Cullen, J. J. 2008. Observation and prediction of harmful algal blooms. Pages 1 - 41 in M. Babin, C. S. Roesler, and J. J. Cullen, eds. *Real-time Coastal Observing Systems for Marine Ecosystem Dynamics and Harmful Algal Blooms: Theory, Instrumentation and Modelling*. UNESCO, Paris.

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Observation and prediction of harmful algal blooms

J. J. Cullen

1.1 INTRODUCTION

Phytoplankton are the principal source of food for life in the sea, and the dynamics of phytoplankton communities are centrally important to the structure and function of pelagic ecosystems. Life forms of phytoplankton have evolved to exploit different regimes of turbulence and hence nutrients (Margalef, 1978) but by their nature, planktonic food webs are structured by grazing and other biological interactions (Kiørboe, 1993; Smetacek, 1998). Consequently, physical processes determine the structure of pelagic ecosystems, directly by their influence on the growth of phytoplankton and indirectly by affecting food-web interactions (Cullen et al., 2002). Phytoplankton dynamics are particularly variable in coastal ecosystems because physical, chemical and biological influences are forced in complex ways: flows of water are constrained by coastlines and shallow, highly variable bathymetry; nutrients are supplied from terrestrial and benthic sources as well as from deeper water offshore; and benthic and intertidal communities actively interact with those in the water column. The increasing concentration of human activities in the coastal region (Nicholls and Small, 2002) and the multifaceted importance of coastal ecosystems to the sustainability of the planet (Costanza et al., 1997) ensure the prominence of biological variability in coastal ecosystems as an environmental concern.

Transient proliferations of phytoplankton, referred to as blooms, are common and natural in coastal environments. In pelagic systems, such outbreaks are the principal means by which flows of matter and energy escape the tightly coupled microbial loop to feed higher trophic levels and export organic matter to deeper waters and the bottom as sinking particles (Michaels and Silver, 1988; Legendre and Le Fèvre, 1989; Kiørboe, 1993). Algal blooms are thus integral to planktonic ecosystem dynamics and biogeochemical cycles. However, some phytoplankton blooms in coastal or brackish waters are perceived as harmful. They can cause massive fish kills, contaminate seafood with toxins, and alter ecosystems in ways that humans do not like. These are harmful algal blooms (HABs), a generic term that glosses over that facts that not all HAB species are classified as algae and some species cause harmful effects when present in low cell densities, nothing like a bloom (Smayda, 1997*b*). A thorough review of the HAB problem was recently prepared as part of the Science Plan for an international research programme on HABs (GEOHAB, 2001). As this chapter shares many objectives with the GEOHAB Science Plan, some material from that document is repeated here, with added emphasis on observation and prediction of HABs in the context of real-time observation systems.

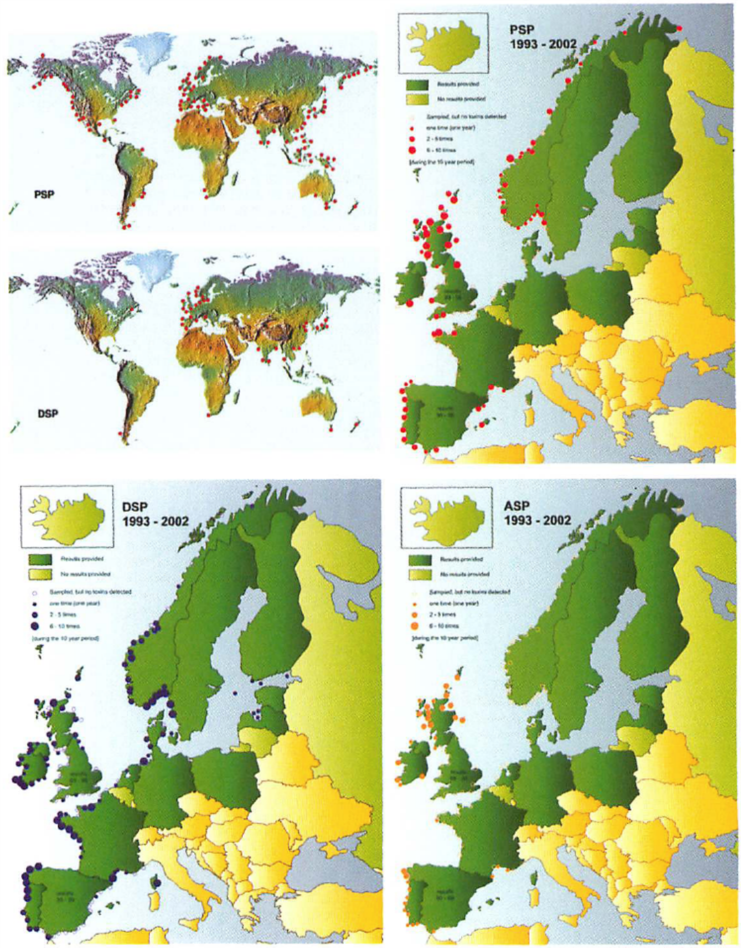

Figure 1.1
Maps of reported occurrences of HAB toxicity demonstrate many aspects of the HAB problem. Top left: global distributions of reported paralytic shellfish poisoning (PSP) and diarrhetic shellfish poisoning (DSP) events show that harmful effects are widespread. Regional patterns are to some extent related to the presence of systems for monitoring and reporting; absence of reports does not necessarily mean that HABs have not occurred (US National Office for Marine Biotoxins and Harmful Algal Blooms). Other panels: Occurrences of PSP, DSP and amnesic shellfish poisoning (ASP) in ICES countries[2] from 1993–2002 show that some locations are affected by several types of HAB, whereas certain types of toxicity are more restricted. None of these maps can show the diversity of species that generate these effects (Table 1.1). The Coastal Module of the Global Ocean Observing System (IOC, 2003) is being established to facilitate more effective monitoring of HABs and other phenomena in coastal environments worldwide, so temporal and spatial patterns can be resolved and explained.[3] *Source*: Harmful Algae Event Data Base (HAEDAT), © IFREMER.

[2] ICES (International Council for the Exploration of the Sea) member countries are Belgium, Canada, Denmark, Estonia, Finland, France, Germany, Iceland, Ireland, Latvia, Netherlands, Norway, Poland, Portugal, Russian Federation, Spain, Sweden, United Kingdom and United States.

[3] http://www.ifremer.fr/envlit/documentation/dossiers/ciem/aciem-c1.htm

1.1.1 Diversity of HABs

The great diversity of HAB species and effects (Table 1.1, Figure 1.1) precludes effective generalization. Still, harmful algae are commonly classified in two groups:

- toxin producers, which can contaminate seafood, kill fish, or cause health problems in humans through direct exposure to the toxins;
- high-biomass producers, which can kill or damage marine life after reaching dense concentrations, for example by causing anoxia after collapse of a bloom or by chronically shading benthic vegetation.

Blooms of high-biomass producers also affect tourism and recreation by discolouring coastal waters and generating noxious foams, slimes or odours. Even this broad classification of harmful algae is not exclusive: several HAB species that are toxic also form dense blooms. To compromise generalization further, closely related species can occur in high concentrations in some regions but not others. For example, *Alexandrium* discolours water in the Gulf of St Lawrence but generally forms only low-density blooms in the Gulf of Maine, although it contaminates shellfish in each environment (Anderson, 1997; Weise et al., 2002). Other species exhibit variable toxicity, for reasons that are as yet unresolved (e.g. Granéli et al., 1993; Scholin et al., 2007 – Chapter 11 this volume). Formal definitions of algal blooms are thus neither practical nor particularly helpful (Smayda, 1997*b*); in this chapter, bloom is synonymous with an increase in the abundance of a phytoplankton species above a background concentration, in either space or time.

Considered broadly, HABs are a grab-bag of phenomena with little in common except for effects that humans perceive as being harmful. Due to their diversity, no

TABLE 1.1 Some deleterious effects caused by harmful algae in coastal and brackish waters

Effect	Examples of causative organisms	
Human health		
Paralytic shellfish poisoning (PSP)	Dinoflagellates	*Alexandrium* spp., *Pyrodinium bahamense* var. *compressum*, *Gymnodinium catenatum*
	Cyanobacteria	*Anabaena circinalis*
Diarrhetic shellfish poisoning (DSP)	Dinoflagellates	*Dinophysis* spp., *Prorocentrum* spp.
Neurotoxic shellfish poisoning (NSP)	Dinoflagellates	*Karenia brevis*
Amnesic shellfish poisoning (ASP)	Diatoms	*Pseudo-nitzschia* spp.
Azaspiracid shellfish poisoning (AZP)	Dinoflagellate	*Protoperidinium crassipes**
Ciguatera fish poisoning (CFP)	Dinoflagellates	*Gambierdiscus toxicus*
Respiratory problems and skin irritation, neurological effects	Dinoflagellates	*Karenia brevis*, *Pfiesteria piscicida*
	Cyanobacteria	*Nodularia spumigena*
Hepatotoxicity	Cyanobacteria	*Microcystis aeruginosa*, *Nodularia spumigena*

(Continued)

TABLE 1.1 *(continued)*

Effect	Examples of causative organisms	
Natural and cultured marine resources		
Hemolytic, hepatotoxic, osmoregulatory effects and other unspecified toxicity	Dinoflagellates	*Gymnodinium* spp., *Cochlodinium polykrikoides, Heterocapsa circularisquama, Pfiesteria piscicida, Gonyaulax* spp.
	Raphidophytes	*Heterosigma akashiwo, Chattonella* spp., *Fibrocapsa japonica*
	Prymnesiophytes	*Chrysochromulina* spp., *Phaeocystis pouchetii, Prymnesium* spp.
	Cyanobacteria	*Microcystis aeruginosa, Nodularia* spp.
Negative effects on feeding behaviour	Pelagophytes	*Aureococcus anophagefferens*
Hypoxia, anoxia	Dinoflagellates	*Prorocentrum micans, Ceratium furca*
Mechanical damage	Diatoms	*Chaetoceros* spp.
Gill clogging and necrosis	Prymnesiophytes	*Phaeocystis* spp.
Tourism and recreational activities		
Production of foam, mucilage, discoloration, repellent odour	Dinoflagellates	*Noctiluca scintillans, Prorocentrum* spp.
	Prymnesiophytes	*Phaeocystis* spp.
	Diatoms	*Cylindrotheca closterium*
	Cyanobacteria	*Nodularia spumigena, Aphanizomenon flos-aquae, Microcystis aeruginosa, Lyngbya* spp.
Marine ecosystem impacts		
Hypoxia, anoxia	Dinoflagellates	*Noctiluca scintillans, Heterocapsa triquetra*
	Diatoms	*Skeletonema costatum*
	Prymnesiophytes	*Phaeocystis* spp.
Negative effects on feeding behaviour and reduction of water clarity	Pelagophytes	*Aureococcus anophagefferens, Aureoumbra lagunensis*
	Dinoflagellates	*Prorocentrum minimum*
Toxicity to marine organisms, including invertebrates, fish, mammals and birds	Dinoflagellates	*Karenia brevis, Alexandrium* spp.
	Diatoms	*Pseudo-nitzschia australis*

Sources: Zingone and Enevoldsen (2000) as modified by GEOHAB (2001), with further modifications.

*Recently described by James et al. (2003).

one cause for HABs can be found, and no single strategy for detection or prediction will suffice. The major challenge for understanding HABs to support management and mitigation is to describe, for each species, what conditions promote its development instead of (or in concert with) other phytoplankton (GEOHAB, 2001).

1.1.2 Harmful algae and environmental variability

It is axiomatic that HAB species have adapted to many niches (suites of ecological factors that determine their distributions and activities), and that the matches between the adaptations of harmful species and oceanographic variability are good enough to ensure their survival from year to year, and their proliferation when conditions are conducive. The great diversity of HABs – with respect to taxonomy, region, hydrographic regime and harmful effects – reflects in a fundamental way that environmental forcing has selected for a wide variety of harmful algae, on timescales from evolutionary to days and spatial scales from ocean basins to bays. For each harmful species, the challenge is to unlock its secrets: why does it bloom or exert its harmful effects in one situation and not in another? The answers lie in detailed information about the distributions and activities of phytoplankton species in relation to the oceanographic and ecological processes that influence them. This should be complemented with experimental results describing how each species responds to these environmental factors, and with models – either conceptual or mechanistic – that describe the principal controls on population dynamics of the target species in relation to the phytoplankton community.

Even though it is an enormously daunting task to resolve the complex interactions that determine the population dynamics of a phytoplankton species in coastal or estuarine waters, significant progress has been made through the careful work of insightful researchers. The contributions of Ramón Margalef (e.g. Margalef, 1978; Margalef et al., 1979) are widely regarded as a seminal influence. Considering life forms of phytoplankton, that is their gross morphological and physiological traits, Margalef and colleagues described how functional groups of phytoplankton (with representative species identified) could be plotted against axes representing nutrient availability and the intensity of turbulence (Margalef, 1978). The typical seasonal succession of phytoplankton, from fast-growing diatoms to motile dinoflagellates, corresponds to the temporal transition from a well-mixed, nutrient-rich water column during winter to a nutrient-poor, stratified environment later in the year. This model was later modified to include a 'red-tide sequence', a trajectory parallel to the typical succession, but in environments with higher levels of nutrients (Figure 1.2). Using a similar approach, Colin Reynolds and colleagues (reviewed briefly by Reynolds and Smayda, 1998; revisited by Smayda, 2002) developed 'habitat matrices' that relate variability of phytoplankton species composition in lakes to several axes of variation, still dominated by nutrients and turbulence.

Summarizing efforts to describe variability in phytoplankton communities, Reynolds (2002) concluded that the dynamics of individual species are unpredictable, except on the scale of days, and only then if based on full knowledge of initial distributions. However, he felt that at a higher lever of generality (i.e. for functional groups or trait-based associations of phytoplankton), responses of phytoplankton communities to environmental conditions would be increasingly predictable. A key link to predictability is that variability in community composition is 'explicable in retrospect' (Reynolds, 2002). That is, the confidence we can have in predictions of phytoplankton communities under future scenarios depends largely on how well the same conceptual models explain historical variability of phytoplankton.

As the ecological implications of morphological (Karp-Boss et al., 1996), physiological and behavioural (Cullen and MacIntyre, 1998) adaptations of harmful algae become better understood, new and more powerful definitions of functional groups will emerge, guiding how phytoplankton species should be classified, and which

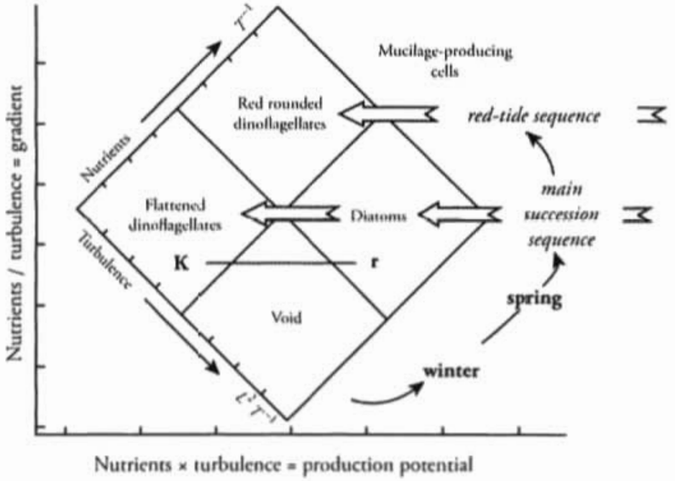

Figure 1.2
The 'Mandala' redrawn from Margalef et al. (1979). This diagram, rich with information on phytoplankton succession, is extremely useful for developing generalizations about relationships between life forms of phytoplankton and hydrographic conditions, particularly during seasonal succession. The 'red-tide sequence' (development of a high-biomass HAB) can be viewed as related to elevated nutrients, independent of changes in turbulence regime. This conceptual model it is not directly applicable to real-time observation and prediction of HABs. Nonetheless, Margalef's framework is a cornerstone of phytoplankton ecology and it should support the roots of any model of seasonal phytoplankton community dynamics as influenced by local conditions.

environmental factors must be considered, when trying to predict their dynamics. These more detailed classifications should lead to improvements in predicting the probability of HAB occurrence for a particular location and time, given measured or modelled scenarios of physical and chemical conditions. Moving beyond probabilities of occurrence, the dynamics of HABs may be predictable over the course of days, given initial data on species distributions from coastal observation systems (Johnsen et al., 1997; Stumpf et al., 2003). Development and testing of any predictive model will thus require effective systems for observing the distributions of phytoplankton, including HABs, in the context of coastal ecosystem dynamics.

