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Biology and ecology of harmful algal species

As discussed in Chapter 1, harmful algal bloom (HAB) problems are associated primarily with two general types of causative organisms: namely, toxin producers and high-biomass producers—some organisms have attributes of both groups. Importantly, toxin producers may lead to harmful consequences even when present in low cell concentrations (Sellner *et al.*, 2003) whereas the impact of algae of the second group only has ecological consequences when their proliferation attains exceptionally high levels (Glibert *et al.*, 2001).

It is acknowledged that the expression of HABs is a function of the physics and environmental controls acting on the HAB species, and from this perspective HABs must be considered as a *systematic–ecological* phenomenon.

There are a number of different and sometimes competing factors that promote preferable growth conditions for a specific group of HAB algae. These factors encompass the natural variability of hydrodynamics, light availability, nutrient loading, individual algal physiological and behavioral patterns, trophodynamic interactions/changes in the grazing community, anthropogenic eutrophication, and, allegedly, global change processes. Further, this combination of factors leads to specific HAB bloom events that, by and large, are generally *monospecific* (although in many cases what was formerly considered a single species is in fact a mixture of genetically similar strains of that species) (Anonymous, 1995).

In the context of the aquatic *ecosystem* approach, open coastal and basin-scale systems are generally those that are more likely controlled by meso-scale to large-scale physical processes as opposed to enclosed or semi-enclosed systems (Filatov *et al.*, 2005). Thus, understanding the dynamics of HABs in these dynamic systems may require close consideration of intimate interactions of in-water biophysical and geochemical processes, as well as external forcing stemming from either direct anthropogenic or climate change impacts/mechanisms.

2.1 ROLE OF HYDRODYNAMICS

Open coastal regions (OCRs) prone to HAB events often have narrow and steep upwelling-dominated regions, as is the case, for example, along the Pacific coast of the U.S.A. and the Atlantic coast of Spain and Portugal. The main function of upwelling movements is the migration of nutrient-rich deep waters into the euphotic zone and promoting conditions for intensive growth of algae there.

On the other hand, there are OCRs frequently or occasionally plagued by HABs where upwelling is *not* a dominant feature, as is found in the broad North Sea region such as Skagerrak and Kattegat (Johannessen *et al.*, 2006; Bratbak *et al.*, 2011) as well as in regions subject to buoyancy-driven currents moving, for example, along the Norwegian Atlantic Coast, the Louisiana–Texas coastline in the Gulf of Mexico (Anonymous, 2003b), and the east coast of Japan bathed by the Kuroshio Current (Anonymous, 1995).

Strong currents promote the origination of meso-scale circulation features such as eddies, which can be critical for algal bloom dynamics. Eddies can have various roles. They can promote algal bloom initiation and rapid growth of cell concentration due to accumulation resulting from retention as a result of circular movement of the water. At the same time, because of the latter, they can trap the bloom and prevent or control its advection to other areas and further development: under such circumstances, the algal mass can be doomed to rapid depletion of nutrients, extensive zooplankton grazing, and, ultimately, premature dwindling of the community population. For example, there were reports that a *Chattonella* bloom was trapped in meso-scale eddies within the Norwegian Coastal Current. This precluded its further spread and transportation along the coastline and resulted in a temporally geographical limitation of the impact of this HAB event on the aquatic environment (Pettersson *et al.*, 2005).

Other hydrodynamic features are also important. Convergence at fronts associated with upward vertical movements of significant water masses or invasion of river plumes may result in a spike of algal concentration enhancement or subduction of algal blooms beneath the surface, as was documented in 1992 for Spain in the vicinity of Prego (Anonymous, 2003b).

Tidal fronts, formed at the abutment of stratified offshore water and tidally mixed waters frequently become areas densely populated by algae (Pingree *et al.*, 1975). Algal accumulations at front systems are well documented for, *inter alia*, the western English Channel (Holligan, 1979), the mouth of the Gulf of Finland (Moisander *et al.*, 1997), Chesapeake Bay (Sellner *et al.*, 1991), and many other locations throughout the world's oceans (for further references see Sellner *et al.*, 2003).

Frontal jets and coastal currents are efficient in effecting the alongshore transport of algal blooms. This in turn is conducive to the initiation of either inshore or offshore blooms depending on the absence or presence of prominent coastal headlands. Thus, topography and shore geometry can significantly influence (H)AB dynamics.

Mesoscale water density stratification can cause subsurface transport of algal

blooms from one area to another *without any visible surface expressions* of this phenomenon. For instance, this frequently occurs in the Skagerrak region where one can observe a subsurface sinking of waters in the Jutland region and its further entrainment by currents along the coast of southern Norway.

It is now common knowledge that HABs are frequently organized into thin layers, not necessarily only at the water surface–atmosphere interface but also at certain depths; these are mainly in the *upper part* of the euphotic zone (e.g., Marcaillou *et al.*, 2000). There are plenty of such reports in relation to *Alexandrium catenella*, *Dinophysis accuminata*, *Chaetoceros debilis*, and others (Anonymous, 2003b). Although there are thermohydrodynamic-based theories of this phenomenon, this issue remains presently unresolved.

In OCRs with shallow waters subjected to strong wind-driven vertical mixing, the algal cysts buried in bottom sediments can be brought back to surface layers and initiate a massive growth of the phytoplankton community. This process is regularly observed, for example, in connection with the winter rest of several algae cysts at the bottom and their activation during early spring blooms.

For OCRs, upwelling events are thus critically important for initiation and proliferation of HABs. These regions are subjected to strong seasonal cycling with intermittent infusions of nutrients from nutrient-rich deeper water layers.

Franks and Anderson (1992) highlighted the critical importance of upwelling and downwelling phenomena for toxic bloom initiation and development. The benthic environment in the Gulf of Maine has been shown to have an extended *Alexandrium tamarense* cyst seabed located offshore at 150 m depth. Importantly, the cyst population proved to be 20 times denser than in shallow waters of the gulf. It has been found that during upwelling a combination of cysts migrating upward from the seabed and the surface-trapped plume of brackish water, originating from river runoff, causes the plume to thin vertically and extend offshore, blanketing the area above the seabed.

Growing from germinated cysts and tending to reach light-rich surface waters, the *A. tamarense* cells end up inhabiting this thin surface layer. However, with the change of wind conditions and origination of downwelling movements at the shoreline, the developed algae are brought back to shore and eventually develop into an extensive bloom.

In those OCRs where upwelling is not typical, early spring algal blooms are supplied with nutrients through winter mixing with deeper layers as a result of spring overturn. Further, with the establishment of stratification, nutrient delivery proceeds through river input as well as tidal and wind-driven mixing.

Hydrodynamics are at the origin of the so-called coastal retention zones, which are different from those discussed above in relation to eddies: water circulation patterns can lead to formation of “reservations”—isolated water masses with specific chemical, biological, and thermohydrodynamic regimes. Such unique properties associated with a relatively long residence time within the retention zones favor rapid and massive development of algae, predominantly of toxic origin as a result of intrinsic biological mechanisms. The latter reside in (i) toxin accumulation from indigenous toxic algae, (ii) sexual cross-breeding effected by toxin egestions,

(iii) genetic modifications, spurring up the development of non-obligatory toxic species capable of developing their toxicity in the course of growth phases, and (iv) low consumption of algal cells by zooplankton as a result of grazing slowdown, etc. As a result, transport from these zones to other regions along the coast can initiate onset of a major bloom of toxic algae uncharacteristic of the local indigenous algal taxonomy (Fermin *et al.*, 1996).

Enclosed and *semi-enclosed* (ESE) marine systems offer suitable conditions not only to accommodate matter brought from land or with river runoff, but also from contiguous ocean waters. Although varying in location, size, bathymetry, and morphology, ESE marine systems have in common their susceptibility to bloom events. This is conditioned not only by shallowness and associated replenishment of nutrients from sediment resuspensions and restrictive circulation but also mostly by the delivery of nutrients through runoff from land and rivers and, generally to a lesser degree, atmospheric deposition.

The most important *physical* factor conditioning the initiation and proliferation of a HAB is the *stability* of the water column. The onset of thermal stratification (e.g., as a result of arrival of buoyant freshwater that prevents both vertical exchange of deep waters with the surface layers and, consequently, channeling of oxygen down to the depth) conditions favorable for establishing such convergent features as fronts may actively contribute to bloom initiation (for the reasons, see above).

