

Harmful microalgae blooms (HAB); problematic and conditions that induce them

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Abstract

HAB occurrence is becoming more frequent and problematic in marine recreational waters. However, the exploitation of the coastal area for recreational use is promoting the necessary conditions for the HAB increase. In terms of the harmful effects, we can consider two types of causative organism: the toxic producers and the high-biomass producers. Toxic events can be produced by a very low concentration of the causative organism. This characteristic implies a difficulty for the monitoring programs in relation to human health. It is important to point out in the context of human health and HAB events, that in some coastal regions (e.g. the Mediterranean basin) HABs are an emerging problem. In these regions, the local population and visitors may face a health risk that is difficult to measure. The monitoring of toxic species has mainly been associated -with shellfish farming. However, the risk of intoxication could become even greater in areas not subject to legislation of aquaculture activities.

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1. Introduction

Coastal systems around the world have suffered a variety of environmental problems, including loss of seagrass habitats, coral reef degradation or destruction, loss of quality of coastal waters for recreational use, deaths of marine mammals, red tides, fish kills, and outbreaks of shellfish poisonings. The last five problems cited above can be attributable to what is called harmful algae blooms (HABs). A term introduced for the first time in 1974 (1st International conference of blooms of toxic dinoflagellates). One of the main problems in coastal regions on a world scale is the increased frequency of HABs.

There is growing international recognition that HAB's are affected by human activities, but its exact causes are still under debate. There are many on-going HAB research

efforts at national and international levels (GEOHAB, ECOHAB, EUROHAB) to address problems associated with HAB and are increased knowledge of the underlying factors for HAB occurrences (Anderson, 1995; Granéli et al., 1999; Granéli and Lipiatou, 2002).

It is essential in this context to clarify that the term HAB is used for a wide range of different phenomena. First, because the microalgae responsible are diverse; harmful species belong to six algal groups (diatoms, dinoflagellates, haptophytes, raphidophytes, cyanophytes, and pelagophytes) and these differ greatly in terms of morphological, physiological and ecological characteristics (Zingone and Enevoldsen, 2000; Garcés et al., 2002). The definition of HABs has been evolving over decades. A phytoplankton bloom (what was known traditionally as a “red tide” because of the water discoloration) is considered to be a sudden increase in the population of a microalgae that has encountered suitable conditions for growth, that, together with their adaptive strategies (i.e migration, active swimming) and the appropriate physical conditions, can

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reach concentrations of 10^4 – 10^5 cell l^{-1} during certain period of time (commonly 1–3 weeks). A proliferation like this can be characterised by the occasional dominance of a particular species (in that case a monospecific bloom) or group of species. The term HABs includes other types of events considered directly or indirectly harmful for humans, and for the biota of the region. The list of harmful species on a world scale is growing as rapidly as its political concern. In terms of harmful effects, we can consider two types of causative organism: the toxin producers and the high-biomass producers. Some HAB species are related to both characteristics. Of the 4000 of marine planktonic microalgae, some 200 can be harmful. Of these, only around 80 (mainly dinoflagellates) have the potential to produce toxins (Zingone and Enevoldsen, 2000; Smayda and Reynolds, 2003).

Problems associated with high biomass blooms and toxic events are different. High biomass blooms may cause significant ecological problems and harmful effects in the biota of the region (anoxia, community and food-web changes) as well as great economic problems connected to the deterioration of the coastal recreational waters (discoloration, odour etc.). The conspicuous nature of these events brings it to the attention of the public and authorities. Moreover, in some cases these bloom events have been confused with waste water pollution (Garcés et al., 1999).

Toxin events can result from very low concentrations of the causative organism. Actually, some toxic events are considered to be HABs, are not blooms. This poses a difficulty for monitoring programs in relation to human health. Moreover, in the case of toxic events co-occurring with high-biomass, in most cases, levels of toxicity considered dangerous have risen before the bloom is conspicuous due to discoloration or cell counts. A specific toxic event with very low cellular concentrations (10^2 – 10^4 cell l^{-1}) is the DSP episodes associated with the dinoflagellates of the genus *Dinophysis* (Reguera et al., 1993; Blanco et al., 1998).

Four main harmful effects on humans are associated with the toxic producers: (i) consumption of toxic shellfish that have accumulated phytoplankton toxins filtered from the water, (ii) consumption of tropical fish that accumulated phytoplankton toxins (ciguatera), (iii) respiratory problems due to inhalation of aerosols from sea water that contains toxic species, and (iv) skin irritations due to allergy-like reactions. A fifth harmful effect, not yet evaluated, is being considered (i.e. the chronic exposure to low toxin levels). Both high biomass and toxic events can also be associated with the mortality of fish. Different causes are associated with these mortalities (low oxygen levels, direct toxicity, hemolysis, and mechanical damages). In many cases, fish mortality events are related to the fact that fish cannot escape from the cages. A complete enumeration of different cases, species, etc. of the various harmful effects on fish produced by microalgae can be found in Landsberg (2002). Cases of toxic events related to drinking waters (cyanobacterial blooms) are also increasing around the

world (Chorus et al., 2000; Pitois et al., 2000; Rao et al., 2002). The listing of harmful effects of high biomass blooms can be found in Zingone and Enevoldsen (2000). In any case, we will focus our attention on the toxic events linked to human health and marine waters. In Table 1, we present a summary of toxins, producer species and symptoms. For a detailed description of the chemical structures of the toxins, see Chapter 9 in Hallegraeff et al. (1995).

It is not written the scope of this paper to give an enumeration of the current most problematic toxic events around the world. Information is available on the WEB sites of the different monitoring programmes around the world. Some of them update the information on a weekly or monthly basis. Currently, approximately 2000 cases of intoxication (with a 15% mortality rate) in humans due to consumption of toxic shellfish or fish are registered annually (Hallegraeff et al., 1995, 2003). In fact, while giving us an idea of the problematic nature of HABs in relationship to human health, it does not reflect the reality of the situation. Much money is being invested nowadays in monitoring programs (Hoagland et al., 2002), as can be also seen in the WEB sites cited above. Monitoring can prevent the consumption of toxic seafood. Most important, the actual number of cases has been underestimated because of incorrect diagnoses, usually where gastro-intestinal symptoms are implicated.

2. Increase of HABs

The apparent global increase in HABs was considered by Hallegraeff (1993). He concluded that: “the effects on public health and economic impacts of HABs are now showing signs of a truly global epidemic”. The history of the different toxic events, i.e. the first association between a human intoxication and the causative organism, and the successive detention of toxic events, is a revealing way of showing the dimension of the problem (see figures in Hallegraeff, 1993). The development of databases such as the IOC HAEDAT (www.ioc.unesco.org/hab/data3.html) have been very useful in understanding the expansion of some species as well as the increase in the frequency of toxic events in the Atlantic and circumscribed areas of the Mediterranean. Decadal maps of toxic events in these areas are available at the WEB site: www.ifremer.fr/envlit/documentation/dossiers/ciem/aindex.html.