1.1.3 Observation and modelling in the 'old days'

Observations of HAB dynamics have seldom been adequate to describe the three stages of an event: development, maintenance and decline (Tester and Steidinger, 1997). So, much of what is known about HABs comes from careful analysis of limited data, with much reliance on inference. Comprehensive observations of events preceding a bloom are particularly rare, because the unpredictability that justifies research on harmful algae also precludes the scheduling of cruises to coincide with HABs. The unpredictable nature of HABs has led to facetious acceptance of the maxim that the best way to prevent them is to schedule a major research programme to study them.

Some of the most effective studies of HABs and other phytoplankton blooms in coastal and estuarine waters come from regions where conditions are similar year to year, and sustained observations have shown relationships between the population dynamics of phytoplankton species and hydrographic conditions. Several are described in this volume. A study by Tyler and Seliger (1978, 1981) is an excellent example of observation and modelling in the days before autonomous observation systems and three-dimensional coupled models. The approach they used is just as appropriate today as it was 25 years ago. The best available sampling techniques were used to characterize the distributions of the target species (*Prorocentrum minimum*, formerly *Prorocentrum mariae-lebouriae*) in relation to light and hydrographic conditions. In turn, the physiological and behavioural responses of these motile algae to the same environmental factors were characterized experimentally. By considering the interaction of physiology and behaviour of the phytoplankton with the vertical structure of the water column and seasonal transport by estuarine circulation, selection for the target species was explained and the general features of population dynamics predicted. All this was done with limited information. Still, it took 128 ship days during 40 cruises over two years (plus hundreds of hours counting cells under a microscope) to acquire the data for describing the dynamics of *Prorocentrum* in Chesapeake Bay (Tyler and Seliger, 1978). Subsequently, much more has been learned about the dynamics of *Prorocentrum minimum* in Chesapeake Bay and elsewhere (Heil et al., 2005), but the validity of Tyler and Seliger's multifaceted approach (observations, experimentation, modelling, validation) has not diminished.

Many of the old limitations on coastal ecological research are vanishing. As described in this volume, advances in observation technology and modelling, supported by greatly enhanced capabilities for communications and computing, are transforming the nature of ecological investigation from a labour-intensive effort to collect precious data, interpreted largely through inference, to a process in which unprecedented quantities of data and model output must be managed effectively to yield useful information. Still, it is essential to remember that the fundamental principles of the research will not change. Species must be identified and their physiological, behavioural and ecological interactions must be considered in the context of oceanographic processes to understand and describe the population dynamics of harmful species as members of phytoplankton communities. Insights from the 'old days' of the twentieth century will certainly help to guide HAB research when the widespread availability of observations threatens to mask the fundamental need for focused questions about controls on the population dynamics of the causative species.

1.2 DETECTION AND PREDICTION FOR MONITORING AND MANAGEMENT OF HABS

The HAB problem is rich with unanswered questions that will occupy scientists for decades. More immediately, it represents threats to coastal ecosystems and activities, and these must be dealt with now (Malone, 2007 – Chapter 14 this volume). Authorities responsible for environmental protection, economic development and public health must develop and implement plans for the monitoring and management of HABs (Anderson et al., 2001; Andersen et al., 2003). These plans may include:

- Strategies for monitoring coastal waters for detection of HABs, including their effects, with an aim to develop early warning systems.
- Development of a modelling system for short-term forecasts of HAB movements.

- Integration of observations, forecasts and communications into an action plan for rapid response to HAB events, including criteria for initiating strategic sampling, beach closures, shellfish bans and communication to the public.
- Mitigation strategies, from direct actions to neutralize blooms or minimize their effects (e.g. application of clay or movement of fish cages) to long-term nutrient management plans or bans on ballast water discharges.
- A programme of research to predict the likelihood of HABs, i.e. changes in their frequency or impacts, in response to human activities or climate change.
- Integration of monitoring, predictions and communications in support of policy decisions.

All aspects of monitoring and management require the means to detect, and broadly to predict, the occurrences and impacts of HABs on scales from days to decades. These challenges can only be met through fundamental scientific research, but there is no benefit in conducting this research independently from ongoing monitoring programmes.

In some jurisdictions, and in the minds of many scientists, basic research has been considered to be distinct from routine activities such as monitoring. As a consequence, monitoring activities may be specifically excluded from funding programmes for research and, in turn, sustained sampling programmes established for research are regularly threatened with cuts or termination, even though they have proved invaluable for describing long-term trends in ecosystems (e.g. Tont, 1976; Roemmich and McGowan, 1995; Fromentin and Planque, 1996; Karl et al., 2001). With the advent of real-time coastal observation systems with capabilities for environmental forecasts, the goals of scientists and coastal managers are aligning, as are the means for attaining these goals: real-time detection of HABs is essential for early warning; prediction of dynamics with forecast models supports rapid response and mitigation; and sustained observations (equivalent to monitoring) are required to develop and validate the long-range models of HAB probabilities needed to develop coastal management strategies.

The conclusion is that the research topics of real-time detection, sustained observations and quantitative prediction of HABs must be integrated with the operational requirements for monitoring and management. To justify the large investment in research and infrastructure, results from real-time coastal observation systems must be accessible, understandable and useful to a broad range of user groups. Research must be more closely coordinated with operational oceanography (Chapter 14), which will have to change with time to serve a wide range of users. This will require restructuring, not only in the way coastal research is organized, but also in the way scientists communicate their results – a healthy challenge.

1.3 CLASSIFICATION OF HABs FOR OBSERVATION SYSTEMS

No observing system can provide the oceanographic ideal of continuous and synoptic measurements of physical, chemical and biological properties and processes, so efforts must be made to match observations and their scales to the HAB phenomena of interest (Franks and Keafer, 2003; Smayda, 2003; Chang and Dickey, 2007 – Chapter 2 this volume). This is no easy task, however. The range of scales for HABs is immense (Hallegraeff, 2003). Some may be confined to inlets (Seliger et al., 1970), others are observed over large expanses (Kahru et al., 1994). Blooms may come and go over days to weeks, often terminated by wind events which may transport the algae offshore or cause direct mortality from turbulence (but see Smayda, 2002). Other blooms can persist for months, for example *Karenia brevis* blooms off Florida (Tester and Steidinger, 1997), or even years (*Aureoumbra lagunensis* in Laguna Madre, Texas; DeYoe and Suttle, 1994). Many are found close to the surface, not surprisingly as discoloration of the water draws attention. Some of these can be traced to subsurface layers, brought near the surface by physical transport, including frontal processes (McMahon et al., 1998) and vertical mixing (see Section 1.5.1). Other surface blooms develop through vertical migration of phytoplankton (Oliver, 1994; Kamykowski, 1995). A coarse classification of HABs can be useful as an initial guide to identify relevant scales and appropriate observation strategies for local or regional observation programmes. The classification is summarized here, with suggestions for observation strategies.

1.3.1 Widespread HABs

Generally, a harmful algal bloom must have widespread effects to attract the attention of the scientific community and the general public. Discoloured water, dead fish and noxious foam, scums or aerosols over hundreds of kilometres of coastline make the news, and with good reason. The blooms are extensive and the algae are easily identified as the cause of harm. The features that make such blooms noteworthy are also useful for classification and the design of strategies for early warning, monitoring and prediction: relatively large extent; persistence; and, often but not always, dominance of the phytoplankton by one species. Three somewhat idealized categories within this loose classification can be proposed.

1.3.1.1 Extensive, progressive coastal blooms

Some of the most challenging oceanographic and ecological questions are raised by extensive blooms, nearly monospecific and often toxic, that appear in a coastal waters and progress along the shoreline, leaving a trail of shellfish closures, ravaged fish farms or spoiled beaches. Some examples include blooms of *Karenia brevis* in the Gulf of Mexico (Tester and Steidinger, 1997; Stumpf et al., 2003), *Karenia mikimotoi* (formerly *Gyrodinium aureolum* or *Gymnodinium mikimotoi*) in northern European shelf waters (e.g. Holligan, 1979; Dahl and Tangen, 1993; Gentien, 1998), the toxic bloom of *Chrysochromulina polylepis* in Scandinavian waters in 1988 (Granéli et al., 1993; Gjøsæter et al., 2000), blooms of *Heterosigma* in the Strait of Georgia and adjacent waters in Canada (Taylor and Haigh, 1993), and the dramatic bloom of *Karenia digitata* in Hong Kong waters in April 1998 (Lee et al., 2007 – Chapter 18 this volume).

Hypotheses about bloom dynamics focus on the processes of initiation, transport and interactions of populations with surface circulation (Tester and Steidinger, 1997). Assessment of impacts requires information on transmission of harm (e.g. decay leading to anoxia, direct contact, toxin transfer through ingestion, production of aerosols), how these processes relate to the distributions of harmful algae, and environmental influences on the production of noxious effects.

Many environmental properties must be measured for effective early warning, monitoring and prediction. When conditions permit, remote sensing of ocean colour and sometimes sea surface temperature from satellites and aircraft can provide key information on distributions and transport (Stumpf et al., 2003; Ruddick et al., 2007 – Chapter 9 this volume), especially when supplemented by observation networks that include direct sampling (Johnsen et al., 1997; Tangen, 1997). Even if surface distributions of developed blooms are resolved with remote sensing, early stages and subsurface distributions must be described by other means. In particular, vertical distributions of phytoplankton should be well resolved because the interaction of swimming, sinking or floating with frontal features (Franks, 1997), aggregation of seed populations in subsurface layers near the pycnocline (McMahon et al., 1998), and changes of behaviour in mixed waters landward of a front (Dahl and Tangen, 1993; Gentien, 1998), possibly associated with nutrition (Cullen and MacIntyre, 1998), all may be important in initiation, maintenance and transport of extensive, progressive, coastal blooms. Consequently, for early warning and monitoring, observation systems must resolve vertical distributions of phytoplankton in relation to temperature, salinity and currents, and they must have the means to identify target species *in situ*. Nutrient availability can influence toxicity (Bates, 1998; Cembella, 1998) and depletion of nutrients can terminate a bloom. So, for effective monitoring and modelling, the nutrient regime should also be assessed.

Progressive coastal blooms move with coastal currents and can appear or disappear on the timescale of days. Effective monitoring thus requires nearly continuous measurements, and mitigation responses (such as the movement of aquaculture cages) require communications in near real time (Tangen, 1997). Strategies for management, such as controls on coastal nutrient loading or site selection for aquaculture, depend on long time series of observations to determine the relationships between environmental variability, human influences, bloom occurrences and their impacts. Sustained deployment of real-time observation systems is thus ideally suited for observation and prediction of extensive, progressive coastal blooms.

1.3.1.2 Extensive blooms in open waters

It has long been recognized that phytoplankton blooms in open waters are part of the natural ecology of the oceans. The phenomenology of some, such as the vernal diatom bloom in temperate waters (Sverdrup, 1953), surface aggregation of *Trichodesmium* during calm periods (Capone et al., 1998), *Phaeocystis* and diatom blooms associated with receding ice edges (Lancelot et al., 1998) and the green waters of upwelling systems (Barber and Smith, 1981) are fairly well understood. The root causes of dramatic expanses of milky water from coccolithophores are open to informed speculation (e.g. Olson and Strom, 2002) and examination through numerical modelling (Merico et al., 2004). Satellite imagery[4] reveals many other blooms in open waters that will remain curiosities until they are studied further. In the context of this chapter, interest is focused on harmful or potentially harmful blooms that occur in open waters in semi-enclosed seas or near coasts, where they can influence coastal ecosystems and be affected by terrestrial inputs of fresh water and nutrients. The Baltic, North Sea and Bohai (China) are exemplary. It serves little purpose to apply this classification strictly; extensive blooms in open waters are grouped so the potential forcing functions – climate change and nutrient sources – can be discussed along with strategies for observing and predicting ecological responses to these influences.

Open water HABs can cause problems when they impinge on the coast, delivering scums, foams or toxicity. For example, summer blooms of nitrogen-fixing cyanobacteria in the Baltic Sea are common (Sellner, 1997). The hepatotoxic *Nodularia spumigena* is conspicuous; during the latter stages of a bloom, filaments form highly visible aggregates at the surface that can be detected from space (Kahru et al., 1994). Nitrogen

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[4] For example: http://visibleearthnasa.gov/

enrichment as well as toxicity on landfall are concerns. Blooms of *Phaeocystis* in the North Sea can deliver prodigious quantities of noxious foams to beaches. Hallegraeff (2003) reviews the relation between eutrophication and occurrences of *Phaeocystis* and other HABs.

Although there is a need to predict the trajectories of open water blooms that may impinge on coastlines, observation and prediction of extensive HABs in open waters tends to focus on their importance as ecological indicators and modifiers of the marine or brackish water environment. Particular emphasis is placed on the interactions of climate, circulation, nutrient inputs and algal physiology. Proposed scenarios include:

- Springtime blooms of *Phaeocystis* in the North Sea can be related to discharges from seven major west European rivers, which introduce new and unbalanced sources of nutrients, including excesses of nitrate and phosphate compared with silicate (Lancelot, 1995; Riegman, 1998).
- Relatively cool and windy conditions favoured the vertically migrating, depth-seeking *Heterocapsa triquetra* over cyanobacteria in the entrance to the Gulf of Finland during summer 1998 (Kononen et al., 2003).
- Eutrophication of the Baltic leads to deep water hypoxia, liberation of phosphorus from sediments, and hence decreased nitrogen:phosphorus ratio in the nutrients supplied to the surface layer; N-fixing cyanobacteria, including toxic bloom-formers, are favoured (discussed and critically evaluated by Bianchi et al., 2000).
- The flow of saline, oxygen depleted water into the Baltic in 1993 triggered the eastward expansion of *Nodularia spumigena* blooms into the Gulf of Finland. *Nodularia* was previously absent due to relatively high N:P ratios, and thus reduced competitive advantage for N-fixers. Salty water increased stratification in the bottom layers; oxygen concentrations decreased, P was liberated from sediments, water-column N:P decreased, and the N-fixing cyanobacteria bloomed (Kahru et al., 2000).

Year-to-year comparisons of bloom dynamics were central to the development and testing of these scenarios. Observation systems, including monitoring programmes, have thus contributed very significantly to these and other studies of algal blooms in open waters. Remote sensing figures prominently, particularly because cyanobacterial blooms can be detected with satellites (AVHRR) that have been deployed for decades (Kahru, 1997). Under-way measurements from ferries[5] have been incorporated into a system that now can describe in some detail the variability, in space and time, of blooms in Scandinavian waters.

For extensive blooms in open waters, the needs for observation and prediction include long records that can characterize fundamental changes in both the physico-chemical environment and the ecological system, including the frequency, duration and extent of blooms. Predictions could include long-term trends in bloom frequency and yearly projections of probabilities. Except for properties like N:P ratios and deep-water salinity and oxygen, periodic surveys are inadequate to develop and test predictive models, because transient and patchy events cannot be resolved. The strategy of routine continuous transects from ferries and remote sensing, supplemented with cruises to monitor physical, chemical and biological conditions, appears to be on the right track. Although the ideal of continuous and synoptic observations cannot be attained, the data can be used to describe the variability of phytoplankton with unprecedented temporal and spatial resolution.

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[5] Alg@line: www.itameriportaali.fi

Smaller than the Baltic Sea, but also subject to HABs and strong anthropogenic influences, the Seto Inland Sea in Japan has been studied intensively to resolve environmental influences on the frequency, species composition and impacts of HABs (Okaichi, 1997). Although near-shore processes figure prominently in many studies, the influences of eutrophication and nutrient controls on long-term trends of bloom frequency and composition are central questions (Yamamoto, 2003), as they are in the Baltic. Research has been backed by a broad range of monitoring, including records of water clarity (Secchi depth) dating back more than 60 years (Yanagi and Okaichi, 1997). These records are an especially useful resource, a prime example of long-term optical monitoring of environmental variability in coastal waters (Cullen et al., 1997). During the 1990s, a programme for high-resolution marine biogeochemical sampling from ferries was used in East Asian marginal seas (Harashima et al., 1997). Ferry tracks included a transect along the Seto Inland Sea.

Examples from Japan and the Baltic illustrate the great value of sustained observations, and the potential uses of continuous measurements, such as those from ferries. The capability for viewing observations in real time is perhaps less important than in near-shore environments, but timely knowledge of offshore events can guide sampling and provide information for early warning systems.

1.3.1.3 Blooms in upwelling systems

Phytoplankton proliferate when hydrographic conditions deliver nutrients to a well-lighted surface layer in the absence of deep vertical mixing, so upwelling systems generate blooms by their nature, forming the bases of the most productive ecosystems in the ocean (Ryther, 1969; Barber and Smith, 1981). Because the wind-driven delivery of nutrients to the surface layer and the coupled transport of developing blooms offshore are dominant influences on phytoplankton population dynamics in coastal upwelling systems, blooms in upwelling regimes are prime examples of phytoplankton dynamics under oceanographic control. Of course, not all blooms in upwelling systems are the same: complex interactions among large-scale circulation, the chemical composition of upwelled water and local circulation (e.g. Tont, 1976; Grantham et al., 2004), plus varying timescales of change of wind-driven circulation (Moloney et al., 1991; Carr, 1998), and frontal dynamics (Franks, 2006 – Chapter 15 this volume) all influence the development of phytoplankton populations and thus the species composition of blooms and their effects on coastal ecosystems.