Importantly, ESE marine systems are retentive not solely because of coastline features. In addition, features such as keys, islands, sandbanks, siltbanks, tidal fronts, etc. restrict hydrodynamic interaction with the open ocean, determining longer residence times not only in the inner but also outer parts of estuaries, fjords, or embayments. From this perspective, the Baltic Sea, which regularly experiences massive cyanobacteria blooms, is an example of an extreme case. Deep-water renewals occur there episodically on decadal scales.

Horizontal transport in a stratified ESE marine system is frequently driven not so much by river runoff, but by local circulation whose strength might be 10 times that of the streams of inflowing rivers.

On short timescales, it is wind-induced circulation that often prevails in determining to a large degree the intensity of upper-layer water exchange with neighboring water masses. However, this exchange is not solely a consequence of water transport by wind-driven currents, it is also one of gravitational force arising from water level differences between the ocean and the linked enclosed water body.

Intermittent, near-instantaneous inputs of freshwater from rivers into an ESE marine system and, conversely, dense saline waters from the contiguous oceanic area can be conducive to algae and other waterborne matter accumulation.

In smaller ESE marine systems this effect may be accentuated by stratified flow interactions with bottom relief, topographically steered river runoff fronts, or hydraulic controls.

In larger ESE marine systems, such as the Baltic Sea, the Coriolis effect plays the role of a retaining and sustaining factor: low-density brackish waters originating from river inflow are drawn to the sea shores while fronts, being fed with additional energy, become more sustainable. In the Baltic Sea, owing to its large dimensions,

strong meso-scale water movements, such as coastal jets, eddies, upwelling, and fronts control hydraulic interactions between shelf and pelagic waters. Thus, large ESE marine systems exhibit features of both ESE and OCR marine systems.

One of the striking phenomena revealed through the comparison of HAB events in ESE and OCR marine systems occurring under various geographic/climatic and biogeochemical conditions is that, notwithstanding sharp contrasts in incidence and extent, the key functional groups and species prove to be common.

At the same time, increasing evidence indicates that species once identified as harmless in some areas become harmful in other areas. For instance, *Prorocentrum minimum* and *Mesodinium rubrum* cause harmful blooms in the Chesapeake Bay (due to high toxic biomass and high non-toxic biomass, respectively) are indigenous components of the plankton community in the Baltic Sea, but they form blooms without harmful effects. Similarly, *Heterocapsa triquetra* and *H. rotundata* cause mahogany tides in Chesapeake Bay but they develop non-harmful blooms in the Baltic Sea (Anonymous, 2003b). These findings warrant the supposition that biogeochemical aspects might play a deciding role given similar types of marine systems (Kudela *et al.*, 2002).

In the open ocean, HAB proliferation in spring is determined principally by the timing of the shutdown of *convective overturning*, although episodic strong winds add to vertical mixing and can potentially affect the onset of stratification and can be at the basis of *interannual variations* in HAB bloom lifecycles: initiation, development, and demise.

In OCRs away from inputs of freshwater, stratification is controlled by competing solar insolation-induced water stratification, convective overturning, wind stress, and tidal-driven vertical mixing. As mentioned above, in tidally energetic regions, such as the shelf seas of northwestern Europe, tidal mixing prevails in determining the summer vertical water column structure.

2.2 ROLE OF BIOGEOCHEMISTRY

The hydrodynamic mechanisms determining HAB initiation, frequency of occurrence, and the vexing expansion across the world's oceans are generally closely related to biogeochemical processes (Holmedal and Utne, 2006). One of the numerous examples is cross-bay tilting of the pycnocline induced by winds shifting from calm/weak westerly winds to strong southerly winds along the axis of Chesapeake Bay drives subpycnocline remineralized nutrients into the euphotic zone, resulting in a bloom outbreak (Sellner *et al.*, 2003). Such phenomena are common along the western coasts of major continents bringing about similar nitrification effects, which spur up enhanced algal production and often harmful algal blooms.

Like all autotrophic algae, growth of autotrophic harmful algae requires some major conditions to be met: availability of nutrients, favorable water temperature, stable vertical stratification (Sharples *et al.*, 2006), and light—although for mixotrophic and, even more so, heterotrophic algae, light availability is optional.

Water column vertical mixing/stratification is controlled by water temperature and salinity, particularly in inshore areas subject to freshwater discharge, offshore currents, and upwelling.

HAB events often follow a period of intense rainfall and runoff—both of which enhance water column stratification and enclose in the upper layer the chemicals favorable to algal growth—followed thereafter by a period of intense solar illumination. It is believed that heavy rainfall can also contribute to coastal water nitrification through provision of some nutrients important for the development of a specific HAB event. For example, Graneli *et al.* (1993) assumed that selenium and cobalt have been partially responsible for blooms of *Chrysochromulina polylepis* in the Skagerrak and Kattegat.

The hydrochemical habitat of planktonic organisms is extremely complex and highly variable temporally, being subject to seasonal, regional, and long-term modifications. For example, seasonal variations of oxygen content in the water column, especially in bottom waters, are full of consequences for shallow poorly flushed coastal waters, at aquaculture sites, and in regions exhibiting environmental degradation.

The effects of hydrochemical conditions/habitat on HABs are thought to be twofold: (1) influencing predominant species selection and (2) promoting algal growth into a bloom. Marine harmful algae¹ are generally nitrogen-limited, although in inland water environments indigenous algae are generally phosphorus-limited. For diatoms, silica levels might also be a limiting factor.

Accordingly, there is growing evidence strongly indicating that HAB outbreaks occur with steadily increasing incidence and spatial extension in nutrient-rich waters (Andersen *et al.*, 2006). The importance of nitrification can be exemplified by well-documented long-term tendencies in escalation of blooms of *Phaeocystis pouchetti* in Dutch coastal waters, *Prorocentrum cordata* in the Black Sea, and there are numerous similar reports from other marine environments (for the Baltic Sea see for example Rönneberg and Bonsdorff, 2004).

In light of the above, coastal eutrophication is considered as one of the major forcing factors in HAB occurrences. Mass introduction of nutrients might proceed in a variety of pathways ranging from cattle/hog farm waste ponds, inefficient use of manure/fertilizers to waste disposal/sewage waters of municipal and industrial origin. However, this list is certainly not exhaustive. For example, huge amounts of nutrients can be dragged up from bottom sediments either due to civil engineering (e.g., dredging) or storm-induced scavenging of bottom sediments in harbors and bays, coastal zones, and even in shallow non-coastal areas. For instance, cyanobacterial pigments likely from the summer dominant taxa *Nodularia* and *Aphanizomenon*, remaining at very low levels in the Baltic Sea for the previous 7,000 years (Poutunen and Nikkilä, 2001) showed a dramatic increase in the 1960s, which is certainly due to the action of two conjoint factors: huge post-

¹ A possible exception is cyanobacteria, which can take up nitrogen from the atmosphere, but need the phosphorus available in the water column, as is the case of cyanobacteria blooms in the Baltic Sea.

World War accumulations of N and P in bottom sediments are recurrently returned (in mineralized form) to the euphotic zone as a result of strong storms typical of the wintertime and springtime.

Aquacultural production of shellfish and finfish generates large amounts of excretory products (feces, pseudofeces, and so on), which are rich in N and P and may also include toxins from the medication of caged fish. Particulates, either defecated matter or the decomposing flesh of dead fish, settle at the bottom and through remineralization yield N and P suitable for algae to feed on. Accordingly the licensing conditions for aquaculture sites may include limitations with respect to the allowed period of operations at one specific location.

However, along with the nutrition factor, the *life cycles* of algae might be very important in the context of the HAB problem (e.g., within the lifecycle of *Alexandrium* spp.). As was discussed above, during periods unfavorable for sustainable development, algae produce resting cysts that settle on the bottom and, after a dormancy term, can break open and release vegetative cells that ascend to the euphotic zone to initiate a spate of extensive algal bloom. Importantly, some diatoms and cyanobacteria are apt to also produce similar resting organisms (called spores and akinetes, respectively). This property gives dinoflagellates and such specific diatoms and cyanobacteria an important advantage over algal populations devoid of such an ability to persist under temporarily unfavorable conditions. Therefore, this may explain the abrupt and massive surging of one algal taxon that occurs in some cases when algae of other taxa remain peripheral in the outbreaking phytoplankton community.