Increased research and knowledge is a cause of new harmful species detection in some areas. Shell-fish farming has been increasing continuously over the past decades and monitoring associated with toxicity in shellfish farming areas has increased. Few doubt nowadays that we are witnessing a real increase in HABs events.

Apart from the more in-depth knowledge due to the increased monitoring, other factors related to human activities can be summarised: (i) the increase in geographical ranges of harmful species distribution due to human-induced transport of resting cysts results from movement of shellfish stocks or ballast waters and floating plastic

Table 1
A summary of syndromes, producer species and symptoms

Paralytic shellfish poisoning (PSP)	Diarrhetic shellfish poisoning (DSP)	Amnesic shellfish poisoning (ASP)	Neurotoxic shellfish poisoning (NSP)	Spirolide (SST)	Azaspiracid shellfish poisoning (AZP)	Ciguatera fish poisoning (CFP)
Causative organism <i>Alexandrium andersoni</i> , <i>A. acatenella</i> , <i>A. catenella</i> , <i>A. cohorticula</i> , <i>A. minutum</i> , <i>A. tamarense</i> , <i>A. tamiyavanichi</i> , <i>Gymnodinium catenatum</i> , <i>Pyrodinium bahamense</i>	<i>Dinophysis acuminata</i> , <i>D. acuta</i> , <i>D. caudata</i> , <i>D. fortii</i> , <i>D. mitra</i> , <i>D. norvergica</i> , <i>D. rotundata</i> , <i>D. rapa</i> , <i>D. sacculus</i> , <i>D. tripos</i> , <i>Prorocentrum lima</i> , <i>P. arenarium</i> , <i>P. belizeanum</i> , <i>P. cassubicum</i> , <i>P. concavum</i> , <i>P. emarginatum</i> , <i>P. hoffmannianum</i> , <i>P. maculosum</i>	<i>Pseudonitzschia australis</i> , <i>P. delicatissima</i> , <i>P. pseudodelicatissima</i> , <i>P. Multiseries</i> , <i>P. fraudulenta</i> , <i>P. multistriata</i> , <i>P. pungens</i> , <i>P. seriata</i> , <i>Nitzschia navis-varingica</i>	<i>Karenia brevis</i> (= <i>Gymnodinium breve</i>); <i>Pfiesteria piscicida</i> (<i>neurotoxic</i>), <i>P. shumwayae</i>	<i>Alexandrium</i> <i>ostenfeldii</i>	<i>Protoperdinium</i> <i>crassipes</i>	<i>Gambierdiscus australes</i> , <i>G. pacificus</i> , <i>G. polynesiensis</i> , <i>G. toxicus</i> , <i>G. yasumotoi</i> <i>Ostreopsis heptagona</i> , <i>Prorocentrum lima</i>
Symptoms <i>Mild care</i> Within 30 min: tingling sensation or numbness around lips, gradually spreading to face and neck; prickly sensation in fingertips and toes; headache, dizziness, nausea, vomiting, diarrhoea	After 30 min to a few hours (seldom more than 12 h): diarrhoea, nausea, vomiting, abdominal pain	After 3–5 h: nausea, vomiting, diarrhoea, abdominal cramps	After 3–6 h: chills, headache, diarrhoea; muscle weakness, muscle and joint pain; nausea and vomiting paraesthesia; altered perception of hot and cold, difficulty in breathing, double vision, trouble in talking and swallowing	Unknown in humans. Injected in to mice, spriolides cause rapid death due to neurointoxication	Gastrointestinal illness, all symptoms similar to DSP. Severe diarrhoea, vomiting, nausea, stomach cramps, headaches and chills, which persisted for 3–5 days	Symptoms develop within 12–24 h of eating fish. Gastrointestinal symptoms: diarrhoea, abdominal pain, nausea, vomiting
<i>Extreme care</i> Muscular paralysis; pronounced respiratory difficulty; choking sensation; death through respiratory paralysis may occur within 2–24 h after ingestion	Chronic exposure may promote tumour formation in the digestive system	Decreased reaction to deep pain; dizziness, hallucinations, confusion; short-term memory loss; seizures				Neurological symptoms: numbness and tingling of hands and feet; cold objects feel hot to touch; difficulty in balance; low heart rate and blood pressure; rashes. In extreme cases, death through respiratory failure
<i>Treatment</i> Patient has stomach pumped and is given artificial respiration. No lasting effects	Recovery after 3 days, irrespective of medical treatment	At this point, the treatment of ASP is symptomatic				No antitoxin or specific treatment is available. Neurological symptoms may last for months and years. Calcium and mannitol may help relieve symptoms

debris is suggested as a potential transport vector of the HAB species (Masó et al., 2003); (ii) stimulation due to the over-enrichment of coastal waters (what is called cultural eutrophication), (iii) human-induced climatic change has also been noted, but the lack of a long term series of monitoring makes it a difficult task to reach any conclusions at the present time, (iv) the increase of confined bodies water in coastal areas due to the exploitation of the coastline has been suggested in the Mediterranean Sea (Garcés et al., 2000; Vila et al., 2001), and (v) the decreasing biomass of filter feeding organisms, due to over fishing, or changing environmental conditions (Rothschild et al., 1994).

We must deal with different interacting factors, and their relevance in most cases is difficult to assess. Indeed, all causes mentioned are products of anthropogenic actions on coastal area. HABs, in fact, are a natural phenomenon that has been reported in many areas around the world, but, it seems, that the special conditions that trigger the possibility of developing a harmful event are more frequent and occur in more areas than before. Due to its problematic nature, HABs research has been enhanced drastically. The international conference on harmful algae blooms held every two years, has had increasing numbers of participants each year. The proceedings of these conferences are valuable sources of information on HABs events around the world (Yasumoto et al., 1995; Reguera et al., 1998; Hallegraeff et al., 2000). Nevertheless, we must say that there are still doubts as to the extent to which human impact (eutrophication, marine pollution, coastal development, fisheries, ballast water, and climatic change) may contribute to HABs. Each species has different adaptive strategies and responds in different ways to the variability of the environment and its changes. So the answers are not unique and would depend on many factors: human, natural and their interaction. There are expectations that micropaleontology could bring many factors to light in that sense. Microfossils can be used to follow the history of HABs incidences and relate it to natural or human environmental changes (Dale et al., 1999; Dale, 2000, 2001).

The diversity of bloom dynamics is another aspect to be taken into account. Different interacting physical, chemical and biological factors can trigger a bloom of a species but in different habitats (Zingone and Enevoldsen, 2000). Evidence shows that the inter-annual variability of some HABs events (*Gymnodinium catenatum* and the *Pyrodinium bahamense*, both PSP producers) are a result of the interaction between local and global forcing (climatic events such as the North Atlantic Oscillation or El Niño respectively) (Fraga and Bakun, 1993; Usup and Azanza, 1998).

The detection of a harmful species in one area, not previously identified, is a common occurrence. The expansion of the geographical distribution of a species could be due to an anthropogenic introduction, a natural phenomenon (i.e. currents), or it could be a “hidden flora” species; the species was already in the area but at undetectable concentrations, (the case of *Gymnodinium breve*, a NSP producer, in New Zealand waters (Hallegraeff et al., 1995)). Moreover,

areas not currently affected by a certain species, could have hold the species in the distant past (Dale et al., 1993). Both natural climatic variability on a global scale, or man induced climatic variability, can provoke changes in the geographical range of the species (Glibert et al., 2001).

