

Review

A Review on Toxic and Harmful Algae in Greek Coastal Waters (E. Mediterranean Sea)

Lydia Ignatiades ^{1,*} and Olympia Gotsis-Skretas ²

¹ National Center of Scientific Research “Demokritos”, Institute of Biology, Aghia Paraskevi, 15310 Athens, Greece

² Hellenic Center for Marine Research, Institute of Oceanography, 19013 Anavyssos, Greece; E-Mail: ogotsis@ath.hcmr.gr

* Author to whom correspondence should be addressed; E-Mail: igna@bio.demokritos.gr; Tel.: +30 210 6503629; Fax: +30 210 6511767.

Received: 22 March 2010; in revised form: 23 April 2010 / Accepted: 5 May 2010 /

Published: 11 May 2010

Abstract: The Greek coastal waters are subjected to harmful algal bloom (HAB) phenomena due to the occurrence of species characterized as toxic (TX), potentially toxic (PT), and non-toxic, high biomass (HB) producers causing harm at multiple levels. The total number of (TX), (PT) and (HB) algae reported in this work are 61, but only 16 species have been associated with the occurrence of important HABs causing damage in the marine biota and the water quality. These phenomena are sporadic in time, space and recurrence of the causative species, and are related to the anthropogenically-induced eutrophication conditions prevailing in the investigated areas.

Keywords: harmful algae; Aegean Sea; Ionian Sea

1. Introduction

The coastline (18,000 km) of the Greek mainland is located in the Eastern Mediterranean Sea, it is surrounded by the Aegean, Ionian and Cretan Seas and its morphological regime shows a variety of gulfs and semi-enclosed gulfs. All these basins are eutrophic [1] since they receive the waters and fertile material from large rivers and/or smaller water outfalls derived from agricultural and industrial activities.

Eutrophication triggers various physical and chemical changes in the marine environment and exerts a pressure on algal populations, allowing the intensive growth of certain harmful-toxin producing species or nuisance blooms that may create problems in the structure of the ecosystem and public health. These blooms are collectively called Harmful Algal Blooms (HABs). The greatest number of toxic species is found among dinoflagellates, but evidence has been provided for several species of other taxa (diatoms, flagellates, cyanobacteria, prymnesiophytes, raphidophytes) suggesting that they belong in this category [2–4].

Concern about harmful algae in Greek coastal waters has been growing since the late 1970s, when the first symptoms of “fish kills” due to the increased anthropogenic effects led to the fact that HABs—often quoted as the phenomenon of red tides—acquired the attention of scientists and the public. Since then, routine records of phytoplankton samples from almost all major gulfs along the Greek coastline during the last 30 years have revealed the presence of toxic and potentially toxic algae (those producing and/or potentially producing toxins) and non-toxic, high biomass producing species (non-toxic producers, but causing harmful blooms at multiple levels), although their destructive effects were occasional.

The European Commission has funded a number of projects such as EUROHAB (European Initiative on Harmful Algal Blooms) to generate the required research to better manage the effects of toxic/harmful marine microalgae that have caused problems in European marine waters [5]. This paper is the first comprehensive presentation of these species in the Eastern Mediterranean Sea, based on a synopsis of all published information for the period 1977–2009.

2. Sampling Areas and Data Collection

The investigated area (Figure 1) is located in the Eastern Mediterranean and presents the sampling regions along the coastlines of the North Aegean Sea (I), the Western Aegean Sea (II), the Southern Aegean Sea (III), the Ionian Sea (IV) and the Mytilini Island, Eastern Aegean Sea (V). These sites include nine major Gulfs (a: Thermaikos; b: Kavalas; c: Pagassitikos; d: Malliakos; e: Evoikos; f: Saronikos; g: Messiniakos; h: Amvrakikos and i: Kalloni), as well as harbors, docks and marinas.

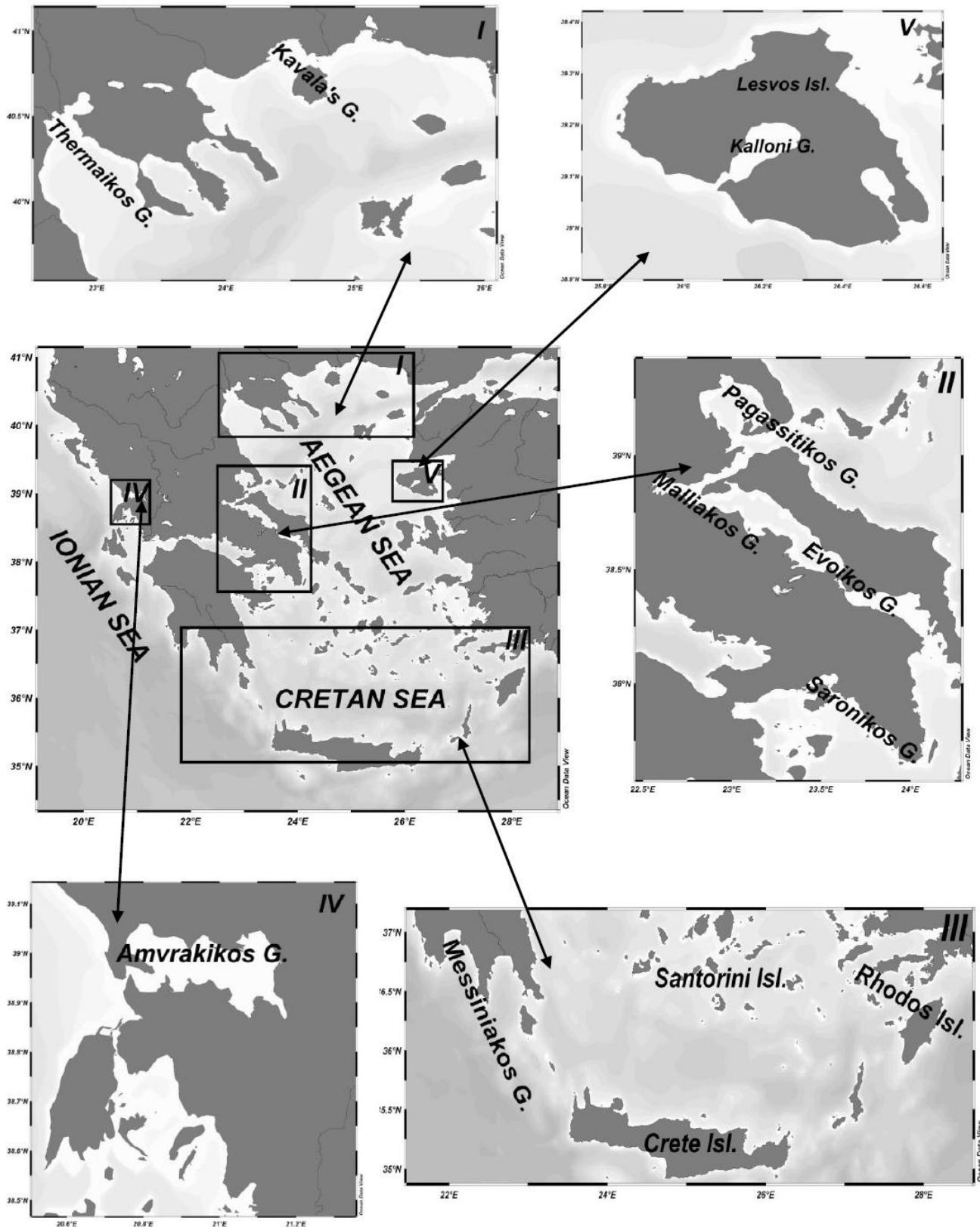
The collection of data covers the period 1977–2008. The methodology of sampling, preservation of samples, quantitative-qualitative analysis and the toxicity detection/evaluation of each one of the phytoplanktonic species under investigation are given in the literature cited in Table 1. The characterization of species as toxic (TX), potentially toxic (PT) and high biomass (HB) harmful blooms in this work was based on publications providing comprehensive descriptions of the current status of knowledge in the field as well as the IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae [4]. The specifications of toxins were also determined from the literature.

3. Results and Discussion

A traditional system has been adopted for the eukaryotic species taxonomy [6]. Cyanobacteria are prokaryotes that may create problems producing diverse neurotoxins hazardous for human health; they have been classified among the HAB species [7] and are therefore included here. The majority of species are autotrophic (photosynthetic algae), but certain species (mostly dinoflagellates) are heterotrophic (feeding on particulate or dissolved organic matter) and their mode of nutrition

(phagotrophy, osmotrophy) has been also taken into consideration [8]. It is interesting to notice that species of the same family differ in toxic properties.