2.3 ROLE PLAYED BY OTHER FACTORS

Meteorological events, atmosphere–ocean variability, and global change implications can reportedly provoke not only bloom formation but also large-scale alterations to the present state of the aquatic ecosystem. For example, the typical vernal *Mesodinium/Noctiluca* blooms in the waters of the northeast coastal zone of New Zealand gave way to summer *Raphidophytae* and *Dinoflagellate* blooms. This succession is uncharacteristic and, in contrast with spring diatoms, summer dinoflagellates and diatoms outburst again in the fall. The revealed change in species succession order was associated with an El Niño that brought lower-than-normal water temperatures (Rhodes *et al.*, 2001).

The North Atlantic Oscillation (NAO) can also be implicated in HAB transportation and proliferation. This can be exemplified by a case recorded in Spain: the bloom initially “ignited” by upwelling-driven nutrification then spread over the northwestern coastal zone by NAO-conditioned alongshore winds (Fraga and Bakun, 1993). In the late 1980s, dedicated studies in Swedish fjords established that the positive phase NAO (i.e., milder winters and higher levels of salinity) were significantly correlated with the growth dynamics of *Dinophysis* species as well as *Chrysochromulina polylepis* and *Gymnodinium aureolum*.

The general mechanisms or processes leading to algal bloom formation, proliferation, and decay can be further specified through the results of a comparative study addressing three geographical regions in European waters: namely, the North Sea/Skagerrak, the Baltic Sea, and the Galician Rías (Pettersson *et al.*, 2005). These case studies provide evidence to support this book's thrust to advocate the importance of combining comprehensive monitoring of HABs with associated ecological modeling with the objective of establishing an efficient integrated system of early warning, detection, monitoring, and forecasting of HAB events. Accordingly, such model simulations have been accomplished for the three abovementioned cases and are presented in Chapter 5 along with a broader discussion of this issue.

2.4 CASE STUDIES

2.4.1 *Chattonella* or *Pseudochattonella* spp. in the North Sea/Skagerrak

During the period 1997–2002, three large blooms of the flagellate *Chattonella* aff. *verruculosa*² occurred in the North Sea/Skagerrak/Kattegat region, in 1998, 2000, and 2001. During the first and the last blooms, fish mortality was registered in fish farms along the southern coast of Norway. It is likely that the above pernicious species had been initially introduced, possibly for example through ballast water, to the area in 1998, and during the following years spread further across the area becoming today a well-established species in the region. A short chronicle of the major *Chattonella* bloom events affecting the waters of Norwegian concern is presented in [Table 2.1](#).

Our analyses of the *Chattonella* bloom occurrences in 1998, 2000, and 2001 match the above discussions in Sections 2.1–2.3 in the following way. The blooms were all observed in coastal water masses characterized by shallow water or a shallow pycnocline, relatively low salinity, and relatively high availability of nutrients due to runoff from land and regeneration of nutrients from the sediment. Distinct coastal water masses (revealed by their temperature signal) are characteristic of *Chattonella* bloom areas along the west coast of Denmark, the west coast of Sweden, and the south Norwegian coast ([Figure 2.1](#)).

The first bloom of *Chattonella* in the North Sea/Skagerrak/Kattegat area observed in 1998 was due to *Chattonella* aff. *verruculosa*. The bloom initially originated off the west coast of Denmark at the beginning of April, and further spread to cover the area extending from the German Bight, along the west coast of Denmark, to Sweden. In May it reached the southern coast of Norway and was advected northward to Boknafjord (Stavanger). The highest algal concentration was recorded off the west coast of Denmark.

This was the first registered large-scale evidence of a *Chattonella* bloom in the Skagerrak area. However, reanalysis of data from the Swedish west coast revealed

² Riisberg and Edvardsen (2008) have reclassified the *Chattonella verruculosa* bloom events in the waters discussed in this book to *Pseudochattonella verruculosa* (see also Section 4.1.9).

Table 2.1. Summary of *Chattonella* blooms in the North Sea/Skagerrak and Kattegat during 1997–2009.

| | |
|------|---|
| 1997 | There was no large-scale <i>Chattonella</i> bloom, but a local bloom was observed in the Århus Bugt, Denmark. |
| 1998 | The first major <i>Chattonella</i> bloom year. The bloom originated off the west coast of Jutland and was transported northward along the west coast by the Jutland Current. The major part of the bloom patch was supposed to be advected from Denmark over to the southern part of Norway as a result of blockage in the eastward direction as a result of the Baltic outflow in the Kattegat. Part of the bloom might have spread to the Swedish west coast, crossing under the Baltic Outflow Current. Following transport to the southern part of Norway the bloom spread to the Swedish coast due to east/southeastern currents compensating the Baltic outflow at the surface. |
| 1999 | No <i>Chattonella</i> bloom reported. |
| 2000 | The second <i>Chattonella</i> bloom year. Occurred only in the North Sea. No further northward transport to the waters of the Swedish west coast and the southern part of Norway, which was presumably as a result of blockage of the Jutland Current south of Skagen. |
| 2001 | The third <i>Chattonella</i> bloom year. Developed mainly in the Kattegat/Skagerrak area, during early spring in cold water. Low algal concentrations in the North Sea: presumably because the bloom originated and developed in the Kattegat and successively in the Baltic Outflow Current with further transportation to the Norwegian coast. |
| 2002 | Late spring <i>Chattonella</i> blooms reported in warm water in April to May. |
| 2004 | Two major <i>Chattonella</i> blooms in the North Sea/Skagerrak region. The first in February and March in the Kattegat affected the Swedish west coast, however it was observed in very low concentrations in Norwegian waters. In April confined to the waters along the west coast of Denmark. |
| 2006 | Early spring <i>Chattonella</i> blooms reported in cold water in January to March. |
| 2007 | A <i>Chattonella</i> bloom in the Kattegat, but with no effects or reports from Norwegian waters. |
| 2009 | <i>Pseudochattonella farcima</i> bloom in west Jutland waters in April. Monitored by ship and satellite measurements and ocean modeling. |

that *Chattonella* was already present there at low levels in 1990, a fact which, in all probability, has been overlooked in routine investigations (L. Edler, pers. commun.).

In late April 2000 a new bloom of *Chattonella* spp. was observed in the southern part of the west coast of Denmark. Between late April and mid-May, the bloom extended from the German Bight to Skagen (northern part of Jutland, Denmark). The entire duration of this HAB event was less than a month.

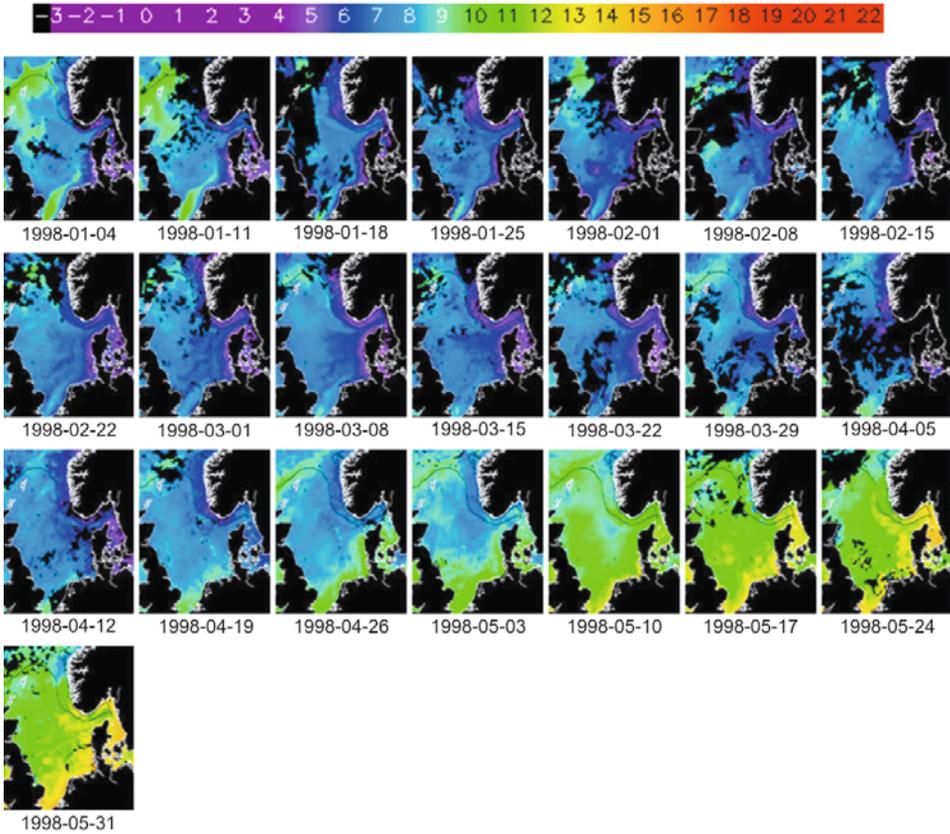


Figure 2.1. Time series of weekly averages of sea surface temperature (SST in $^{\circ}\text{C}$) in the North Sea for the period January–May 1998 derived from the NOAA AVHRR sensor.

