LIFE HISTORIES OF MICROALGAL SPECIES CAUSING HARMFUL BLOOMS

Esther Garcés, Marta Estrada
Departament de Biologia Marina i Oceanografia, Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas (CSIC), Pg. Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain

Rosa Isabel Figueroa
Instituto Español de Oceanografia (IEO), C.O. Vigo, 36280 Vigo, Spain
Aquatic Ecology Division, Department of Biology, Lund University, S-22362 Lund, Sweden

Keywords: Harmful algal species, life history, harmful algal blooms, environmental and physiological factors, resting stages, management, models

Contents

Summary

In coastal and offshore waters, harmful algal blooms (HABs) are recurrent events affecting localized or widespread areas. In either case, they threaten human health, marine ecosystems, and economic resources, such as tourism, fisheries, and aquaculture, and as such are one of the major problems currently faced by coastal countries. However, the challenge posed by HABs is complicated by the fact that they are the product of diverse phenomena and are caused by organisms from multiple algal classes, each with its own unique characteristics.

HAB dynamics also vary from one site to another, depending on hydrographic and ecological conditions and on biological features of the causative organisms, including the characteristics of their life histories. Understanding the life cycle of HAB producers appears to be the key to the prediction of bloom initiation, maintenance and decline. Most HAB-forming species display heteromorphic life cycles, and different life stages of the same organism interact with the environment in highly distinct ways. Indeed, in many species, planktonic stages are an ephemeral phase of the organism's life cycle. By contrast, resistant stages enable a species to withstand adverse conditions for prolonged periods in addition to facilitating its dispersal.

Moreover, the accumulation of resistant stages in coastal sediments provides dormant reservoirs for eventual HABs. Although the relevance of the different life stages of a species with respect to its population dynamics is well appreciated, the full life cycle has only been determined for less than 1% of the described species and both the dynamics of the dormant phases and their interactions with the surrounding environment are poorly understood.

Likewise, the factors triggering transitions between the different phases have yet to be identified, although knowledge of the transition rates between life cycle stages is fundamental in efforts aimed at realistically predicting HABs. In this chapter, we review current knowledge on life cycle strategies of major groups of HAB producers in marine and brackish waters and summarize existing field observations. Next, we review relevant field observations and finally, we present an overview of simple mathematical models that have been used to explore the significance of life cycle characteristics for bloom dynamics.

1. Harmful Algal Blooms as Recurring Events World Wide

Phytoplankton or microalgae are unicellular photosynthetic organisms that inhabit freshwater, brackish water and seawater environments and are the most important phototrophs in the aquatic systems of the Earth. In general, both eukaryotic protists and prokaryotic cyanobacteria are considered within the microalgae. These organisms are able to synthesize organic compounds from CO_2 and water using sunlight as energy and are thus essential components of aquatic food webs.

Harmful algal blooms (HABs) are due to species that produce negative impacts by different means. Some species produce toxins that are harmful through direct effects on humans and others by killing fish species. Microalgal toxins are accumulated by marine animals and bivalves that filter seawater to obtain food. The consumption of toxic seafood by humans results in a number of disease syndromes, such as paralytic shellfish poisoning (PSP), diarrheic shellfish poisoning (DSP), and amnesic shellfish poisoning (ASP).

Ichthyotoxic species produce toxins that cause the death of fishes and other aquatic organisms. Some other species produce high-biomass blooms that may exceed 10^5–10^6 cells l^{-1} and are harmful not because of the release of toxins but mainly because the intense production of organic matter may cause significant ecological damage to the regional biota (anoxia, community and food-web alterations) as well as major economic problems related to the deterioration of coastal recreational waters (discoloration, odor, etc.). These blooms are commonly known as "red tides" but they may, in fact, confer a brown, green, or white discoloration to the affected waters (Figure 1). Some marine planktonic dinoflagellates belong to all three of the above-listed categories of HABs. In coastal and offshore waters, HABs are recurrent events that affect localized or widespread areas. In either case, they threaten marine ecosystems, human health, and activities such as tourism, fisheries, and aquaculture. Indeed, HABs pose a major environmental threat to coastal countries. Some HABs are a response to the natural physicochemical variability of the environment, such as changes in hydrodynamics, turbulence, temperature, or nutrient availability.

Figure 1. A dinoflagellate bloom at a NW Mediterranean beach. Foto by Agència Catalana de l'Aigua, Catalonia, Spain.

However, in other cases, the expansion of human activities is thought to underlie the increase in HAB incidence. The relative contributions of these causes are still under debate. It may be that recent regular monitoring of HAB outbreaks, to safeguard human health, has improved the recording of these incidents, but it is also widely accepted that anthropogenic factors promote HABs by: i) increasing the geographical range of harmful species through human-mediated transport of resting cysts, e.g., during the movement of shellfish stocks, in ballast water, or on floating plastic debris; ii) increasing the number of confined water bodies where HABs can proliferate, such as harbors and protected beaches in coastal areas; iii) nutrient enrichment of coastal waters (anthropogenic eutrophication), e.g., by the runoff of fertilizers used in agricultural fields; and iv) reducing the biomass of filter-feeding organisms through overfishing or the disturbance of environmental conditions. Human-induced climatic change has also been mentioned as a factor in the apparent increase of HABs, but the scarcity of data from long-term monitoring does not allow definitive conclusion yet.