Figure 1. Location of the investigated Gulfs on the map of Greece.



3.1. Taxonomy and toxic properties of detected HAB species in Greek coastal waters

3.1.1. Class Bacillariophyceae (Diatoms)

3.1.1.1. Order Thalassiophysales

Family Catenulaceae. A strain of the species *Amphora coffeaeformis* (from Canada) was found to produce Domoic acid. Other strains examined so far were non-toxic. However, the precise identification of the Canadian strain has been questioned [4,9]. It is also a mucilage producer [10].

3.1.1.2. Order Bacillariales

Family Bacillariaceae. The five species of this family are Domoic acid producers: *Pseudo-nitzschia delicatissima* [11], *Pseudo-nitzschia pseudodelicatissima* [12], *Pseudo-nitzschia seriata* [13], *Pseudo-nitzschia pungens* [14] and *Pseudo-nitzschia calliantha* [15].

3.1.2. Class Dinophyceae (Dinoflagellates)

There are five important orders of Dinophyceae identified and presented in this work: Peridiniales, Prorocentrales, Dinophysiales, Gymnodiniales, and Noctilucales.

3.1.2.1. Order Peridiniales

Family Goniodomataceae. This family comprises six species of the genus *Alexandrium* and one of the genus *Gambierdiscus* that are among the well known harmful algae. *A. catenella* is a producer of c1-c4 toxins, Saxitoxins and Gonyautoxins [16,17]. *A. tamarense*, *A. minutum* and *A. taylori* produce Gonyautoxins [18,19]. *A. balechii* and *A. insuetum* have been characterized in the literature as species of unknown toxicity, but they have been associated with harmful algal blooms [14,20] and *Gambierdiscus* sp. is known to be toxic producing Ciguatoxin and Maitotoxine [21].

Family Ostreophidaceae. *Coolia monotis* produces Cooliatoxin, an analog of Yessotoxin [22].

Family Heterocapsaceae. *Heterocapsa circularisquama* produces the photosensitizing hemolytic toxins H2-a, H3-a [23].

Family Ostreopsidaceae. The two toxic species of the genus *Ostreopsis* are *O. ovata* producing putative Palytoxin and Ovatoxin compounds and *O. siamensis*, putative Palytoxin [24–26].

Family Gonyaulacaceae. *Protoceratium reticulatum* is a species known as a Yessotoxin toxin producer [27]. *Scrippsiella trochoidea* is a bloom forming species of unknown toxicity [28].

Family Protoperidiniaceae. Two species of this family have been recorded, *Diplopsalis lenticula*, a bloom forming species [29] of unknown toxicity and *Protoperidinium crassipes*, producing Azaspiracid toxins [30].

Family Peridiniaceae. *Peridinium quinquecorne* is a bloom forming species [31].

Family Ceratiaceae. The four species of the genus *Ceratium*, *C. furca*, *C. fusus*, *C. lineatum*, and *C. tripos* occasionally form non-toxic blooms [32] that may cause discoloration of the water and undesirable aesthetic symptoms, but without toxic signs [33–36].

3.1.2.2. Order Prorocentrales

Family Prorocentraceae. All species of this family are in the genus *Prorocentrum*. The four toxic species are: *P. borbonicum*, producing Borbotoxins [37], *P. levis* and *P. lima*, producing Okadaic acid and Dinophysistoxins [38,39], and the Okadaic acid producer *P. rhathymum* [40]. Species associated with high biomass harmful blooms are: *P. arcuatum* [41], *P. obtusidens* [43], *P. redfeldii* [43], *P. micans* [44], *P. minimum* [45], *P. dentatum* [46] and *P. emarginatum* [47].

3.1.2.3. Order Dinophysiales

Family Dinophysiaceae. All species of this family representing the genus *Dinophysis* are toxic. *D. sacculus* produces Okadaic acid [48]; *D. tripos* and *D. rotundata*, Dynophysistoxin [48,49]; *D. acuminata* and *D. acuta*, Okadaic acid/Dynophysistoxin [48]; *D. fortii*, Okadaic acid/Dynophysistoxin/Palytoxin [48]; *D. caudata*, Okadaic acid/Palytoxin [48].

3.1.2.4. Order Gymnodiniales

Family Gymnodiniaceae. All species of this family are toxic except *Gyrodinium impudicum*, a non-toxic, bloom forming species [50]. *Amphidinium carterae*, is a producer of the Maitotoxin [51] and *G. aureolum* produces 1-acyl-3-digalactosylglycerol and octadecapentaenoic acid [52]. One of the two toxic species of the genus *Karenia*, *K. brevis* produces Polyether Neurotoxins called Brevetoxins [53] and *K. mikimotoi* Gymnocin-A [54]. The species *Gymnodinium catenatum* produces Gonyautoxins and Saxitoxin [55], whereas *Karlodinium veneficum*, Karlotoxins [56].

3.1.2.5. Order Noctilucales

Family Noctilucaceae. *Noctiluca scintillans* is the single species of this family. It is a non-toxic bloom forming species [57] responsible for harmful outbursts (water discoloration, anoxic events).

3.1.3. Class Prymnesiophyceae (Haptophytes)

3.1.3.1. Order Phaeocystales

Family Phaeocystaceae. *Phaeocystis puchetii*: toxic species producing polyunsaturated aldehyde [58].

3.1.3.2. Order Prymnesiales

Family Prymnesiaceae. *Prymnesium parvum*: toxic species producing Prymnesins [59].

3.1.4. Class Rhaphidophyceae (Chloromonadophytes)

Order Chattonellales

Family Chattonellaceae. Both species of this family *Chattonella globosa* and *C. verucolosa* are unknown toxicity high biomass forming species [60].

3.1.5. Class Cyanophyceae (Cyanobacteria)

3.1.5.1. Order Chroococales

Family Chroococaceae. The species *Microcystis aeruginosa* produces the toxin Microcystin-LR [61], and the species *Chroococcus gelatinosus* and *Synechocystis sellensis* are bloom forming species [62].

3.1.5.2. Order Nostocalles

Family Oscillatoriaceae. *Lyngbya agardhii* is a high biomass forming species [62] and *Trichodesmium erythraeum* produces Saxitoxin [63].

Table 1 presents alphabetically the list of species, their toxic properties and the area of their occurrence given in the literature.

Table 1. Toxic (TX), potentially toxic (PT) and high biomass (HB) nuisance species in Greek coastal waters. Shaded rows demarcate species that have caused toxic events.

Species	Toxins	Category	Area	Source
Diatoms				
<i>Amphora coffeaeformis</i> (C. Agardh) Kützing	Domoic acid	(PT)	V	[29]
<i>Pseudo-nitzschia calliantha</i> Lundholm, Moestrup et Hasle	Domoic acid	(PT)	V	[29]
<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden	Domoic acid	(PT)	I, II, III	[73,77]
<i>Pseudo-nitzschia pseudodelicatissima</i> (Hasle) Hasle	Domoic acid	(PT)	I, II, IV, V	[43,78,79]
<i>Pseudo-nitzschia pungens</i> (Grunow ex Cleve) Hasle	Domoic acid	(PT)	I, II, III, IV, V	[29,43,73]
<i>Pseudo-nitzschia seriata</i> (Cleve) H. Peragallo	Domoic acid	(PT)	I, II, III, V	[78,80,81]
Dinoflagellates				
<i>Alexandrium balechii</i> (Steidinger) Balech	Unknown toxicity	(PT)	II	[82]
<i>Alexandrium catenella</i> (Whedon et Kofoid) Balech	Saxitoxin, Gonyautoxin, c1-c4 toxins	(PT)	I, II	[82]
<i>Alexandrium insuetum</i> Balech	Unknown toxicity	(HB)	IV, V	[29,43]
<i>Alexandrium minutum</i> Halim	Gonyautoxins (1–4)	(PT)	I, II, IV, V	[43,64,83]
<i>Alexandrium tamarensense</i> (Lebour) Balech	Gonyautoxins (1–4)	(PT)	I, II	[82,84]

Table 1. Cont.