Upwelling systems, such as those off the coast of Portugal and Spain, Peru, the west coast of the United States and Mexico, West Africa, Southern Africa, Japan and Australia, are affected by HABs (GEOHAB, 2001). Effects include anoxia associated with accumulation and degradation of organic material from blooms, and toxicity associated with blooms of toxic algae brought into contact with shellfish, for example. Wind-driven transport is a major theme; it can have a direct influence by bringing populations in contact (or not) with shellfish (Fraga et al., 1988; Franks and Anderson, 1992*a*), or in setting up circulation patterns that encourage the development of migrating populations (Weise et al., 2002) or the concentration of organic matter leading to anoxia (Pitcher et al., 1998). The turbulence regime is important, because HABs are often associated with the relaxation of upwelling (Anderson, 1995). This relationship might reflect direct influences of turbulence on the growth of dinoflagellates (Pollingher and Zemel, 1981; Juhl and Latz, 2002), or indirect effects related more to upwelling circulation and transport (Smayda, 2002).

Because of their oceanographic significance and commercial importance, upwelling regions are among the best studied of coastal environments, providing opportunities to integrate targeted observation of HAB phenomena with broader-based research and monitoring programmes (Pitcher, 2007 – Chapter 21 this volume). The new tools and approaches for real-time observations described elsewhere in this volume are almost all well suited for observation and prediction of HABs in upwelling systems.

1.3.2 Localized blooms

When they occur, HABs cause local problems, regardless of regional extent. Within regions (defined as the next larger scale that must be observed to understand the local scale of interest, IOC, 2003) some locations experience recurrent, though not necessarily predictable, HABs; other nearby locations are spared. Even though the phenomena are likely to be related to larger-scale forcings, for many types of HAB, local conditions have a strong influence on occurrence and impacts and thus merit direct focus in the development of observation and prediction systems for monitoring and management.

Almost any recurrent HAB could be studied as a local phenomenon, at least partially explainable by local conditions. A few of many examples include:

- Blooms of *Heterosigma akashiwo* (Honjo, 1993) or *Alexandrium tamarense* (Yamamoto et al., 2002) in Hiroshima Bay, which can be related to patterns of eutrophication and local hydrography, invoking cyst dynamics, growth and behaviour of the algae.
- Paralytic shellfish poisoning (PSP) toxicity in oceanic bays (*rias*) of north-west Spain, where *Gymnodinium catenatum* is transported from elsewhere but exerts its effects on local mussel farms due to interactions between longshore transport, estuarine circulation under the influence of winds, and swimming behaviour of the dinoflagellates (Figueiras et al., 1996; Hallegraeff and Fraga, 1998).
- Brown tides of the pelagophyte *Aureococcus anophagefferens* (Bricelj and Lonsdale, 1997) in US mid-Atlantic coastal waters. Blooms are recurrent and persistent, but not predictable. Explanatory hypotheses invoke preferences for organic nitrogen and other nutrients that could be advantageous when estuarine flushing is reduced, and also top-down control as influenced by suppressed grazing (Gobler et al., 2002).

Description and prediction of localized blooms requires assessment of their extent and duration in relation to local conditions, quantification of exchanges with adjacent waters, and enough observations of nearby systems to explain why the HABs occur in one location and not another. The design of an appropriate observation system and the development of hypotheses and predictive models requires careful consideration of the life history of the alga (including cyst dynamics, when relevant), its buoyancy or swimming behaviour, important effects on growth, and local oceanographic conditions and ecological interactions. Clearly, these can be developed only through an iterative procedure of observation, analysis and improved observations. The example of *Prorocentrum* in Chesapeake Bay (Section 1.1.3; Tyler and Seliger, 1981) illustrates the kinds of processes and interactions that should be observed and modelled. The emphasis should be different for each localized bloom phenomenon, guided by targeted research.

1.3.3 Blooms strongly influenced by buoyancy or swimming behaviour

Some of the most dramatic pictures of blooms depict strong discoloration of water near frontal features in coastal waters (Figure 1.3). These phenomena can have significant impacts, for example when they impinge on aquaculture sites or decay in restricted

Figure 1.3
Dense blooms associated with physical discontinuities in the water demonstrate the interaction of swimming, sinking or floating of phytoplankton with small-scale circulation and interfaces (Franks, 1997). A, *Noctiluca* (from GEOHAB, 2001)
Source: after Malone (2001).

inlets, causing anoxia. Regardless, the patterns are spectacular, clearly illustrating the importance of biological-physical interactions in determining the patterns of algal blooms. A hallmark of these aggregations is a concentration of nutrient in phytoplankton cells (e.g. mmol particulate N m^{-3} of seawater) greater than what could have been available as dissolved nutrient in the water (Holmes et al., 1967); this explicitly demonstrates movement of cells relative to the water, in a sense scavenging nutrients from the water column.

Dense aggregations of phytoplankton, such as those at fronts, surface scums, concentrated subsurface layers, and transient surface accumulations due to diel vertical migration (DVM), are all associated with interactions between vertical movements of phytoplankton and discontinuities in the water column (Franks, 1997). Buoyancy and swimming behaviour are thus integral to the determination of population growth and transport (Kamykowski, 1995; Donaghay and Osborn, 1997). In turn, algal adaptations for vertical movements are important determinants of ecological selection (Levandowsky and Kaneta, 1987; Oliver, 1994; Cullen and MacIntyre, 1998). Consequently, detection and description of these blooms requires effective sampling of phytoplankton and physical-chemical properties on the scales of the biological-physical interaction, and modelling to describe the consequences of these interactions in three dimensions.

Subsurface layers illustrate the challenges of observation and modelling. Many species of phytoplankton, including dinoflagellates (Margalef et al., 1979; Eppley et al., 1984; Gentien et al., 1995), the prymnesiophyte *Chrysochromulina polylepis* (Granéli et al., 1993) and diatoms of the genus *Pseudo-nitzschia* (Rines et al., 2002) can form subsurface thin layers, thereby evading detection with conventional sampling. Considering that thin layers are commonly found when appropriate sampling is conducted, and that specialized sampling and analysis has not been widely employed, it is reasonable to guess that many toxic species (and other phytoplankton species) will be found in thin layers of stratified coastal waters (Dekshenieks et al., 2001). Highly resolved vertical profiles, for example with special samplers (Dekshenieks et al., 2001; Cowles, 2003; Kononen et al., 2003) and moored, towed, or autonomous under-way profiling systems (Griffiths, 2007 – Chapter 13 this volume), are required to describe the distributions of subsurface blooms. Because buoyancy and swimming behaviour of phytoplankton are strongly influenced by nutrition (Oliver, 1994; Kamykowski, 1995; Cullen and MacIntyre, 1998), the association of subsurface layers with nutrient gradients is quite likely, though only rarely explored on this scale of thin layers (e.g. Kononen et al., 2003). Well-resolved determination of nutrient concentrations (Hanson and Donaghay, 1998; Johnson and Coletti, 2002), as well as temperature, salinity and currents, is thus needed to resolve causes and dynamics of subsurface blooms in thin layers (Cowles, 2003).

1.3.3.1 Modelling phytoplankton behaviour in coastal waters

Models of biological-physical interactions in behaviourally influenced blooms have described important processes that generate patterns observed in nature (Kamykowski, 1974; Donaghay and Osborn, 1997; Franks, 1997; Franks, 2007 – Chapter 15 this volume). Models designed to simulate local dynamics, including behaviour (Levandowsky and Kaneta, 1987; Kamykowski, 1995), describe the conditions conducive to bloom development (Tyler and Seliger, 1981; Amano et al., 1998; Yamamoto et al., 2002). Detailed prognostic modelling of behaviourally influenced bloom dynamics is quite difficult because not only must the three-dimensional evolution of physical discontinuities be described realistically, but also the physiological control on depth regulation, be it buoyancy regulation or swimming (Cullen and MacIntyre, 1998; Kamykowski et al., 1999). Fortunately, general features of transport and dynamics can be described without specifying the details of swimming and buoyancy by making simplifying assumptions, such as prescribed scavenging of nutrients in the surface layer by a population implicitly capable of migration (e.g. McGillicuddy et al., 2007 – Chapter 16 this volume), or confinement of a population to the pycnocline.

1.3.4 Toxic HABs

Blooms of toxic algae can be studied in the framework described in the previous sections, but toxic HABs merit special consideration for several reasons:

- They can have harmful effects even if the species is not dominant (e.g. Anderson, 1997), so effective detection at species level against a background of more abundant phytoplankton may be required.
- However, some HAB species cannot be distinguished on the basis of gross morphology or pigmentation, for example the toxic species of the diatom genus *Pseudo-nitzschia*.
- The production of toxin can vary among strains within a species (Anderson, 1990), and because it is under physiological control (Bates, 1998; Cembella, 1998) will vary with environmental conditions during the course of a bloom. Toxicity must therefore be detected in concert with distributions of the toxic species and, if possible, assessment of their physiological state (Scholin et al., 2007 – Chapter 11 this volume).
- The effects of toxic HABs depend on the toxin, the targets, and how the toxin gets to the target. Pathways of transfer must be understood and assessed (GEOHAB, 2001).
- Effective prediction of toxic HABs (especially as a phenomenon that occurs instead of a non-toxic bloom) requires an understanding of how toxicity influences ecological interactions, particularly loss processes such as grazing by zooplankton (Turner

and Tester, 1997) and shellfish (e.g. Tracey, 1988), and competition through allelopathy (Pratt, 1966; Gentien and Arzul, 1990; Schmidt and Hansen, 2001). Consequently, studies of toxic HABs should include several components in addition to characterization of phytoplankton biomass in relationship to oceanographic processes: detection and physiological characterization at the species level; measurement of toxin; assessment of toxic effects; and description of how toxins reach the target species. Toxic effects on competitors, grazers or predators that feed back on population dynamics should also be explored.

Observation and prediction of algal blooms is a challenge that requires a multidisciplinary approach to detect phytoplankton (Cullen et al., 1997; Schofield et al., 1999) and to describe physical-biological interactions (Donaghay and Osborn, 1997). With the inclusion of toxic effects as a factor, the problem becomes even more multidisciplinary, complicated and challenging. Fortunately, the tools (Chapter 11) and the willingness to collaborate in multidisciplinary research and monitoring are developing rapidly.

1.4 PREDICTION OF HABs

In the context of ocean observation systems, prediction can be defined as the estimation of properties that are not observed directly with known certainty (IOC, 2003). This broad and etymologically incorrect, but practical, definition includes hindcasts, nowcasts and forecasts of conditions:

- Hindcasts can be used to test if events are 'explicable in retrospect' (Reynolds, 2002), critical for the development and testing of models. For example, Franks and Anderson (1992*b*) compared historical records of PSP toxicity with hindcasts based on a model of wind-induced transport of *Alexandrium* to test hypotheses about physical control of toxicity in the Gulf of Maine.
- Nowcasts (comparable to weather maps) are essentially interpolations and extrapolations of observations, including those obtained in real time. They might include maps of the distributions of blooms in relation to currents. A time series of nowcasts (which become hindcasts as time passes and can be supplemented with more data) can serve as a record of environmental change that is richer than a compilation of direct observations alone; this is the future of coastal monitoring.
- Forecasts are the ultimate goal of marine prediction. The timescale could be hours to days, for predicting the course of events such as HABs; months, for prediction of seasonal bloom probabilities; or years to decades or longer, in simulations of eutrophication and climate change to support integrated coastal management.

A prediction with no bounds on its certainty has little practical value, so predictions should include estimation of associated errors (assessment of skill). Estimation of error is integral to some types of predictive model (Walstad and McGillicuddy, 2000; Pinardi et al., 2007 – Chapter 20 this volume), but hardly a feature of others. It may be some time before a requirement for error estimation in the prediction of ecological processes is universally embraced, but the need for error estimation is immediate.

There are many ways to model coastal ecosystems and HABs, and predictions span a large range of spatial and temporal scales and levels of biological detail. Some analytical models and a broad range of numerical predictive models are reviewed in this volume, so only the one class of prediction not explicitly addressed, empirical models, is discussed in the following section.

1.4.1 Empirical models

Many existing models of HABs are based on empirical relationships between the dynamics of HAB species and environmental variables measured concurrently over an extended period of observations. Generally backed up by a large amount of supplementary observations and research, empirical models may be formulated as statements, such as that of Taylor and Haigh (1993), based on figures reproduced here (Figure 1.4): 'The appearance of substantial numbers of *Heterosigma* at Jericho coincides with both a rise in temperature of about 15°C and a decrease in salinity below 15 ppt.' This straightforward prediction is both interpretable in ecological terms and suitable for forecasting the likelihood of blooms in the region, given information on temperature and salinity. With the availability of suitable data, such predictions can be evaluated statistically and refined. The same general approach can apply for empirical models relating HABs to eutrophication (Lam and Ho, 1989; Zhang, 1994).

By definition, empirical models must be based on observations. And, as predictions must have bounds, statistical validation and estimation of error is necessary at some point. Unbiased and unaliased data on the distributions of HAB species in relation to relevant environmental factors are thus centrally important. This is where multi-platform real-time coastal observation systems assume prominence (Chang and Dickey, 2007 – Chapter 2 this volume). As described in Section 1.2, and discussed in some detail below (Section 1.5.1), the observation strategy must be appropriate for the phenomena being observed, in discrimination (bulk phytoplankton biomass in some

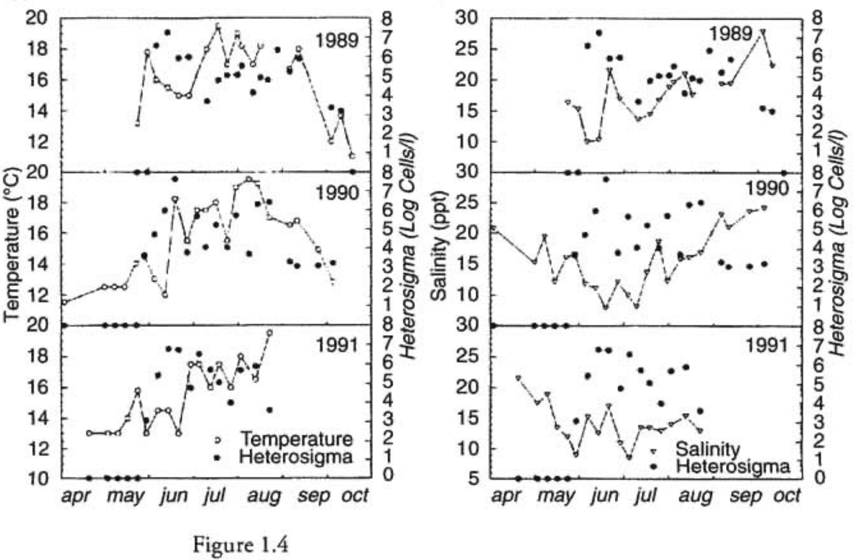

Figure 1.4
A, temperature, B, salinity, and concentrations of *Heterosigma* at Jericho Pier, in English Bay, Vancouver, Canada.
Source: Taylor and Haigh (1993). Copyright 1993, reprinted with permission from Elsevier.

cases, species and toxicity in others), environmental properties measured (temperature, salinity, currents, nutrients), vertical and temporal resolution, and spatial scale.

As reviewed in this volume, sophisticated and powerful modelling techniques, mostly numerical, are being developed for prediction of HABs. Empirical models will nonetheless retain an important role in predicting probabilities of HABs. As for all approaches, the quality of the predictions will depend on the data, and coastal observation systems will have to be designed with these applications in mind.

1.5 OBSERVATION TECHNOLOGIES

For any HAB phenomenon and scale of interest, development and evaluation of early warning and prediction systems requires observations to characterize algal distributions in relation to environmental factors, and models that relate algal population dynamics to the observed properties of the environment (Anderson et al., 2001; GEOHAB, 2001; IOC, 2003). Algal blooms are episodic and patchy, so observations of algal distributions in relation to physical and chemical properties should be both continuous and synoptic. This ideal is unachievable, but a new generation of oceanographic instruments can provide continuous measurements of many physical, chemical and biological properties from autonomous moorings and underwater vehicles, in vertical profile and along ship-tracks. Also, remote sensing from aircraft and satellites can provide synoptic views of coastal processes when conditions allow. Many of these relatively new technologies and approaches are reviewed in this volume. The following discussion highlights a few approaches and raises some issues that have general relevance to observation and prediction of HABs.