Genetic analysis is essential to confirm the invasion of alien microalgae in different coastal areas affected by ballast water or the transfer of shellfish stocks, i.e. *Alexandrium* species expansion in Tasmanian Waters (Scholin, 1996). The expansion of *Alexandrium catenella* (a PSP and high biomass producer) in the Mediterranean is yet another example. Its huge blooms are a natural phenomenon in upwelling areas (South Africa, Chile) after certain hydrographical conditions (Pitcher and Calder, 2000; Uribe and Espejo, 2003). In the Mediterranean, it has been detected in three regions: in the last 5 years, the Catalan Coast (Tarragona and Barcelona harbours) (Vila et al., 2001) and Valencia, the Sardinia Coast (Gulf of Olbia) (Lugliè et al., 2003) and in the Thau lagoon (French Mediterranean). Genetic analysis shows that *A. catenella* from the Mediterranean is closely related to the *A. catenella* of Asia (Lilly et al., 2002; Penna et al., 2005). For that reason it is supposed that *A. catenella* is an alien species introduced by human ways. However, we don't know if its current distribution in the Mediterranean is due to a natural expansion of the species or the result of successive anthropogenic introductions. Indeed, *A. catenella* was described in the North-western Mediterranean as a rare species by Margalef and Estrada (1987). Frequently, it is challenging to arrive at concrete conclusions. In any case, numerous studies confirm the presence of resting cysts of harmful species in ballast water (Hallegraeff, 1998; Dickman and Zhang, 1999; Blackburn et al., 2001; Marangoni et al., 2001).

One of the most significant anthropogenic forces to the marine environment is the introduction of excessive nutrients, particularly nitrogen and phosphorus. The relationship between the increase of HAB events on a world scale and the increase of anthropogenic nutrient flux in the last decades has been repeatedly discussed.

3. HAB and nutrients. What we know

Anthropogenic sources of nutrients include fertilisers, combustion of fossil fuels, discharge of human waste, and the consequences of animal production (Nixon, 1995; National Research Council, 2000). Coastal zones around the world are subjected to increasingly nutrient inputs as related to human activities including direct discharges and via rivers, ground water and atmospheric deposition. These inputs not only originate from land but also increase in aquaculture activities can result in increased nutrient loading in certain areas. The load of P in the marine waters has increased 3-fold compared to pre-industrial, pre-agricultural levels; the flux of N has increased even more (i.e. 4-fold in the Mississippi River, and more than 10-fold in the rivers entering the North Sea) (National Research Council, 2000).

There are well-established positive relationships among nutrient loads in marine systems, and phytoplankton primary production, and fisheries yield (Rabalais and Nixon, 2002). However, the amount of nutrients discharged can surpass the capacity of the system to assimilate the nutrient-enhanced production, and water-quality degradation occurs. This over-enrichment leads to diverse impacts including increase turbidity with a subsequent loss of submerged aquatic vegetation, oxygen deficiency, disruption of ecosystem functioning, loss of habitat, loss of biodiversity, shifts in food webs, and loss of harvestable fisheries and HABs (National Research Council, 2000; Rabalais and Nixon, 2002).

Existing nutrient records provide evidence of a rapid change in the fertility of coastal ecosystems over the last half of the 20th century (Cloern, 2001). While the scientific community agrees, in general, on the key role of coastal over-enrichment in the increase of HABs, there are few cases where this relationship has been thoroughly proven. HAB research, although an active area of research, is a relatively new science, as is marine coastal eutrophication (Cloern, 2001), although this may seem surprising. The lack of long term series of monitoring data in the majority of the coastal areas is a great handicap. We refer the readers to the reviews of Smayda (1989), Hallegraeff (1993), Hallegraeff et al. (1995), Zingone and Enevoldsen (2000), Anderson et al. (2002), where concrete examples of HABs events around the world, and their relationship with cultural over-enrichment, can be found. Without going into this any further it should be noted that new studies have successfully related over-enrichment with HAB events. Some of these findings are based in sediment analyse such as in the case of *Pseudonitzschia* blooms in the Gulf of Mexico (Parsons et al., 2002).

Nutrients reach the coastal area via non-point and point sources. It is considered in a global context that point sources such as urban waste water and industrial discharges are less important nutrient contributors than non point-sources. The amount of nutrient loading in the marine environment brought via non-point sources is very difficult to evaluate. A variety of human activities such as the use of fertilisers, fossil-fuel combustion or animal feeding operations contribute to non-point sources of nutrient loading. The different contributions of human activities and ways of arriving depend on the area (National Research Council, 2000; UNEP/WHO, 1996) and are very difficult to control. Paerl (2002) stated that among the non-point sources atmospheric deposition of nitrogen would play a determining role in the global increase of HABs. Atmospheric nitrogen deposition is a greater source of nitrogen enrichment to nitrogen (N)-limited estuarine and coastal waters than anthropogenic emissions. Local riverine inputs is a determining factor in specific sites, and when combined with low flushing rates, it can lead to huge toxic events, for example, *Alexandrium minutum* blooms in the Mediterranean (Vila et al., 2005). See Anderson et al. (2002) for a review of the rela-

tive importance of point and non-point sources in HAB increase.

One point that has frequently been discussed in the context of nutrient over-enrichment and HABs is why certain harmful species are favoured above others. Nutrient enrichment will lead to an increase in phytoplankton biomass. Why are some species favoured over the rest of the community? Indeed, why the toxic ones? It is obvious that a high biomass bloom needs high nutrient levels. But, dinoflagellates, the taxa that proportionally causes, high biomass blooms have developed adaptive strategies for nutrient uptake at low levels of concentration (Smayda, 1997). If it is sometimes difficult in the case of high biomass forming species to find answers, it is even more difficult in the case of toxic events, where there is not a huge increase of certain species. Its presence at low levels of concentration can produce very harmful effects. For these two reasons the statement “over-enrichment-HAB increment” has been questioned.

High-biomass blooms (concomitant or not with toxic events), which result from the interaction of biological, physical and chemical mechanisms, are, with some exceptions, poorly understood. Bloom dynamics are controlled internally (through behavioural adaptation). Adaptive strategies such as mobility behaviour (phototaxis, vertical migration, swimming patterns, and aggregation) and life cycle strategies (which include temporary phases and resting cysts) interact with the surrounding environment in development and maintenance of blooms. The dynamics of the HABs, varies from place to place, not depending alone of the hydrographic and topographical conditions, but also on ecological and biological characteristics of the causative organism(s). Each species has a specific life history adapted to the surrounding environment, and that gives them advantage over the rest of the community. For this reason knowledge of growth, the phases of the life cycle, the mortality rates, and their relationships with the local circulation, and the biological environment, is basic. Vertical migration is a mechanism to seek nutrients, but is also a determining factor in the spatial distribution of the population (Prego, 1992; Liu et al., 2002) as well as an adaptation to minimize population loss. Basterretxea et al. (2004) demonstrated the key role of summer breeze forcing and its coupling with organism behavior in determining the occurrence and persistence of the high biomass blooms that occurs recurrently during summer in some Mediterranean beaches. A low water renewal favors nutrient availability and maintenance of certain positions for species with swimming ability, enabling them to avoid being washed seaward. Nutrient input is a necessary but not sufficient condition.