The last bloom of this case series occurred in the Skagerrak area in March–April 2001. The bloom was first observed off the Swedish west coast at the beginning of March, extending to the southern coast of Norway during the second half of March. At the beginning of April, the bloom covered the Swedish west coast and the southern coast of Norway up to Mandal (southern tip of Norway). The bloom disappeared from the area on or about April 20, and the total lifetime of this bloom was nearly two months.

In situ observations indicate that *Chattonella* takes about 2–3 weeks of growth to turn into a major bloom. During the pre-bloom/initiation period, nutrients were abundant, solar illumination was substantial (high-pressure periods over the North Sea), and winds were weak enough to minimize the advection of *Chattonella* cells and nutrients from the coastal waters out to the North Sea. It is evidenced that since 1998 to date, *Chattonella* is invariably present in the spring constituting an inherent constituent of the late spring phytoplankton community.

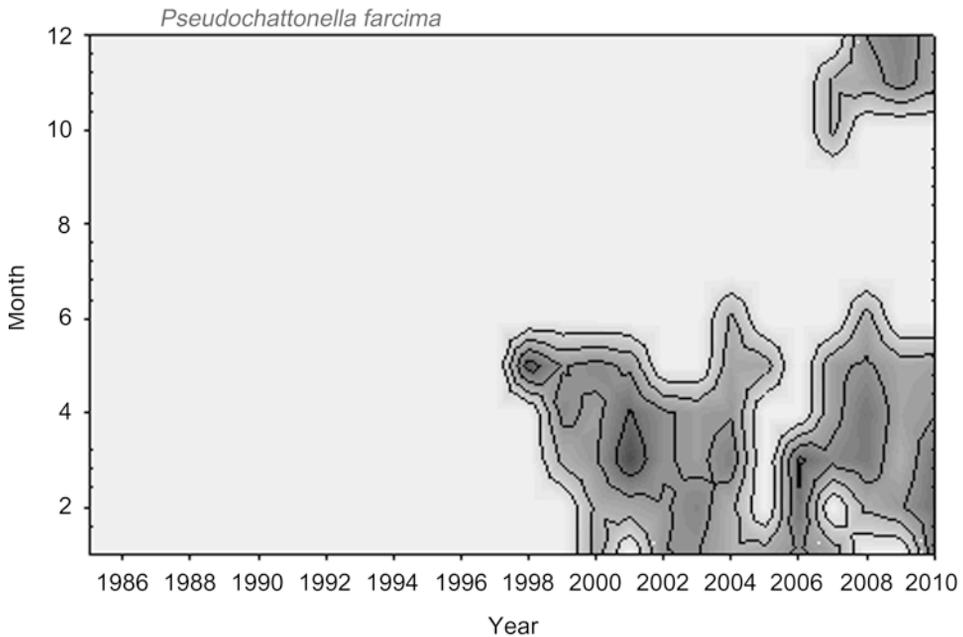


Figure 2.2. Measurements of *Pseudochattonella farcima* at Flødevigen Research Station (1986 to 2010), illustrating its abundance and the expanded seasonal (y -axis) intensity and increased frequency of occurrence during the most recent years. The data are log-transformed. *Courtesy:* Lars Johan Naustvoll, IMR.

The Institute of Marine Research in Flødevigen (Lars Johan Naustvoll, pers. commun.) has extensively studied *Pseudochattonella farcima* and monitored its abundance at its research station location since 1986. As indicated above, it is a species that proliferates in Norwegian waters during the spring and winter period and has done so predominantly since 1997, with some irregular interannual variations in bloom intensity. During recent years it has also been observed during December and to some extent in November (see [Figure 2.2](#)). The abundance of *Pseudochattonella farcima* seems to be a more regular and annual phenomenon in the Kattegat (eastern Danish waters) and farther south in the German Bight.

These studies of *Chattonella* bloom development confirmed the aforementioned worldwide observations in enclosed or semi-enclosed, as well as open, coastal marine ecosystems of HAB evolution in space and time: this process can largely be characterized as a four-stage process:

Phase 1. In the *pre-bloom* phase the species is present only in very low concentrations in either pelagic areas or in bottom sediments in encysted form. To proceed to the next phase of bloom development, the cysts undergo germination and encysted specimens enter the pelagic environment.

Phase 2. In the *growth phase*, as a result of light harvesting and uptake of nutrients (which need to be present in ample amounts), primary production increases very rapidly but is dependent on water temperature, salinity, and slight vertical mixing within the euphotic zone. At the population level, the growth rate is controlled by an algal physiological growth process in combination with loss processes such as zooplankton grazing and cyst sinking as well as dispersion/advection intervention.

Phase 3. The *bloom phase* is the period of algal maximum concentration; its duration varies, but is usually not in excess of a couple of months.

Phase 4. The *declining phase* begins when the dynamic balance between algal growth and loss shifts to the latter. This is the result of a number of factors such as prevailing grazing pressure, depletion of nutrients, encystment, intervention of bacteria and/or viruses, and dispersion (e.g., as a result of a storm event).

The *Chattonella* case study has revealed that, although the duration of blooms has not shown any tendency to increase or decrease, the onset of blooms occurred progressively earlier during the study period (Figure 2.3). To be more specific, the

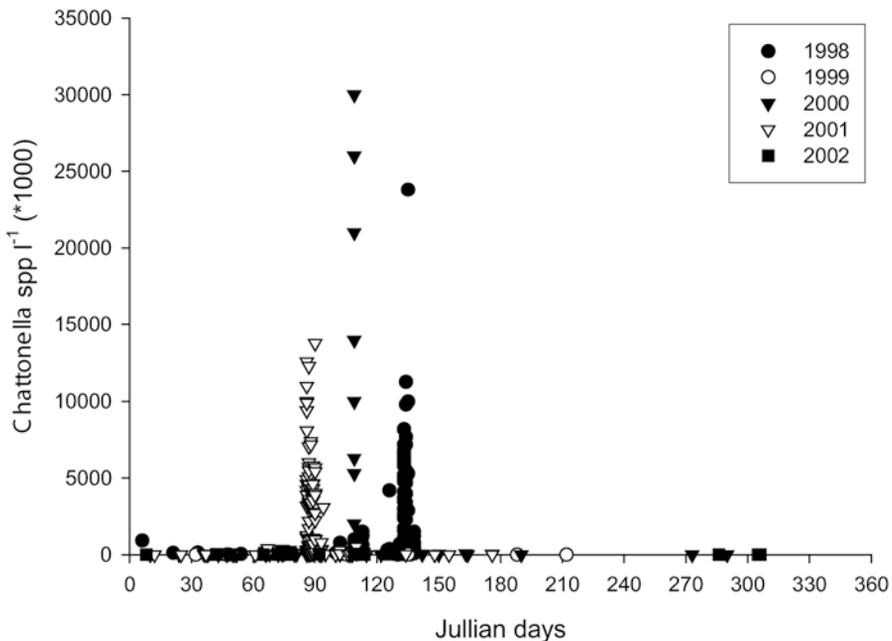


Figure 2.3. *Pseudochattonella* spp. abundance and timing of onset in the North Sea/Skagerrak/Kattegat area, during the period 1998 to 2002. Courtesy: L. J. Naustvoll, IMR.

2001 bloom started one month earlier than the other two blooms (Table 2.1). The bloom in 2001 occurred just after the early spring diatom bloom partly overlapping with the spring bloom, whereas the previous blooms occurred well after the spring bloom had completely disappeared. The bloom most likely started off the southern coast of the Swedish Kattegat and was entrained later on by the Baltic Outflow Current northward along the west coast of Sweden.

Regional ocean circulation modeling results indicate that there was a pronounced outflow from Kattegat to Skagerrak at the beginning of March 2001. At the time of the bloom apex, it covered the entire Swedish west coast and the Norwegian Skagerrak coast as far as Mandal. Incidentally, a *Chattonella* bloom was not reported from the Danish west coast in March 2001, but was observed there much later, in mid-April, when it was also reported along the Norwegian coast east of Lindesnes. Ocean circulation models for this area indicate that the bloom has been restricted due to the northeasterly winds and eddies formed in the Lindesnes area, which efficiently restricted further advection of the bloom northwestward along the Norwegian coast.