<i>Alexandrium taylori</i> Balech	Gonyautoxin-4, Gonyautoxin-6	(PT)	I, II	[82]
<i>Amphidinium carterae</i> Hulburt	Maitotoxin	(PT)	IV, V	[29,85]
<i>Ceratium furca</i> (Ehrenberg) Claparède et Lachmann	Unknown toxicity	(PT)	I, II, III, IV, V	[29,73,78,80]
<i>Ceratium fusus</i> (Ehrenberg) Dujardin	Unknown toxicity	(PT)	I, II, III, IV, V	[29,73,78,80]
<i>Ceratium lineatum</i> (Ehrenberg) Cleve	Unknown toxicity	(PT)	IV, V	[29,79]
<i>Ceratium tripos</i> (Müller) Nitzsch	Unknown toxicity	(PT)	I, II, III, IV, V	[29,73,78–80]
<i>Coolia monotis</i> Meunier	Cooliatoxin	(PT)	I, III, IV	[79,86,87]
<i>Dinophysis acuminata</i> Claparède et Lachmann	Okadaic acid, Dinophysistoxin-2	(TX)	I, II, IV	[42,43,71,85]
<i>Dinophysis acuta</i> Ehrenberg	Okadaic acid, Dinophysistoxin-2	(PT)	I	[88]
<i>Dinophysis caudata</i> Saville-Kent	Okadaic acid, Palytoxin	(PT)	I, II, IV, V	[29,42,43]
<i>Dinophysis fortii</i> Pavillard	Okadaic acid, Dinophysistoxin-1, Palytoxin	(PT)	I	[42]
<i>Dinophysis rotundata</i> Claparède et Lachmann	Dinophysistoxin-1	(PT)	I, IV	[42,79]
<i>Dinophysis sacculus</i> Stein	Okadaic acid	(PT)	I, II, III, IV, V	[29,43,73]
<i>Dinophysis tripos</i> Gourret	Dinophysistoxin-1	(PT)	I, II	[82,88]
<i>Diplopsalis lenticula</i> Bergh	Unknown toxicity	(PT)	I, V	[29,88]
<i>Gambierdiscus</i> sp.	Ciguatoxin, Maitotoxine	(PT)	III	[87]
<i>Gymnodinium catenatum</i> Graham	Gonyautoxins (1–4), Saxitoxin	(PT)	I	[84,88]
<i>Gyrodinium aureolum</i> Hulburt	1-acyl-3- digalactosyl glycerol, Octadeca- pentaenoic acid	(TX)	I, II	[46,88]
<i>Gyrodinium impudicum</i> Fraga et Bravo	Unknown toxicity	(PT)	I, IV	[79,84]
<i>Heterocapsa circularisquama</i> Horiguchi	hemolytic toxin2-a, hemolytic toxin 3-a	(PT)	V	[29]
<i>Karenia brevis</i> (<i>Gymnodinium breve</i>) (Davis) G. Hansen et Moestrup	Brevetoxin-1, Brevetoxin-2, Brevetoxin-3	(TX)	I, II, III	[46,70,73,78]
<i>Karenia mikimotoi</i> (Miyake et Kominami ex Oda) Hansen et Moestrup	Gymnocin-A	(PT)	IV	[79]
<i>Karlodinium veneficum</i> (Ballantine) J. Larsen	Karlotoxin-1, Karlotoxin-2	(PT)	V	[29]
<i>Noctiluca scintillans</i> (Macartney) Kofoid et Swezy	Unknown toxicity	(HB)	I	[43]
<i>Ostreopsis ovata</i> Fukuyo	Putative Palytoxin, Ovatoxin-a	(PT)	I, III, V	[29,86,87]

Table 1. Cont.

<i>Ostreopsis siamensis</i> Schmidt	Putative Palytoxin	(PT)	I, III	[86,87]
<i>Peridinium quinquecorne</i> Ab é	Unknown toxicity	(PT)	V	[29]
<i>Prorocentrum arcuatum</i> Issel	Unknown toxicity	(PT)	V	[29]
<i>Prorocentrum borbonicum</i> Ten-Hage, Turquet, Quod, Puiseux-Dao et Cout é	Borbotoxins	(PT)	I, III	[87,89]
<i>Prorocentrum dentatum</i> Stein	Unknown toxicity	(HB)	I, II	[46]
<i>Prorocentrum emarginatum</i> Fukuyo	Unknown toxicity	(PT)	I, III, IV	[79,87,89]
<i>Prorocentrum levis</i> M.A. Faust, Kibler, Vandersea, P.A. Tester & Litaker	Okadaic acid, Dinophysistoxin-2	(PT)	I	[89]
<i>Prorocentrum lima</i> (Ehrenberg) Stein	Okadaic acid, Dinophysistoxin-1, Dinophysistoxin-2	(PT)	I, II, III, V	[29,73,87,89]
<i>Prorocentrum micans</i> Ehrenberg	Putative Palytoxin, Ovatoxin-a	(PT)	I, II, III, IV	[73,77–79]
<i>Prorocentrum minimum</i> (Pavillard) Schiller	Unknown toxicity	(HB)	I, II, IV, V	[29,43,46]
<i>Prorocentrum obtusidens</i> Schiller	Unknown toxicity	(HB)	I	[42,43]
<i>Prorocentrum redfeldii</i> Bursa	Unknown toxicity	(HB)	I, IV	[43,79]
<i>Prorocentrum rhathymum</i> Loeblich III, Sherley et Schmidt	Okadaic acid	(PT)	I, III, IV	[85,87,89]
<i>Protoceratium reticulatum</i> (Clapar ède et Lachmann) B ütschli	Yessotoxin	(PT)	I	[84]
<i>Protoperidinium crassipes</i> (Kofoid) Balech	Azaspiracid toxin-1 Azaspiracid toxin-2 Azaspiracid toxin-3	(PT)	V	[29]
<i>Scrippsiella trochoidea</i> (Stein) Loeblich	Unknown toxicity	(HB)	I, II, III, IV, V	[29,46,73,78,79]
Prymnesiophytes				
<i>Phaeocystis pouchetii</i> (M.P. Hariot) G. Lagerheim	Polyunsaturated aldehydes	(HB)	I, II, III	[46,62,73]
<i>Prymnesium parvum</i> N. Carter	Prymnesin-1, Prymnesin-2	(PT)	I, IV	[85,88]
Rhaphidophytes				
<i>Chattonella globosa</i> Y. Hara et Chihara	Unknown toxicity	(HB)	I, IV	[42,43]
<i>Chattonella verucolosa</i> Y. Hara et Chihara	Unknown toxicity	(HB)	I, IV	[42,43]
Cyanobacteria				
<i>Microcystis aeruginosa</i> (Kützing) Kützing	Microcystin-LR	(TX)	II	[62]
<i>Lyngbya agardhii</i> P.L.Crouan & H.M.Crouan ex Gomont	Unknown toxicity	(HB)	II	[62]
<i>Chroococcus gelatinosus</i> Geitler	Unknown toxicity	(HB)	II	[62]
<i>Synechocystis sellensis</i> Skuja	Unknown toxicity	(HB)	II	[62]
<i>Trichodesmium erythraeum</i> Ehrenberg	Saxitoxin	(TX)	II	[62]

3.2. The ecological role of toxic, potentially toxic and bloom forming species in Greek coastal waters

In the present article (Table 1) we nominate toxic (TX) as the species producing blooms associated with evident toxic symptoms in the marine ecosystem, e.g., fish and shellfish death, or in humans consuming the poisoned fish and shellfish populations. Thus, consumption of contaminated shellfish by (a) the diatom *Pseudonitzschia seriata*, a domoic acid producer, caused [13] amnesic shellfish poisoning (ASP), (b) the dinoflagellate *Dinophysis sacculus*, an okadaic acid producer, caused [48] diarrhetic shellfish poisoning (DSP) and (c) the cyanobacterium *Microcystis aeruginosa*, a microcystin-LR producer, caused [61] extensive liver damage.

Potentially toxic (PT) are characterized as species carrying the toxigenic potential according to toxicological analyses, but their presence in an area has not been accompanied by toxic blooms and the relevant symptoms. A noticeable example is the toxic dinoflagellate (GTX1-4) *Alexandrium minutum*, whose presence did not produce toxic symptoms in the Greek coastal waters since their nutritional status did not favor blooms of this species [64].