1.5.1 Need for observations on relevant scales

As discussed in Section 1.2, HABs encompass a very broad range of scales, and detecting them involves many different challenges, depending on the species, its proclivities and the associated properties that should be measured. Considering that coastal observation systems should serve many purposes (IOC, 2003), technological approaches and scales of measurement must be very carefully chosen to provide data of maximum usefulness. This requires explicit consideration of the important phenomena to be detected and predicted, the scales of variability to be addressed, and the environmental forcings that should be characterized (Chang and Dickey, 2007 – Chapter 2 this volume).

The implications of sampling strategies are illustrated by an example from Bedford Basin, Nova Scotia, a well-studied coastal embayment (Li and Dickie, 2001). A dense subsurface bloom of *Gonyaulax digitale* persisted in a thin subsurface layer during summertime in the Basin, exposing itself to observers in the afternoons when winds eroded the pycnocline and the water turned reddish-brown (Cullen et al., 1994). Shortly after detailed observations were made (Figure 1.5), the bloom collapsed, leading to anoxia, a fish kill and considerable public concern. Key aspects of bloom dynamics were easy to document with frequent, highly resolved vertical profiles of optical and physical properties. Critical observations included weekly vertical profiles of temperature, salinity and chlorophyll fluorescence over the course of the summer (Bedford Institute, 2003), repeated profiles over the course of a day (Figure 1.5), targeted sampling of the thin layer to determine species composition, and measurement of meteorological conditions.

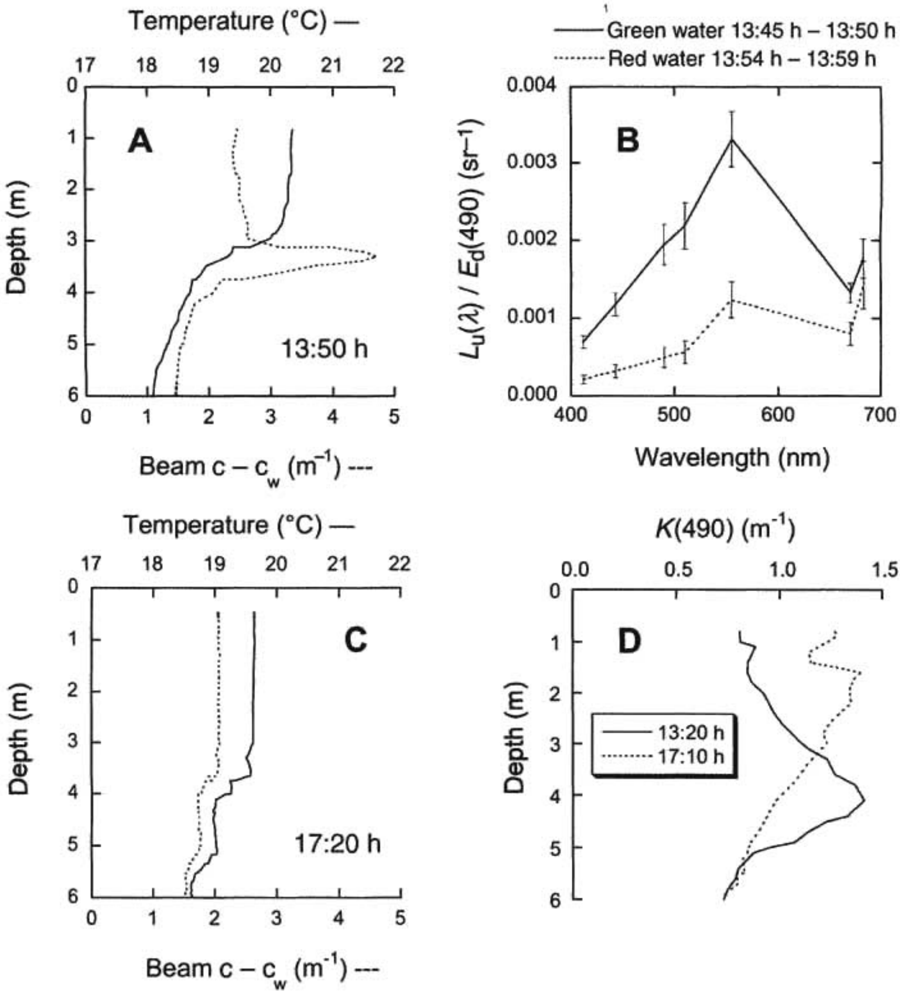

Figure 1.5
Changes in the vertical distribution of a *Gonyaulax digitale* bloom in Bedford Basin on 18 August 1993.
A, profiles of temperature (solid line) and beam attenuation, corrected for the contribution of pure water ($c - c_w$, m^{-1}; dotted line) show dinoflagellates predominantly confined to a thin subsurface layer at 13:50 h. This was the typical distribution during the morning and early afternoon.
B, measurements from a tethered spectral radiometer buoy show green water (solid line) changing rapidly to reddish-brown water (dotted line) as wind-mixing eroded the mixed layer and entrained the dinoflagellates into the surface layer.
C, mixing is demonstrated in profiles taken at 17:20 h.
D, the subsurface layer, and its entrainment into the surface layer, could also be resolved with measurements of light attenuation ($k_d(490)$, m^{-1}), which was profiled here, but could be measured with a chain of irradiance sensors. Measurements of ocean colour or samples from fixed depths could not describe the temporal changes of this population.
Source: Cullen et al. (1994).

Dynamics of the *Gonyaulax digitale* HAB would have been impossible to describe if observations were available only from the surface (ocean colour) or from conventional sampling at fixed depths. It is thus not surprising that an earlier study of *G. digitale* dynamics in Bedford Basin (Amadi et al., 1992), conducted with conventional periodic sampling, did not reveal clear patterns, and that a time series of chlorophyll concentration at 5 m detected the bloom on only one weekly sampling (Li and Dickie, 2001) when the layer happened to be at the nominal depth. The records from 5 m, especially when sustained for many years, are nonetheless extremely useful for describing annual and interannual trends of phytoplankton and nutrients, for example as influenced by increased nutrient loading and changes in climate (Li et al., 2003).

The message is that the same sampling programme can be used in different ways, depending on the questions, but that if the spatial or temporal resolution of sampling is inadequate, some phenomena cannot be described. In turn, measurements must be repeated for years to reveal trends and to test predictive models. Therefore, to address the range of scales that influence HABs and coastal ecosystems, observations must be highly resolved and sustained. With the advent of autonomous systems with sensors for physical, chemical, optical and biological properties, this is possible.

1.5.2 Fundamental strengths and limitations of bio-optical observations

The following chapters describe a stunning array of approaches for observing and describing the distributions of phytoplankton in relation to the oceanography and ecology of coastal systems. Bio-optical measurements are among the most promising, especially when integrated with systems to measure physical, chemical and biological properties on similar scales from a variety of platforms, in support of modelling. Using a few examples and without going into much detail, it is possible to illustrate some fundamental strengths and limitations that are generic to bio-optical observations.

1.5.2.1 Apparent optical properties

The absorption and scattering of light by algae, other micro-organisms, detrital and inorganic particles, dissolved substances and water modify both the underwater and upwelling (emergent) light fields. The influences of algae, which are generally distinct from those of other components (Morel and Bricaud, 1986; Morel, 2006 – Chapter 4 this volume), can be detected and quantified by determining the fate of sunlight in the ocean from measurements of apparent optical properties (AOPs) such as spectral reflectance or attenuation coefficients (Sosik, 2007 – Chapter 8 this volume). Consequently, where algal blooms occur in sufficient biomass, they may be detected by passive optical instruments (radiometers), including ocean-colour sensors on moorings, aircraft, or satellites (Lewis, 2007; Ruddick et al., 2007 – Chapters 6 and 9 this volume). Passive optical sensors cannot detect toxic algae that occur as minor components of the phytoplankton, but estimates of total pigment and information such as spectral attenuation from these sensors can provide important data for biological-chemical-physical models of algal dynamics.

One great strength of AOP measurements is that they are derived from radiometric quantities that retain their validity for long-term and wide-ranging comparisons over time or between sites (e.g. for resolving influences of eutrophication or climate variability). Interpretations of the measurements may change for the better, but if proper calibration is ensured, comparability and continuity of records should be guaranteed (Cullen et al., 1997). This contrasts with techniques for other observations, such as determination of chlorophyll concentration, measurement of turbidity, and enumeration

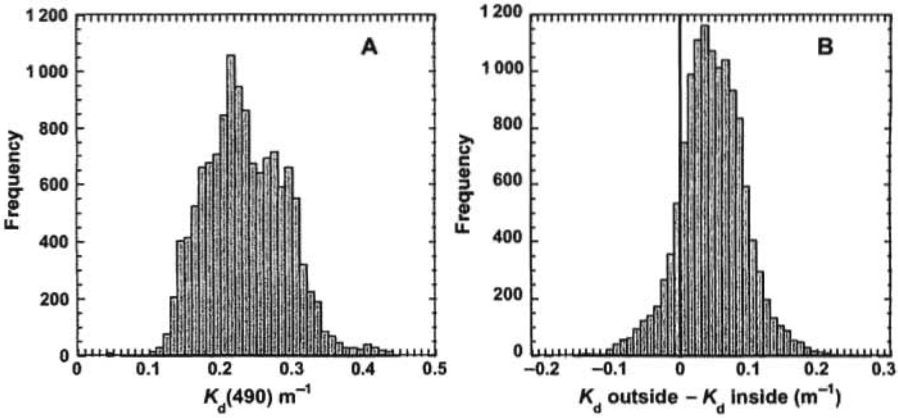

Figure 1.6
Diffuse attenuation coefficient at 490 nm ($k_d(490)$, m^{-1}) for the depth range 4–8 m, measured with moored irradiance sensors (Tethered Attenuation Coefficient Chain Sensor, TACCS, Satlantic, Inc.) in Ship Harbour, Nova Scotia, during summer 2002.
A, these observations from a mooring near a mussel farm provide a permanent record of water clarity, with statistical moments. Although they do not reveal the sources of variability, simple, direct and robust measurements like this could be compared over decades to reveal secular trends in water clarity and changes in seasonal patterns.
B, comparison with concurrent measurements at a second mooring within the mussel farm show depletion of absorbing substances (seston) within the farm. The average change is significantly different from zero, and it could be related directly to feeding by mussels. But variability was such that direct sampling from boats on a regular schedule (hourly, daily, weekly) would be unlikely to distinguish the pattern. Measurements of attenuation have the added advantage of integrating the influence of all substances in the depth range between sensors (corresponding to the suspended mussels), so the scale is correct and thin layers should not be missed.
Source: D. A. Ibarra, Dalhousie University.

of picoplankton, which have changed over the years and still vary today, complicating the interpretation of long time series and regional comparisons, despite the availability of some overlap of newer and older measurements (Karl et al., 2001).

Measurements of diffuse attenuation in a coastal inlet (Figure 1.6) illustrate the simple power of radiometric measurements for quantifying conditions in coastal waters: the nearly continuous records are valid for direct comparison with the nearby measurements made concurrently (Figure 1.6B). Comparisons could also be made over decades at the same site, or among sites in regional or global networks (IOC, 2003).

Attenuation at one wavelength (Figure 1.6) is an excellent comparative measure of water clarity, much better than the attenuation coefficient for photosynthetically available radiation (PAR), which will vary with depth even in optically uniform waters due to the spectral filtering effect (Kirk, 1994). However, measurements at one

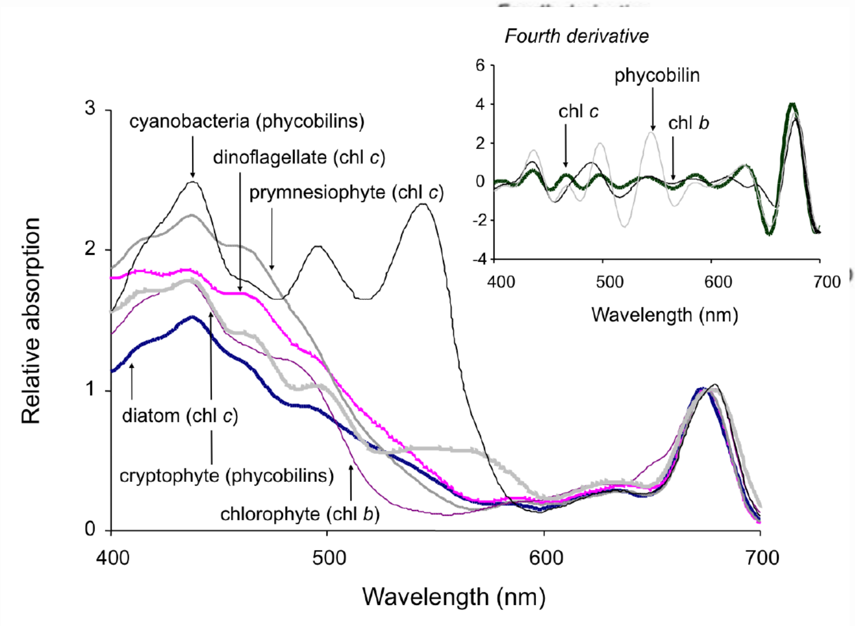

Figure 1.7
The absorption characteristics of photosynthetic pigments, and differences in pigment composition among phytoplankton taxa, are used to discriminate taxonomic status of phytoplankton from optical measurements. Absorption for representatives of the major phytoplankton taxa are presented here, normalized at 675 nm. Measurements, including these, are made using samples collected on glass-fibre filters, but new systems, including a flow-through spectrometer (Schofield et al., 2007 – Chapter 3 this volume), measure absorption characteristics in real time. Variability in spectral shapes reflects the presence of different accessory chlorophyll and carotenoid pigments, with a major contributor identified for each group.
Sources: after Johnsen et al. (1994); Schofield et al. (1996).
Inset: fourth-derivative spectra for the major spectral classes of algae are used to resolve the positions of absorption features attributable to specific pigments (Bidigare et al., 1989; Millie et al., 1995; Schofield et al., 2007 – Chapter 3 this volume).
Source: Bissett et al., 2001.

wavelength reveal nothing about the attenuating substances in the water. Spectrally resolved measurements are required to retrieve information about the constituents of the water, including phytoplankton (Figure 1.7). For example, highly resolved spectra of reflectance (ratio of upwelling radiance to downwelling irradiance, an AOP) from the Bering Sea (Figures 1.8B, 1.8C) show several distinguishing features that were repeatable over the course of a research cruise and surely related to pigmentation and fluorescence characteristics of assemblages dominated by diatoms and *Phaeocystis*, in fairly close proximity (lighter- and darker-green regions in Figure 1.8A as deduced from shipboard sampling). We have not yet perfected an analytical procedure to

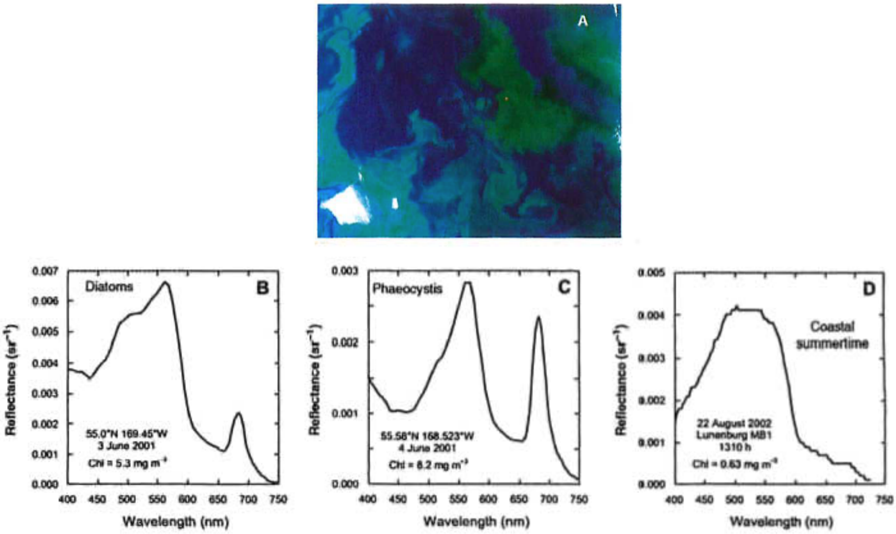

Figure 1.8
A, satellite image of a phytoplankton bloom in the Bering Sea on 7 June 2001 (292 km by 200 km centred near 58.7°N, 177°W). During this period, shipboard sampling and measurements of reflectance indicated blooms dominated by diatoms and *Phaeocystis*, in close proximity, probably corresponding to the lighter and darker green features in the image. Coccolithophore blooms are highly reflective and may be responsible for the brighter features in the SW corner of the image. *Sources*: SeaWiFS Project, NASA Goddard Space Flight Center and ORBIMAGE.
B, C, in-water measurements of hyperspectral reflectance at the surface in the Bering Sea during early June reveal irregularities between 400 nm and 550 nm that are associated with pigment absorption, which reduces reflectance (Sosik, 2006 – Chapter 8 this volume), and large peaks near 680 nm from sun-induced chlorophyll fluorescence (Babin, 2007 – Chapter 7 this volume). Here, reflectance is upwelling radiance at 65 cm divided by downwelling irradiance above the surface, measured with a Hyperspectral TSRB Tethered Spectral Radiometer Buoy (Satlantic, Inc.)
D, similar measurements from a mooring in Lunenburg Bay, Nova Scotia, show much less interpretable structure because pigment concentrations are about 10-fold lower, and much of the absorption in blue wavelengths is due to chromophoric dissolved organic matter (CDOM).

distinguish these groups and perhaps their physiological status from such measurements, but we are working on it. The spectra show that we have much information with which to work, but analyses (Brown, Huot and Cullen, unpublished) indicate that the influences of chromophoric dissolved organic matter (CDOM) represent a chronic problem that is not easily addressed.