At present there is no general consensus about the ecological roles of toxins and therefore the evolutionary reasons for their appearance. A large part of HABs, species research has been dedicated to toxin production and factors that control it. The issue gets more complicated since environmental conditions (light, temperature, salinity and

nutrients) can increase or diminish the capability of some species to produce toxins (Cembella, 1998). It has also been said that the same species can be toxic in one area (with very harmful effects), not toxic in other areas, or lose their capability of producing toxins in culture. This statement must be treated with caution; in fact, it may be due to confusion in the identification of the species. Cembella (1998), argued that it is impossible to eliminate completely the toxicity in a strain with the capacity to produce toxins and, in the same way, it is impossible for non-toxic strains to become toxic. Several laboratory experiments have been dedicated to elucidating the relationship between “toxin-production” and nutrients. In fact, different results have been obtained depending on the species and also on the life cycle stage, or indeed, on the different phases of the population growth (exponential, maintenance, end) (Anderson et al., 1990; Cembella et al., 1990; Flynn et al., 1994). Bacteria have been implicated in the production and biotransformation of microalgae toxins (Falconer, 1993). What is certain is that bacterial–algal interactions play a role in dynamics HABs. This is an ongoing area of research, and efforts are addressed to isolating and identifying the bacteria associated with the species during bloom conditions (Alavi et al., 2001; Hold et al., 2001; Tobe et al., 2001; Vasquez et al., 2001; Biegala et al., 2002; Uribe and Espejo, 2003). Although our knowledge of toxin production has increased substantially in recent years, there are not any conclusive answers as to what factor, or interaction of factors, control toxin production in natural environments.

One of the hypotheses explaining the increase in toxic events is that toxic production can provide advantages over other organisms of the community. Toxin production has been associated with allelochemical and allelopathic activities, which inhibit the growth of co-occurring phytoplankton species (Arzul et al., 1999), and act as a deterrent to grazers (see Turner and Tester, 1997). Teegarden and Cembella (1996) and Teegarden (1999) found selective feeding at high, but not low, concentrations of *Alexandrium fundyense*, suggesting that PSP toxins deter grazers only when higher cell concentrations are reached. One hypothesis is that as dinoflagellates seem to produce more toxins under nutrient limitation (Bechemin et al., 1999; John and Flynn, 2000; Guisande et al., 2002; John and Flynn, 2002), toxin production could be an adaptation developed to offset the negative effects of interspecific competition in conditions of nutrient limitation by increasing grazing pressure on non-toxic competitors (Guisande et al., 2002).

In fact, *A. minutum* (a PSP producer), the subject of the laboratory study on which this hypothesis was based, was more negatively affected by interspecific competition than by predation. However, the hypothesis of Wyatt and Jenkinson (1997)—that toxins could act as pheromones—could explain why such a diversity of composition and differences among populations of different areas exists. Max Taylor, in the conclusions of the Ninth International Conference on Harmful Algal Blooms (2000) said, referring to the toxins, “This raises once again the question of the func-

tions of such substances. While past experiments have supported the notion of an antipredation role for the saxitoxins and possible allelopathy by the bloom-forming chloromonads, the physiological or genetic variability of production raises doubts about them playing an essential role. Are toxin-producing strains more successful than non-toxic ones?” Actually, it is not known if the limitation of nutrients plays an important role in the production of toxins in natural proliferations.

Human activities on land are drastically changing the characteristics of the trophic conditions in coastal waters. The alteration of the nutrient loadings to the coastal area not only implies higher greater quantities of inorganic nutrients and organic compounds, but also its quality and composition, flux frequency and places of delivery.

Anthropogenic changes in the ratio of nutrient availability could be one of the key factors in some areas. This means that human activities have altered the relative quantity of a certain nutrient with respect to the others. Moreover, each species has its own characteristic nutritional requirements, and therefore some species could be favoured under certain human-altered conditions. In other words, some species (that could be classified “harmful for humans”) could be enhanced more than other microalgae of the community. A key element in the context of HABs is silica (the nutrient ratio hypothesis) (Smayda, 1997). An element required by diatoms in their walls, their growth ceases when Si becomes depleted. The ratios N:Si and P:Si have increased substantially in coastal areas affected by human stresses (Justic et al., 1995; Olivos, 2000). Sewage and agricultural discharges are rich in N and P not in Si. This has been proposed as one of the causes of the increase of HABs species on a global scale: dinoflagellates (in which group most HAB species belong) would be favoured over diatoms, the other important constituent of the phytoplankton community in marine waters. Laboratory experiments have shown that diatoms out-compete flagellates at higher levels; in contrast, flagellates dominate at lower ratios (Sommer, 1994; Schöllhorn and Granéli, 1996). However, the statement “silicate deficiency-HAB events increase on a global scale” remains to be verified. This statement implies changes in the structure of the phytoplankton community and these alterations could be slow and difficult to detect.

The evidence for the relationship regarding over-enrichment and HABs is clearer each day due to the fact that HABs tend to decrease when nutrient loading is reduced. The already classic instance of Hong Kong harbour is a clear example of how a reduction of nutrient loading reduces the number of problems associated with algae blooms (Hodgkiss and Ho, 1997). However, many HABs are natural phenomenon; some of them develop in pristine waters, such as in the case of *Alexandrium* blooms in Canadian waters (Prakash et al., 1971; Horner et al., 1997). Indeed the reduction of nutrients loadings has caused some unexpected results in certain places. a classical example is Seto Inland where a reduction of nutrient loading

effectively cause a reduction of phytoplankton biomass, but it seems that some toxic species are favoured (Anderson et al., 2002).

Links between HABs and nutrient loading are complex and imply an understanding of the physiological requirements and the mechanisms of nutrient acquisition by each species. Why doesn't a direct relationship exist between external nutrient concentration and HABs? The rate of nutrient supply will not necessarily correlate with the rate of nutrient assimilation. Nutrient assimilation depends on a variety of factors such as the nutritional preferences, uptake capabilities or nutritional status. In relationship with the nutritional strategies, flagellates, including dinoflagellates, have considerable nutritional strategies such as: (i) low nutrient affinity (Smayda, 1997), (ii) preference for reduced N forms (i.e. ammonium and urea) (DeYoe and Suttle, 1994), and (iii) mixotrophy (the ability to acquire N and C via particle ingestion or by the uptake of dissolved organic compounds) (Carlsson et al., 1998; Lomas and Glibert, 1999; Berg et al., 2002, 2003) and reviewed in Granéli and Carlsson (1998). Lower nutrient affinity means that diatoms have an advantage, with respect to flagellates, at low nutrient conditions. For that reason, flagellates would have developed alternative strategies, as the mixotrophic or heterotrophic tendencies that allow them to dominate in an environment where the nutrients may be insufficient for normal nutritional demands.