Certain non-toxic species create high biomass (HB) blooms that have been characterized as harmful, because their occurrence produces discoloration of the water, undesirable aesthetic symptoms and anoxic harmful conditions to the ecosystem. They also cause severe economic problems due to loss to fisheries and tourism operations [65]. Massive growth of the dinoflagellates *Noctiluca scintillans* (late winter-early spring), *Chatonella globosa* (spring) and several species of the genus *Prorocentrum* in autumn (*P. micans*, *P. triestinum*, *P. obtusidens* and *P. rostratum*) caused severe water discoloration in Thermakos Gulf during the years 2000–2004 [43].

The total numbers of (TX), (PT) and (HB) algae reported in this work are 61 species. Dinoflagellates included 46 species contributing the 75% of total number (Table 1). Among them, three species are toxic (*Dinophysis acuminata*, *Gyrodinium aureolum*, *Karenia brevis*), seven species are forming high biomass (HB) harmful blooms and the rest (36) are potentially toxic species. Dinoflagellates are referred [66] as the group producing the most potent biotoxins known and with the largest number of HAB species, and the present data (75% dinoflagellates of total number of HAB species) are in accordance with this information.

Diatoms were represented by only six species—all potentially toxic—and this might be attributed to their nutrition requirements for a well balanced ratio (N:P:Si) of all nutrients. This necessity makes them poorer competitors than the non-siliceous dinoflagellates that seem to have a competitive advantage over diatoms if the stoichiometry of nutrients is deviated from its normal status in seawater [67].

Another advantage of dinoflagellates over diatoms is their nutritional mode, since several dinoflagellates are not exclusively phototrophic but heterotrophic/mixotrophic because they can shift to osmotrophy (uptake of dissolved organic substances) and/or phagotrophy (feeding on particulate organic carbon) under changes in nutrient supply ratios (N:P, C:P) and light-depleted conditions [8].

Table 2. Trophic strategies of heterotrophic HAB species.

Species	Feeding mechanism	Food type	Source
<i>Alexandrium catenella</i>	Osmotrophy	Urea, dextrans	[90]
<i>Alexandrium minutum</i>	Osmotrophy-Phagotrophy	Urea, Cyanobacteria	[91,92]
<i>Alexandrium tamarense</i>	Osmotrophy-Phagotrophy	Urea, Cyanobacteria, Cryptophytes	[92–94]
<i>Ceratium furca</i>	Phagotrophy	Ciliates	[95]
<i>Dinophysis acuminata</i>	Phagotrophy	Ciliates	[96]
<i>Gambierdiscus sp.</i>	Phagotrophy	Unknown pray	[8]
<i>Gymnodinium catenatum</i>	Phagotrophy	Cyanobacteria	[92]
<i>Gyrodinium impudicum</i>	Phagotrophy	Cyanobacteria, Algae	[94,97]
<i>Karenia brevis</i>	Osmotrophy-Phagotrophy	Urea, Cyanobacteria	[92,98]
<i>Karlodinium veneficum</i>	Osmotrophy-Phagotrophy	Urea, Cryptophytes	[99,100]
<i>Noctiluca scintillans</i>	Phagotrophy	Algae	[101]
<i>Ostreopsis ovata</i>	Phagotrophy	Unknown pray	[8]
<i>Ostreopsis siamensis</i>	Phagotrophy	Unknown pray	[8]
<i>Prorocentrum micans</i>	Phagotrophy	Cyanobacteria, Algae	[92,94]
<i>Prorocentrum minimum</i>	Osmotrophy-Phagotrophy	Urea, Cyanobacteria, Algae	[92,99,102]
<i>Protoperidinium crassipes</i>	Phagotrophy	Algae	103
<i>Scrippsiella trochoidea</i>	Phagotrophy	Cyanobacteria, Algae	[92,94]
<i>Prymnesium parvum</i>	Phagotrophy	Algae	[104]
<i>Microcystis aeruginosa</i>	Osmotrophy	Leucine	[69]

The 19 identified mixotrophic species in this investigation (Table 2) included 17 dinoflagellates, one prymnesiophyte and one cyanobacterium. Mixotrophic dinoflagellates comprised 40% of the total (46) species in the Dinophyceae class (Table 1) and their feeding types are well known. Nine mixotrophic species (*Ceratium furca*, *Dinophysis acuminata*, *Gymnodinium catenatum*, *Gyrodinium impudicum*, *Noctiluca scintillans*, *Prorocentrum micans*, *Protoperidinium crassipes*, *Scrippsiella trochoidea*, *Prymnesium parvum*) have been reported as phagotrophic, having the ability to feed on prokaryote prey (e.g., cyanobacteria) and/or eukaryote algae (dinoflagellates, cryptophytes). However, the prey of phagotrophic *Gambierdiscus sp.*, *Ostreopsis ovata*, *O. siamensis*, is unknown. For species supplementing their nutrition with osmotrophy (*Alexandrium catenella*) or osmotrophy and phagotrophy (*Alexandrium minutum*, *A. tamarense*, *Karenia brevis*, *Karlodinium veneficum*, *Prorocentrum minimum*), urea proved to be an important nitrogen source, with the exception of the cyanobacterium *Microcystis aeruginosa*, which may utilize leucine.

Among the 61 species presented in Table 1, certain algae (16) have been associated with the occurrence of important HAB incidents in the investigated areas during the last 30 years, and six among these are heterotrophic species. Table 3 presents the seasonal and spatial distribution of the HAB incidents and the associated impact in the biotic community and water quality.

Table 3. Important HAB incidents in Greek coastal waters.

Species	Season/year of max. abundance (Cells.L ⁻¹)	Gulf	Impact	Source
<i>Alexandrium insuetum</i>	April 2003 (2.5×10^6) May 2004 (4.7×10^5)	Amvrakikos	Water discoloration	[43]
<i>Dinophysis acuminata</i>	Jan. 2000 (8.5×10^4) Feb. 2002 (3.7×10^4) March 2003 (2.2×10^3) May 2004 (1.1×10^4)	Thermaikos	Diarrhetic shellfish toxins	[42,71]
<i>Karenia brevis</i>	Sept. 1977 (1.0×10^7) Sept. 1978 (5.0×10^7) Oct. 1987 (2.7×10^7)	Saronikos	Massive fish kill	[70,105]
<i>Noctiluca scintillans</i>	February–March 2000–2004 ($>1.0 \times 10^6$) March 1978 (1.1×10^5)	Thermaikos, Kavalas	Water discoloration Water discoloration	[43] [105]
<i>Prorocentrum micans</i>	April 1994 (3.7×10^7) May 1993 (1.1×10^6)	Thermaikos Saronikos	Water discoloration Water discoloration	[43] [46]
<i>Prorocentrum minimum</i>	April 2003 (1.2×10^5) April 2003 (1.1×10^5) Autumn 2003 (1.0×10^5)	N. Aegean coastal area, Saronikos, Amvrakikos	Water discoloration	[43]
<i>Prorocentrum obtusidens</i>	Jan. 2000 (1.2×10^6) Jan. 2001 (1.2×10^6)	Thermaikos	Water discoloration	[43]
<i>Prorocentrum redfieldii</i>	Winter 2000 (1.2×10^6) Winter 2001 (6.0×10^6)	Thermaikos	Water discoloration	[43]
<i>Phaeocystis pouchetii</i>	March 1989 (2.5×10^6) August 1993 (3.5×10^7) Sept. 1999 (2.7×10^6)	Saronikos Evoikos	Water discoloration Mucilage	[46] [62]
<i>Chattonella globosa</i>	Spring 2001 ($>10^4$) Spring 2002 ($>10^4$) Spring 2003 ($>10^4$)	Thermaikos	Water discoloration	[43]
<i>Chattonella verucolosa</i>	Dec. 1998 (Massive presence)	Amvrakikos	Mass finfish mortality	[43]
<i>Microcystis aeruginosa</i>	Sept. 1999 (9.9×10^5)	Evoikos	Mucilage	[62]
<i>Lynghya agardhii</i>	Sept. 1999 (4.8×10^3 filaments.L ⁻¹)	Evoikos	Mucilage	[62]
<i>Chroococcus gelatinosus</i>	Sept. 1999 (8.2×10^5)	Evoikos	Mucilage	[62]
<i>Synechocystis sellensis</i>	Sept. 1999 (8.9×10^4)	Evoikos	Mucilage	[62]
<i>Trichodesmium erythraeum</i>	Sept. 1999 (7.1×10^4 trichomes.L ⁻¹)	Evoikos	Mucilage	[62]