Measurements representing non-bloom conditions illustrate some limitations of using AOPs such as reflectance for discerning species composition, or even for obtaining accurate estimates of chlorophyll concentration, in coastal waters. In a coastal bay of Nova Scotia (Figure 1.8D), the absorption by pigments in the 400–550 nm range is overwhelmed by CDOM so the reflectance spectrum shows little structure associated with phytoplankton pigments, clearly evident as depressed reflectance in Figures 1.8B and 1.8C. Sustained observations backed up by careful analysis will show, for different regions, what can be discerned about phytoplankton dynamics from measurements of AOPs in coastal waters.

This discussion of AOPs hardly scratches the surface. The important message of this overview is that the fate of light in the ocean is strongly determined by its constituents, so when effectively analysed, variability in AOPs reflects variability of what is in the water. When measured with properly constructed and calibrated instruments, AOPs represent a permanent and robust record of environmental variability that is certainly relevant to HABs and ecosystem dynamics. Apparent optical properties can be measured on many scales (Lewis, 2007; Ruddick et al., 2007 – Chapters 6 and 9 this volume) and will be centrally important to developing coastal observation systems (Malone, 2007 – Chapter 14 this volume). Enthusiasm for bio-optical interpretation of AOPs is warranted, but it should be tempered with a healthy appreciation of the difficulties encountered when working in optically complex coastal waters (IOCCG, 2000). Research on the interpretation of AOPs in coastal waters will continue for years; it is important that the technology becomes recognized more widely, so that it can be incorporated into coastal monitoring programmes.

1.5.2.2 Inherent optical properties

In the context of coastal observing systems and ecosystem dynamics, optical properties of the water are measured primarily to infer the distributions of phytoplankton and other constituents in the water. Inherent optical properties (IOPs) are the bio-optical connection between what is in the water and the AOPs that can be observed with passive optical instruments. The IOPs – coefficients for absorption and scattering, and the volume scattering function – do not depend on the geometry of the ambient light field; they are inherent to water, particles and dissolved substances, and can generally be assumed to act additively (Roesler and Boss, 2007 – Chapter 5 this volume). The bio-optical chain of evidence therefore can go:

- from AOPs to IOPs, using some quantitative guesswork to find the combination of IOPs that best explains observations, with consideration of the ambient light field and generalizations about the optical properties of phytoplankton, other particles and CDOM; and
- from IOPs to the concentration of constituents, using those same generalizations about their optical properties.

Approaches for inferring the constituents of water from optical properties are reviewed in Chapter 8 (Sosik, 2007). Progress has been rapid in recent years, bolstered by enhanced appreciation of optics by biologists and greater incorporation of biological and ecological processes into the growing field of bio-optical oceanography.

For coastal observing systems, it makes theoretical and practical sense to measure IOPs directly and make inferences about the constituents of the water directly from the measurements. Why try to infer optical properties from AOPs when the optical properties can be measured directly? Instruments are now available to characterize spectral absorption and scattering well enough to contribute significantly to the description of phytoplankton communities in coastal waters (Roesler and Boss, 2007; Schofield et al., 2007 – Chapters 5 and 3 this volume). The instruments have their own light sources and therefore operate day and night. Some, such as absorption-attenuation meters with and without prefiltration units (Chapter 5) and a capillary flow-through spectrometer system (Chapter 3), can use physical separation to discriminate contributions of particles versus dissolved constituents. When designed, constructed, calibrated and operated correctly (Chapter 5), their measurements are robust and comparable, just as are measurements of AOPs. And, just as with other optical measurement systems, fouling and instrument drift can be major problems during prolonged deployment. Fouling can be assessed and addressed (Chang and Dickey, 2007; Lehaitre et al., 2007 – Chapters 2 and 12 this volume). However, instrument drift, for example in the blank, can be a particular problem during long deployments (Davis et al., 2000) and when appropriate blanks are not or cannot be measured (Cullen and Davis, 2003).

The measurement and interpretation of IOPs should have a central role in coastal observing systems. As with any analytical approach, the value of the measurements will largely depend on careful design and operation of instruments and informed interpretation of the measurements (Chapter 5). Continued research, and a commitment to training those who will use the instruments operationally, should ensure that IOPs are used effectively in early warning, prediction and monitoring of HABs.

1.5.2.3 Fluorescence

Of all the optical properties observable in the ocean, chlorophyll fluorescence is the only one directly attributable to phytoplankton. Also, the method for estimating chlorophyll concentration from the measurement of *in vivo* fluorescence has been with us for nearly 40 years (Lorenzen, 1966) and small, relatively inexpensive *in situ* fluorometers are widely available. Consequently, stimulated fluorescence (i.e. as detected with a fluorometer) is the most commonly used measure of phytoplankton distributions in vertical profile and on moorings and under-way systems. It is also well established that sun-induced chlorophyll fluorescence can be detected with passive radiometers, including airborne imagers and satellite sensors, and related to both the biomass and photosynthetic properties of phytoplankton (reviewed by Babin, 2007 – Chapter 7 this volume).

Early on (reviewed by Cullen, 1982), it was well established that fluorescence was an imprecise measure of chlorophyll, strongly influenced by irradiance *in situ*, dark adaptation of samples (if any), species composition, physiological state and light history of the phytoplankton. Beyond that, excitation light sources in fluorometers differ significantly in spectral quality, duration and magnitude of exposure (Cullen et al., 1988; Chapter 7), making comparisons between instruments difficult (see also Neale et al., 1989). To compound the uncertainty, chlorophyll *a* constitutes a variable proportion of phytoplankton biomass, varying more than a factor of 10 with species group and environmental conditions (Geider, 1987; Cullen et al., 1993). The ease of measuring fluorescence to assess the distributions of phytoplankton thus invites trouble, as illustrated in Figure 1.9, in which one of the simpler environmental influences on fluorescence yield, sunlight, is shown to affect the measurement in a way that is seldom accounted for in calibrations (but see Marra, 1992).

As reviewed by Babin in Chapter 7, fluorometers that are now commercially available provide much more than a simple index of chlorophyll concentration. Some (for example the bbe Moldenke Fluoroprobe 2 and the SAFire by WET Labs) are capable of discriminating phytoplankton groups on the basis of their different photosynthetic absorption characteristics (see Figure 1.7) detected on the basis

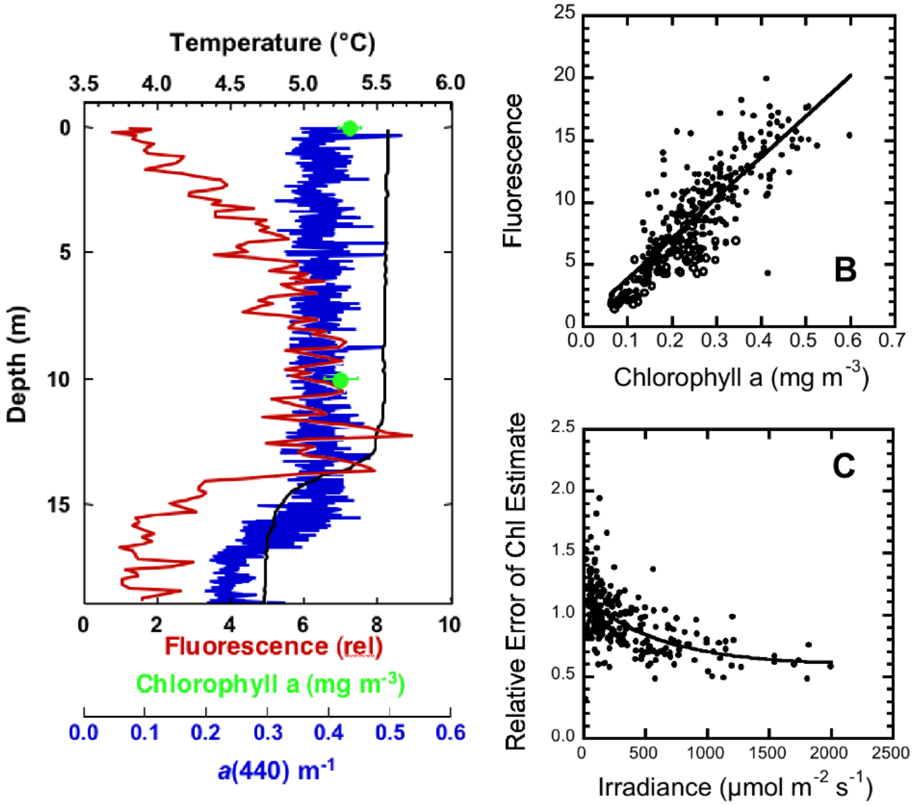

Figure 1.9
Effects of irradiance on fluorescence yield.
A, this profile from the Bering Sea shows an optically uniform mixed layer of about 12 m in which chlorophyll concentration (filled grey circles: ± s.e., *n* = 3) is the same at top and bottom, and the absorption coefficient at 440 nm (WET Labs ac-9; middle line), an IOP strongly influenced by phytoplankton pigment, is vertically uniform. It may be concluded that the concentration of phytoplankton is uniform in the upper 10 m. Fluorescence (WET Labs WETStar; left-hand line), however, is suppressed near the surface by nonphotochemical quenching (Babin, 2007 – Chapter 7 this volume). This distribution of fluorescence could be incorrectly interpreted as surface avoidance by phytoplankton.
Source: J.J. Cullen, unpublished.
B, when fluorometers are calibrated with concurrent measurements of chlorophyll concentration, the observations near the surface (open symbols) may not have a particularly strong influence on the regression, so the effect of bright light can be ignored while maintaining a fairly good regression coefficient.
C, the effect of bright light is real, though, and readily accounted for with a simple model that quantifies the underestimate of chlorophyll due to fluorescence quenching as a function of ambient irradiance.
Source: Cullen and Lewis (1995).

of relative fluorescence yield under multispectral excitation (Beutler et al., 2002). The physiology of phytoplankton can also be explored: by measuring fluorescence yield while manipulating flash intensity or background irradiance, it is possible to determine parameters that describe the photosynthetic apparatus – maximum quantum yield for charge separation, photosynthetic cross-section, and turnover time of photosystem II (e.g. Schreiber et al., 1986; Kolber and Falkowski, 1993; Falkowski and Kolber, 1995). In principle, these parameters can be used to calculate the rate of photosynthesis (Kolber and Falkowski, 1993; Suggett et al., 2003). More importantly, perhaps, they are very sensitive to physiological state and environmental conditions and thus may be excellent diagnostics of environmental stresses such as nutrient limitation (e.g. Kolber et al., 1988; Geider et al., 1993; Parkhill et al., 2001). The development of robust diagnostics and their measurement in the field is anything but straightforward, however: differences in culture conditions can have a strong influence on the relationship between nutrient stress and maximum quantum yield (Cullen et al., 1992; Parkhill et al., 2001); little experimental work has been done on phytoplankton grown under high irradiance characteristic of the sea surface (Cullen and Lewis, 1995); and critical evaluation of the new generation of fluorometers under a range of conditions at sea is difficult and not yet widely demonstrated (Cullen and Davis, 2003; Chapter 7).

A fundamental strength and an unfortunate limitation of fluorescence as an optical measurement is that it is very strongly tied to photosynthesis and physiology of phytoplankton. This is a strength, because the measurement has such great potential (which has already been demonstrated) – it is also a limitation, because interpretation of the measurements requires a working knowledge of algal physiology, including the fundamentals of fluorescence and photosynthesis (Chapter 7). Experience has shown that the fluorescence literature seems nearly impenetrable to many aquatic scientists, though perseverance pays off. Even if the process is understood, the measurement needs further attention: the design of instruments and evaluation of their performance requires a good appreciation of the principles of measuring fluorescence and, for fluorometers such as the fast repetition rate fluorometer (Kolber and Falkowski, 1993), the statistical determination of parameters from kinetic curves (Laney, 2003). The rewards from measuring fluorescence are potentially great, and the pitfalls are many.

1.6 TOWARDS REAL-TIME OBSERVATION AND PREDICTION OF HABs

As amply demonstrated in this volume (see also Glasgow et al., 2004), advances in observation technology and modelling, along with greatly enhanced capabilities for communications and computing, make a revolution in coastal oceanography, monitoring and management inevitable. Much as remote sensing from space has fundamentally changed our view of the oceans and allowed questions to be addressed that could hardly be posed before (e.g. mesoscale variability, discussed by Lewis, 2002), automated, real-time observing systems will transform the way the ocean is sampled and understood. With advancing technology, the potential for describing biological and physical variability on a very broad range of scales is almost limitless, and many applications will be directly relevant to the coastal ocean (IOC, 2003). Science will deliver the capability to detect ecosystem processes and the dynamics of some harmful algae in real time, and predictive models will improve. Continued progress will require large investments of time and resources, and this can be justified only with the promise of operational monitoring and prediction systems for HABs and other ecological phenomena. Consequently, scientific research and operational oceanography must work together as never before (Malone, 2007 – Chapter 14 this volume). An assessment of the present capabilities and limitations of real-time observation and prediction systems, and their links to monitoring and management, can be helpful in preparing for the challenges and opportunities that lie ahead.

1.6.1 Enabling research

1.6.1.1 Observation technologies

Progress in the observation of ecosystem processes in coastal waters has been rapid and significant. Optical and acoustical instruments, mounted on a variety of platforms, can already provide unprecedented views of coastal processes on scales from those relevant to cellular interactions all the way to climate change (Chang and Dickey, 2007; Griffiths, 2007; Jaffe, 2007; Schofield et al., 2007 – Chapters 2, 13, 10 and 3 this volume). The measurements are not direct assessments of species distributions and activities – they are proxies that must be interpreted through careful analysis (e.g. Sosik, 2007 – Chapter 8 this volume); quantitative evaluation of analytical approaches and widespread acceptance for use in monitoring are major challenges (Figure 1.10). To foster effective development of coastal observation systems, the users of measurements from optical or acoustical instruments should have a good appreciation of their theoretical foundations and limitations. In turn, designers of the instruments can do their jobs better if the biological reasons for variations in instrument response (e.g. environmental influences on fluorescence yield; effects of plankton community structure on scattering) are more fully understood. Enhanced collaboration among scientists from different disciplines and the designers of instruments is the key to rapid advancement, and in many research communities this is being pursued actively with good results.

Detection of HABs cannot rely completely on indirect measurements of phytoplankton abundance. In many situations there is a need for identification of species or assessment of toxicity, sometimes at cellular level. As with other fields of ocean observation, progress has been rapid (Scholin et al., 2007 – Chapter 11 this volume) and collaborations have been effective. As methods for autonomous assessment of HABs become more developed, approaches for quantifying the abundance of zooplankton and other consumers will become increasingly important (Jaffe, 2007 – Chapter 10 this volume).

Judging by the leading edge, research on coastal observation technologies is a major success story, on a good track and gaining momentum. Sustained progress of widespread significance depends on expanding the base of scientists who use these tools for coastal research, so observation of HABs and ecosystem dynamics can be addressed under a broad range of conditions worldwide. This can be accomplished through education, for example inclusion of bio-optics in curricula, and enhanced accessibility of instruments or data. The latter is a challenge well beyond the scope of a scientific review; nonetheless, many observation systems provide free access to data over the internet and several provide opportunities for collaborative deployment of new instruments. This, along with development, testing, acceptance and commercialization of robust and more affordable instruments, should help to sustain the ongoing revolution in coastal observation.