Studies of the *vertical profiles* of *Chattonella* blooms have indicated that algal cells were mainly accumulated in the upper few meters of the water column. During the bloom in 1998 *Chattonella* was observed down to 30 meters at the Danish Skagerrak coast. The highest abundance was observed in the upper 10 meters. More or less the same pattern was observed in 2001. A high abundance of *Chattonella* was observed above the halocline at most stations and the highest concentrations were found in the upper 5 meters (Figure 2.4). However, *Chattonella* may also be present as a subsurface maximum.

Regarding the aquatic environment parameters favorable for the massive growth of *Chattonella*, the following water salinity and temperature regimes were identified. *Chattonella* spp. were observed in waters with salinity (S , psu) levels between 12 psu and 35 psu (Figure 2.5), and preferably at $20 \leq S \leq 34$ psu. These observations are backed up by experiments with the Norwegian strain of *Chattonella* aff. *verruculosa*, which showed positive growth within salinity S in the range 15–35 psu (Ref.).

Importantly, this species is found to be unable to grow at salinities less than 10 psu (D. Naustvoll, unpublished data). Therefore, there are reasons to presume that at least *Chattonella* aff. *verruculosa* cannot be responsible for major bloom events in Baltic Sea waters characterized by low salinity levels.

Nonetheless, *Chattonella* aff. *verruculosa* has an exemplary tolerance of broad (0–21°C) water temperature (T) excursions (Figure 2.6) and can produce blooms in Scandinavian waters during the time period extending from late winter to early summer. Laboratory experiments indicate that this species has the highest growth rate at $T \leq 10^\circ\text{C}$ (D. Naustvoll, unpublished data). Thus, this species qualifies as a cold-water organism.

Comparing the pre-spring bloom nutrient content variations during the studied period, it was found not unexpectedly that in 2002 and especially in 1998 there were exceptionally high concentrations of inorganic N near the coast, which by the mechanisms described in Sections 2.1–2.3 were subsequently drawn away from the

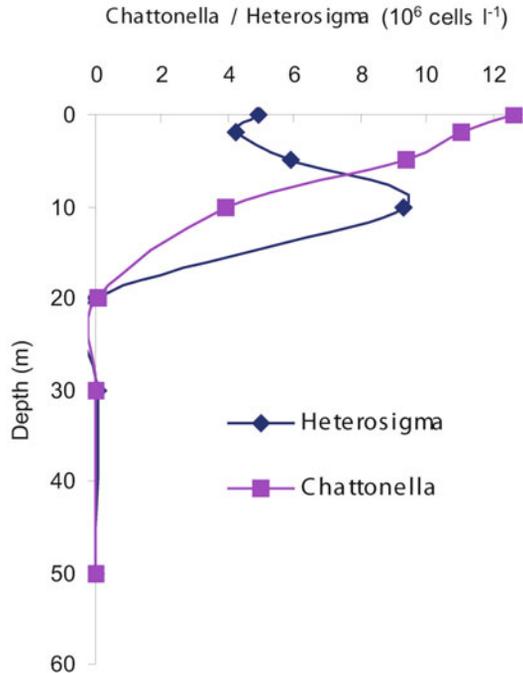


Figure 2.4. Vertical profiles of *Pseudochattonella* aff. *verruculosa* and *Heterosigma* at Lyngør during the 2001 bloom. The profile from this station was found to be typical of the coastal zone of southern Norway, except for stations heavily affected by freshwater runoff. Courtesy: L. J. Naustvoll, IMR.

immediate proximity to the coast. It conforms to the paradigm that *Chattonella* is predominantly nitrogen (N) limited. However, it is interesting to note that even though the highest biomass of *Chattonella* was registered in waters with rather high N concentrations, no clear relationship between the concentrations of inorganic N and *Chattonella* abundance has been found (Figure 2.7).

In contrast to N, the observed (rather moderate) concentrations of inorganic P showed significantly less interannual variability. The concentrations of dissolved silicate were rather high throughout the years 1998–2002 (although *Chattonella*, unlike diatoms, is known not to be silicate limited).

Analyses of the influence of meteorology and irradiance on *Chattonella* blooms have revealed that in 1998, 2000, and 2001 wind energy was low from mid April to mid May whereas during the same period in 1999 and 2002 it was definitely higher. Regarding insolation, in 1998 and 2000 there was a stable increase in downwelling irradiance from mid April to mid May, but in 1999 the irradiance was very low in early May, and in 2002 it was only at moderate levels in late April–early May. These data are consistent with what was pointed out in this respect in Sections 2.1–2.3.

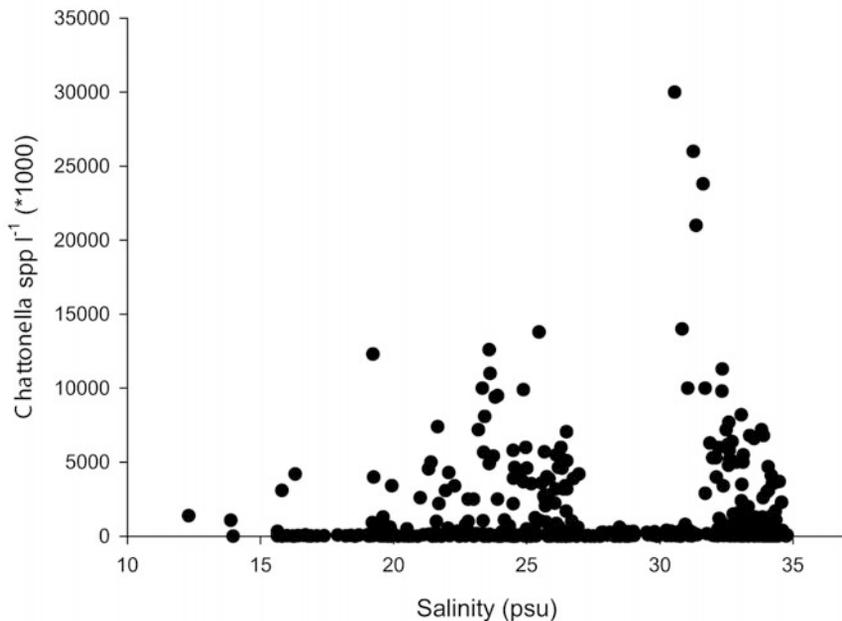


Figure 2.5. *Pseudochattonella* spp. abundance vs. salinity in the North Sea/Skagerrak/Kattegat area during the period 1998–2003. *Courtesy:* L. J. Naustvoll, IMR.

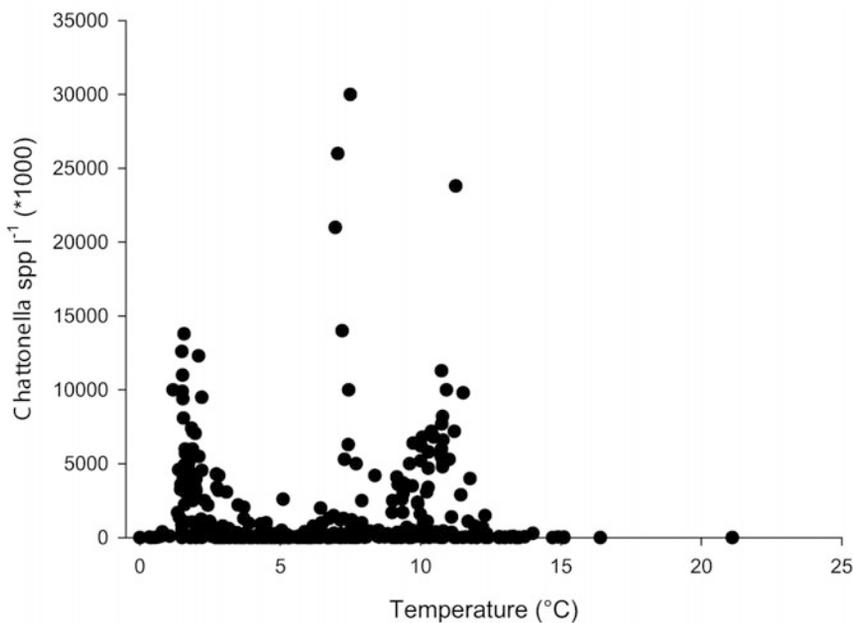


Figure 2.6. *Pseudochattonella* spp. abundance vs. sea surface temperature in the North Sea/Skagerrak/Kattegat area, during the period 1998–2003. *Courtesy:* L. J. Naustvoll, IMR.