HABs encompass a diverse range of phenomena and are caused by a number of species in multiple algal classes. Consequently, the characteristics of each bloom are in many ways unique. The dynamics of an outbreak also vary from one site to another, depending on the physicochemical and hydrological conditions of the water column and on the ecological and biological characteristics of the causative organism. In particular, an understanding of the life cycle of harmful microalgal species is fundamental to understand the occurrence and dynamics of HABs (Garcés et al., 2010). The life cycle of many causative species includes a resistant stage that allows for survival under adverse environmental conditions. The transitions from active growth to the resting stage determine the timing of appearance of many HA species in the water column and facilitates the successful dispersal of the organisms, thus giving rise to blooms in previously unaffected waters.

2. Life Strategies in Microalgal Species

Most HA species have complex life cycles during which the organism may adopt radically different morphologies. Prior to the development of the appropriate techniques for identification, this resulted in considerable confusion and numerous erroneous classifications.

These life stages typically consist of vegetative planktonic cells and benthic resting stages such as cysts, spores, etc. (Figs 2, 3). During the vegetative planktonic phase, a species typically grows in the water column, where it can cause noxious blooms. The timing and abundance of the planktonic stage has thus been intensively studied in marine and freshwater ecosystems and the resulting information can tell us when, why and for how long harmful blooms will occur.

By contrast, little is known about the resting stage of microalgae, which remains dormant in the sediments on the sea bottom until environmental conditions are adequate to re-establish the vegetative stage. Even less is known about the transitional processes between these two stages.

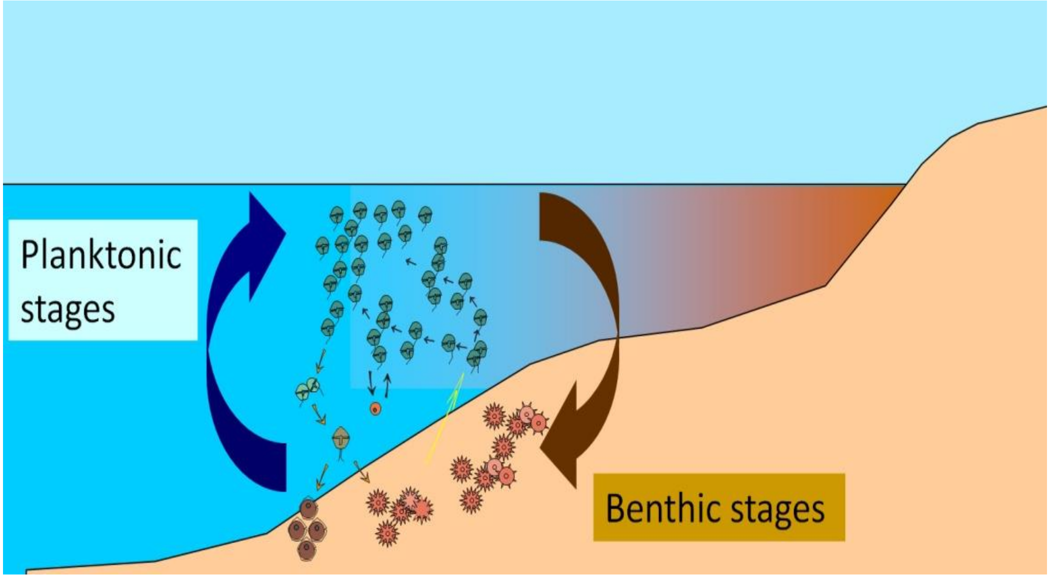

Figure 2. Schematic drawing of a dinoflagellate life cycle showing the planktonic (cell) and benthic (cyst) stages and the transition between them (arrows).

Generally, the different life stages (vegetative cell and cyst) of a single species inhabit distinct environments and are exposed to different ranges of variability. Indeed, for many species, the planktonic phase accounts for only a brief period of the life cycle; nonetheless, it is during this stage that the cells are exposed to the wide variability in temperature, salinity, turbulence, and nutrient supply of the water column. By contrast, the benthic stage, in which cysts or spores are buried in the marine sediments, accounts for a large part of plankton organism existence. Furthermore, the sedimentary environment is relatively stable: there is little, if any, penetration of light and the temperature is relatively constant.

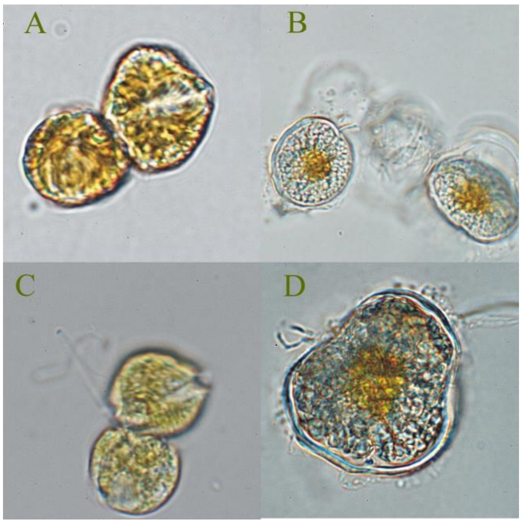

Figure 3. Gametes (A and C) and resting cysts (B and D) from the dinoflagellates *Alexandrium minutum* (A, B) and *Alexandrium taylori* (C, D). Photos R. I. Figueroa.