The forms of nitrogen available in marine coastal areas are changed drastically due to human activities, therefore not only can the nutrient ratio enhance some species or groups of species, but the several N forms have to be considered as a key element in the increase of HABs. Organic forms may play a key role in the development and maintenance of blooms of some species (Glibert et al., 2001).

4. Concluding remarks

Although the geographic extent of nutrient enrichment and its consequences are spread around the globe, much remains to be understood about differences in the susceptibility of the different coastal ecosystems. It is known that water renovation and flushing rates are key factors. The increase in artificial environments (ports, breakwaters and semi-closed beaches) in highly populated coastal areas multiplied those habitats favourable for the HABs species, as discussed in section of HABs increase. Coastal sheltered areas are increasing in direct relationship with recreational use of near-shore waters. A consequence is the evident variation of the small-scale coastal dynamics.

Vila and Masó (2005) analysed the phytoplankton community in anthropogenically impacted waters of the NW Mediterranean. Their results show that bloom forming dinoflagellates group in clear clusters preferentially occurring in large harbours (low flushing rates), and in summer. However, toxin producers are scattered across the four functional groups that resulted from the multivariate analysis (Fig. 1); results indicated that the most probable species

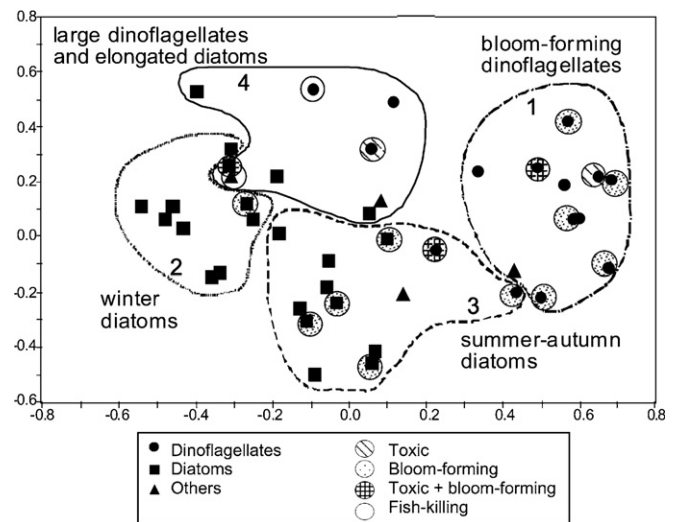


Fig. 1. Phytoplankton functional groups that characterize the anthropogenic impacted waters of the Catalan coast (Northwestern Mediterranean). The different harmful species have been pointed out according to their potential harm (from Vila and Masó, 2005).

associations are predictable in the area; however there is limited probability of predicting a toxic event. What is certain in the context of toxic events or, in general, HAB events, is that humans are increasing habitats favourable for these events to occur in. Favourable habitats are created by an interaction of factors that could be anthropogenic or not. For instance, large harbours may foster habitat conditions for HAB events in the Mediterranean (Vila and Masó, 2005). Harbours may have low flushing rates and are also situated in populated areas, which, in general, mean high nutrient contents. They are also subjected to a high traffic of commercial vessels that are known to be important vectors in the translocation of resting cyst of harmful phytoplanktonic species, and thus act as reservoirs for resting cysts (Garcés et al., 2004). This means recurrent events that can provoke the expansion of the species in the area.

HABs are, nowadays, considered one of the major problems that the coastal countries must face, and it seems that this will be even greater in the near future. But when we are talking of HABs we are referring to a diverse type of phenomenon caused by different organisms, with each case having its own concrete characteristics. To now we have left out, in this document, examples of HAB events around the world because an extensive literature is available on this topic. Instead, our intention has been to give an image of the HAB research that is currently being carried out, mentioning those reviews on the different topics where the different cases around the world are summarised.

The occurrence of HAB is becoming more frequent and problematic in recreational waters. However, exploitation for recreational use is fosters the conditions necessary for the HAB increase. Apparent increases respond to the current coastal zone management schemes that protect habitats encouraging the growth of dinoflagellates or the possibility of annual recurrence and the expansion of

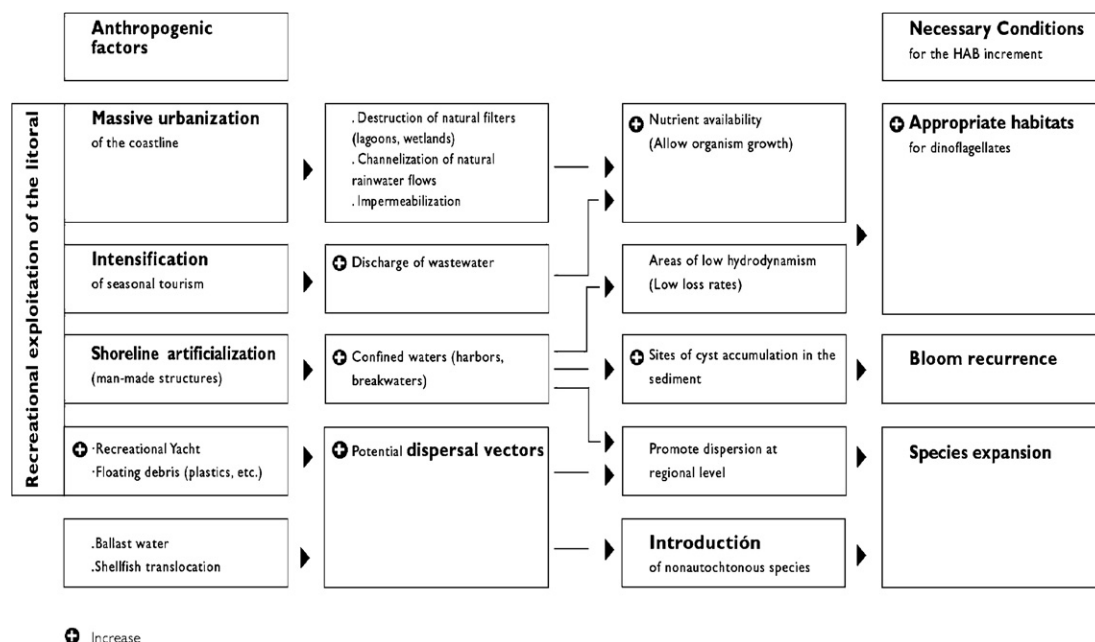


Fig. 2. Scheme of anthropogenic factors related with recreational activities promoting HAB increase (from Action plans and measures for an integrated control of Mediterranean recreational waters in relationship with harmful algae blooms. <http://www.icm.csic.es/bio/projects/wscalvia>).

species of concern (Fig. 2). It is important to point out in the context of human health and HAB events, that in some coastal regions (e.g. the Mediterranean basin) HABs are an ever increasing problem. Before the 1980s, blooms in the Mediterranean were considered rare events. Therefore, we do not have the appropriate societal responses thus, there is neither norms for action, nor strategic plans. In these regions, the local population and visitors may face a health risk that is difficult to measure.