The present data demonstrate that HAB episodes in Greek coastal waters are sporadic in time, space and recurrence of the causative species. Blooms (up to 5.0×10^7 cells.L⁻¹) of *Karenia brevis* (*Gymnodinium breve*) were recorded only in the Saronikos Gulf, three times (September 1977, September 1978, and October 1987) with massive fish kill. Outbreaks of *Dinophysis acuminata* (up to 8.5×10^4 cells.L⁻¹) were recorded only in the Thermaikos Gulf in January 2000, April 2001, February 2002, March 2003 and May 2004, and they were associated with extensive shellfish deaths. However, this species was also observed in the Amvrakikos and Malliakos Gulfs at several times in low

abundances and without toxic symptoms. The huge growth (5.4×10^6 cells.L⁻¹) of *Noctiluca scintillans* caused water discoloration in late winter-early spring occasionally during 2000–2004 in Thermaikos and in Kavala Gulfs. The outbursts of four species of the genus *Prorocentrum* were also associated with water discoloration. *P. obtusidens*, *P. redfeldii* and *P. micans* occurred in the Thermaikos Gulf during the winter 2000–2001 at abundances up to 6.0×10^6 cells.L⁻¹ and *P. minimum* was recorded (up to 1.2×10^5 cells.L⁻¹) in April 2003 along the N. Aegean coastal line and in the Saronikos Gulf, and in autumn 2003 in the Amvrakikos Gulf. However, the presence of *P. minimum* in the Kalloni Gulf did not cause any undesirable incidents [29]. Mass occurrence (4.7×10^5 – 2.5×10^6 cells.L⁻¹) of *Alexandrium insuetum* caused water discoloration in the Amvrakikos Gulf in the spring of 2003 and 2004, but in Kalloni Gulf did not create harmful effects [29].

The two Rhaphidophyte species of *Chattonella* were also involved in severe HAB phenomena. The species *C. globosa* grew massively ($>10^4$ cells.L⁻¹), causing water discoloration during spring 2001–2003 in the Thermaikos Gulf, whereas considerable growth of *C. veruculosa* caused finfish mortality in the Amvrakikos Gulf in December 1998. The Prymnesiophyte *Phaeocystis pouchetii*, growing at concentrations up to 3.5×10^7 cells.L⁻¹, caused water discoloration in the Saronikos Gulf (March 1989, August 1993) and “mucilage” problems in the Evoikos Gulf (September 1999). In September 1999, the co-occurrence of five species of the cyanophyceae, *Microcystis aeruginosa* (9.9×10^5 cells.L⁻¹), *Lyngbya agardhii* (4.8×10^3 filaments.L⁻¹), *Chroococcus gelatinosus* (8.2×10^5 cells.L⁻¹), *Synechocystis sellensis* (8.9×10^4 cells.L⁻¹) and *Trichodesmium erythraeum* (7.1×10^4 trichomes.L⁻¹) produced a serious harmful bloom in the Evoikos Gulf. The sea surface was covered by mucus-forming “blankets” and “marine snow” transported horizontally and vertically and causing problems to recreation, public health and fish harvesting.

From the ecological point of view, most (TX), (PT) and (HB) algae (Table 1) are “normal” components of inshore waters [72,73]. However, major gaps still exist in our understanding of the factors triggering only certain species to initiate and develop harmful populations. There is evidence that HABs are eutrophication-induced phenomena thriven by anthropogenic activities. Records on the trophic status of the Aegean and Ionian Gulfs [1] proved that the investigated areas (Figure 1) were characterized “eutrophic” because the chl α concentrations were higher ($>>1.0$ mg chl α . m⁻³) in relation to the values ($<<0.5$ mg chl α . m⁻³) prevailing in the oligotrophic open oceanic waters [74]. The information available on the eutrophication-HAB relationship has recently increased, regarding the general explanation of the competition of phytoplankton species in relation to overall nutrient availability and the ratio between different nutrient species [65].

It is interesting to notice that the species *Alexandrium insuetum*, *A. tamarense*, *Gymnodinium catenatum*, *Gyrodinium aureolum*, *Coolia monotis*, *Ostreopsis ovata* and *O. siamensis* are not indigenous, but alien species of the Mediterranean Sea. They have been introduced via ship traffic for the Atlantic, Pacific and Indian Oceans [75] and it is obvious that the “ballast water” problem needs urgent attention [76].

4. Conclusions

The available data indicate that 61 identified HAB species (toxic, potentially toxic and high biomass producing algae) have spread across the Greek coastline during the last 30 years. Among

these, certain algae (16) were associated with the occurrence of important HAB incidents causing damage in the marine biota and the water quality. There is a strong indication that these incidents were eutrophication-induced phenomena, but sporadic in time, space and recurrence of the causative species.

References

1. Gotsis-Skretas, O.; Ignatiades, L. Distribution of chlorophyll α in the Aegean and Ionian Sea. In *State of the Hellenic Fisheries*; Papaconstantinou, C., Zenetos, A., Vassilopoulou, V., Tserpes, G., Eds.; HCMR: Athens, Greece, 2007; pp. 24–27.
2. Codd, G.A. Cyanobacterial toxins: Their occurrence in aquatic environments and significance to health. In *Marine Cyanobacteria*; Charpy, L., Larkum, A.W.D., Eds.; Bulletin De L'Institut Oceanographique: Paris, France, 1999; pp. 483–500.
3. Vershinin, A.O.; Orlova, T.Y. Toxic and harmful algae in the coastal waters of Russia. *Mar. Biol.* **2008**, *48*, 524–537.
4. Moestrup, Ø.; Akselman, R.; Cronberg, G.; Elbraechter, M.; Fraga, S.; Halim, Y.; Hansen, G.; Hoppenrath, M.; Larsen, J.; Lundholm, N.; Nguyen, L.N.; Zingone, A. IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae (HABs). <http://www.marinespecies.org/hab/>, accessed 3 March 2010.
5. Anon. *EUROHAB Science Initiative Part B: Research and Infrastructural Need*; National European and International Programmes; Gran ċi, E., Lipiatou, E., Eds.; Office for Official Publications of the European Communities: Luxembourg, 2002.
6. Sournia, A. *Atlas du Phytoplankton Marin. Cyanophycees, Dictyochophycees, Dinophycees, Raphidophycees*; Centre National de la Recherche Scientifique: Paris, France, 1986; Volume 1, pp. 1–219.
7. Zingone, A.; Evenoldsen, H.O. The diversity of algal blooms: A challenge for science and management. *Ocean Coast. Manage.* **2000**, *43*, 725–748.
8. Burkholder, J.M.; Gilbert, P.M.; Skelton, H.M. Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae* **2008**, *8*, 77–93.
9. Sala, S.E.; Sar, E.A.; Ferrario, M.E. Review of materials reported as containing *Amphora coffeaeformis* (Agardh) Kützing in Argentina. *Diatom Res.* **1998**, *13*, 323–336.
10. Bruno, M.; Coccia, A.; Volterra, L. Ecology of mucilage production by *Amphora coffeaeformis* var. *perpusilla* blooms of Adriatic Sea. *Water Air Soil Pollut.* **1993**, *69*, 201–207.
11. Todd, E.C.D. Amnesic shellfish poisoning—a new seafood toxin syndrome. In *Toxic Marine Phytoplankton*; Gran ċi, E., Sundström, B., Edler, L., Anderson, D.M., Eds.; Elsevier: Amsterdam, The Netherland, 1990; pp. 504–508.
12. Kaczmarska, I.; LeGresley, M.M.; Martin, J.L.; Ehrman, J. Diversity of the diatom genus *Pseudo-nitzschia* Peragallo in the Quoddy region of the Bay of Fundy, Canada. *Harmful Algae* **2005**, *4*, 1–19.
13. Lundholm, N.; Skov, J.; Pocklington, R.; Moestrup, Ø. Domoic acid, the toxic amino acid responsible for amnesic shellfish poisoning, now in *Pseudo-nitzschia seriata* (Bacillariophyceae) in Europe. *Phycologia* **1994**, *33*, 475–478.