Based on their life histories, microalgae species can be classified into two groups: i) holoplankton, which only include planktonic life stages and ii) meroplankton, which spend only a part of their life cycle in the plankton and the rest in the sediments. It is important to note that, even though resting stages are considered to provide a "seed bank" for bloom recurrence, many harmful algal species appear to lack them. One example of a potentially harmful holoplanktonic organism is the diatom *Pseudo-nitzschia multiseries*, for which the ability to form a resting stage has not been documented, neither in culture, nor in planktonic field samples, nor in sediments. This species probably survives year-round always as a component of the plankton but at very low cell densities. Meroplankton includes several dinoflagellates, with species of the genera *Alexandrium* and *Gymnodinium*, the freshwater raphidophyte *Gonyostomum*, and cyanobacteria such as *Anabaena*.

2.1. Dinoflagellates

Dinoflagellates are a phylum of marine and freshwater unicellular microalgae that can present a highly diverse morphology. Among the characteristics of dinoflagellates, are their two dimorphic flagella and certain features of their nuclei (e.g., high DNA-copy number and permanently condensed chromosomes). Some of them are surrounded by an armour-like structure called a theca. The nutritional modes of dinoflagellates can vary from autotrophic (able to produce organic carbon through photosynthesis) to mixotrophic (able to produce organic carbon but also to acquire it from outside) but nearly half of the known extant dinoflagellate species are heterotrophic (using externally produced organic carbon for growth). Many species are nearly ubiquitous and are thus referred to as cosmopolitan. In addition, they occupy marine as well as freshwater habitats, in pelagic (open water) or benthic zones. Some species are symbionts, others are parasites. Several dinoflagellates produce toxins that contaminate seafood and cause various syndromes (e.g. PSP, DSP) and some are poisonous to aquatic organisms. Other species produce high-biomass proliferations, which, as previously mentioned, cause discoloration of the water and other problems. In the vegetative planktonic stage of their life cycles, dinoflagellates usually multiply by simple fission (asexual division). The vegetative cell's response to the actual environmental conditions (e.g., photoperiod, nutrient availability, temperature, turbulence, grazing) determines its growth rate and thus the extent of the population increase. In the planktonic stage, the motility and migration behavior is in itself an important survival strategy. For example, vertical migration can allow the cells to avoid predation and increase nutrient uptake, and chain formation enables faster swimming speeds. These and other mechanisms have been proposed as adaptations that allow dinoflagellates to maintain local cell concentrations and to produce blooms. Current knowledge on the life cycle stages of harmful dinoflagellates is summarized in Table 1. As can be appreciated, detailed life history information is available only for a few dinoflagellate species; for some genera, such as *Karenia* and *Gambierdiscus*, almost nothing is known about their essential life cycle aspects. Some species present self-mating capability to complete the sexual process (homothallic behavior) while others require gametes of a different mating group for successful sexual reproduction (heterothallic behavior). This mating systems exhibited by the species during the sexual process are also poorly known.

Species	**Harmful effect**	**Life history**			
		Resting cysts	**Pellicle cyst**	**He /ho**	**Chain formers**
Alexandrium andersoni	Paralytic shellfish poisoning	+			
A. catenella	Paralytic shellfish poisoning	+	+	he	+
A. cohorticula	Paralytic shellfish poisoning	+			+
A. hiranoi	Goniodomin producer	+	+		
A. margalefi	Ichthyotoxic	+	+	he	
A. minutum	Paralytic shellfish poisoning	+	+	he	
A. monilatum	Ichthyotoxic	+			+
A. ostenfeldii	Spirolide, Paralytic shellfish poisoning	+	+	he/ho	
A. peruvianum	Spirolide producer	+	+	he	
A. tamarense	Paralytic shellfish poisoning	+	+	he	
A. tamiyavanichi	Paralytic shellfish poisoning				+
A. taylori	Discoloration	+	+	ho	
Amphidinium carterae	Ichthyotoxic haemolytic			ho	
Cochlodinium polykrikoides	Ichthyotoxic	+			
Coolia monotis	Cooliatoxin producer	+		ho	