The monitoring of toxin producing species has mainly been associated with shellfish farming. Moreover, the risk of toxin contamination could become even greater in areas not subject to legislation of local/regional aquaculture activities. For example, the CEE legislation regarding HABs deals with areas of shellfish farming activities (91/492/CEE). At present, there is neither legislation nor even monitoring in relationship to HABs in areas free of commercial activities in most of the Nations of the European Union. To reduce impacts in human health and economic activities, the following elements are considered immediately necessary to have: (a) reliable monitoring networks and databases that allow for the analyses of the expansion of these organisms, (b) established channels of exchange of information among scientific and environmental managers, (c) outreach and education programs and easy access for users to monitoring networks results (e.g. Institution's WEB sites) and, (d) implication of the medical sector (the consequences in public health are underestimated, necessity of epidemiological studies).¹

¹ Conclusions of the workshop "Management of recreational waters in relationship with harmful microalgae blooms in the Mediterranean" <http://www.icm.csic.es/bio/projects/wscalvia>.

The sanitary conditions of the near-coastal waters have improved substantially from the 1960s, due largely to the sewage treatment. Toxic event increase would need more complicated measurements but what is certain is that more work must be done to follow the range expansions and human introduction of alien species. In the recent past, even HABs increment was sometimes questioned; because routine monitoring (mainly related to shellfish farming) was not addressed to establish if an increase was actually occurring. The design of monitoring strategies to detect and follow the expansion of harmful species is an urgent task that has to be taken into account in the HABs monitoring programs. Management strategies in regard to ballast waters and introductions are already considered a key element. It is also becoming increasingly common to see notices warning local populations of an occurrence of HABs in some affected areas. This kind of action should be applied to areas where toxic events are, in some sense, new events.

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References

- Alavi, M., Miller, T., Erlandson, K., Schneider, R., Belas, R., 2001. Bacterial community associated with *Pfiesteria*-like dinoflagellate cultures. *Environmental Microbiology* 3, 380–396.

- Anderson, D.M. (Ed.), 1995. ECOHAB. The ecology and oceanography of harmful algal blooms. A national research agenda, vol. Woods Hole, MA.
- Anderson, D.M., Kulis, D.M., Sullivan, J.J., Hall, S., 1990. Toxin composition variations in one isolate of the dinoflagellate *Alexandrium fundyense*. *Toxicon* 28, 885–893.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25, 704–726.
- Arzul, G., Seguel, M., Guzman, L., ErardLeDenn, E., 1999. Comparison of allelopathic properties in three toxic *Alexandrium* species. *Journal of Experimental Marine Biology and Ecology* 232, 285–295.
- Basterretxea, G., Garcés, E., Jordi, A., Masó, M., Tintoré, J., 2004. Breeze as *Alexandrium taylori* bloom favoring mechanism in a Mediterranean pocket beach. *Estuarine, Coastal and Shelf Science* 32, 1–12.
- Bechemin, C., Grzebyk, D., Hachame, F., Hummert, C., Maestrini, S.Y., 1999. Effect of different nitrogen/phosphorus nutrient ratios on the toxin content in *Alexandrium minutum*. *Aquatic Microbial Ecology* 20, 157–165.
- Berg, G.M., Repeta, D.J., Laroche, J., 2002. Dissolved organic nitrogen hydrolysis rates in axenic cultures of *Aureococcus anophagefferens* (Pelagophyceae): comparison with heterotrophic bacteria. *Applied and Environmental Microbiology* 68, 401–404.
- Berg, G.M., Balode, M., Purina, I., Bekere, S., Béchemin, C., Maestrini, S.Y., 2003. Plankton community composition in relation to availability and uptake of oxidized and reduced nitrogen. *Aquatic Microbial Ecology* 30, 263–274.
- Biegala, I.C., Kennaway, G., Alverca, E., Lennon, J.F., Vaultot, D., Simon, N., 2002. Identification of bacteria associated with dinoflagellates (Dinophyceae) *Alexandrium* spp. using tyramide signal amplification-fluorescent in situ hybridization and confocal microscopy. *Journal of Phycology* 38, 404–411.
- Blackburn, S.I., Bolch, C.J.S., Haskard, K.A., Hallegraeff, G.M., 2001. Reproductive compatibility among four global populations of the toxic dinoflagellate *Gymnodinium catenatum* (Dinophyceae). *Phycologia* 40, 78–87.
- Blanco, J., Moróño, A., Pazos, Y., Maneiro, J., Mariño, J., 1998. Trends and variations of the abundance of a PSP and DSP producing species in the Galician Rias: environmental and biological influences. In: Reguera, B., Blanco, J., Fernandez, M.L., Wyatt, T. (Eds.), *Harmful Algae*. Xunta de Galicia & IOC of UNESCO, Santiago de Compostela, Spain, pp. 204–207.
- Carlsson, P., Edling, H., Bechemin, C., 1998. Interactions between a marine dinoflagellate (*Alexandrium catenella*) and a bacterial community utilizing riverine humic substances. *Aquatic Microbial Ecology* 16, 65–80.
- Cembella, A.D., 1998. Ecophysiology and metabolism of paralytic shellfish toxins in marine microalgae. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*, vol. NATO ASI Series; vol. G 41: Ecol. Sciences. Springer-Verlag, Berlin, pp. 381–403.
- Cembella, A.D., Destombe, C., Turgeon, J., 1990. Toxin composition of alternative life history stages of *Alexandrium excavatum* as determined by high-performance liquid chromatography. In: Granéli, E., Sandström, B., Edler, L., Anderson, D.M. (Eds.), *Toxic Marine Phytoplankton*. Elsevier Science Publishing Co., New York, pp. 333–338.
- Chorus, I., Falconer, I.R., Salas, H.J., Bartram, J., 2000. Health risks caused by freshwater cyanobacteria in recreational waters. *Journal of Toxicology and Environmental Health Part B Critical Reviews* 3, 323–347.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210, 223–253.
- Dale, B., 2000. Dinoflagellate cysts as indicators of cultural eutrophication and industrial pollution in coastal sediments. In: Martin, R.E. (Ed.), *Environmental Micropaleontology*. Plenum Press Div Plenum Publishing Corp, 233 Spring St/New York/NY 10013/USA, pp. 305–321.
- Dale, B., 2001. The sedimentary record of dinoflagellate cysts: looking back into the future of phytoplankton blooms. *Scientia Marina* 65, 257–272.
- Dale, B., Madsen, A., Nordberg, K., Thorsen, T.A., 1993. Evidence for prehistoric and historic ‘blooms’ of the toxic dinoflagellate *Gymnodinium catenatum* in the Kattegat-Skagerrak region of Scandinavia. In: Smayda, T.J., Shimizu, Y. (Eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier, Amsterdam, pp. 47–52.
- Dale, B., Thorsen, T.A., Fjellsa, A., 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuarine Coastal and Shelf Science* 48, 371–382.
- DeYoe, H.R., 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. *Journal of Phycology* 30, 800–806.
- Dickman, M., Zhang, F.Z., 1999. Mid-ocean exchange of container vessel ballast water. 2: Effects of vessel type in the transport of diatoms and dinoflagellates from Manzanillo, Mexico, to Hong Kong, China. *Marine Ecology Progress Series* 176, 253–262.
- Falconer, I. (Ed.), 1993. *Algal Toxins in Seafood and Drinking Water*. Academic Press, London.
- Flynn, K., Franco, J.M., Fernandez, P., Reguera, B., Zapata, M., Wood, G., Flynn, K.J., 1994. Changes in toxin content, biomass and pigments of the dinoflagellate *Alexandrium minutum* during nitrogen refeeding and growth into nitrogen or phosphorus stress. *Marine Ecology Progress Series* 111, 99–109.
- Fraga, S., Bakun, A., 1993. Global climate change and harmful algal blooms: the example of *Gymnodinium catenatum* on the Galician coast. In: Smayda, T.J., Shimizu, Y. (Eds.), *Toxic Phytoplankton Blooms in the Sea*, vol. 3. Elsevier, Amsterdam, pp. 59–66.
- Garcés, E., Masó, M., Camp, J., 1999. A recurrent and localized dinoflagellate bloom in Mediterranean beach. *Journal of Plankton Research* 21, 2373–2391.
- Garcés, E., Masó, M., Vila, M., Camp, J., 2000. HABs events in the Mediterranean Sea: Are they increasing? A case study the last decade in the NW Mediterranean and the genus *Alexandrium*. *Harmful Algal News* 20, 1–11.
- Garcés, E., Zingone, A., Montresor, M., Reguera, B., Dale, B. (Eds.), 2002. LIFEHAB: life histories of microalgal species causing harmful blooms. Office for the Official Publications of the European Communities, Luxembourg.
- Garcés, E., Bravo, I., Vila, M., Figueroa, R.I., Maso, M., Sampedro, N., 2004. Relationship between vegetative cells and cyst production during *Alexandrium minutum* bloom in Arenys de mar harbour (NW Mediterranean). *Journal of Plankton Research* 26, 1–9.
- Glibert, P.M., Magnien, R., Lomas, M.W., Alexander, J., Fan, C.K., Haramoto, E., Trice, M., Kana, T.M., 2001. Harmful algal blooms in the Chesapeake and coastal bays of Maryland, USA: comparison of 1997, 1998, and 1999 events. *Estuaries* 24, 875–883.
- Granéli, E., Carlsson, P., 1998. The ecological significance of phagotrophy in photosynthetic flagellates. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. Springer-Verlag, Berlin, pp. 539–557.
- Granéli, E., Lipiatou, E., (Eds.), 2002. EUROHAB Science Initiative Part B: Research and Infrastructural Need. National European and International Programmes. Office for Official Publications of the European Communities, Luxembourg.
- Granéli, E., Codd, G.A., Dale, B., Lipiatou, E., Maestrini, S.Y., Rosenthal, H., (Eds.), 1999. EUROHAB Science initiative. Harmful algal blooms in European marine and brackish waters. Office for Official Publications of the European Communities, Luxembourg.
- Guisande, C., Frangopulos, M., Maneiro, I., Vergara, A.R., Riveiro, I., 2002. Ecological advantages of toxin production by the dinoflagellate *Alexandrium minutum* under phosphorus limitation. *Marine Ecology Progress Series* 225, 169–176.
- Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32, 79–99.
- Hallegraeff, G.M., 1998. Transport of toxic dinoflagellates via ships’ ballast water: bioeconomic risk assessment and efficacy of possible