14. Moestrup, Ø.; Codd, G.A.; Elbrächter, M.; Faust, M.A.; Fraga, S.; Fukuyo, Y.; Cronberg, G.; Halim, Y.; Taylor, F.J.R.; Zingone, A. IOC Taxonomic Reference List of Toxic Algae; Intergovernmental Oceanographic Commission of UNESCO: 2004. <http://www.ioc.unesco.org/hab/data.htm> (accessed on 18 March 2009).
15. Thessen, A.E.; Stoecker, D.K. Distribution, abundance and domoic acid analysis of the toxic diatom genus *Pseudo-nitzschia* from the Chesapeake Bay. *Estuar. Coast.* **2008**, *31*, 664–672.
16. Faust, M.A.; Gulledge, R.A. Identifying harmful marine dinoflagellates. *Contr. US Nat. Herb.* **2002**, *42*, 1–144.
17. Krock, B.; Seguel, C.G.; Cembella, A.D. Toxin profile of *Alexandrium catenella* from the Chilean coast as determined by liquid chromatography with fluorescence detection and liquid chromatography coupled with tandem mass spectrometry. *Harmful Algae* **2007**, *6*, 734–744.
18. Frangopoulos, M.; Guisande, C.; de Blas, E.; Maneiro, I. Toxin production and competitive abilities under phosphorus limitation of *Alexandrium* species. *Harmful Algae* **2004**, *3*, 131–139.
19. Lim, P.T.; Usup, G.; Leaw, C.P.; Ogata, T. First report of *Alexandrium taylori* and *Alexandrium peruvianum* (Dinophyceae) in Malaysia waters. *Harmful Algae* **2005**, *4*, 391–400.
20. Congestri, R.; Bianco, I.; Albertano, P. Potentially toxic thecate dinoflagellates of middle Tyrrhenian coastal waters (Mediterranean Sea). In *Harmful Algae*; Steidinger, K.A., Landsberg, J.H., Tomas, C.R., Vargo, G.A., Eds.; Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO, 2002; pp. 332–334.
21. Durand-Clement, M. Study of production and toxicity of cultured *Gambierdiscus toxicus*. *Biol. Bull.* **1987**, *172*, 108–121.
22. Holmes, M.J.; Lewis, R.J.; Jones, A.; Hoy, A.W. Cooliatoxin, the first toxin from *Coolia monotis* (Dinophyceae). *Nat. Toxins* **1995**, *3*, 355–362.
23. Miyazaki, Y.; Nakashima, T.; Iwashita, T.; Fujita, T.; Yamaguchi, K.; Odaa, T. Purification and characterization of photosensitizing haemolytic toxin from harmful red tide phytoplankton, *Heterocapsa circularisquama*. *Aquat. Toxicol.* **2005**, *73*, 382–393.
24. Aligizaki, K.; Katikou, P.; Nikolaidis, G.; Panou, A. First episode of shellfish contamination by palytoxin-like compounds from *Ostreopsis* species (Aegean Sea, Greece). *Toxicon* **2008**, *51*, 418–427.
25. Guerrini, F.; Pezzolesi, L.; Feller, A.; Riccardi, M.; Ciminiello, P.; Dell’Aversano, C.; Tartaglione, L.; Lacovo, E.D.; Fattorusso, E.; Forino, M.; Pistocchi, R. Comparative growth and toxin profile of cultured *Ostreopsis ovata* from the Tyrrhenian and Adriatic Seas. *Toxicon* **2009**, in press.
26. Rhodes, L.; Towers, N.; Briggs, L.; Munday, R.; Adamson, J. Uptake of palytoxin-like compounds by shellfish fed *Ostreopsis siamensis* (Dinophyceae). *N.Z. J. Mar. Freshw. Res.* **2002**, *36*, 631–636.
27. Howard, M.D.A.; Smith, G.J.; Kudela, R.M. Phylogenetic relationships of yessotoxin-producing dinoflagellates, based on the large subunit and internal transcribed spacer ribosomal DNA domains. *Appl. Environ. Microbiol.* **2009**, *75*, 54–63.

28. Gárate-Lizárraga, I.; Band-Schmidt, C.J.; Lopez-Cortés, D.J.; Muneton-Gomez, M.D. Bloom of *Scrippsiella trochoidea* (Gonyaulacaceae) in a shrimp pond in the southwestern Gulf of California, Mexico. *Mar. Pollut. Bull.* **2009**, *58*, 145–149.
29. Spatharis, S.; Dolapsakis, N.P.; Economou-Amilli, A.; Tsirtsis, G.; Danielidis, D.B. Dynamics of potentially harmful microalgae in a confined Mediterranean Gulf—Assessing the risk of bloom formation. *Harmful Algae* **2009**, *8*, 736–743.
30. Magdalena, A.B.; Lehane, M.; Krys, S.; Fernández, M.L.F.; Furey, A.; James, K.J. The first identification of azaspiracids in shellfish from France and Spain. *Toxicon* **2003**, *42*, 105–108.
31. Gárate-Lizárraga, I.; Muneton-Gomez, M.D. Bloom of *Peridinium quinquecorne* Abé in La Ensenada de La Paz, Gulf of California (July 2003). *Acta Bot. Mex.* **2008**, *83*, 33–47.
32. Baek, S.H.; Shimode, S.; Han, M.S.; Kikuchi, T. Population development of the dinoflagellates *Ceratium furca* and *Ceratium fusus* during spring and early summer in Iwa Harbor, Sagami Bay, Japan. *Ocean Sci. J.* **2008**, *43*, 49–59.
33. Glibert, P.M.; Landsberg, J.H.; Evans, J.J.; Al-Sarawi, M.A.; Faraj, M.; Al-Jarallah, M.A.; Haywood, A.; Ibrahim, S.; Klesius, P.; Powell, K.; Shoemaker, C. A. Fish kill of massive proportion in Kuwait Bay, Arabian Gulf, 2001: the roles of bacterial disease, harmful algae, and eutrophication. *Harmful Algae* **2002**, *1*, 215–231.
34. Onoue, Y. Massive fish kills by a *Ceratium fusus* red tide in Kagoshima Bay, Japan. *Red Tide Newslett.* **1990**, *3*, 2.
35. Rost, B.; Richter, K.U.; Riebesell, U.; Hansen, P.J. Inorganic carbon acquisition in red tide dinoflagellates. *Plant Cell Environ.* **2006**, *29*, 810–822.
36. Weaver, S.S. *Ceratium* in Fire Island Inlet, Long-Island New-York (1971–1977). *Limnol. Oceanogr.* **1979**, *24*, 553–558.
37. Ten-Hage, L.; Turquet, J.; Quod, J.P.; Puiseux-Da, S.; Couté, A. *Prorocentrum borbonicum* sp. nov. (Dinophyceae), a new toxic benthic dinoflagellate from southwestern Indian Ocean. *Phycologia* **2000**, *39*, 296–301.
38. Faust, M.A.; Vandersea, M.W.; Kibler, S.R.; Tester, P.A.; Litaker, R.W. *Prorocentrum levis*, a new benthic species (Dinophyceae) from a mangrove island, Twin Cays, Belize. *J. Phycol.* **2008**, *44*, 232–240.
39. Vale, P.; Veloso, V.; Amorim, A. Toxin composition of *Prorocentrum lima* strain isolated from the Portuguese coast. *Toxicon* **2009**, *54*, 145–152.
40. Tianying, A.; Winshell, J.; Scorzetti, G.; Fell, J.W.; Rein, K.S. Identification of okadaic acid production in the marine dinoflagellate *Prorocentrum rhathymum* from Florida Bay. *Toxicon* **2009**, in press.
41. Baric, A.; Grbec, B.; Kuspilic, G.; Marasovic, I.; Nincevic, Z.; Grubelic, I. Mass mortality event in a small saline lake (Lake Rogoznica) caused by unusual holomictic conditions. *Sci. Mar.* **2003**, *67*, 129–141.
42. Koukaras, K.; Nikolaidis, G. *Dinophysis* blooms in Greek coastal waters (Thermaikos Gulf, NW Aegean Sea). *J. Plankton Res.* **2004**, *26*, 445–457.
43. Nikolaidis, G.; Koukaras, K.; Aligizaki, K.; Heracleous, A.; Kalopesa, E.; Moschandreu, K.; Tsolaki, E.; Mantoudis, A. Harmful microalgal episodes in Greek coastal waters. *J. Biol. Res.-Thessal.* **2005**, *3*, 77–85.