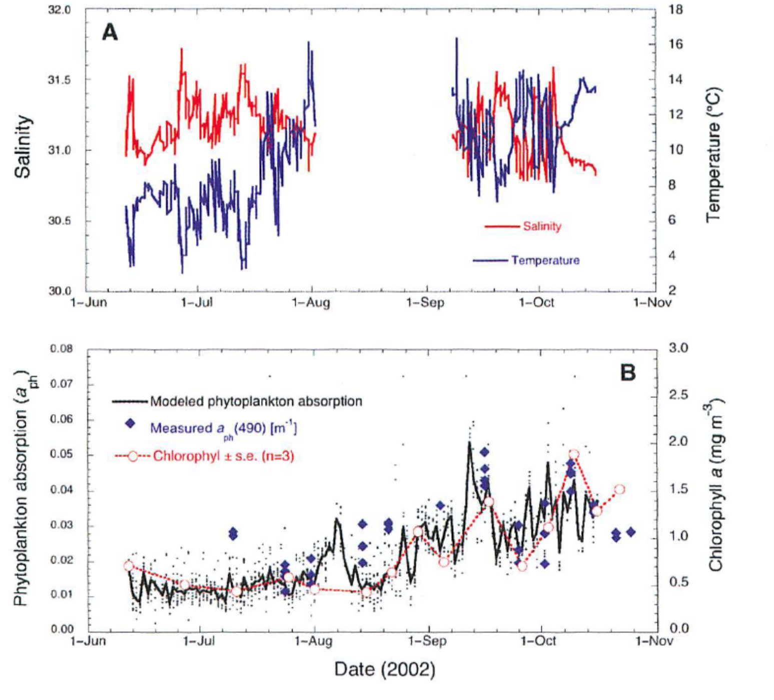

Figure 1.10
Early results from a coastal observatory illustrate some of the promise of coastal observing systems and many of the challenges that must be overcome before systems for research and development become operational and comparable between sites (Glenn et al., 2000; IOC, 2003; Malone, 2007 – Chapter 14 this volume). The MEPS-Bay system[6] has three moorings with temperature-salinity chains, current meters, meteorology and optics; a data assimilation model is being developed to incorporate these data and other local observations into a real-time, coupled, atmosphere-ocean simulation of the bay (Sheng and Wang, 2004).
A, the records of temperature and salinity from the 11 m conductivity-temperature (CT) sensor on a mooring (Lunenburg Bay, MB1) show the seasonal development of temperature, and many event-scale changes of water in the bay that could not be resolved with conventional monitoring. It also shows a gap corresponding to a technical failure; operational systems must be robust and provision must be made to correct such problems quickly.
B, nearly continuous measurements of hyperspectral ocean colour (as in Figure 1.8D) were analysed by Brown and Huot (unpublished) with an inverse model, generating relative estimates of phytoplankton absorption (Roesler and Perry, 1995; Sosik, 2007 – Chapter 8 this volume) corrected for the substantial contribution of CDOM and other constituents of the water (black dots; the black line is a locally weighted least-squares regression to indicate trends). Blue symbols show direct measurements of phytoplankton absorption (filter pad method, corrected for detritus) and open red symbols are determinations of extracted chlorophyll. Development, quantitative evaluation and widespread acceptance of robust optical measures of phytoplankton is required for routine monitoring. This is a major challenge.

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[6] Marine Environmental Prediction System-Bay; Lunenburg, Nova, Scotia; www.cmep.ca/bay

1.6.1.2 Prediction systems

For a long time, the development and evaluation of marine models was fundamentally limited by availability of data. A prediction was untestable if the process could not be resolved with real measurements. This has not stopped the development of models, but it has certainly limited their rigorous evaluation in the context of predicting the occurrence of HABs. Until recently, most models of HABs have been either conceptual descriptions, somewhat general predictions based on empirical data or theoretical models, or idealized simulations of responses to forcing factors. Such models are valuable – to a large extent, they represent the foundations of our understanding of HABs. However, data-limited models are not suitable for real-time forecasts of HABs. With the advent of coastal observation systems, this is changing. It is now possible to construct numerical simulations of ecosystem dynamics and HABs in local flow fields (Bissett et al., 2007; Fennel and Neumann, 2007; Lee et al., 2007; McGillicuddy et al., 2007 – Chapters 17, 18 and 16 this volume), and data assimilation procedures for integrating observations into models (Pinardi et al., 2007 – Chapter 20 this volume) are being extended to include biological processes (Walstad and McGillicuddy, 2000). Also, blooms have been detected by remote sensing and tracked, with forecasts of trajectories (Stumpf et al., 2003). Prediction of ecosystem dynamics in the coastal zone is in its infancy, so expectations for immediate successes should not be too high. Still, results to date and the confluence of observation and modelling systems suggest that research will provide the means to predict the dynamics of HABs for some, but certainly not all, scales and locations.

Many of the limitations of predictive models have to do with scales of prediction and the limits of predictability. As with all ecological models, a tradeoff will always exist between generality and realistic simulation. No deterministic model will ever simulate the time-dependent evolution of a natural algal bloom in three dimensions at the scale of a cell's interaction with the environment. Predictive models will adopt different approaches, relying on carefully chosen schemes for generalization. Success will depend to a large extent on the suitability of the approach for the coastal system being modelled, and the accuracy of the ecological information on which the model is constructed. Close ties between biological and modelling research will be essential.

Many aspects of phytoplankton dynamics can be modelled using functions based on experimental results (e.g. growth rate as a function of temperature and irradiance, grazing rate as a function of cell concentration). However, important ecological properties and processes must be better resolved to improve the prediction of HABs. For example:

- There is a need for information on what ecophysiological factors distinguish a HAB species from a closely related species that does not cause the harmful effects (Smayda, 1997*a*; GEOHAB, 2001).
- Descriptions of food-web interactions should be better constrained with observations and experimental results, including more assessments of grazing and grazers in coastal observation systems, and descriptions of chemical and other defences against grazing (Smetacek, 1998).
- Research is needed to improve the predictability of algal growth and behaviour in a complex environment, including variable light and nutrients (and vertical migration when warranted). Currently, most experimental results are obtained for one isolate of a species grown in well-defined conditions (Cullen and MacIntyre, 1998).

These examples from biology are only a few of the many gaps in knowledge that should be filled as predictive models are developed. Other requirements for ecological information, observations, physical models and numerical techniques are identified in this volume (see also GEOHAB, 2001).

Even if the research is done, there is a great need for effective transfer of information between experimentalists, oceanographers and modellers (by no means mutually exclusive categories). This could be accelerated through the development of interactive modelling and visualization systems. Working together, biologists and modellers could 'tinker' with a model while discussing the merits of different biological parameterizations and their consequences for output from the model. Turnaround time for feedback would be reduced by orders of magnitude from the old model of scientific publication or annual meetings. Implementation of these interactive systems could transform coastal ecosystem modelling and, with modifications, serve an important role in coastal management and education of the public.

1.6.2 Transition to routine operations

An ultimate goal of research on observation and prediction of HABs is the establishment of real-time systems for routine monitoring, early warning and prediction. This is operational oceanography. Malone (2007 – Chapter 14 this volume) explains why the requirements for operational oceanography are much different than for research, and suggests that fundamental changes in the relationships between scientists, managers and society in general are needed not only to meet societal goals, but also to maintain the integrity of the scientific process as it serves the many stakeholders who invest in it and depend on it for their livelihoods, enjoyment, safety or survival. This grand challenge must be met if the revolution in coastal observation technology is to spread. Here, the discussion is confined to some practical issues that are nearly universal and must be addressed.

Early results from a nascent coastal observing system, under development as a research project, demonstrate the great value of autonomous systems for monitoring and prediction (Figure 1.10). They also illustrate many of the scientific, logistical and structural problems that must be confronted as observation systems for research contribute to and eventually merge with operational oceanography. The record of temperature and salinity from one of many sensors in the observation system (Figure 1.10A) shows the temporal resolution of moored observatories (Chang and Dickey, 2007 – Chapter 2 this volume). Nothing less would serve to describe hydrographic variability in the bay. A record with a gap is shown to highlight the importance of continuous observations in operational systems. Researchers are familiar with such technical problems, and fix them as quickly as is feasible under a broad range of constraints; as coastal observation systems become established and more useful for sustained monitoring and detection, it will be important to develop support systems for the operational components. That is, as the systems become operational, responsibility for running them should migrate from scientists to agencies. The necessary coordination is not well developed in many jurisdictions.

Novel optical observations from the coastal observatory reveal difficulties that will arise during the integration of results from research systems into coastal monitoring for operational oceanography (Figure 1.10B):

- Measurements of ocean colour from a mooring provide nearly continuous records of phytoplankton absorption, an optical estimate of phytoplankton abundance. It could be argued that the measure is as good as chlorophyll *a*, the widely used indicator of phytoplankton, and better than *in vivo* fluorescence. The estimate is generated using a fairly complicated inverse model, however, and many other bio-optical models exist (Sosik, 2007 – Chapter 8 this volume). Is it reasonable to expect that regional or global observing systems will adopt highly derived data products as operational measures of phytoplankton or other constituents of the water? Who will decide, and how?

- Evaluation of the model for phytoplankton absorption must include direct comparison with sea-truth samples. Although collection and analysis of water samples is straightforward, comprehensive evaluation is difficult and expensive: regular sampling at our site (about three times per month; discrete samples in Figure 1.10B) required a substantial commitment of time and resources, yet obviously it missed interesting and possibly important events. Statistical analysis of results will not be as powerful as we would like. Adaptive sampling based on cues from real-time sensors, and participation of community volunteers who can easily visit the sites for sampling, will help us to acquire more and better data.
- More broadly, the measurements that form the foundations of operational systems for monitoring and prediction of HABs and ecosystem dynamics will have to be reliable and affordable, and they should be simple to operate, with measurements that are easy to interpret. Currently, the triumvirate of optical measurements for environmental monitoring are *in vivo* fluorescence, turbidity and PAR. Bio-optical research, reviewed in this volume, has shown that much more discriminating measurements are now available. Greater efforts should be made to develop and test robust sensors so that emerging observation systems can start out with newer measurements that are likely to be the standards in coming decades.

The gap between the state of the art in bio-optical oceanography and well established practices in coastal monitoring has parallels in almost every other aspect of observation and prediction of HABs. Given the promise of the science and the immediacy of its practical application, there is excellent justification for pursuing new ways to coordinate research with operational oceanography, using observation and prediction for monitoring and management. This will come through education, training, communication and genuine interest in cooperation.

1.7 CONCLUSIONS

Excitement about real-time coastal observing systems is developing rapidly, and systems are being deployed worldwide (Glasgow et al., 2004). Scientific and technical advances are building a capability for observing and describing dynamics of the coastal ocean in real time on the scales that really matter, rather than poring over sparse, hard-fought data to infer what occurred months or years before. Ironically, achievements in specialized fields (e.g. optics, acoustics, algal physiology, molecular biology, ocean engineering, numerical modelling techniques) have led to the development of a truly interdisciplinary approach for describing ecosystem dynamics. Interactions among biologists, physicists, engineers and modellers are stronger than ever before, and better links with managers and policy-makers are sure to develop. Classic research of the data-starved but thinking-rich 'old days' is highly relevant as efforts to describe HABs progress. This is a dynamic time, with much to do. As technology and research march forward, we should remember to maintain our roots in ecology and oceanography and to pay special attention to making our work accessible to those who will use it.

REFERENCES

AMADI, I., SUBBA RAO, D. V. and PAN, Y. 1992. A *Gonyaulax digitale* red water bloom in the Bedford Basin, Nova Scotia, Canada. *Bot. Marina*, 35, pp. 451–55.

AMANO, K., WATANABE, M., KOHATA, K. and HARADA, S. 1998. Conditions necessary for *Chattonella antiqua* red tide outbreaks. *Limnol. Oceanogr.*, 43, pp. 117–28.

ANDERSEN, P., ENEVOLDSEN, H. and ANDERSON, D. 2003. Harmful algal monitoring programme and action plan design. In: Hallegraeff et al. (eds), op. cit., pp. 627–47.

ANDERSON, D. M. 1990. Toxin variability in *Alexandrium* species. In: E. Granéli, B. Sundström, L. Edler and D. M. Anderson (eds), *Toxic Marine Phytoplankton*. Elsevier, New York, pp. 41–51.

ANDERSON, D. M. 1995. Toxic red tides and harmful algal blooms: a practical challenge in coastal oceanography. *Rev. Geophys.*, 33, Suppl., pp. 1189–200. (US National Report to IUGG 1991–1994.)

ANDERSON, D. M. 1997. Bloom dynamics of toxic *Alexandrium* species in the northeastern US. *Limnol. Oceanogr.*, 42, pp 1009–22.

ANDERSON, D. M., ANDERSEN, P., BRICELJ, V. M., CULLEN, J. J. AND RENSEL, J. E. 2001. *Monitoring and Management Strategies for Harmful Algal Blooms in Coastal Waters*. Paris, Intergovernmental Oceanographic Commission of UNESCO. (IOC Technical Series 59.)

ANDERSON, D. M., CEMBELLA, A. D. and HALLEGRAEFF, G. M. (eds). 1998. *Physiological Ecology of Harmful Algal Blooms*. Heidelburg, Springer-Verlag.

BABIN, M. 2007. Phytoplankton fluorescence: theory, current literature and in situ measurement. In: Babin et al. (eds), op. cit., this volume.

BARBER, R. T. and SMITH, R. L. 1981. Coastal upwelling ecosystems. In: A. R. Longhurst (ed.), *Analysis of Marine Ecosystems*. San Diego, Calif., Academic Press, pp. 31–68.

BATES, S. S. 1998. Ecophysiology and metabolism of ASP toxin production. In: Anderson et al. (eds), op. cit., pp. 405–26.

BEDFORD INSTITUTE. 2003. www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/CTD/

BEUTLER, M., WILTSHIRE, K. H., MEYER, B., MOLDAENKE, C., LÜRING, C., MEYERHÖFER, M., HANSEN, U.P. and DAU, H. 2002. A fluorometric method for the differentiation of algal populations *in vivo* and *in situ*. *Photosyn. Res.*, 72, pp. 39–53.

BIANCHI, T. S., ENGELHAUPT, E., WESTMAN, P., ANDRÉN, T., ROLFF, C. and ELMGREN, R. 2000. Cyanobacterial blooms in the Baltic Sea: natural or human-induced? *Limnol. Oceanogr.*, 45, pp. 716–26.

BIDIGARE, R. R., MORROW, J. H. and KIEFER, D. A. 1989. Derivative analysis of spectral absorption by photosynthetic pigments in the western Sargasso Sea. *J. Mar. Res.*, 47, pp. 323–41.

BISSETT, W. P., SCHOFIELD, O., GLENN, S., CULLEN, J. J., MILLER, W. L., PLUEDDEMANN, A. J. and MOBLEY, C. D. 2001. Resolving the impacts and feedback of ocean optics on upper ocean ecology. *Oceanogr. Mag.*, 14, pp. 30–53.

BISSETT, W. P., ARNONE R., DEBRA S., DYE D., KIRKPATRICK G., MOBLEY C. and SCHOFIELD O. M. 2007. Integration of ocean-colour remote sensing with coastal nowcast/forecast simulations of harmful algal blooms. In Babin et al (eds) op. cit., this volume.

BRICELJ, V. M. and LONSDALE, D. J. 1997. *Aureococcus anophagefferens*: causes and ecological consequences of brown tides in US mid-Atlantic coastal waters. *Limnol. Oceanogr.*, 42, pp. 1023–38.

CAPONE, D. G., SUBRAMANIAM, A., MONTOYA, J. P., VOSS, M., HUMBORG, C., JOHANSEN, A. M., SIEFERT, R. L. and CARPENTER, E. J. 1998. An extensive bloom of the N_2-fixing cyanobacterium *Trichodesmium erythraeum* in the central Arabian Sea. *Mar. Ecol. Progr. Ser.*, 172, pp. 281–92.

CARR, M. E. 1998. A numerical study of the effect of periodic nutrient supply on pathways of carbon in a coastal upwelling regime. *J. Plankton Res.*, 20, pp. 491–516.

CEMBELLA, A. D. 1998. Ecophysiology and metabolism of paralytic shellfish toxins in marine microalgae. In: Anderson et al. (eds), op. cit., pp. 381–403.

CHANG, G. C. and DICKEY, T. D. 2007. Interdisciplinary sampling strategies for detection and characterization of harmful algal blooms. In: Babin et al. (eds), op. cit., this volume.

Costanza, R., d'Arge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., Sutton, P. and Vandenbelt, M. 1997. The value of the world's ecosystem services and natural capital. *Nature*, 387, pp. 253–60.

Cowles, T. J. 2003. Planktonic layers: physical and biological interactions on the small scale. In: *Handbook of Scaling Methods in Aquatic Ecology: Measurements, Analysis, Simulation*. Boca Raton, Fl., CRC Press, pp. 31–49.

Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.*, 39, pp. 791–803.

