

# Chapter 8

## The Role of Life Cycle Characteristics in Harmful Algal Bloom Dynamics



Rhodora V. Azanza, Michael L. Brosnahan, Donald M. Anderson, Inga Hense, and Marina Montresor

### 8.1 Introduction

Many phytoplankton species have multiphasic life cycles that include stages with different morphologies, behaviours, and functional roles. Studies of life cycles under controlled conditions in the laboratory, observations in species' natural environments, and model simulations have all provided valuable insights on species-specific bloom dynamics and associated impacts. This chapter presents an overview of the role that life cycles play in the bloom dynamics of representative, diverse, toxic harmful algal bloom (HAB)-forming taxa: specifically, the dinoflagellates *Pyrodinium bahamense* and *Alexandrium fundyense*, diatom species of the genus *Pseudo-nitzschia*, and the cyanobacterium *Nodularia spumigena*. These are among the most widespread harmful algal species described, causing a range of impacts from human illness and death from ingestion of potent toxins via the food chain to fish and wildlife mortalities and ecosystem disruption. There are many other HAB species that cause these and other impacts, but the four species highlighted here are selected because features of their life cycles are representative of many different HAB species that undergo sexuality or have resting stages in their

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R.V. Azanza (✉)

The Marine Science Institute, University of the Philippines, Quezon City, Philippines

e-mail: [rvazanza@up.edu.ph](mailto:rvazanza@up.edu.ph)

M.L. Brosnahan • D.M. Anderson

Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

I. Hense

Institute for Hydrobiology and Fisheries Science, Center for Earth System Research and Sustainability, University of Hamburg, Hamburg, Germany

M. Montresor

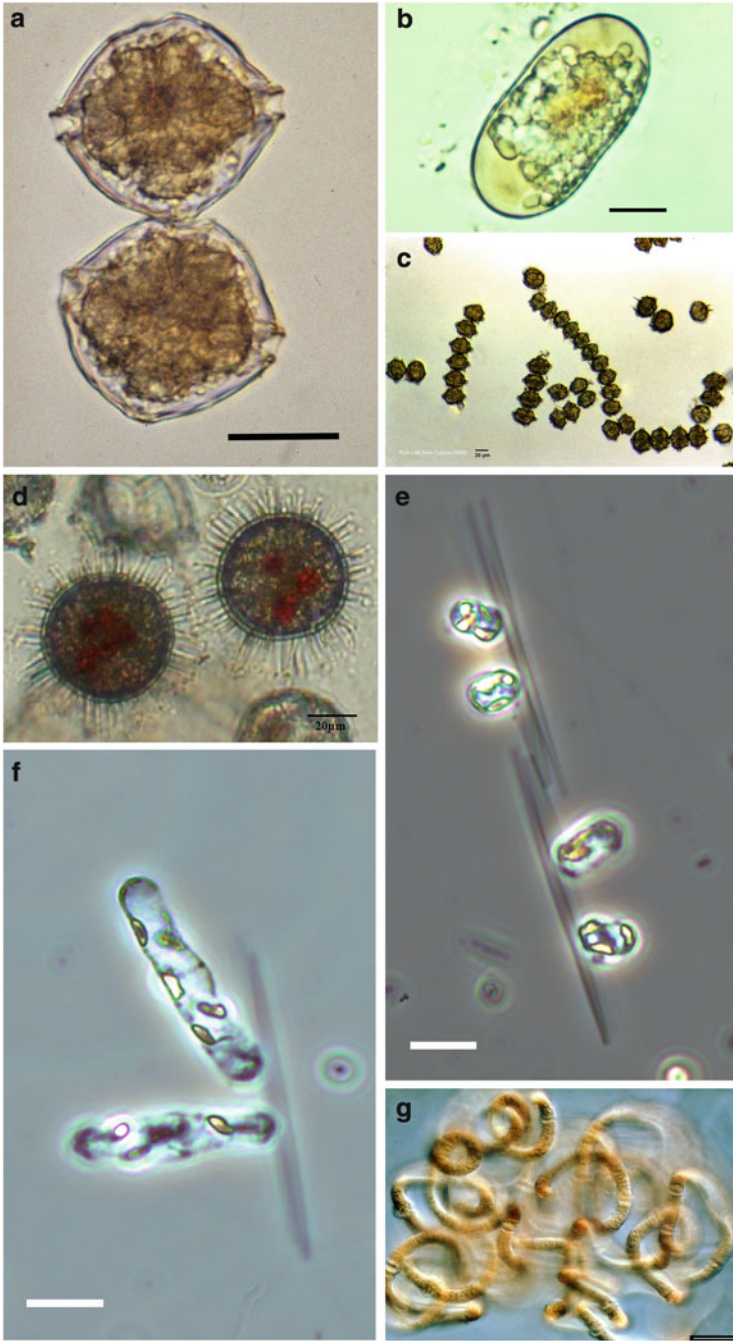
Integrative Marine Ecology Department, Stazione Zoologica Anton Dohrn, Naples, Italy