44. Lassus, P.; Berthome, J.P. Status of 1987 algal blooms in IFREMER. ICES/annex III C.M. 1988, 33A, 5–13.
45. Berden-Zrimec, M.; Flander-Putrlle, V.; Drinovec, L.; Zrimec, A.; Monti, M. Growth, delayed fluorescence and pigment composition of four *Prorocentrum minimum* strains growing at two salinities. *Biol. Res.* **2008**, *41*, 11–23.
46. Moncheva, S.; Gotsis-Skretas, O.; Pagou, K.; Krastev, A. Phytoplankton blooms in Black Sea and Mediterranean coastal ecosystems subjected to anthropogenic eutrophication: Similarities and differences. *Est. Coast. Shelf Sci.* **2001**, *53*, 281–295.
47. Faust, M.A. Morphologic details of six benthic species of *Prorocentrum* (Pyrrhophyta) from a mangrove island, Twin Cays, Belize, including two new species. *J. Phycol.* **1990**, *26*, 548–558.
48. Wright, J.L.C.; Cembella, A.D. Ecophysiology and biosynthesis of polyether marine biotoxins. In *Physiological Ecology of Harmful Algal Blooms*; Anderson, D.M., Cembella, A.D., Hallegraeff, G.M., Eds.; Springer: Berlin Heidelberg, Germany; 1998; pp. 427–451.
49. Lee, J.S.; Igarashi, T.; Fraga, S.; Dahl, E.; Hovgaard, P.; Yasumoto, T. Determination of diarrhetic shellfish toxins in various dinoflagellate species. *J. Appl. Phycol.* **1989**, *1*, 147–152.
50. Fraga, S.; Bravo, I.; Delgado, M.; Franco, J.M.; Zapata, M. *Gymnodinium impudicum* sp. nov. (Dinophyceae), a non-toxic, chain forming red tide dinoflagellate. *Phycologia* **1995**, *34*, 514–521.
51. Fessard, V.; Diogène, G.; Dubreuil, A.; Quod, J.P.; Durand-Clément, M.; Legay, C.; Puiseux-Dao, S. Selection of cytotoxic responses to maitotoxin and okadaic acid and evaluation of toxicity of dinoflagellate extracts. *Nat. Toxins* **2006**, *2*, 322–328.
52. Smolowitz, R.; Shumway, S.A. Possible cytotoxic effects of the dinoflagellate, *Gyrodinium aureolum*, on juvenile bivalve molluscs. *Aquac. Int.* **1997**, *5*, 29–300.
53. Pierce, R.H.; Henry, M.S. Harmful algal toxins of the Florida red tide (*Karenia brevis*): Natural chemical stressors in South Florida coastal ecosystems. *Ecotoxicology* **2008**, *17*, 623–631.
54. Satake, M.; Shoji, M.; Oshima, Y.; Naoki, H.; Fujita, T.; Yasumoto, T. Gymnocin-A, a cytotoxic polyether from the noxious red tide dinoflagellate, *Gymnodinium mikimotoi*. *Tetrahedron Lett.* **2002**, *43*, 5829–5832.
55. Gárate-Lizárraga, I.; Bustillos-Guzmán, J.J.; Alonso-Rodríguez, R.; Luckas, B. Comparative paralytic shellfish toxin profiles in two marine bivalves during outbreaks of *Gymnodinium catenatum* (Dinophyceae) in the Gulf of California. *Mar. Pollut. Bull.* **2004**, *48*, 397–402.
56. Galimany, E.; Place, A.R.; Ramón, M.; Jutson, M.; Pipe, R.K. The effects of feeding *Karlodinium veneficum* (PLY # 103; *Gymnodinium veneficum* Ballantine) to the blue mussel *Mytilus edulis*. *Harmful Algae* **2008**, *7*, 91–98.
57. Mohamed, A.Z.; Mesaad, I. First report on *Noctiluca scintillans* in the Red Sea off the coasts of Soudi Arabia: Consequencies of eutrophication. *Oceanologia* **2007**, *49*, 337–351.
58. Hansen, E.; Ernstsén, A.; Eilertsen, H.C. Isolation and characterization of a cytotoxic polyunsaturated aldehyde from the marine phytoplankter *Phaeocystis puchettii* (Hariot) Lagerheim. *Toxicology* **2004**, *199*, 207–217.
59. Igarashi, T.; Satake, M.; Yasumoto, T. Structures and partial stereochemical assignments for prymnesin-1 and prymnesin-2: potent hemolytic and ichthyotoxic glycosides isolated from the red tide alga *Prymnesium parvum*. *J. Am. Chem. Soc.* **1999**, *121*, 8499–8511.

60. Moestrup, Ø.; Thomsen, H.A. Taxonomy of toxic haptophytes (prymnesiophytes). In *Manual on Harmful Marine Microalgae*, 2nd ed.; Hallegraeff, G.M., Anderson, D.M., Cembella, A.D., Eds.; IOC-UNESCO: Paris, France, 2003; Volume 11, pp. 433–464.
61. Raabergh, C.M.I.; Bylund, G.; Eriksson, J.E. Hystopathological effects of microcystin-LR a cyclic peptide toxin from the cyanobacterium (blue-green alga) *Microcystis aeruginosa* on common carp (*Cyprinus carpio* L.). *Aquat. Toxicol.* **1991**, *20*, 131–146.
62. Metaxatos, A.; Panagiotopoulos, C.; Ignatiades, L. Monosaccharide and aminoacid composition of mucilage material produced from a mixture of four phytoplanktonic taxa. *J. Exp. Mar. Biol. Ecol.* **2003**, *294*, 203–217.
63. Negri, A.P.; Bunter, O.; Jones, B.; Llewellyn, L. Effects of the bloom-forming alga *Trichodesmium erythraeum* on the pearl oyster *Pinctada maxima*. *Aquaculture* **2004**, *232*, 91–102.
64. Ignatiades, L.; Gotsis-Skretas, O.; Metaxatos, A. Field and culture studies on the ecophysiology of the toxic dinoflagellate *Alexandrium minutum* (Halim) grown in Greek coastal waters. *Harmful Algae* **2007**, *6*, 153–165.
65. Smayda, T.J. Harmful algal blooms: Their ecotoxicology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* **1997**, *42*, 1137–1153.
66. Cembella, A.D. Chemical ecology of eukaryotic microalgae in marine ecosystems. *Phycologia* **2003**, *42*, 420–44.
67. Riegman, R.; Colijn, F.; Malschaert, J.F.P.; Kloosterhuis, H.T.; Cadee, G.C. Assessment of growth rate limiting nutrients in the North Sea by the use of nutrient-uptake kinetics. *Neth. J. Sea Res.* **1990**, *26*, 53–60.
68. Faust, M.A. Mixotrophy in tropical benthic dinoflagellates. In *Harmful Algae*; Reguera, B., Blanco, J., Fernandez, M.L., Watt T., Eds.; Xunta de Galicia and IOC–UNESCO: Paris, France, 1998; pp. 390–393.
69. Kamjunke, N.; Tittel, J. Utilisation of leucine by several phytoplankton species. *Limnologia* **2008**, *38*, 360–366.
70. Pagou, K.; Ignatiades, L. The periodicity of *Gymnodinium breve* (Davis) in Saronikos Gulf, Aegean Sea. In *Toxic Marine Phytoplankton*; Granđi, E., Sundström, B., Edler, L., Anderson, D.M., Eds.; Elsevier: Amsterdam, The Netherland, 1990; pp. 206–208.
71. Reizopoulou, S.; Stroglyoudi, E; Giannakourou, A.; Pagou K.; Chatzianestis I.; Pyrgaki C.; Granđi E. Okadaic acid accumulation in macrofilter feeders subjected to natural blooms of *Dinophysis acuminata*. *Harmful Algae* **2008**, *7*, 228–234.
72. Ignatiades, L. 1969. Annual cycle, species diversity and succession of phytoplankton in lower Saronikos Gulf, Aegean Sea. *Mar. Biol.* **1969**, *3*, 196–200.
73. Ignatiades, L.; Georgopoulos, D.; Karydis, M. Description of phytoplanktonic community of the oligotrophic waters of S.E. Aegean Sea. *Mar. Ecol.* **1995**, *16*, 13–26.
74. Ignatiades, L. 2005. Scaling the trophic status of the Aegean Sea, Eastern Mediterranean. *J. Sea Res.* **2005**, *54*, 51–57.
75. Gómez, F. Endemic and Indo-Pacific plankton in the Mediterranean Sea: a study based on dinoflagellate records. *J. Biogeogr.* **2006**, *33*, 261–270.