Dinophysis acuminata	Diarrheic shellfish poisoning	?			
D. acuta	Diarrheic shellfish poisoning	?			
D. caudata	Diarrheic shellfish poisoning	?			
D. tripos	Diarrheic shellfish poisoning	?			
Gymnodinium catenatum	Paralytic shellfish poisoning	+	+	ho/he	
G. pulchellum	Ichthyotoxic				
Gyrodinium corsicum	Ichthyotoxic				
Heterocapsa circularisquama	Ichthyotoxic		+		
Karenia brevis	Neurotoxic shellfish poisoning	+		ho/he	+
Lingulodinium polyedrum	Yessotoxin producer	+	+	he	
Noctiluca scintillans	Discoloration anoxia				
Ostreopsis heptagona	Ciguatera?				
O. lenticularis	Ostreotoxin producer				
O. mascarenensis	Toxic compound producer				
O. ovata	Palytoxin and ovatoxin-a	+		?	
O. siamensis	Ostreocine/ palytoxin	+		?	
Pfiesteria piscicida	Neurotoxic ichthyotoxic	+	+	ho	
P. shumwayae	Neurotoxic ichthyotoxic	+		he	
Prorocentrum lima	Diarrheic shellfish poisoning	+			
P. minimum	Ichthyotoxic		+		
Protoceratium reticulatum	Yessotoxin producer	+			
Protoperidinium crassipes	Azaspiracid producer				
Pyrodinium bahamense v. compressum	Paralytic shellfish poisoning	+	+	he ?	+

Table 1. Life cycles of dinoflagellate HAB species. The information is rewritten from the report of the LIFEHAB workshop and scientific references therein. (http : / / www . icm . csic . es / bio / projects / lifehab / LIFEHAB . pdf). The harmful effect of a species is listed, as are the known stages of its life history, such as resting or pellicle cysts. he = heterothallic; ho = homothallic.

In most of the investigated HAB dinoflagellates, resting cysts, or benthic stages, derive from sexual reproduction. However, generally, this is not the only route of cyst production in dinoflagellates, as asexual resting cysts have been documented for several species (Kremp and Parrow, 2006, Figueroa et al. 2009). In some dinoflagellate species, sexuality is facultative but in some others is an essential process in which a resting cyst is produced (Figure 2). Resting cyst formation is initiated by the fusion of two compatible gametes, forming a zygote that after some variable time in the water column, loses its mobility, encysts, and sinks to the sea floor, where it can survive in the sediments for several years (Figueroa and Garcés, 2010). Not only is the benthic environment more stable than the pelagic one, but the resting stage is much more resistant than the vegetative stage to unsuitable environmental conditions. Consequently, cysts can remain viable in the sediments for years, until biological and environmental conditions favor germination. Indeed, recent studies showed that cells retain the ability to germinate from resting stages even after a century of dormancy (Ribeiro et al., 2011). Certain species produce a different kind of cysts with thinner walls than resting cysts and less resistant to adverse environmental conditions. These cysts are referred to in the literature as temporal, pellicle, or ecdysal cysts (Bravo et al., 2010).

-

-

-

Bibliography

Alpermann T. J., Beszteri B., John U., Tillmann U. and Cembella A. D. (2009). Implications of life-history transitions on the population genetic structure of the toxigenic marine dinoflagellate *Alexandrium tamarense*. *Molecular Ecology* 18, 2122-2133. [Authors propose how the sexuality in dinoflagellates can modulate the population genetic structure]

Anderson D. M., Stock C. A., Keafer B. A., Nelson A. B., Thompson B., McGillicuddy D. J., Keller M., Matrai P. A. and Martin J. (2005). *Alexandrium fundyense* cyst dynamics in the Gulf of Maine. *Deep-Sea Research Part II-Topical Studies in Oceanography* 52, 2522-2542. [The paper describes large-scale cyst surveys to yield a cyst distribution map for the Gulf of Maine]

Anderson D. M. and Rengefors K. (2006). Community assembly and seasonal succession of marine dinoflagellates in a temperate estuary: The importance of life cycle events. *Limnology and Oceanography* 51, 860-873. [A study of the dinoflagellate community and their life cycle strategies]

Anglès S., Jordi A., Garcés E., Basterretxea G. and Palanques A. (2010). *Alexandrium minutum* resting cyst distribution dynamics in a confined site. *Deep-Sea Research Part II-Topical Studies in Oceanography* 57, 210-221. [In this paper the cyst distribution in an enclosed coastal area was quantified]

Bravo I., Figueroa R. I., Garcés E., Fraga S. and Massanet A. (2010). The intricacies of dinoflagellate pellicle cysts: The example of *Alexandrium minutum* cysts from a bloom-recurrent area (Bay of Baiona, NW Spain). *Deep-Sea Research Part II-Topical Studies in Oceanography* 57, 166-174. [This paper describes a new terminology and understanding for the pellicle cysts in dinoflagellates]

Chepurnov VA, Mann DG, Sabbe K, Vyverman W (2004) Experimental studies on sexual reproduction in diatoms. International Review of Cytology 237:91-154 [A review on the sexual development in diatoms]

D'Alelio D., d'Alcala M. R., Dubroca L., Sarno D., Zingone A. and Montresor M. (2010). The time for sex: A biennial life cycle in a marine planktonic diatom. *Limnology and Oceanography* 55, 106-114. [A study on the in situ sex development in planktonic diatoms]

Dale B. (1983). Dinoflagellate resting cysts: "benthic plankton". In Fryxell, G. A. (ed), In: *Survival Strategies of the Algae.* Cambridge University Press, Cambridge, pp. 69-136. [This paper reviews the state-of-the-art of resting cysts]