life cycles. *Pyrodinium* and *Alexandrium* are representative of cyst-forming dinoflagellates and illustrate some of the ways that dinoflagellate life cycles are adapted to tropical and temperate habitats, respectively. *Pseudo-nitzschia* species undergo sexuality, but have no resting stage, similar to many other diatoms, and *Nodularia* is an example of a bloom-forming, toxic cyanobacteria that form akinetes as a resting stage. Consistent with the comparative approach in Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB 2001), these four species are compared and contrasted to identify common and unique strategies for survival and proliferation within varied aquatic environments. This chapter also illustrates the research conducted under the GEOHAB Programme to clarify adaptive strategies of harmful species.

## 8.2 Dinoflagellates: *Alexandrium fundyense* and *Pyrodinium bahamense*

Dinoflagellates represent a disproportionate fraction of all HAB species and are further overrepresented among those shown to be expanding globally in recent decades (Anderson 1989; Smayda 1997). These patterns are attributable in large part to the meroplanktonic life cycles of these organisms (including both benthic and free-swimming stages). Benthic stages, particularly diploid and haploid cysts, enable many dinoflagellates to endure short- and long-term periods of adverse conditions and also facilitate dispersal through currents and other natural mechanisms, as well as anthropogenic processes such as global shipping and aquaculture transplantations (Hallegraeff 1998). Planktonic stages are similarly adaptable as swimming cells that can migrate to exploit gradients in nutrient and light availability or, for mixotrophic and kleptoplastic species, to locate and capture prey. These same swimming behaviours facilitate dispersal within coastal current systems and contribute to patterns of cyst deposition that sustain recurrent threats to public health and ecosystems. Here, we highlight research exploring the ecology and life cycle characteristics of two marine cyst-forming species, *A. fundyense* and *P. bahamense*.

*Alexandrium fundyense* (Fig. 8.1a) is one of multiple species within the *Alexandrium* genus that cause outbreaks of paralytic shellfish poisoning (PSP) in temperate, subtropical, and subpolar regions around the world and is one of three toxic species within the *A. tamarensis* species complex. Species boundaries within this subgroup were long delineated using morphological criteria including the presence/absence of chain formation and/or an apical pore within the 1' Kofoidian thecal plate. However, these criteria are now known to be polyphyletic (and therefore invalid), and the formerly recognized morphospecies designations *A. tamarensis*, *A. fundyense*, and *A. catenella* have been redefined or replaced using molecular characters that divide the complex into five distinct species (John et al. 2014). *A. fundyense* is the most widespread of these and is known to cause PSP on the east and west coasts of North and South America as well as in areas along the northeast Asian coast and in northern Europe (Lilly et al. 2007).



**Fig. 8.1** Various life cycle stages of four HAB species. (a) Vegetative cell pair after division and (b) resting cyst of *Alexandrium fundyense*, scale bars = 10  $\mu\text{m}$ ; (c) vegetative cells and (d) resting resting cells of another species; (e) vegetative cells of a third species; (f) vegetative cells of a fourth species; (g) resting cysts of a fifth species.