76. Granéli, E.; Codd, G.A.; Dale, B.; Lipiatou, E.; Maestrini, S.Y.; Rosenthal, H. *Harmful Algal Blooms in European Marine and Brackish Waters*; EUR 18592; European Commission: Belgium, 1999.
77. Gotsis-Skretas, O.; Ignatiades, L. Phytoplankton in pelagic and coastal waters, In *State of the Hellenic Marine Environment*; Papathanassiou, E., Zenetos, A., Eds.; HCMR: Athens, Greece, 2005; pp.187–193.
78. Gotsis-Skretas, O; Friligos, N. Contribution to eutrophication and phytoplankton ecology in the Thermaikos Gulf. *Thalassographica* **1990**, *13*, 1–12.
79. Nikolaidis, G.; Koukaras, K.; Aligizaki, K; Kalopesa, E.; Moschandreu, K.; Tsolaki, E. Phytoplankton. In *Monitoring of Water Quality in the Coastal Area of Kalamitsi—Preveza* (2nd phase); Final Report, Aristotle University of Thessaloniki (A.U.Th.): Thessaloniki, Greece, 2006; pp. 90–106.
80. Friligos, N.; Gotsis-Skretas, O. Relationships of phytoplankton with certain environmental factors in the South Euboikos Gulf (Greece). *P.S.Z.N.I.: Mar. Ecol.* **1987**, *8*, 59–73.
81. Spatharis, S.; Mouillot, D.; Danielidis, D.B.; Karydis, M.; Chi, T.D.; Tsirtsis, G. Influence of terrestrial runoff on phytoplankton species richness-biomass relationships: A double stress hypothesis. *J. Exp. Mar. Biol. Ecol.* **2008**, *362*, 55–62.
82. Gotsis-Skretas, O.; Ignatiades, L.; Pavlidou, A.; Metaxatos, A.; Papadopoulos, A.; Pappas, G. *Alexandrium* spatio-temporal distribution in the STRATEGY areas (WP1) March 2002–October 2002): Greek Area; In *Second Year Report of the EU Project “STRATEGY” New Strategy of Monitoring and Management of HABs in the Mediterranean Sea*, 2003; Annex III, pp. 1–14.
83. Spatharis, S.; Dolapsakis, N.P.; Danielidis, D.B.; Tsirtsis, G. Dynamics of a HAB developed after an episodic rainfall event in a coastal area. *Rapp. Comm. Int. Mer. Medit.* **2007**, *38*, 396.
84. Giannakourou, A.; Orlova, T.; Assimakopoulou, G.; Pagou, K. Dinoflagellate cysts in recent marine sediments from Thermaikos Gulf, Greece. Possible implications of resuspension events on the onset of phytoplankton blooms. *Cont. Shelf Res.* **2005**, *25*, 2585–2596.
85. Dolapsakis, N.P.; Tzovenis, I.; Kantourou, P.; Bitis, I.; Economou-Amilli, A. Potentially harmful microalgae from lagoons of the NW Ionian Sea, Greece. *J. Biol. Res.-Thessalon.* **2008**, *9*, 89–95.
86. Aligizaki, K.; Nikolaidis, G. The presence of the potentially toxic genera *Ostreopsis* and *Coolia* (Dinophyceae) in the North Aegean Sea, Greece. *Harmful Algae* **2006**, *5*, 717–730.
87. Aligizaki, K.; Nikolaidis, G. Morphological identification of two tropical dinoflagellates of the genera *Gambierdiscus* and *Sinophysis* in the Mediterranean. *J. Biol. Res.-Thessalon.* **2008**, *9*, 75–82.
88. Nikolaidis, G.; Moustaka-Gouni, M. The structure and dynamics of phytoplankton assemblages from the inner part of the Thermaikos Gulf, Greece. I. Phytoplankton composition and biomass from May 1988 to April 1989. *Helgolander Meeresunters* **1990**, *44*, 487–501.
89. Aligizaki, K.; Nikolaidis, G.; Katikou, P.; Baxevanis, A.D.; Abatzopoulos, T.J. Potentially toxic epiphytic *Prorocentrum* (Dinophyceae) species in Greek coastal waters. *Harmful Algae* **2009**, *8*, 299–311.
90. Dyhrman, S.T.; Anderson, D.M. Urease activity in cultures and field populations of the toxic dinoflagellate *Alexandrium*. *Limnol. Oceanogr.* **2003**, *48*, 647–655.

91. Chang, F.H.; McClean, M. Growth responses of *Alexandrium minutum* (Dinophyceae) as a function of three different nitrogen sources and irradiance. *N.Z. J. Mar. Freshwater Res.* **1997**, *31*, 1–7.
92. Jeong, H.J.; Park, J.Y.; Nho, J.H.; Park, M.O.; Ha, J.H.; Seong, K.A.; Jeng, C.; Seong, C.N.; Lee, K.Y.; Yih, W.H. Feeding by red tide dinoflagellates on the cyanobacterium *Synechococcus*. *Aquat. Microb. Ecol.* **2005a**, *41*, 1331–2143.
93. Leong, S.C.Y.; Murata, A.; Nagashima, Y.; Taguchi, S. Variability in toxicity of the dinoflagellate *Alexandrium tamarense* in response to different nitrogen sources and concentrations. *Toxicon* **2004**, *43*, 407–415.
94. Jeong, H.J.; Yoo, D.Y.; Park, J.Y.; Song, J.Y.; Kim, S.T.; Lee, S.H.; Kim, K.Y.; Yih, W.H. Feeding by phototrophic red-tide dinoflagellates: five species newly revealed and six species previously known to be mixotrophic. *Aquat. Microb. Ecol.* **2005b**, *40*, 133–150.
95. Smalley, G.W.; Coats, D.W. Ecology of the red-tide Dinoflagellate *Ceratium furca*: distribution, mixotrophy and grazing impact on ciliate populations of Chesapeake Bay. *J. Eukaryot. Microbiol.* **2002**, *49*, 63–73.
96. Jacobson, D.M.; Anderson, D.M. Widespread phagocytosis of ciliates and other protists by marine mixotrophic and heterotrophic thacate dinoflagellates. *J. Phycol.* **1996**, *32*, 279–285.
97. Jeong, H.J.; Yoo, D.Y.; Seong, K.A.; Kim, J.H.; Park, J.Y.; Kim, S.T.; Lee, S.Y.; Ha, J.H.; Yih, W.H. Feeding by the mixotrophic red-tide dinoflagellate *Gonyaulax polygramma*: mechanisms, prey species, effects of prey concentration and grazing impact. *Aquat. Microb. Ecol.* **2005**, *38*, 133–150.
98. Sinclair, G.; Kamykowski, D.; Glibert, P.M. Growth, uptake, and assimilation of ammonium, nitrate, and urea, by three starins of *Karenia brevis* grown under low light. *Harmful Algae* **2009**, *8*, 770–780.
99. Solomon, C.M.; Glibert, P.M. Urease activity in five phytoplankton species. *Aquat. Microb. Ecol.* **2008**, *52*, 149–157.
100. Adolf, J.E.; Bachvaroff, T.; Place, A.R. Can Cryptophyte abundance trigger toxic *Karlodinium veneficum* blooms in eutrophic estuaries? *Harmful Algae* **2008**, *8*, 119–128.
101. Hansen, P.J.; Miranda, L.; Azanza, R. Green *Noctiluca scintillans*: a dinoflagellate with its own greenhouse. *Mar. Ecol. Prog. Ser.* **2004**, *275*, 79–87.
102. Stoecker, D.K.; Li, A.; Coats, D.W.; Gustafson, D.E.; Nannen, M.K.; Mixotrophy in the dinoflagellate *Prorocentrum minimum*. *Mar. Ecol. Prog. Ser.* **1997**, *152*, 1–12.
103. Jeong, H.J.; Latz, M.I. Growth and grazing rates of the heterotrophic dinoflagellates *Protoperdinium* spp. on red tide dinoflagellates. *Mar. Ecol. Prog. Ser.* **1994**, *106*, 173–185.
104. Tillmann, U. Kill and eat your predator: a winning strategy of the plankton flagellate *Prymnesium parvum*. *Aquat. Microb. Ecol.* **2003**, *32*, 73–84.
105. Satsmadjis, J.; Friligos, N. Red tide in Greek waters. *Vie et Milieu* **1983**, *33*, 111–117.