Davidovich N. A. and Bates S. S. (2002). Pseudo-nitzschia life cycle and the sexual diversity of clones in diatom populations. In Garcés, E., Zingone, A., Dale, B., Montresor, M. and Reguera, B. (eds), LIFEHAB Workshop: Life history of microalgal species causing harmful algal blooms. Luxembourg: Office for the Official Publications of the European Commission, pp. 31-36. [This paper reviews the state-of-the-art of the life cycle knowledge in a diatom genus]

Edvardsen B. (2002). Life cycle strategies in the haptophyte genera *Chrysochromulina* and *Prymnesium*. In Garcés, E., Zingone, A., Montresor, M., Reguera, B. and Dale, B. (eds), LIFEHAB: Life histories of microalgal species causing harmful blooms. Luxembourg: Office for the Official Publications of the European Commission, pp. 67-70. [This paper reviews the state-of-the-art of the life cycle knowledge in a haptophyte genus]

Eilertsen H. C. W., T. 1998. (1998). A model of *Alexandrium* population dynamics, Ed, Vol Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO. [This paper is focusing on the population dynamics of a toxic dinoflagellate genus]

Estrada M., Arin L., Blasco D., Blauw A., Camp J., Garcés E., Sampedro N., Vila M. (2008). Ø. Moestrup et al (Eds). A fuzzy logic model for *Alexandrium* proliferations in harbours of the Catalan coast. Proceedings of the 12th International Conference on Harmful Algae. ISSHA and IOC of UNESCO 2008. pp. 111-113. Description of a fuzzy logic model of the intensity of HAB events caused by *Alexandrium minutum* in a typical Mediterranean harbour. [A modeling study on a toxic dinoflagellate genus focusing in the life cycle transitions]

Estrada M., Sole J., Anglès S. and Garcés E. (2010). The role of resting cysts in *Alexandrium minutum* population dynamics. *Deep-Sea Research Part II-Topical Studies in Oceanography* 57, 308-321. [A modeling study on a toxic dinoflagellate genus focusing in the life cycle transitions]

Figueroa R. I. and Bravo I. (2005). Sexual reproduction and two different encystment strategies of *Lingulodinium polyedrum* (Dinophyceae) in culture. *Journal of Phycology* 41, 370-379. [This paper focuses on the life cycle of a toxic dinoflagellate species and presenting new pathways]

Figueroa R. I., Bravo I. and Garcés E. (2005). Effects of nutritional factors and different parental crosses on the encystment and excystment of *Alexandrium catenella* (Dinophyceae) in culture. *Phycologia* 44, 658-670. [This paper focuses on the life cycle of a toxic dinoflagellate species]

Figueroa R. I., Bravo I. and Garcés E. (2006a). Multiple routes of sexuality in *Alexandrium taylori* (Dinophyceae) in culture. *Journal of Phycology* 42, 1028-1039. [This paper focuses on new pathways of the life cycle of a toxic dinoflagellate species]

Figueroa R. I. and Rengefors K. (2006). Life cycle and sexuality of the freshwater raphidophyte *Gonyostomum semen* (Raphidophyceae). *Journal of Phycology* 42, 859-871. [This paper focuses on the life cycle of a noxious raphidophyte species]

Figueroa R. I., Rengefors K. and Bravo I. (2006b). Effects of parental factors and meiosis on sexual offspring of *Gymnodinium nolleri* (Dinophyceae). *Journal of Phycology* 42, 350-362. [This paper focuses on sexual life cycle of a toxic dinoflagellate species modulated by the parental factors]

Figueroa R. I., Garcés E. and Bravo I. (2007). Comparative study of the life cycles of *Alexandrium tamutum* and *Alexandrium minutum* (Gonyaulacales, Dinophyceae) in culture. *Journal of Phycology* 43, 1039-1053. [This paper focuses on the life cycle of two toxic dinoflagellate species, morphologically similar]

Figueroa R. I., Bravo I. and Garcés E. (2008a). The life significance of sexual versus asexual cyst formation in the life cycle of the noxious dinoflagellate *Alexandrium peruvianum* (Dinophyceae) in culture Harmful Algae 7, 653-663. [This article presents the importance of the asexual versus sexual phase on the life cycle of two toxic dinoflagellate species]

Figueroa R. I., Bravo I., Ramilo I., Pazos Y. and Moroño A. (2008b). New life-cycle stages of *Gymnodinium catenatum* (Dinophyceae): laboratory and field observations. *Aquatic Microbial Ecology*

52, 13-23. [This article presents new stages of the life cycle of on toxic dinoflagellate species in natural samples]

Figueroa R. I. and Garcés E. (2010). Dinoflagellate Life Cycles, Ed K. Schulz, Vol http : // tolweb . org / articles / ? article _ id = 5512 in The Tree of Life Web Project, http://tolweb.org/[A review of the state-of-the-art of the dinoflagellate life cycles]

Franks P. (1997). Models of harmful algal blooms. *Limnology and Oceanography* 42, 1273-1282. [A review of the state-of-the-art of the modeling studies on a harmful species]