- ballast water management strategies. Marine Ecology Progress Series 168, 297–309.
- Hallegraeff, G.M., Anderson, D.M., Cembella, A.D. (Eds.), 1995. Manual on Harmful Marine Microalgae, vol. 33. UNESCO.
- Hallegraeff, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), 2000. Harmful algal blooms 2002. In: Proceedings of the Ninth International Conference on Harmful Algal Blooms, Hobart, Tasmania (Australia).
- Hallegraeff, G.M., Anderson, D.M., Cembella, A.D. (Eds.), 2003. Manual on Harmful Marine Microalgae, vol. 33. UNESCO.
- Hoagland, P., Anderson, D.M., Kaoru, Y., White, A.W., 2002. The economic effects of harmful algal blooms in the United States: estimates, assessment issues, and information needs. Estuaries 25, 819–837.
- Hodgkiss, I.J., Ho, K.C., 1997. Are changes in N:P ratios in coastal waters the key to increased red tide blooms? Hydrobiologia 352, 141–147.
- Hold, G.L., Smith, E.A., Rappe, M.S., Maas, E.W., Moore, E.R.B., Stroempl, C., Stephen, J.R., Prosser, J.I., Birkbeck, T.H., Gallacher, S., 2001. Characterisation of bacterial communities associated with toxic and non-toxic dinoflagellates: *Alexandrium* spp. and *Scripsiella trochoidea*. FEMS Microbiology Ecology 37, 161–173.
- Horner, R.A., Garrison, D.L., Plumley, F.G., 1997. Harmful algal blooms and red tide problems on the US west coast. Limnology and Oceanography 42, 1076–1088.
- John, E.H., Flynn, K.J., 2000. Growth dynamics and toxicity of *Alexandrium fundyense* (Dinophyceae): the effect of changing N:P supply ratios on internal toxin and nutrient levels. European Journal of Phycology 35, 11–23.
- John, E.H., Flynn, K.J., 2002. Modelling changes in paralytic shellfish toxin content of dinoflagellates in response to nitrogen and phosphorus supply. Marine Ecology Progress Series 225, 147–160.
- Justic, D., Rabalais, N.N., Turner, R.E., Dortch, Q., 1995. Changes in nutrient structure of river-dominated coastal waters: stoichiometric nutrient balance and its consequences. Estuarine, Coastal and Shelf Science 40, 339–356.
- Landsberg, J.H., 2002. The effects of harmful algal blooms on aquatic organisms. Reviews in Fisheries Science 10, 113–390.
- Lilly, E., Kulis, D., Gentien, P., Anderson, D., 2002. Paralytic shellfish poisoning toxins in France linked to a human-introduced strain of *Alexandrium catenella* from the western Pacific: evidence from DNA and toxin analysis. Journal of Plankton Research 24, 443–452.
- Liu, G., Janowitz, G.S., Kamykowski, D., 2002. Influence of current shear on *Gymnodinium breve* (Dinophyceae) population dynamics: a numerical study. Marine Ecology Progress Series 231, 47–66.
- Lomas, M.W., Glibert, P.M., 1999. Interactions between NH_4^+ and NO_3^- uptake and assimilation: comparison of diatoms and dinoflagellates at several growth temperatures. Marine Biology 133, 541–551.
- Lugliè, A., Giacobbe, M., Sannio, A., Fiocca, F., Sechi, N., 2003. First record of the dinoflagellate *Alexandrium catenella* (Whedon & Kofoid) Balech (Dinophyta), a potential producer of paralytic shellfish poisoning, in Italian waters (Sardinia, Tyrrhenian Sea). In: X Congresso di OPTIMA (Organization for the Phyto-Taxonomic Investigation of the Mediterranean Area), Palermo (Sicily).
- Marangoni, C., Pienaar, R.N., Sym, S.D., 2001. Possible introduction of alien phytoplankton via shipping ballast water: a South African perspective. South African Journal of Botany 67, 465–474.
- Masó, M., Garcés, E., Pages, F., Camp, J., 2003. Drifting plastic debris as a potential vector for dispersing Harmful Algal Bloom (HAB) species. Scientia Marina 67, 107–111.
- Nixon, S.W., 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia 41, 199–219.
- Olivos, A., 2000. Nutrientes inorgánicos disueltos en aguas litorales próximas del Mar Catalán. PhD Marine Biology Department. Barcelona, Universitat de Barcelona, 195.
- Parsons, M.L., Dortch, Q., Turner, R.E., 2002. Sedimentological evidence of an increase in *Pseudonitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication. Limnology and Oceanography 47, 551–558.
- Penna, A., Garcés, E., Vila, M., Giacobbe, M.G., Fraga, S., Lugliè, A., Bravo, I., Bertozzini, E., Vernesi, C., 2005. *Alexandrium catenella* (Dinophyceae), a toxic ribotype expanding in the NW Mediterranean Sea. Marine Biology 148, 13–23.
- Pitcher, G.C., Calder, D., 2000. Harmful algal blooms of the southern Benguela Current: a review and appraisal of monitoring from 1989 to 1997. South African Journal of Marine Science 22, 255–271.
- Pitois, S., Jackson, M.H., Wood, B.J.B., 2000. Problems associated with the presence of cyanobacteria in recreational and drinking waters. International Journal of Environmental Health Research 10, 203–218.
- Prakash, A., Medcot, J.C., Tennant, A.D., 1971. Paralytic shellfish poisoning in eastern Canada. Bulletin of Fisheries Research Board of Canada 177, 1–87.
- Prego, R., 1992. Flows and budgets of nutrient salts and organic carbon in relation to a red tide in the Ria of Vigo (NW Spain). Marine Ecology Progress Series 79, 289–302.
- Rabalais, N.N., Nixon, S.W., 2002. Preface: nutrient over-enrichment of the coastal zone. Estuaries 25, 639.
- Rao, P.V.L., Gupta, N., Bhaskar, A.S.B., Jayaraj, R., 2002. Toxins and bioactive compounds from cyanobacteria and their implications on human health. Journal of Environmental Biology 23, 215–224.
- Reguera, B., Bravo, I., Mariño, J., Campos, M.J., Fraga, S., Carbonell, A., 1993. Trends in the occurrence of *Dinophysis* spp in Galician coastal waters. In: Samyda, T.J., Shimizu, Y. (Eds.), Toxic Phytoplankton Blooms in the Sea. Elsevier, Amsterdam, pp. 559–564.
- Reguera, B., Blanco, J., Fernandez, M.L., Wyatt, T. (Eds.), 1998. In: VIII International Conference on Harmful algae, vol. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Vigo.
- Rothschild, B.J., Ault, J.S., Goulletquer, P., Heral, M., 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Marine Ecology Progress Series 111, 29–39.
- Scholín, C.A., 1996. Morphological, genetic and biogeographic relationships of toxic dinoflagellates *Alexandrium tamarense*, *A. catenella* and *A. fundyense*. In: Anderson, D.A., Cembella, A.D., Hallegraeff, G.M. (Eds.), The Physiological Ecology of Harmful Algal Blooms. Springer, Bermuda Biological Station, pp. 13–28.
- Schöllhorn, E., Granéli, E., 1996. Influence of different nitrogen to silica ratios and artificial mixing on the structure of a summer phytoplankton community from the Swedish west coast (Gullmar fjord). Journal of Sea Research 35, 159–167.
- Smayda, T., 1997. What is a bloom? A commentary. Limnology and Oceanography 42, 1132–1136.
- Smayda, T.J., Reynolds, C.S., 2003. Strategies of marine dinoflagellate survival and some rules of assembly. Journal of Sea Research 49, 95–106.
- Sommer, U., 1994. Are marine diatoms favoured by high Si N ratios? Marine Ecology Progress Series 115, 309–315.
- Teegarden, G.J., 1999. Copepod grazing selection and particle discrimination on the basis of PSP toxin content. Marine Ecology–Progress Series 181, 163–176.
- Teegarden, G.J., Cembella, A.D., 1996. Grazing of toxic dinoflagellates, *Alexandrium* spp; by adult copepods of coastal Maine: Implications for the fate of paralytic shellfish toxins in marine food webs. J. Exp. Mar. Biol. Ecol. 196, 145–176.
- Turner, J.T., Tester, P.A., 1997. Toxic marine phytoplankton, zooplankton grazers, and pelagic food webs. Limnology and Oceanography 42, 1203–1214.
- Tobe, K., Ferguson, C., Kelly, M., Gallacher, S., Medlin, L.K., 2001. Seasonal occurrence at a Scottish PSP monitoring site of purportedly toxic bacteria originally isolated from the toxic dinoflagellate genus *Alexandrium*. European Journal of Phycology 36, 243–256.
- Uribe, P., Espejo, R.T., 2003. Effect of associated bacteria on the growth and toxicity of *Alexandrium catenella*. Applied and Environmental Microbiology 69, 659–662.
- Usup, G., Azanza, R.V., 1998. Physiology and bloom dynamics of the tropical dinoflagellate *Pseudonitzschia bahamense*. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), Physiological Ecology