Cullen, J. J., Ciotti, A. M., Davis, R. F. and Lewis, M. R. 1997. Optical detection and assessment of algal blooms. *Limnol. Oceanogr.*, 42, pp. 1223–39.

Cullen, J. J., Ciotti, A. M. and Lewis, M. R. 1994. Observing biologically induced optical variability in coastal waters. *Ocean Optics XII, Proc. SPIE*, 2258, pp. 105–15.

Cullen, J. J. and Davis, R. F. 2003. The blank can make a big difference in oceanographic measurements. *Limnol. Oceanogr. Bull.*, 12, pp. 29–35.

Cullen, J. J., Franks, P. J. S., Karl, D. M. and Longhurst, A. 2002. Physical influences on marine ecosystem dynamics. In: A. R. Robinson, J. J. McCarthy and B. J. Rothschild (eds), *The Sea.* Vol. 12: *Biological-Physical Interactions in the Ocean.* New York, John Wiley & Sons, pp. 297–335.

Cullen, J. J., Geider, R. J., Ishizaka, J., Kiefer, D. A., Marra, J., Sakshaug, E. and Raven, J. A. 1993. Toward a general description of phytoplankton growth for biogeochemical models. In: G. T. Evans and M. J. R. Fasham (eds), *Towards a Model of Ocean Biogeochemical Processes*. Berlin, Springer-Verlag, pp. 153–76.

Cullen, J. J. and Lewis, M. R. 1995. Biological processes and optical measurements near the sea-surface: some issues relevant to remote sensing. *J. Geophys. Res.*, 100, pp. 13255–66.

Cullen, J. J. and MacIntyre, J. G. 1998. Behavior, physiology and the niche of depth-regulating phytoplankton. In: Anderson et al. (eds), op. cit., pp. 559–80.

Cullen, J. J., Yang, X. and MacIntyre, H. L. 1992. Nutrient limitation of marine photosynthesis. In: P. G. Falkowski and A. Woodhead (eds), *Primary Productivity and Biogeochemical Cycles in the Sea*. New York, Plenum Press, pp. 69–88.

Cullen, J. J., Yentsch, C. S., Cucci, T. L. and MacIntyre, H. L. 1988. Autofluorescence and other optical properties as tools in biological oceanography. *Proc. SPIE*, 925, pp. 149–56.

Dahl, E. and Tangen, K. 1993. 25 years experience with *Gyrodinium aureolum* in Norwegian waters. In: Smayda and Shimizu (eds), op. cit., pp. 15–21.

Davis, R. F., Stabeno, P. J. and Cullen, J. J. 2000. Use of optical measurements from moorings to detect coccolithophore blooms in the Bering Sea. *Ocean Optics XV, Proc. SPIE*, (CD-ROM)

Dekshenieks, M. M., Donaghay, P. L., Sullivan, J. M., Rines, J. E. B., Osborn, T. R. and Twardowski, M. S. 2001. Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. *Mar. Ecol. Progr. Ser.*, 223, pp. 61–71.

Deyoe, H. R. and Suttle, C. A. 1994. The inability of the Texas 'brown tide' alga to use nitrate and the role of nitrogen in the initiation of a persistent bloom of this organism. *J. Phycol.*, 30, pp. 800–06.

Donaghay, P. L. and Osborn, T. R. 1997. Toward a theory of biological-physical control of harmful algal bloom dynamics and impacts. *Limnol. Oceanogr.*, 42, pp. 1283–96.

Eppley, R. W., Reid, F. M. H., Cullen, J. J., Winant, C. D. and Stewart, E. 1984. Subsurface patch of a dinoflagellate (*Ceratium tripos*) off Southern California: patch length, growth rate, associated vertically migrating species. *Mar. Biol.*, 80, pp. 207–14.

Falkowski, P. G. and Kolber, Z. 1995. Variations in chlorophyll fluorescence yields in phytoplankton in the world oceans. *Aust. J. Plant Physiol.*, 22, pp. 341–55.

Fennel, W. and Neumann, T. 2007. Modelling coastal dynamics and harmful algal blooms in the Baltic Sea. In: Babin et al. (eds), op. cit., this volume.

Figueiras, F. G., Gomez, E., Nogueira, E. and Villarino, M. L. 1996. Selection of *Gymnodinium catenatum* under downwelling conditions in the Ria del Vigo. In: T. Yasumoto, Y. Oshima and Y. Fukuyo (eds), *Harmful and Toxic Algal Blooms*. Paris, Intergovernmental Oceanographic Commission of UNESCO, pp. 215–18.

FRAGA, S., ANDERSON, D. M., BRAVO, I., REGUERA, B., STEIDINGER, K. A. and YENTSCH, C. M. 1988. Influence of upwelling relaxation on dinoflagellates and shellfish toxicity in Ria de Vigo, Spain. *Estuar. Coast. Mar. Sci.*, 27, pp. 349–61.

FRANKS, P. J. S. 1997. Spatial patterns in dense algal blooms. *Limnol. Oceanogr.*, 42, pp. 1297–305.

FRANKS, P. J. S. 2007. Physics and physical modelling of harmful algal blooms. In: Babin et al. (eds), op. cit., this volume.

FRANKS, P. J. S. and ANDERSON, D. M. 1992*a*. Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. *Mar. Biol.*, 112, pp. 153–64.

FRANKS, P. J. S. and ANDERSON, D. M. 1992*b*. Toxic phytoplankton blooms in the southwestern Gulf of Maine: testing hypotheses of physical control using historical data. *Mar. Biol.*, 112, pp. 165–74.

FRANKS, P. J. S. and KEAFER, B. A. 2003. Sampling techniques and strategies for coastal phytoplankton blooms. In: Hallegraeff et al. (eds), op. cit., pp. 51–76.

FROMENTIN, J. M. and PLANQUE, B. 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Progr. Ser.*, 134, pp. 111–18.

GEIDER, R. J. 1987. Light and temperature dependence of the carbon to chlorophyll *a* ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. *New Phytol.*, 106, pp. 1–34.

GEIDER, R. J., GREENE, R. M., KOLBER, Z., MACINTYRE, H. L. and FALKOWSKI, P. G. 1993. Fluorescence assessment of the maximum quantum efficiency of photosynthesis in the western North Atlantic. *Deep Sea Res.*, 40, pp. 1204–24.

GENTIEN, P. 1998. Bloom dynamics and ecophysiology of the *Gymnodinium mikimotoi* species complex. In: Anderson et al. (eds), op. cit., pp. 155–73.

GENTIEN, P. and ARZUL, G. 1990. Exotoxin production by *Gyrodinium* cf. *aureolum* (Dinophyceae). *J. Mar. Biol. Assoc. UK*, 70, pp. 571–81.

GENTIEN, P., LUNVEN, M., LEHAITRE, M. and DUVENT, J. L. 1995. *In situ* depth profiling of particles sizes. *Deep Sea Res.*, 42, pp. 1297–312.

GEOHAB. 2001. *Global Ecology and Oceanography of Harmful Algal Blooms, Science Plan.* Baltimore/Paris, Scientific Committee on Oceanic Research/Intergovernmental Oceanographic Commission of UNESCO.

GJØSÆTER, J., LEKVE, K., STENSETH, N. C., LEINAAS, H. P., CHRISTIE, H., DAHL, E., DANIELSSEN, D. S., EDVARDSEN, B., OLSGARD, F., OUG, E. and PAASCHE, E. 2000. A long-term perspective on the *Chrysochromulina bloom* on the Norwegian Skagerrak coast 1988: a catastrophe or an innocent incident? *Mar. Ecol. Progr. Ser.*, 207, pp. 201–18.

GLASGOW, H. B., BURKHOLDER, J. M., REED, R. E., LEWITUS, A. J. and KLEINMAN, J. E. 2004. Real-time remote monitoring of water quality: a review of current applications, and advancements in sensor, telemetry, and computing technologies. *J. Exp. Mar. Biol. Ecol.*, 300, pp. 409–48.

GLENN, S. M., DICKEY, T. D., PARKER, B. and BOICOURT, W. 2000. Long-term real-time coastal ocean observation networks. *Oceanogr. Mag.*, 13, pp. 24–34.

GOBLER, C. J., RENAGHAN, M. J. and BUCK, N. J. 2002. Impacts of nutrients and grazing mortality on the abundance of *Aureococcus anophagefferens* during a New York brown tide bloom. *Limnol. Oceanogr.*, 47, pp. 129–41.

GRANÉLI, E., PAASCHE, E. and MAESTRINI, S. Y. 1993. Three years after the *Chrysochromulina polylepis* bloom in Scandinavian waters in 1988: some conclusions of recent research and monitoring. In: Smayda and Shimizu (eds), op. cit., pp. 23–32.

GRANTHAM, B. A., CHAN, F., NIELSEN, K. J., FOX, D. S., BARTH, J. A., HUYER, A., LUBCHENCO, J. and MENGE, B. A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature*, 249, pp. 749–54.

GRIFFITHS, G. 2007. Glider and autonomous underwater vehicle observing systems. In: Babin et al. (eds), op. cit., this volume.

HALLEGRAEFF, G. M. 2003. Harmful algal blooms: a global overview. In: Hallegraeff et al. (eds), op. cit., pp. 25–49.

Hallegraeff, G. M., Anderson, D. M. and Cembella, A. D. (eds). 2003. *Manual on Harmful Marine Microalgae*. Paris, Intergovernmental Oceanographic Commission of UNESCO. (Monographs on Oceanographic Methodology 11.)

Hallegraeff, G. M. and Fraga, S. 1998. Bloom dynamics of the toxic dinoflagellate *Gymnodinium catenatum*, with emphasis on Tasmanian and Spanish coastal waters. In: Anderson et al. (eds), op. cit., pp. 59–80.

Hanson, A. K. Jr and Donaghay, P. L. 1998. Micro- to fine-scale chemical gradients and layers in stratified coastal waters. *Oceanogr. Mag.*, 11, pp. 10–17.

Harashima, A., Tsuda, R., Tanaka, Y., Kimoto, T., Tatsuta, H. and Furusawa, K. 1997. Monitoring algal blooms and related biogeochemical changes with a flow-through system deployed on ferries in the adjacent seas of Japan. In: Kahru and Brown (eds), op. cit., pp. 85–112.

Heil, C. A., Glibert, P. M. and Fan, C. 2005. *Prorocentrum minimum* (Pavillard) Schiller: a review of a harmful algal bloom species of growing worldwide importance. *Harmful Algae*, 4, pp. 449–70.

Holligan, P. M. 1979. Dinoflagellate blooms associated with tidal fronts around the British Isles. In: Taylor and Seliger (eds), op. cit., pp. 249–56.

Holmes, R. W., Williams, P. M. and Eppley, R. W. 1967. Red water in La Jolla Bay, 1964–1966. *Limnol. Oceanogr.*, 12, pp. 503–12.

Honjo, T. 1993. Overview on bloom dynamics and physiological ecology of *Heterosigma akashiwo*. In: Smayda and Shimizu (eds), op. cit., pp. 33–42.

IOC. 2003. *The Integrated, Strategic Design Plan for the Coastal Ocean Observations Module of the Global Ocean Observing System*. Paris, Intergovernmental Oceanographic Commission of UNESCO.

IOCCG. 2000. *Remote Sensing of Ocean Colour in Coastal, and Other Optically-Complex, Waters*. Dartmouth, Nova Scotia, International Ocean-Colour Coordinating Group.

Jaffe, J. S. 2007. Sensing plankton: acoustics and optical imaging. In: Babin et al. (eds), op. cit., this volume.

James, K., Moroney, C., Roden, C., Satake, M., Yasumoto, T., Lehane, M. and Furey, A. 2003. Ubiquitous 'benign' alga emerges as the cause of shellfish contamination responsible for the human toxic syndrome, azaspiracid poisoning. *Toxicon*, 41, pp. 145–51.

Johnsen, G., Samset, O., Granskog, L. and Sakshaug, E. 1994. *In vivo* absorption characteristics in 10 classes of bloom-forming phytoplankton: taxonomic characteristics and responses to photoadaptation by means of discriminant and HPLC analysis. *Mar. Ecol. Progr. Ser.*, 105, pp. 149–57.

Johnsen, G., Volent, Z., Tangen, K. and Sakshaug, E. 1997. Time series of harmful and benign phytoplankton blooms in northwest European waters using the Seawatch buoy system. In: Kahru and Brown (eds), op. cit., pp. 115–43.

Johnson, K. S. and Coletti, L. J. 2002. *In situ* ultraviolet spectrophotometry for high resolution and long-term monitoring of nitrate, bromide and bisulfide in the ocean. *Deep Sea Res. I.*, 49, pp. 1291–305.

Juhl, A. R. and Latz, M. I. 2002. Mechanisms of fluid shear-induced inhibition of population growth in a red-tide dinoflagellate. *J. Phycol.*, 38, pp. 683–94.

Kahru, M. 1997. Using satellites to monitor large-scale environmental change: case study of cyanobacterial blooms in the Baltic Sea. In: Kahru and Brown (eds), op. cit., pp. 43–61.

Kahru, M. and Brown, W. (eds). 1997. *Monitoring Algal Blooms: New Technologies for Detecting Large-Scale Environmental Change*. Austin, Tex., Landes Bioscience.

Kahru, M., Horstmann, U. and Rud, O. 1994. Satellite detection of increased cyanobacterial blooms in the Baltic Sea: natural fluctuation or ecosystem change? Ambio, 23, pp. 469–72.

Kahru, M., Leppänen, J.-M., Rud, O. and Savchuk, O. P. 2000. Cyanobacteria blooms in the Gulf of Finland triggered by saltwater inflow into the Baltic Sea. *Mar. Ecol. Progr. Ser.*, 207, pp. 13–18.

Kamykowski, D. 1974. Possible interactions between phytoplankton and semidiurnal internal tides. *J. Mar. Res.*, 32, pp. 67–89.

Kamykowski, D. 1995. Trajectories of autotrophic marine dinoflagellates. *J. Phycol.*, 31, pp. 200–08.

Kamykowski, D., Milligan, E. J., Reed, R. E. and Liu, W. 1999. Geotaxis/phototaxis and biochemical patterns in *Heterocapsa illdefina* (Dinophyceae) during vertical migrations. *J. Phycol.*, 35, pp. 1397–1403.

Karl, D. M., Bidigare, R. R. and Letelier, R. M. 2001. Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: the domain shift hypothesis. *Deep Sea Res.* II, 48, pp. 1449–70.

Karp-Boss, L., Boss, E. and Jumars, P. A. 1996. Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanogr. Mar. Biol. Ann. Rev.*, 34, pp. 71–107.

Kiørboe, T. 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.*, 29, pp. 1–72.

Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge, UK, Cambridge University Press, 509 pp.

Kolber, Z. and Falkowski, P. G. 1993. Use of active fluorescence to estimate phytoplankton photosynthesis *in situ*. *Limnol. Oceanogr.*, 38, pp. 1646–65.

Kolber, Z., Zehr, J. R. and Falkowski, P. G. 1988. Effects of growth irradiance and nitrogen limitation on photosynthetic energy conversion in photosystem II. *Plant Physiol.*, 88, pp. 923–29.

Kononen, K., Huttunen, M., Hällfors, S., Gentien, P., Lunven, M., Huttula, T., Laanemets, J., Lilover, M. and Pavelson, J. 2003. Development of a deep chlorophyll maximum of *Heterocapsa triquetra* Ehrenb. at the entrance to the Gulf of Finland. *Limnol. Oceanogr.*, 48, pp. 594–607.

Lam, C. W. Y. and Ho, K. C. 1989. Red tides in Tolo Harbour, Hong Kong. In: T. Okaichi, D. M. Anderson and T. Nemoto (eds), *Red Tides: Biology, Environmental Science, and Toxicology*. New York, Elsevier, pp. 49–52.

Lancelot, C. 1995. The mucilage phenomenon in the continental coastal water of the North Sea. *Sci. Total Environ.*, 165, pp. 83–102.

Lancelot, C., Keller, M. D., Rousseau, V., Smith, W. O. Jr and Mathot, S. 1998. Autecology of the marine haptophyte *Phaeocystis* sp. In: Anderson et al. (eds), op. cit., pp. 209–24.

Laney, S. R. 2003. Assessing the error in photosynthetic properties determined by fast repetition rate fluorometry. *Limnol. Oceanogr.*, 48, pp. 2234–42.

Lee, J. H. W., Choi, D. K. W., Wong, K. T. M., Qu, B. and Arega, F. 2007. Modelling algal dynamics in eutrophic coastal waters. In: Babin et al. (eds), op. cit., this volume.

Legendre, L. and Le Fevre, J. 1989. Hydrodynamic singularities as controls of recycled versus export production in oceans. In: W. H. Berger, V. S. Smetacek and G. Wefer (eds), *Productivity of the Ocean: Present and Past*. New York, John Wiley & Sons, pp. 49–63.