Like *A. fundyense*, *P. bahamense* (Fig. 8.1c) causes PSP through its synthesis of saxitoxins. It is identifiable by its Kofoidian plate pattern of (Po, Pi) 4', 6'', 6c, 8s, 6''', 2'''' and was first described from the Bahamas (Plate 1906). The species occurs in both the Atlantic-Caribbean and Indo-Pacific tropics (Bohm 1931; Steidinger et al. 1980), but early workers sometimes differentiated two varieties, *P. bahamense* var. *bahamense* and var. *compressum*, on the basis of cell shape. More thorough investigation by Balech (1985) failed to detect consistent morphological differences, however, and subsequent genetic analyses showed differentiation between Indo-Pacific and Atlantic-Caribbean populations but not morphotypes (Mertens et al. 2015). Fossil cysts of *P. bahamense* are called *Polysphaeridium zoharyii* and are widely distributed globally, but living populations of resting cysts appear to be restricted to Southeast Asia, the Gulf of California, the Caribbean, and Western Europe (Amorim and Dale 1998; Furio et al. 2012; Morquecho et al. 2014).

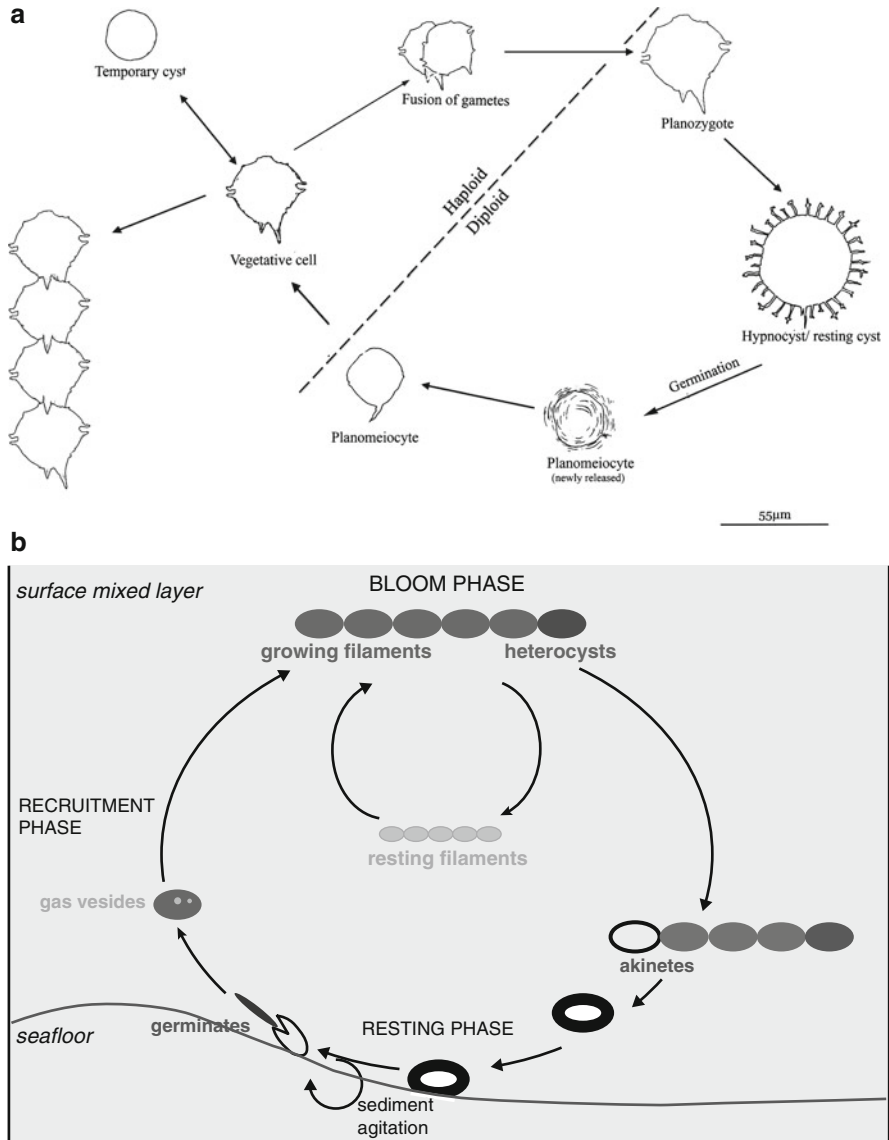
In several respects, *A. fundyense* and *P. bahamense* are highly similar—both are thecate, cyst formers that cause PSP through the synthesis of saxitoxins—but are also distinct in their phenology and geographical distribution. *P. bahamense* forms sustained, late summer/rainy season blooms and is primarily found in tropical regions, while *A. fundyense* impacts temperate and subpolar coasts during spring, summer, and fall seasons. The aim in choosing these two species is to present ways that their unique, species-specific adaptations within a single, common life cycle have enabled them to exploit very different climate regimes.