Garcés E., Bravo I., Vila M., Figueroa R. I., Masó M. and Sampedro N. (2004). Relationship between vegetative cells and cyst production during *Alexandrium minutum* bloom in Arenys de Mar harbour (NW Mediterranean). *Journal Plankton Research* 26, 1-9. [This paper presents the in situ encystment pattern of one toxic dinoflagellate species]

Garcés E., Montresor M., Lewis J., Rengefors K., Anderson D. M. and Brath H. (2010). Preface for the special issue on Phytoplankton Life Cycles and Their Impacts on the Ecology of Harmful Algal Bloom. *Deep-Sea Research Part II-Topical Studies in Oceanography* 57, 159-161. [This paper presents an special issue of 14 papers by specialists on life cycles]

Garcés E., Zingone A., Montresor M., Reguera B. and Dale B. (2002). LIFEHAB: Life histories of microalgal species causing harmful blooms. Luxembourg: Office for the Official Publications of the European Commission.[This book reviews the state-of-the-art of the knowledge of the life cycles of harmful algal species]

Garcés E. and Camp J. (2012). Habitat changes in the Mediterranean Sea and the consequences for Harmful Algal Blooms formation. In “Life in the Mediterranean Sea: A look at habitat changes” Noga Stambler editor, Nova Science Publishers, Inc. New York, US, ISBN: 978-1-61209-644-5, pp. 519-541 .[This chapter book reviews the knowledge of the small scale blooms in the Mediterranean Sea in relation to coastal habitat changes]

Han M. S., Kim Y. P. and Cattolico R. A. (2002). *Heterosigma akashiwo* (Raphidophyceae) resting cell formation in batch culture: Strain identity versus physiological response. *Journal of Phycology* 38, 304-317. [This paper focuses on physiological response of the sexual phase in a Raphidophyceae]

Hense I. and Beckmann A. (2006). Towards a model of cyanobacteria life cycle—effects of growing and resting stages on bloom formation of N2-fixing species. *Ecological Modelling* 195, 205-218. [A modeling study on a toxic dinoflagellate genus focusing in the life cycle transitions]

Hense I. (2010). Approaches to model the life cycle of harmful algae. *Journal of Marine Systems* 83, 108-114. [A study centerd on cyanobacteria life cycle models]

Hense I. and Beckmann A. (2010). The representation of cyanobacteria life cycle processes in aquatic ecosystem models. *Ecological Modelling* 221, 2330-2338. [An overview on the application of models to microalgal life cycles]

Hense I. and Burchard H. (2010). Modelling cyanobacteria in shallow coastal seas. *Ecological Modelling* 221, 238-244. [A study on cyanobacteria life cycle models]

Holtermann K. E., Bates S. S., Trainer V. L., Odell A. and Armbrust E. V. (2010). Mass sexual reproduction in the toxigenic diatoms *Pseudo-nitzschia australis* and *P. pungens* (Bacillariophyceae) on the Washington coast, USA. *Journal of Phycology* 46, 41-52. [This article presents sexuality on diatoms in natural samples]

Iglesias-Rodriguez M. D., Schofield O. M., Batley J., Medlin L. K. and Hayes P. K. (2006). Intraspecific genetic diversity in the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae): The use of microsatellite analysis in marine phytoplankton population studies. *Journal of Phycology* 42, 526-536. [In this work genetic diversity on one species of Prymnesiophyceae was presented using molecular markers]

Impai I. and Itoh K. (1988). Cysts of *Chatonella antiqua* and *C. marina* (Raphidophyceae) in sediments of the Inland Sea of Japan. *Bulletin of the Plankton Society of Japan* 35, 35-44. [A study on the resting cyst production of Raphidophyceae]

Jordi A., Basterretxea G., Casas B., Anglès S. and Garcés E. (2008). Seiche-forced resuspension events in a Mediterranean harbour. *Continental Shelf Research* 28, 505-515. [This paper presents how physical forcing modulate harmful algal bloom dynamics in enclosed coastal systems]

Kononen K. (2002). Life cycles in cyanobacteria. In Garcés, E., Zingone, A., Montresor, M., Reguera, B. and Dale, B. (eds), LIFEHAB: Life histories of microalgal species causing harmful algal blooms. 12. European Commission, Luxembourg, pp. 85-86. [This paper reviews the state-of-the-art of the knowledge of the life cycle of cyanobacteria]

Kremp A. and Heiskanen A. S. (1999). Sexuality and cyst formation of the spring-bloom dinoflagellate *Scrippsiella hangoei* in the coastal northern Baltic Sea. *Marine Biology* 134, 771-777. [This paper studies sexual cycles of target dinoflagellate species in the Baltic sea]

Kremp, A. and Parrow, M. W. 2006 Evidence for asexual resting cysts in the life cycle of the marine peridinoid dinoflagellate, *Scrippsiella hangoei*. *Journal of Phycology*, 42, 2, 400-409. [This paper propose an asexual route for the resting cyst of target dinoflagellate species in the Baltic Sea]