Lehaitre, M., Delauney, L. and Compère, C. 2007. Biofouling and underwater measurements. In: Babin et al. (eds), op. cit., this volume.

Levandowsky, M. and Kaneta, P. J. 1987. Behaviour in dinoflagellates. In: F. J. R. Taylor (ed.), *The Biology of Dinoflagellates*. Oxford, Blackwell Scientific Publications, pp. 360–97.

Lewis, M. R. 2002. Variability of plankton and plankton processes on the mesoscale. In: P. J. L. Williams, D. N. Thomas and C. S. Reynolds (eds), *Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems*. Oxford, Blackwell Science, pp. 141–55.

Lewis, M. R. 2007. Measurement of apparent optical properties for diagnosis of harmful algal blooms. In: Babin et al. (eds), op. cit., this volume.

Li, W. K. W. and Dickie, P. M. 2001. Monitoring phytoplankton, bacterioplankton, and virioplankton in a coastal inlet (Bedford Basin) by flow cytometry. *Cytometry*, 44, pp. 236–46.

Li, W. K. W., Dickie, P. M., Spry, J. A., Perry, T. and Head, E. J. H. 2003. Bedford Basin Plankton Monitoring Program: 1992–2002. Department of Fisheries and Oceans Canada. www.mar.dfompo.gc.ca/science/ocean/BedfordBasin/Publications/BBPMP_Poster.pdf

Lorenzen, C. J. 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. *Deep Sea Res.*, 13, pp. 223–27.

Malone, T. C. 2001. Harmful Algal Events. In: *GOOS Data Products and Services Bulletin.* http://ioc.unesco.org/gpsbulletin/GPS1&2/issue2.htm

Malone, T. C. 2006. Ecosystem dynamics, harmful algal blooms and operational oceanography. In: Babin et al. (eds), op. cit., pp. 237–280 this volume.

Margalef, R. 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, 1, pp. 493–509.

Margalef, R., Estrada, M. and Blasco, D. 1979. Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In: Taylor and Seliger (eds), op. cit., pp. 89–94.

Marra, J. 1992. Diurnal variability in chlorophyll fluorescence: observations and modelling. *Ocean Optics XI, Proc. SPIE*, 1750, pp. 233–44.

McGillicuddy, D. J. Jr, Anderson, D. M., Stock, C. A., Lynch, D. R. and Townsend, D. W. 2007. Modelling blooms of *Alexandrium fundyense* in the Gulf of Maine. In: Babin et al. (eds), op. cit., this volume.

McMahon, T., Raine, R. and Silke, J. 1998. Oceanographic control of harmful phytoplankton blooms in and around southwestern Ireland. In: Reguera et al. (eds), op. cit., pp. 128–30.

Merico, A., Tyrrell, T., Lessard, E. J., Oguz, T., Stabeno, P. J., Zeeman, S. I. and Whitledge, T. E. 2004. Modelling phytoplankton succession on the Bering Sea shelf: role of climate influences and trophic interactions in generating *Emiliania huxleyi* blooms 1997–2000. *Deep Sea Res.* I, 51, pp. 1803–26.

Michaels, A. F. and Silver, M. W. 1988. Primary production, sinking fluxes and the microbial food web. *Deep Sea Res.*, 35, pp. 473–90.

Millie, D. F., Kirkpatrick, G. J. and Vinyard, B. T. 1995. Relating photosynthetic pigments and *in vivo* optical density spectra to irradiance for the Florida red-tide dinoflagellate *Gymnodinium breve. Mar. Ecol. Progr. Ser.*, 120, pp. 65–75.

Moloney, C. L., Field, J. G. and Lucas, M. I. 1991. The size-based dynamics of plankton food webs. II: Simulations of three contrasting southern Benguela food webs. *J. Plankton Res.*, 13, pp. 1039–92.

Morel, A. 2007. Introduction to optical properties in the sea: theoretical aspects. In: Babin et al. (eds), op. cit., this volume.

Morel, A. and Bricaud, A. 1986. Inherent properties of algal cells including picoplankton: theoretical and experimental results. In: T. Platt and W. K. W. Li (eds), *Photosynthetic Picoplankton*. Toronto, *Can. Bull. Fish. Aquat. Sci.*, 214, pp. 521–59.

Neale, P. J., Cullen, J. J. and Yentsch, C. M. 1989. Bio-optical inferences from chlorophyll *a* fluorescence: what kind of fluorescence is measured in flow cytometry? *Limnol. Oceanogr.*, 34, pp. 1739–48.

Nicholls, R. J. and Small, C. 2002. Improved estimates of coastal population and exposure to hazards. *EOS: Trans. Am. Geophys. Union*, 83, p. 301.

Okaichi, T. 1997. Red tides in the Seto Inland Sea. In: T. Okaichi and T. Yanagi (eds), *Sustainable Development in the Seto Inland Sea, Japan – From the Viewpoint of Fisheries*. Tokyo, Terra Scientific Publishing Company, pp. 251–304.

Oliver, R. L. 1994. Floating and sinking in gas-vacuolate cyanobacteria. *J. Phycol.*, 30, pp. 161–73.

Olson, M. B. and Strom, S. L. 2002. Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom. *Deep Sea Res. II*, 49, pp. 5969–90.

Parkhill, J.-P., Maillet, G. and Cullen, J. J. 2001. Fluorescence-based maximal quantum yield for photosystem II as a diagnostic of nutrient limitation. *J. Phycol.*, 37, pp. 517–29.

Pinardi, N., Fratianni, C. and Adani, M. 2007. Use of real-time observations in an operational data assimilation system: the Mediterranean case. In: Babin et al. (eds), op. cit., this volume.

Pitcher, G. C., Bernard, S. and Fawcett, A. 2007. Real-time coastal observing systems for ecosystem dynamics and harmful algal blooms: needs and expectations of users. In: Babin et al. (eds), op. cit., this volume.

PITCHER, G. C., BOYD, A. J., HORSTMAN, D. A. and MITCHELL-INNES, B. A. 1998. Subsurface dinoflagellate populations, frontal blooms and the formation of red tide in the southern Benguela upwelling system. *Mar. Ecol. Progr. Ser.*, 172, pp. 253–64.

POLLINGHER, U. and ZEMEL, E. 1981. *In situ* and experimental evidence of the influence of turbulence on cell division processes of *Peridinium cinctum* forma *westii* (Lemm.) Lefevre. *Br. Phycol. J.*, 16, pp. 281–87.

PRATT, D. M. 1966. Competition between *Skeletonema costatum* and *Olisthodiscus luteus* in Narragansett Bay and in culture. *Limnol. Oceanogr.*, 11, pp. 447–55.

REGUERA, B., BLANCO, J., FERNÁNDEZ, M. L. and WYATT, T. (eds), 1998. *Harmful Algae*. Proc. VIII International Conference on Harmful Algae (June 1997, Vigo, Spain). Santiago de Compostela/Paris, Xunta de Galicia/Intergovernmental Oceanographic Commission of UNESCO.

REYNOLDS, C. S. 2002. On the interannual variability in phytoplankton production in freshwaters. In: P. J. L. Williams, D. N. Thomas and C. S. Reynolds, (eds), *Phytoplankton Productivity: Carbon Assimilation in Marine and Freshwater Ecosystems*. Oxford, UK, Blackwell Science, pp. 187–221.

REYNOLDS, C. S. and SMAYDA, T. J. 1998. Principles of species selection and community assembly in phytoplankton; Further explorations of the mandala. In: Reguera et al. (eds), op. cit., pp. 8–10.

RIEGMAN, R. 1998. Species composition of harmful algal blooms in relation to macronutrient dynamics. In: Anderson et al. (eds), op. cit., pp. 475–86.

RINES, J. E. B., DONAGHAY, P. L., DEKSHENIEKS, M. M., SULLIVAN, J. M. and TWARDOWSKI, M. S. 2002. Thin layers and camouflage: hidden *Pseudo-nitzschia* spp. (Bacillariophyceae) populations in a fjord in the San Juan Islands, Washington, USA. *Mar. Ecol. Progr. Ser.*, 225, pp. 123–37.

ROEMMICH, D. and MCGOWAN, J. 1995. Climatic warming and the decline of zooplankton in the California Current. *Science*, 267, pp. 1324–26.

ROESLER, C. and PERRY, M. J. 1995. *In situ* phytoplankton absorption, fluorescence emission, and particulate backscattering spectra determined from reflectance. *J. Geophys. Res.*, 100, pp. 13279–94.

ROESLER, C. S. and BOSS, E. 2007. *In situ* measurement of inherent optical properties and potential for harmful algal bloom detection and coastal ecosystem observations. In: Babin et al. (eds), op. cit., this volume.

RUDDICK, K., LACROIX, G., PARK, Y., ROUSSEAU, V., DE CAUWER, V. and STERCKX, S. 2007. Overview of ocean colour: theoretical background, sensors and applicability to detection and monitoring of harmful algal blooms (capabilities and limitations). In: Babin et al. (eds), op. cit., this volume.

RYTHER, J. H. 1969. Photosynthesis and fish production in the sea. *Science*, 166, pp. 72–76.

SCHMIDT, L. E. and HANSEN, P. J. 2001. Allelopathy in the prymnesiophyte *Chrysochromulina polylepis*: effect of cell concentration, growth phase and pH. *Mar. Ecol. Progr. Ser.*, 216, pp. 67–81.

SCHOFIELD, O., BOSCH, J., GLENN, S., KIRKPATRICK, G., KERFOOT, J., LOHRENZ, S., MOLINE, M., OLIVER, M. and BISSETT, P. 2007. Bio-optics in integrated ocean observing networks: potential for studying harmful algal blooms. In: Babin et al. (eds), op. cit., this volume.

SCHOFIELD, O., GRZYMSKI, J., BISSETT, W. P., KIRKPATRICK, G. J., MILLIE, D. F., MOLINE, M. and ROESLER, C. S. 1999. Optical monitoring and forecasting systems for harmful algal blooms: possibility or pipe dream? *J. Phycol.*, 35, pp. 1476–96.

SCHOFIELD, O., PRÉZELIN, B. B. and JOHNSEN, G. 1996. Wavelength dependency in the photosynthetic parameters for two dinoflagellate species *Heterocapsa pygmaea* and *Prorocentrum minimum*, implications for the bio-optical modeling of photosynthetic rates. *J. Phycol.*, 32, pp. 574–83.

SCHOLIN, C. A., DOUCETTE, G. J. and CEMBELLA, A. D. 2007. Prospects for developing automated systems for *in situ* detection of harmful algae and their toxins. In: Babin et al. (eds), op. cit., this volume.

SCHREIBER, U., SCHLIWA, U. and BILGER, B. 1986. Continuous recording of photochemical and nonphotochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosyn. Res.*, 10, pp. 51–62.

SELIGER, H. H., CARPENTER, J. H., LOFTUS, M. and MCELROY, W. D. 1970. Mechanism for the accumulations of high concentrations of dinoflagellates in a bioluminescent bay. *Limnol. Oceanogr.*, 15, pp. 234–45.

SELLNER, K. G. 1997. Physiology, ecology, and toxic properties of marine cyanobacteria blooms. *Limnol. Oceanogr.*, 42, pp. 1089–1104.

SHENG, J. and WANG, L. 2004. A high-resolution coastal circulation model for Lunenburg Bay, Nova Scotia. *Proc. 8th International Conference on Estuarine and Coastal Modeling*, pp. 372–87.

SMAYDA, T. J. 1997*a*. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.*, 42, pp. 1137–53.

SMAYDA, T. J. 1997*b*. What is a bloom? A commentary. *Limnol. Oceanogr.*, 42, pp. 1132–36.

SMAYDA, T. J. 2002. Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as 'pelagic seed banks'. *Harmful Algae*, 1, pp. 95–112.

SMAYDA, T. J. 2003. Environmental monitoring, with examples from Narragansett Bay. In: Hallegraeff et al., op. cit., pp. 595–625.

SMAYDA, T. J. and SHIMIZU, Y. (eds). 1993. *Toxic Phytoplankton Blooms in the Sea*. Amsterdam, Elsevier.

SMETACEK, V. 1998. How mainstream biological oceanography can profit from harmful-algal-bloom studies and vice versa. In: Reguera et al. (eds), op. cit., pp. 109–13.

SOSIK, H. M. 2007. Characterizing seawater constituents from optical properties. In: Babin et al. (eds), op. cit., this volume.

STUMPF, R. P., CULVER, M. E., TESTER, P. A., TOMLINSON, M., KIRKPATRICK, G. J., PEDERSON, B. A., TRUBY, E., RANSIBRAHMANAKUL, V. and SORACCO, M. 2003. Monitoring *Karenia brevis* blooms in the Gulf of Mexico using satellite ocean color imagery and other data. *Harmful Algae*, 2, pp. 147–60.

SUGGETT, D. J., OXBOROUGH, K., BAKER, N. R., MACINTYRE, H. L., KANA, T. M. and GEIDER, R. J. 2003. Fast repetition rate and pulse amplitude modulation chlorophyll *a* fluorescence measurements for assessment of photosynthetic electron transport in marine phytoplankton. *Eur. J. Phycol.*, 38, pp. 371–84.

SVERDRUP, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. Int. Explor. Mer.*, 18, pp. 287–95.

TANGEN, K. 1997. Monitoring phytoplankton blooms continuously with SEAWATCH technology. In: J. H. Stel, H. W. A. Behrens, J. C. Borst, L. J. Droppert and J. V. D. Meulen (eds), *Operational Oceanography: The Challenge for European Cooperation*. Amsterdam, Elsevier Science, p. 539.

TAYLOR, D. L. and SELIGER, H. H. (eds). 1979. *Toxic Dinoflagellate Blooms*. New York, Elsevier-North Holland.

TAYLOR, F. J. R. and HAIGH, R. 1993. The ecology of fish-killing blooms of the chloromonad flagellate *Heterosigma* in the Strait of Georgia and adjacent waters. In: Smayda and Shimizu (eds), op. cit., pp. 705–10.

TESTER, P. A. and STEIDINGER, K. A. 1997. *Gymnodinium breve* red tide blooms: initiation, transport, and consequences of surface circulation. *Limnol. Oceanogr.*, 42, pp. 1039–51.

TONT, S. A. 1976. Short-period climatic fluctuations: effects on diatom biomass. *Science*,194, pp. 942–44.

TRACEY, G. A. 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 'brown tide' in Narragansett Bay, Rhode Island. *Mar. Ecol. Progr. Ser.*, 50, pp. 73–81.

TURNER, J. T. and TESTER, P. A. 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. *Limnol. Oceanogr.*, 42, pp. 1203–14.

TYLER, M. A. and SELIGER, H. H. 1978. Annual subsurface transport of a red tide dinoflagellate to its bloom area: water circulation patterns and organism distributions in the Chesapeake bay. *Limnol. Oceanogr.*, 23, pp. 227–46.

TYLER, M. A. and SELIGER, H. H. 1981. Selection for a red tide organism: physiological responses to the physical environment. *Limnol. Oceanogr.*, 26, pp. 310–24.

WALSTAD, L. J. and MCGILLICUDDY, D. J. 2000. Data assimilation for coastal observation systems. *Oceanography Mag.*, 13, pp. 47–53.

WEISE, A. M., LEVASSEUR, M., SAUCIER, F. J., SENNEVILLE, S., BONNEAU, E., ROY, S., SAUVE, G., MICHAUD, S. and FAUCHOT, J. 2002. The link between precipitation, river runoff, and blooms of the toxic dinoflagellate *Alexandrium tamarense* in the St. Lawrence. *Can. J. Fish. Aquat. Sci.*, 59, pp. 464–73.

YAMAMOTO, T. 2003. The Seto Inland Sea – eutrophic or oligotrophic? *Mar. Poll. Bull.*, 47, pp. 37–42.

YAMAMOTO, T., SEIKE, T., HASHIMOTO, T. and TARUTANI, K. 2002. Modelling the population dynamics of the toxic dinoflagellate *Alexandrium tamarense* in Hiroshima Bay, Japan. *J. Plankton Res.*, 24, pp. 33–47.

YANAGI, T. and OKAICHI, T. 1997. Seto Inland Sea — historical background. In: T. Okaichi and T. Yanagi (eds), *Sustainable Development in the Seto Inland Sea, Japan — From the Viewpoint of Fisheries.* Tokyo, Terra Scientific Publishing Company, pp. 9–14.

ZHANG, J. 1994. Atmospheric wet depositions of nutrient elements: Correlations with harmful biological blooms in the northwest Pacific coastal zones. *Ambio.*, 23, pp. 464–68.

ZINGONE, A. and ENEVOLDSEN, H. O. 2000. The diversity of harmful algal blooms: a challenge for science and management. *Ocean Coast. Manag.*, 43, pp. 725–48.