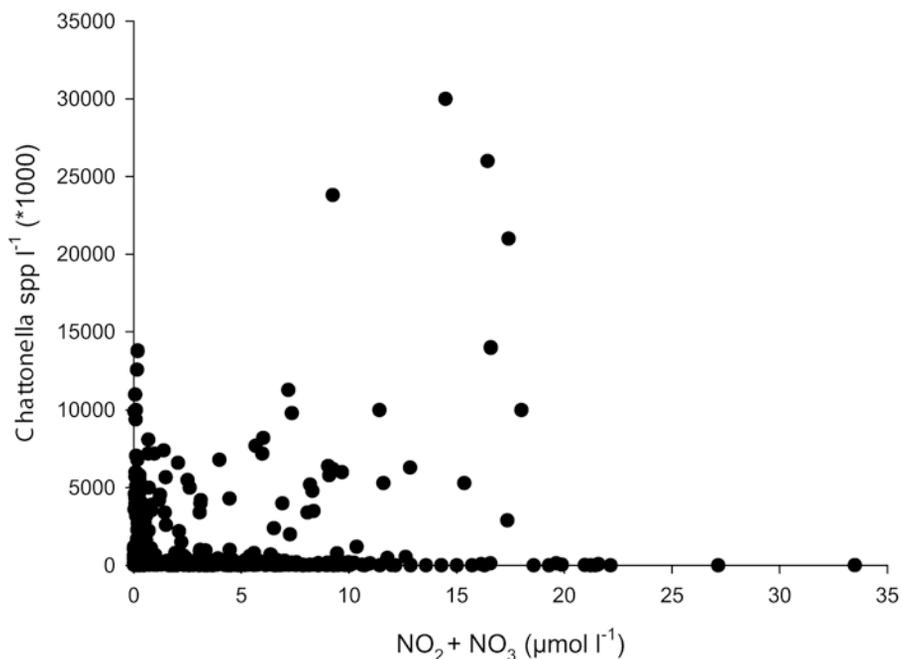


Figure 2.7. *Pseudochattonella* spp. abundance vs. $\text{NO}_2 + \text{NO}_3$ concentration ($\mu\text{mol L}^{-1}$) in the North Sea/Skagerrak/Kattegat area, during the period 1998–2003. *Courtesy:* L. J. Naustvoll, IMR.

2.4.2 Cyanobacteria blooms in the Baltic Sea

The Baltic Sea is among the largest seas with brackish water, with salinities (S) ranging from almost freshwater in the Bay of Bothnia to 15 psu in the Belt Sea. The vertical profile of S exhibits strong variations; for example, in the Baltic proper S varies from 7 psu at the surface to 11 psu at the bottom.

The nutrient load in the Baltic Sea has increased since 1900 by a factor of 4 for N and a factor of 8 for P, turning this water body into a mesotrophic one. While the issue of nutrient limitation for pelagic algae in the Baltic Sea remains a subject of debate, a common concern is intensified eutrophication.

Salinity and temperature stratification, which develops in the Baltic Sea especially during summer, inhibits vertical mixing and hence cuts down the input of inorganic nutrients from below the thermocline to the surface; under such conditions, only cyanobacteria (as an alga capable of nitrogen uptake directly from the atmosphere) have the advantage of growing and generating summertime blooms, provided that enough P has been brought into the euphotic zone by vernal overturning and left after the preceding vernal bloom. Moreover, high internal phosphorus storage in cells is supposed to enable cyanobacteria to grow even under limiting external phosphate concentrations.

Thus, the triggering factors for cyanobacteria bloom initiation in the Baltic Sea are as discussed in Sections 2.1–2.3: namely, a stratified water column, calm weather (wind speed <5 m/s), and high water temperature (>15°C) for 1–2 weeks.

Cyanobacteria occurrence in the Baltic Sea was evaluated according to the Finnish Alg@line data (for data description see Ruokanen *et al.* 2003) for the years 1997–2002. The data for the most common cyanobacteria species *Nodularia spumigena* Mertens and *Aphanizomenon flos-aquae* Ralfs (hereinafter referred to as *Nodularia* and *Aphanizomenon*) were analyzed in this case study.

Although there are various algal species capable of producing toxins in the Baltic Sea, the real damage is generally caused by frequent and vast blooms of *Nodularia* (Laamanen *et al.*, 2001). Also, the frequently occurring cyanobacteria species *Aphanizomenon* is considered as a serious nuisance for fishing and recreation.

Field data from the discussed case study indicate that these cyanobacteria species have different demands on their environment: *Aphanizomenon* prefers lower temperatures and salinities than *Nodularia* (Figures 2.8 and 2.9). *Aphanizomenon* also prefers a lower dissolved inorganic nitrogen (DIN):dissolved inorganic phosphorus (DIP) ratio (Figure 2.10). These different responses may be rooted in the different vertical, horizontal, and temporal distributions of the two genera in the Baltic Sea.

Different preferences in water salinity, temperature, and DIN/DIP ratio conditions determine seasonal and interannual variability in the spatial distributions of these two cyanobacteria species. After the vernal diatom bloom, cyanobacteria start to accumulate the intercellular phosphorus necessary for their later growth. In

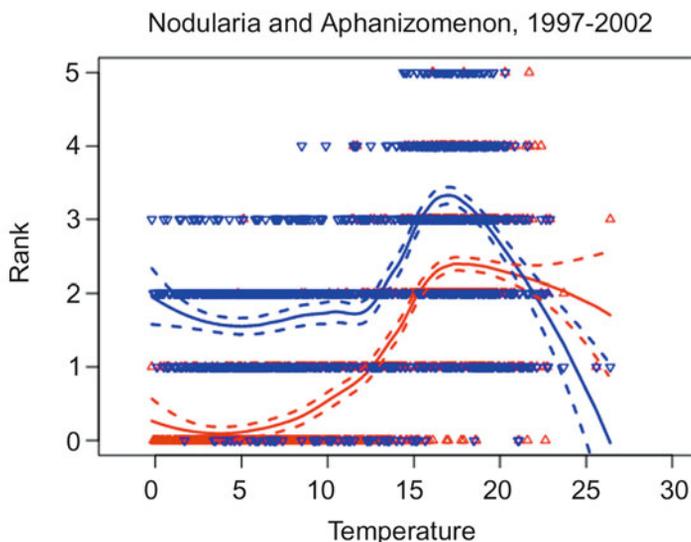


Figure 2.8. Occurrence of cyanobacteria in relation to water temperature. Red lines—*Nodularia*, blue lines—*Aphanizomenon*. Courtesy: S. Kaitala, FIMR.

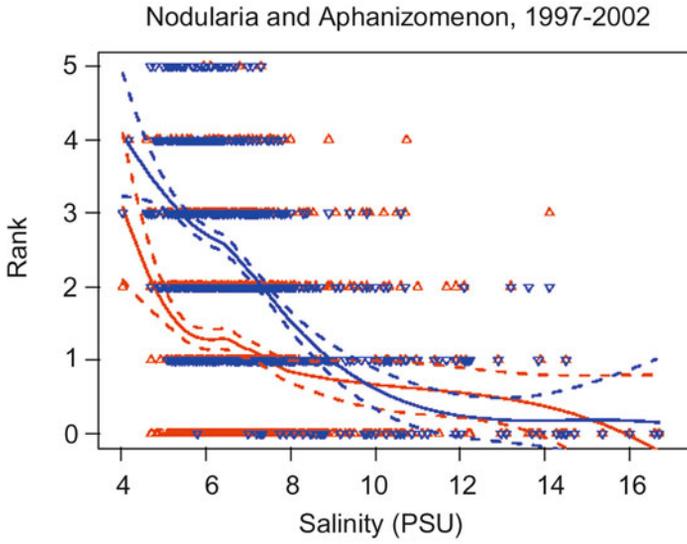


Figure 2.9. Occurrence of cyanobacteria in relation to salinity. Red lines—*Nodularia*, blue lines—*Aphanizomenon*. Courtesy: S. Kaitala, FIMR.