- of Harmful Algal Blooms. Springer-Verlag, Berlin, Heidelberg, pp. 81–94.
- Vasquez, M., Gruttner, C., Gallacher, S., Moore, E.R.B., 2001. Detection and characterization of toxigenic bacteria associated with *Alexandrium catenella* and *Aulacomya* after contaminated with PSP. *Journal of Shellfish Research* 20, 1245–1249.
- Vila, M., Masó, M., 2005. Phytoplankton functional groups and harmful algal species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina* 69, 31–45.
- Vila, M., Camp, J., Garcés, E., Masó, M., Delgado, M., 2001. High resolution spatio-temporal detection of potentially harmful dinoflagellates in confined waters of the NW Mediterranean. *Journal of Plankton Research* 23, 497–514.
- Vila, M., Giacobbe, M.G., Masó, M., Gangemi, E., Penna, A., Sampedro, N., Azzaro, F., Camp, J., Galluzzi, L., 2005. A comparative study on recurrent blooms of *Alexandrium minutum* in two Mediterranean coastal areas. *Harmful Algae* 4, 673–695.
- Wyatt, T., Jenkinson, I.R., 1997. Notes on *Alexandrium* population dynamics. *Journal of Plankton Research* 19, 551–575.
- Yasumoto, T., Oshima, Y., Fukuyo, Y., (Eds.), 1995. Harmful and toxic algal blooms. In: *Proceedings of the Seventh International Conference on Toxic Phytoplankton*, vol. IOC (UNESCO), Sendai, Japan.
- Zingone, A., Enevoldsen, H.O., 2000. The diversity of harmful algal blooms: a challenge for science and management. *Ocean and Coastal Management* 43, 725–748.