### 8.2.1 Life Cycle of Cyst-Forming Dinoflagellates

Both *A. fundyense* and *P. bahamense* (Fig. 8.2a) have haplontic life cycles in which motile, haploid, vegetative cells divide and proliferate within the plankton and, then, under certain conditions transform into gametes that then fuse to form swimming zygotic cells called planozygotes. These diploid planozygotes in turn transform into immobile resting cysts, which are sometimes called hypnocysts or hypnozygotes (Pfiester and Anderson 1987). *A. fundyense* resting cysts (Fig. 8.1b) are smooth, elongate, double-walled cells that are highly resistant to temperature, mechanical, and osmotic stresses. These characteristics enable *A. fundyense* cysts to remain viable for decades, particularly when lying within anoxic habitats

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**Fig. 8.1** (continued) cysts of *Pyrodinium bahamense*, scale bar = 20  $\mu\text{m}$ ; (e) young auxospores still attached to the empty/negative mating type gametangia joined in a chain and (f) more auxospores connected to the gametangial frustule of *Pseudo-nitzschia* cf. *delicatissima* from Gulf of Naples, scale bars = 10  $\mu\text{m}$ ; (g) filaments of *Nodularia spumigena*, scale bar = 30  $\mu\text{m}$ . Photos by D.M. Anderson (a and b), R.V. Azanza culture, photo taken by Y. Fukuyo (c), R.V. Azanza (d), Diana Sarno of Stazione Zoologica Anton Dohrn (e and f), Seija Hällfors of Finnish Environment Institute Syke (g)



**Fig. 8.2** Schematic representation of the life cycle of *Pyrodinium bahamense* (a), based on Azanza (1997) and *Nodularia spumigena* (b), modified after Hense and Beckmann (2006)

(Anderson et al. 1987; Feifel et al. 2015). The cysts' durability also facilitates their spread via a wide range of natural and anthropogenic vectors, the latter including dredging and sediment relocation, ballast water transport, and aquaculture (Hallegraeff and Bolch 1991; Anderson et al. 2012). *P. bahamense* resting cysts (Fig. 8.1d) in contrast are spherical and chorate, having trumpet-shaped processes

distributed over the cyst wall surface (Wall and Dale 1969). It remains to be shown to what extent *P. bahamense* cysts remain viable when displaced or buried through various mechanisms, but these cysts similarly are able to survive long periods in anoxic marine sediments (Azanza et al. 2004; Siringan et al. 2008). Both *P. bahamense* and *A. fundyense* cysts tend to accumulate in areas that collect fine sediment, leading to formation of “seedbeds” or areas of high cyst concentration that inoculate new blooms when cysts germinate (e.g., Anderson et al. 2014a).

Before transformation back to the haploid phase of the life cycle, diploid resting cysts must undergo a maturation process that can last several weeks or months, after which they may be stimulated to germinate, giving rise to a short-lived stage called a planomeiocyte that reverts back to the haploid, vegetative stage through meiotic divisions. Despite very different temperature regimes in their habitats, cyst maturation periods for both species are similar, 1–3 months for *A. fundyense* (Anderson and Morel 1979) and 2.5–3 months for *P. bahamense* (Corrales et al. 1995). For *Alexandrium*, the maturation interval is shortest at warmer temperatures. After completion of their initial maturation, *A. fundyense* resting cysts are known to cycle between germinable and non-germinable states: dormancy, a condition in which cysts are not responsive to ambient environmental conditions, and quiescence, a condition in which cysts will germinate if exposed to oxygen and elevated temperatures. In deepwater cyst seedbeds, the cycling of *A. fundyense* cysts between dormancy and quiescence is governed by an endogenous, circannual rhythm that ensures germination can only occur in spring (Anderson and Keafer 1987; Matrai et al. 2005). Within more seasonally variable inshore habitats, cysts may transition between the dormant and quiescent states in response to seasonal conditions (Anderson and Keafer 1987; Rathaille and Raine 2011). The precise control of transitions between states is yet to be described, but endogenous rhythmicity may be a “backup” adaptation, enabling germlings to best time their emergence when seasonal environmental signals are absent or muted (e.g., in deepwater habitats).