Kremp, A. Rengefors, K. and Montresor, M. (2009) Species-specific encystment patterns in three Baltic cold-water dinoflagellates: The role of multiple cues in resting cyst formation. Limnol Oceanogr 54: 1125-1138. [This paper present how sexual differentiation and cyst formation of non-toxic *Biecheleria baltica* (*W. halophila*) is initiated at growth stimulating conditions]

Lancelot C. (1995). The mucilage phenomenon in the continental coastal waters of the North Sea. *Science of the Total Environment* 165, 83-102. [This paper presents noxious effects caused by microalgal mucilage in a costal system]

Lancelot C., Rousseau V., Schoeman S. and Becquevort S. (2002). On the ecological role of the different life forms of Phaeocystis. In Garcés, E., Zingone, A., Montresor, M., Reguera, B. and Dale, B. (eds), LIFEHAB: Life histories of microalgal species causing harmful blooms. Luxembourg: Office for the Official Publications of the European Commission, pp. 67-70. [This paper reviews the importance of life cycle stages of *Phaeocystis* in their bloom dynamics]

Li Y., He R. Y., McGillicuddy D. J., Anderson D. M. and Keafer B. A. (2009). Investigation of the 2006 *Alexandrium fundyense* bloom in the Gulf of Maine: In-situ observations and numerical modeling. *Continental Shelf Research* 29, 2069-2082. [The paper presented a case study of cyst surveys and a modeling study of a dinoflagellate species]

Lynch D. R., McGillicuddy D. J. and Werner F. E. (2009). Skill assessment for coupled biological/physical models of marine systems. *Journal of Marine Systems* 76, 1-3. [A study on modeling]

Mann D. G. (2002). Life cycles in diatoms. In Garcés, E., Zingone, A., Montresor, M., Reguera, B. and Dale, B. (eds), LIFEHAB: Life histories of microalgal species causing harmful blooms. Luxembourg: Office for the Official Publications of the European Commission, pp. 13-26. [This reviews the state-of-the-art of the diatom life cycles]

Margalef R. (1994). Diversity and biodiversity. Their possible meaning in relation with the wish for sustainable development. *Anais da Academia Brasileira de Ciencais* 66, 3-14. [This paper describes concepts about diversity and biodiversity and their implications]

McGillicuddy D. J., Anderson D. M., Lynch D. R. and Townsend D. W. (2005). Mechanisms regulating large-scale seasonal fluctuations in *Alexandrium fundyense* populations in the Gulf of Maine: Results from a physical-biological model. *Deep-Sea Research Part II*-Topical Studies In *Oceanography* 52, 2698-2714. [A study on modeling of one harmful species]

McGillicuddy D. J. (2010). Models of harmful algal blooms: Conceptual, empirical, and numerical approaches. *Journal of Marine Systems* 83, 105-107. [This paper reviews the application of models in the harmful algal species]

Nakamura Y., Umemori T., Watanabe M., Kulis D. M. and Anderson D. M. (1990). Encystment of *Chattonella antiqua* in laboratory cultures. *Journal of the Oceanographical Society of Japan* 46, 35-43. [This paper describes encystment process in laboratory of one species]

Quijano-Scheggia S., Garcés E., Andree K., Fortuño J. M. and Camp J. (2009). Homothallic auxosporulation in *Pseudo-nitzschia brasiliana* (Bacillariophyta). *Journal of Phycology* 45, 100-107.

[This paper describes the self-mating capability for the completion of the sexual process in a diatom species]

Ribeiro S., Berge T., Lundholm N., Andersen T. J., Abrantes F. and Ellegaard M. (2011). Phytoplankton growth after a century of dormancy illuminates past resilience to catastrophic darkness. *Nature Communication* 2, 311. [This paper describes long survival of the phytoplankton species in the sediments through the resting cyst stage]

Rousseau V., Chrétiennot-Dinet M. J., Jacobsen A., Verity P. and Whipple S. (2007). The life cycle of *Phaeocystis*: state of knowledge and presumptive role in ecology. *Biogeochemistry* 83, 29-47. [This paper describes the new life cycle of one species]

Rynearson T. A. and Armbrust E. V. (2004). Genetic differentiation among populations of the planktonic marine diatom *Ditylum brightwellii* (Bacillariophyceae). *Journal of Phycology* 40, 34–43. [This paper presents the population genetic structure for the planktonic diatom]

Sarno D., Zingone A. and Montresor M. (2010). A massive and simultaneous sex event of two *Pseudo-nitzschia* species. *Deep-Sea Research Part II-Topical Studies in Oceanography* 57, 248-255. [This paper describes sexual process in nature of one diatom species]

Steidinger K. A. (1975). Implications of dinoflagellate life cycles on initiation of *Gymnodinium breve* red tides. *Environmental letters* 9, 129-139. [This paper describes the importance of the life cycle stage of one species for the bloom initiation]

Steidinger K. A. and Garcés E. (2006). Importance of life cycles in the ecology of harmful microalgae. In Graneli, E. and Turner, J. T. (eds), *Ecology of Harmful Algae*. 189. Springer-Verlag Berlin, Berlin, pp. 37-49. [This paper reviews the importance of life cycle stages in the bloom dynamics of the harmful algal species]