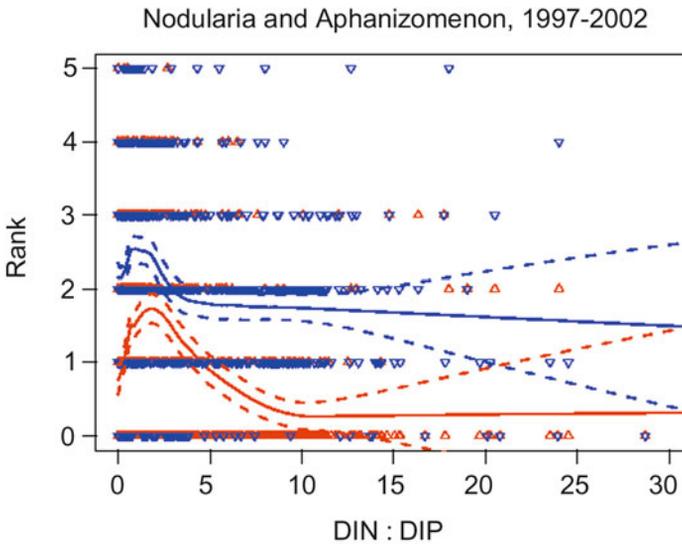


Figure 2.10. Occurrence of cyanobacteria in relation to DIN:DIP ratio. Red lines—*Nodularia*, blue lines—*Aphanizomenon*. Courtesy: S. Kaitala, FIMR.

June–July begins the major onset of the rapid buildup of *Aphanizomenon* accumulations, most expressed in the Gulf of Finland. However, by late spring, appreciable concentrations of *Aphanizomenon* can be found as a result of this species' better (than *Nodularia*) adaptation to low temperatures. The summertime increase in water temperature T in excess of 15°C causes a significant enhancement of *Nodularia* content.

The highest counts of *Nodularia* cells in most years were observed in the central Baltic Sea, where generally the highest sea surface temperature (SST) occurs. In the fall, the growth of *Nodularia* starts to ebb as a consequence of decreasing T , and by late December it has all but disappeared.

In winter, low water temperature and decreased incident solar radiation in combination with enhanced mixing drastically reduce phytoplankton concentrations, but not completely. During this period, a number of complex processes occur that are important for phytoplankton community resuscitation in the following year. First and foremost, nutrient mineralization in sediments and the late winter–early spring overturning of water masses lead to a replenishment of nutrients in the mixed layer. At the same time, water salinity invariably exhibits no seasonal cycle.

The frequent occurrences of massive outbreaks of *Nodularia* in the Baltic Sea in summer are spurred on by low DIN/DIP ratios (resulting from depletion of inorganic nitrogen). Such conditions, as discussed earlier in this section, promote the growth of cyanobacteria. Blooms of *Nodularia*, as a cyanobacterium species, are certainly partially the result of sufficient phosphate concentrations left after the spring bloom, but more strongly by warm and calm weather conditions, low wind, high water temperature, and strong stratification.

Interannual variations in *cyanobacteria* blooms are brought about by atmospheric (both physical and chemical) oceanic parameters that force excursions. The highest interannual variability is found in the Gulf of Finland whereas fluctuations in the southern and central Baltic Sea are comparatively small. In 1997 and 1998, in all three regions of the Baltic Sea lower SST and chlorophyll concentrations were observed in February compared with the time period 1998–2002. However, a rapid increase of T in 1997 caused fast growth of diatom phytoplankton in spring followed by *Aphanizomenon* and *Nodularia* blooms in summer.

2.4.3 *Gymnodinium catenatum* blooms in the Galician Rías

Blooms of dinoflagellates, often harmful, are relatively frequent in the Rías Baixas of Galicia in four bays along the northwestern Iberian Peninsula where seasonal upwelling–downwelling events are among the main oceanographic features (Figueiras *et al.*, 2002).

Study of these blooms has provided a coherent picture of HAB dynamics in the region. Seasonal upwelling on the northwestern Iberian shelf occurs on average between March and September when northerly winds are dominant, whereas downwelling motions prevail during the rest of the year owing to the predominance of southerly and westerly winds. Coastal upwelling and downwelling phenomena

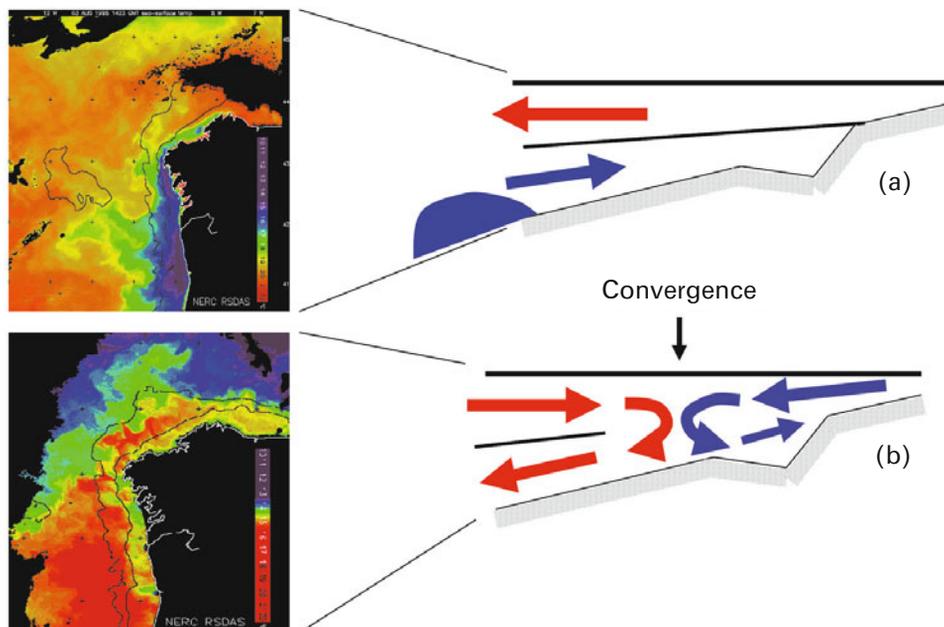


Figure 2.11. Schematic representation of circulation in the Spanish Rías during (a) upwelling and (b) downwelling conditions and their typical off-shore sea surface temperature (SST) conditions revealed in satellite images. *Courtesy:* F.G. Figueras, IIM.

greatly influence circulation in the rías (Figure 2.11) and hence the exchange processes between the rías and the adjacent shelf (Álvarez-Salgado *et al.*, 2000; Tilstone *et al.*, 2000). Upwelling forces two-layer density-induced positive circulation in the rías characterized by the outflow of surface waters and a compensating inflow of upwelled water at the bottom.

The transition to seasonal downwelling, which coincides with the rapid change to southerly winds, establishes a *reversal circulation*, during which surface coastal water enters the rías to develop a downwelling front at the location where it meets inner waters that are under higher continental influence. During this reversal circulation, the outflow towards the ocean in the outer circulation cell (Figure 2.10b) takes place at the *bottom layer*.

Reversal circulation modifies the distribution of algal assemblages along the rías and in the nearest shelf: under upwelling conditions, it is characterized by the predominance of diatoms in the inner waters as well as by higher concentrations of dinoflagellates towards the shelf (Tilstone *et al.*, 1994). Downwelling causes the advection of dinoflagellates to the interior of the rías and promotes their accumulation in the downwelling front (Fermín *et al.*, 1996). This accumulation occurs because the capability of dinoflagellates to swim vertically allows them to compensate for the downward velocity generated in this convergence. Diatoms, unable to counteract such downward velocity, are pushed down in the water column to be then exported towards the shelf by bottom outflow (Figure 2.12).

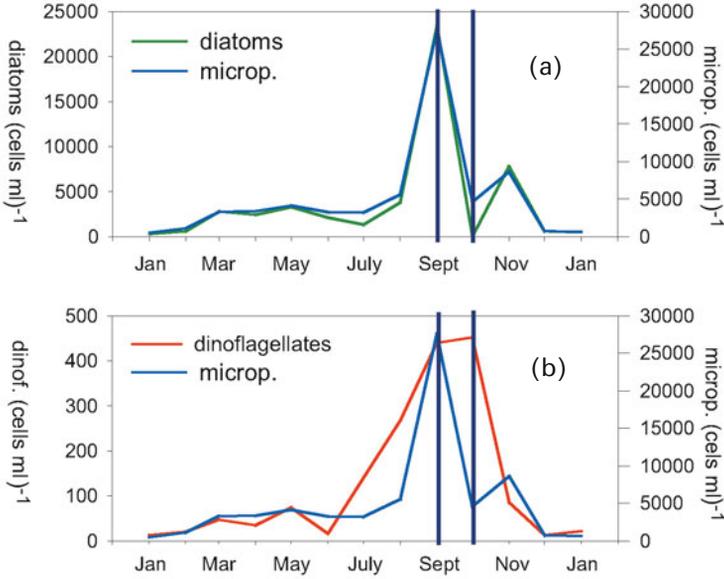


Figure 2.12. Time evolution of (a) total phytoplankton and diatom abundance and (b) total phytoplankton and dinoflagellate abundance in the surface waters of a sampled station in the Ria de Vigo in 1987–1988. Values in (a) and (b) are monthly averages. Vertical bars mark the autumn transition to downwelling. *Courtesy:* F.G. Figueras, IIM.