Both species can also form haploid (or asexual) pellicle cysts directly from the vegetative stage of the life cycle (e.g., Anderson and Wall 1978). Such pellicle cysts are able to revert back to the vegetative cell stage directly and on relatively short time scales (~1 day). The formation of this stage enables shallow water populations to weather and rapidly recover from transient, poor growth conditions during blooms (Pfiester and Anderson 1987; Azanza 1997). The formation and excystment from the temporary cyst stage is especially important for the dynamics of *P. bahamense* blooms (Onda et al. 2014) and is known to play a more significant role in the dynamics of some other *Alexandrium* HABs (e.g., Bravo et al. 2010).

Further differences between *A. fundyense* and *P. bahamense* include the propensity of vegetative cells to form chains and the nature of their gamete stages. *P. bahamense* commonly forms long chains of up to 16 cells in both natural populations and in cultures (Fig. 8.1c). *A. fundyense* on the other hand is often present only as single or paired cells though can occur in chains of up to eight cells. Isolates from these chain-forming *A. fundyense* populations tend not to form chains unless stimulated by turbulence (Sullivan et al. 2003). Gametes of the two species

differ in their size relative to progenitor vegetative cells. *P. bahamense* forms isogametes that are smaller than vegetative cells (20–25  $\mu\text{m}$  versus 25–45  $\mu\text{m}$  diameter). *A. fundyense* gametes may be similar in size to vegetative cells (30–35  $\mu\text{m}$  diameter) or smaller in different populations and are more variable in size, forming both isogamous and anisogamous mating pairs (Pfiester and Anderson 1987). Both species have a heterothallic mating system (i.e., clonal daughters will not pair), and gametes fuse to form nondividing planozygotes that grow progressively larger until encystment (diameter of 50–55  $\mu\text{m}$  in *P. bahamense* and  $>43$   $\mu\text{m}$  in *A. fundyense*).

## 8.2.2 Bloom Dynamics

### 8.2.2.1 Major Study Areas

Bloom dynamics are the result of a species' behaviour within its environment. Therefore, when reviewing the interactions between these species life cycles and their ecology, it is important to also consider the environments in which blooms of these species have been most heavily studied.

*Pyrodinium* blooms routinely affect areas throughout Southeast Asia (Furio et al. 2012 and references therein) but have been characterized most extensively in the Philippines, where the intensity of *Pyrodinium* blooms is often correlated with cyst dynamics, i.e., cyst availability/concentration, cyst bed location, cyst distribution by currents and waves, etc. (Villanoy et al. 1996; Azanza et al. 2004; Siringan et al. 2008; Azanza 2013). Sediment surveys have indicated that cysts can be found year round, especially in seedbed areas of high cyst concentrations (similar to *A. fundyense*). Increased rainfall triggers higher land-based nutrient discharge during southwest (SW) monsoon periods when temperature and salinity conditions also tend to be highly favourable for *Pyrodinium* growth and bloom development (29–32 °C and 26–30 salinity, respectively). In small embayments, such as Manila Bay and Sorsogon Bay (Philippines), there are sometimes massive, sustained blooms lasting weeks to months. Throughout the Philippines, blooms typically occur in late summer, a period that marks the start of SW monsoon when waters tend to be (at least initially) stratified. Within shallow systems like these, *Pyrodinium* often undergoes several cycles of transformation between its pellicle cyst stage and its vegetative stage during a single bloom period (Azanza 1997; Azanza et al. 2004; Onda et al. 2014). This life cycle behaviour enables *P. bahamense* to withstand shear stress associated with the high-energy SW monsoon. The bloom period ends with the beginning of northeast (NE) monsoon, when waters in the Philippines are more well mixed (Azanza and Taylor 2001; Azanza 2013).