Suikkanen S., Kaartokallio H., Laamanen M., Rintala J. M. S. and Huttunen M. (2010). Life cycle strategies of bloom-forming, filamentous cyanobacteria in the Baltic Sea. *Deep Sea Research Part II-Topical Studies in Oceanography* 57, 199-209. [This paper describes life cycle stages of cyanobacteria]

Wall D. (1971). Biological problems concerning fossilizable dinoflagellates. *Geoscience and Man* 3, 1-15. [This paper reviews the importance of resting cysts]

Wyatt T. and Jenkinson I. R. (1997). Notes on *Alexandrium* population dynamics. *Journal of Plankton Research* 19, 551-575. [This paper describes a conceptual model of one dinoflagellate species based on the life cycle stages]

Yamaguchi M. and Imai I. (1994). A microfluorometric analysis of nuclear DNA at different stages in the life history of *Chattonella antiqua* and *Chatonella marina* (Raphidophyceae). *Phycologia* 33, 163-170. [This paper clarify the life cycle stages of two harmful algal species]

Yamamoto T., Seike T., Hashimoto T. and Tarutani K. (2002). Modelling the population dynamics of the toxic dinoflagellate *Alexandrium tamarense* in Hiroshima Bay, Japan. *Journal of Plankton Research* 24, 33-47. [This paper presents a modeling study of one dinoflagellate species]

Biographical Sketches

Esther Garcés, has a PhD in Marine Sciences from the University of Barcelona. As a marine biologist, she is interested in plankton dynamics and physical-biological interactions in marine systems, particularly noxious and toxic phytoplankton species, their abundance and activity, and the ecosystem effects of their proliferations. This involves the study of these species and the factors that regulate their abundance. The focus of Esther's studies has been the life cycles and strategies of these species, empirical measures of their growth and loss rates, and their cell cycle dynamics. The necessity to revise the life cycle and its role in the capacity to maintain and to produce blooms gave place to European funding allocated as part of the 5th and 6th Framework Programmes (LIFEHAB, STRATEGY, SEED) and international, national and regional funding. Esther coordinated and participated in these studies of the adaptive strategies of the species. Currently, Esther is serving in the international panel, in the Steering Committee of International Society for the Study of Harmful Algae, ISSHA (2010-now). More recently, the international scope of our research projects and their broad support are reflected in Esther's participation in expert panels involved in the formulation of the European Water Framework Directive and the more recent European

Marine Strategy Directive. This has extended Esther's input to the field of environmental law and has thus enabled Esther's team to actively influence environmental policy and promote environmental conservation.

Rosa Figueroa, has a degree in Marine Sciences from the University of Vigo (Spain), with specialization in marine biology. Rosa did PhD between the Spanish Institute of Oceanography (IEO) in Vigo and the University of Lund (Sweden), university and got PhD in Limnology and Marine Ecology (2005), with a thesis totally focused on the description and study of sexual stages and factors promoting resting cyst formation in 4 species of toxic marine microalgae responsible for Harmful Algae Blooms. These studies allowed Rosa to obtain a prize as young scientific researcher in 2008 from the International Society for the Study of Harmful Algae Blooms (ISSHA). Although Rosa's research continues focusing on this topic, Rosa's main objective moved to the understanding of the genetic regulation controlling the life cycle transitions undergone by these algae. Nowadays, Rosa is an assistant professor at Lund University, and coordinator of two National projects dealing with the study of the genetic changes undergone during the shift from asexual to sexual reproduction in dinoflagellates, and on the study of the genome and species boundaries in a genus of algae parasites. The first project objective is to practically use the knowledge gathered during these years to make possible the identification of sexual stages in the National Monitoring Programs around Europe, making feasible the early detection of bloom initiation and collapse, and cyst beads localization. Previously, Rosa participated in European projects as well as in Swedish National projects, all of them focused on the study of algae life cycle transitions and on its relevance for the management and forecasting of toxic algal outbreaks.

Marta Estrada holds degrees in Biology and in Medicine and Surgery from the University of Barcelona, as well as a Ph. D. in Biology. She is Research Professor (Profesora de Investigación) of the Consejo Superior de Investigaciones Científicas (CSIC) and is a member of the staff of the Institut de Ciències del Mar, CMIMA (CSIC), Barcelona, Spain. Estrada has more than 30 years of experience in biological oceanography. Her career has focused on marine phytoplankton ecology and her primary research interests are the diversity and dynamics of phytoplankton communities, and the interactions between physical and biological processes in the pelagic ecosystem. Her work has taken her on oceanographic cruises in the Mediterranean, Atlantic, Pacific, and Southern Oceans. She has served in numerous national and international panels, including the Steering Committee (1999-2003) of GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms), an international program of SCOR-IOC. Estrada is a member of the Reial Acadèmia de Ciències i Arts of Barcelona and of the Institut d'Estudis Catalans. Currently, she is the Spanish representative for SCOR (Scientific Committee on Oceanic Research).