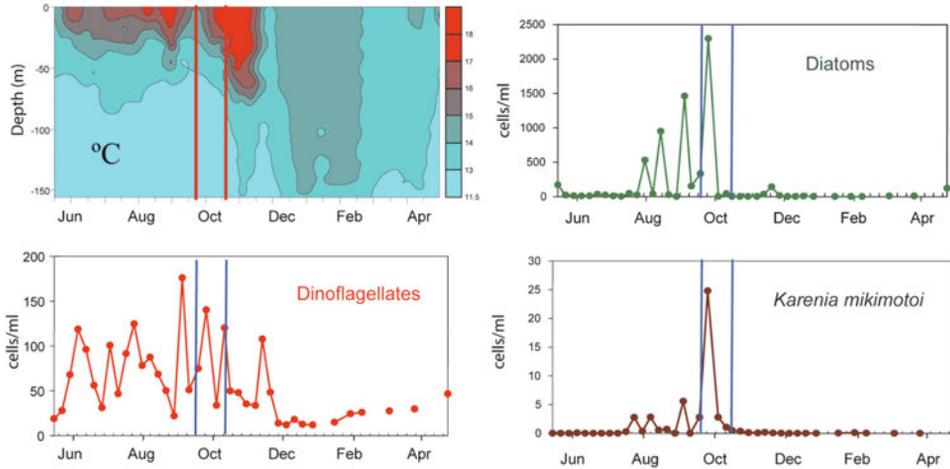


Figure 2.13. Time evolution (June to April) of temperature (upper left) and mean abundance (cells/ml) of diatoms, dinoflagellates, and the swimmer species *Karenia mikimotoi* in shelf waters in front of the Ria de Vigo in 2001–2002. Vertical bars mark the autumn downwelling transition. *Courtesy:* F. G. Figueras, IIM.

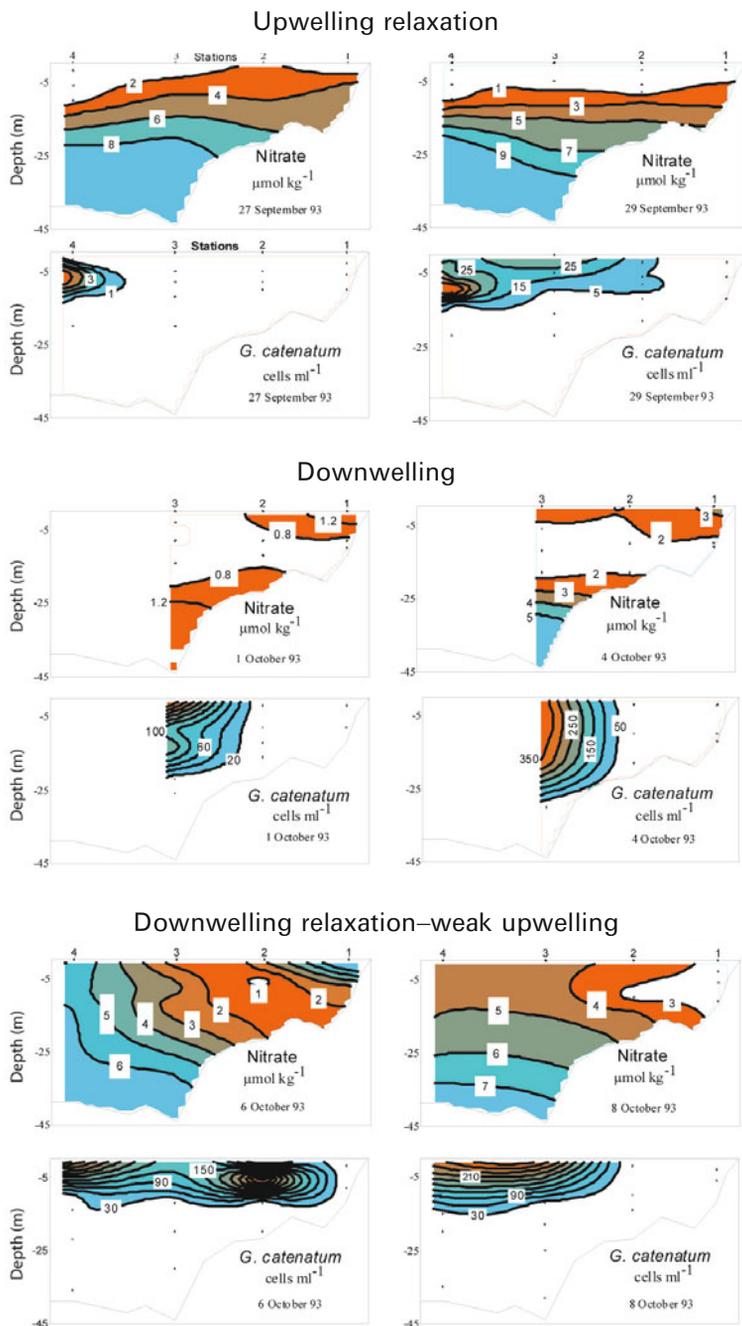


Figure 2.14. Sequence showing the initiation and development of a *Gymnodinium catenatum* bloom in the Ria de Vigo in September–October 1993. Nitrate distribution can be used as a tracer of upwelling/downwelling. *Courtesy:* F. G. Figueras, IIM.

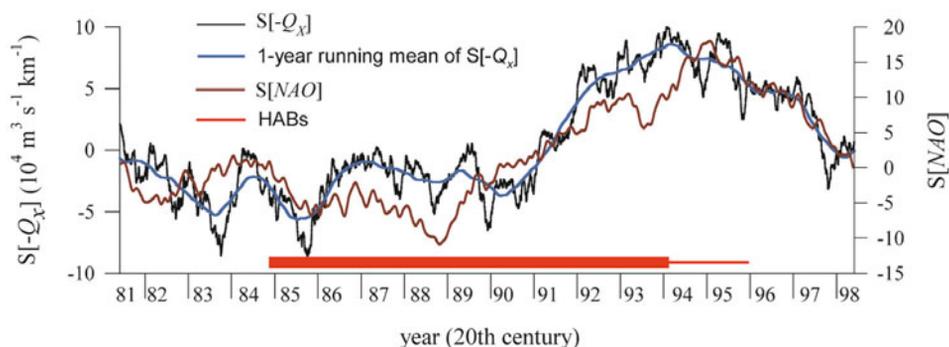


Figure 2.15. Graph showing the possible long-term relationship between climate variability and PSP events caused by *Gymnodinium catenatum* in the Galician Rías Baixas (NW Iberian Peninsula) during the years 1981 to 1998. *Courtesy:* F. G. Figueras, IIM.

This kind of HAB initiation has also been observed in a one-year-long record of data from a station on the shelf with a sampling frequency of once per week (Figure 2.13). Consequently, it can be assumed that autumn downwelling is the key oceanographic process for HAB initiation off the coast of Galicia in the northwestern Iberian Peninsula.

Regardless of which dinoflagellate species predominates as a consequence of downwelling, the actual development of the alga into a bloom also needs an appropriate nutrient supply, which is provided by the return of moderate upwelling conditions (Fermín *et al.*, 1996): strong upwelling enhances positive circulation and favors diatom growth (Figure 2.14). Large runoff during downwelling, another nutrient source for the surface layer, also enhances positive circulation and hence displacement of the downwelling front toward the shelf.

Therefore, the two processes—strong upwelling and runoff—tend to disperse dinoflagellates into shelf waters. Historical data also suggest that HAB episodes are related to long-term variability in upwelling (Figure 2.15), which in turn is connected with interannual climatic variations such as the North Atlantic Oscillation (NAO).

After this analysis of general mechanisms controlling the incidence, surficial extension, and variation of HABs brought about by a multitude of internal and external factors, which were further exemplified by a few case studies, we now turn to a discussion of harmful algal cellular properties, principally from the perspective of their optical attributes. The latter form the basis for remote monitoring of HABs. The approaches and methods used for this are elaborated in Chapter 4.



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