The dynamics of *A. fundyense* blooms and associated outbreaks of PSP have been studied most intensively in the northwest Atlantic, along the coast of maritime Canada and within the Gulf of Maine (GOM), areas that span a broad continental

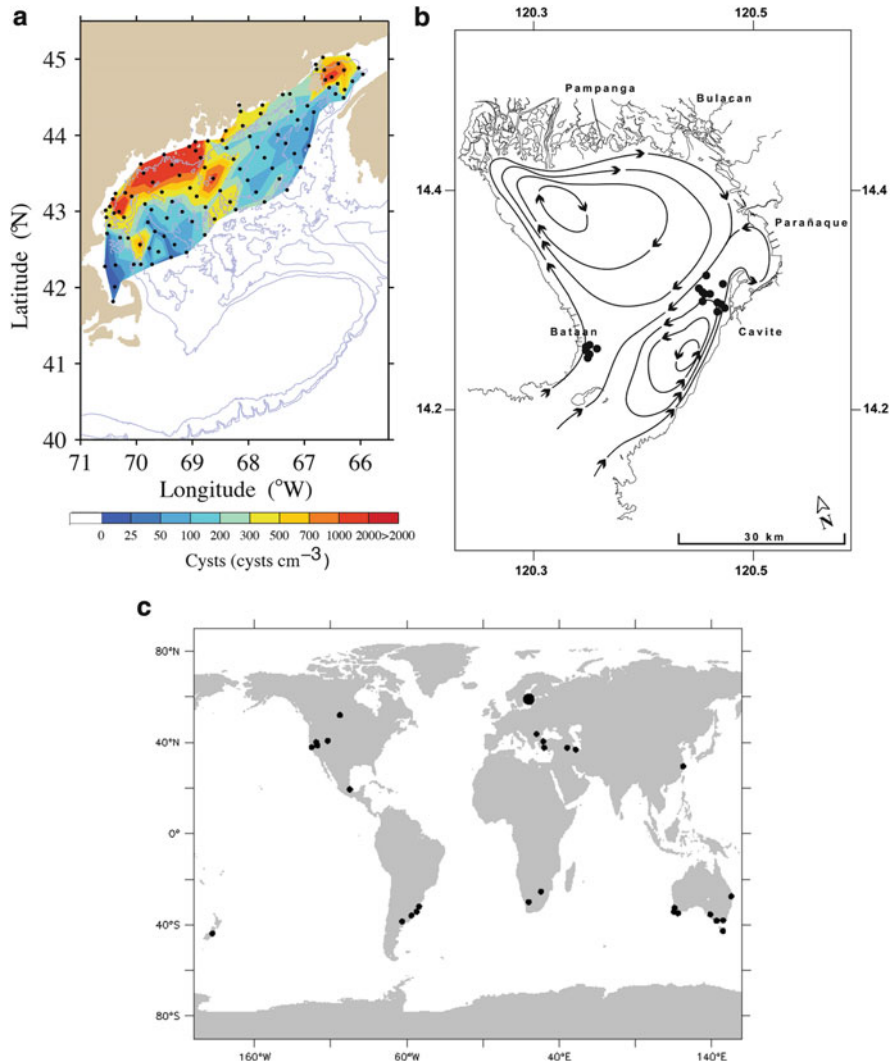
shelf sea and support productive shellfisheries. Within this region, coastal blooms extending for hundreds of kilometres along the coast annually cause toxicity in both nearshore and offshore shellfish beds (e.g., Anderson et al. 2014b). There are also inshore populations of *A. fundyense* that cause localized blooms within embayments only a few km<sup>2</sup> in size (Anderson 1997). These inshore blooms have been especially valuable in revealing details of life cycle transitions due to the localized or captive nature of their blooms, which can be studied from beginning to end, sometimes with novel in situ instruments that greatly enhance the frequency and resolution of observations [e.g., Brosnahan et al. 2014, 2015; see also Chap. 18, Glibert et al. (2018)].

### 8.2.2.2 Cyst Distributions and Initiation of Planktonic Blooms

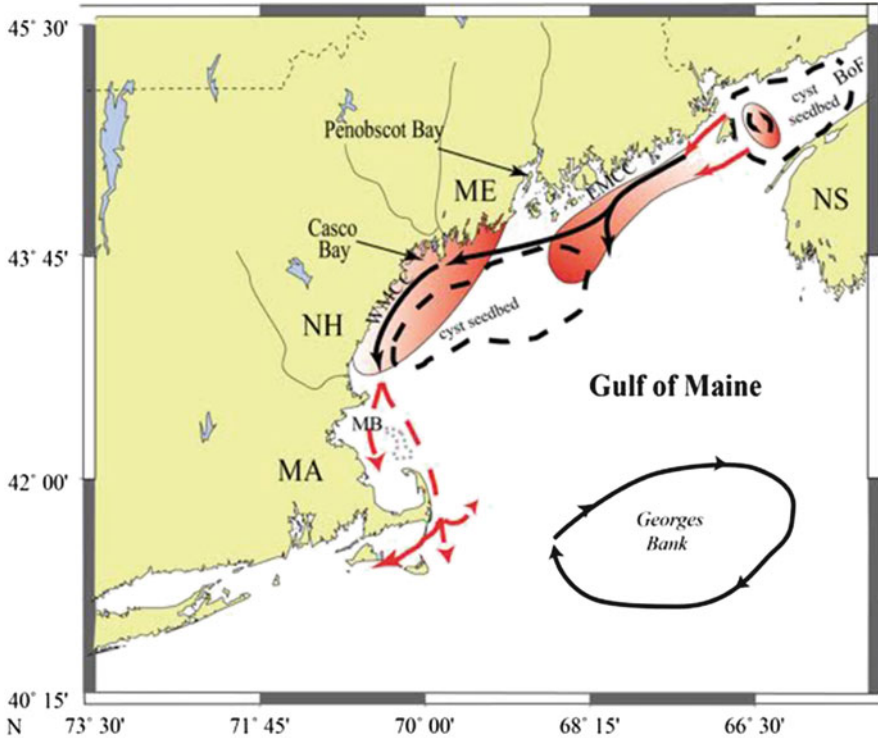
Study of any phytoplankton species on the geographical scale of coastal blooms is challenging because populations are patchy in space, depth, and time. In this respect, studies of cyst-forming dinoflagellates have had the advantage that significant insights into bloom ecology are possible through surveys of their immobile cysts, which are also typically concentrated in thin layers (TLs) at the sediment-water interface [see also Chap. 9, Raine et al. (2018)]. Such surveys of both *A. fundyense* and *P. bahamense* have documented large seedbeds that provide inoculums to major coastal blooms of these two species.

Within the GOM, the vast majority of *A. fundyense* cysts accumulate within two major seedbeds, one within the Bay of Fundy and the other offshore from the central Maine coast (Anderson et al. 2014a). These accumulation zones have been documented repeatedly through mapping cruises in 1997 and annually from 2004 to 2016 (Fig. 8.3a), and their persistence attributed to the combination of the region's bathymetry, sediment characteristics, currents, and annual replenishment from spring-summer blooms along the Maine coast. Still, there is significant interannual variability in total cyst abundance across these areas (up to tenfold between years) which is strongly correlated with geographic measures of bloom extent the subsequent year (e.g., the length of coastline closed due to shellfish toxicity or the southernmost latitude of shellfish closures). It is thus possible to use cyst abundance to empirically forecast the geographic extent of the forthcoming bloom (Anderson et al. 2014a). Statistical assessment of the GOM cyst distributions has further shown that many locations within the GOM harbour a relatively consistent proportion of its total cysts in a given year (Fig. 8.4). This discovery has led to development of a structure-based model of cyst distribution for estimation of the total number of cysts during interbloom periods (Solow et al. 2014). Guided by this model, annual cyst surveys could effectively allow future annual forecasts using a significantly smaller number of stations (e.g., 40% of those sampled in past surveys), greatly reducing the cost of future survey efforts. Similar approaches have great promise for other dinoflagellate species and regions but require multi-year data sets to establish common patterns of cyst abundance and distribution.





**Fig. 8.3** (a) Map of the mean *Alexandrium fundyense* cyst abundance in the Gulf of Maine, calculated for years 2004–2009, showing the two main cyst seedbeds; *black dots* are station locations (modified from Solow et al. 2014). (b) Map of Manila Bay (Philippines) showing cyst beds (*black dots*), sources of *Pyrodinium bahamense* blooms, distribution of which follows two cyclonic wind-driven current systems during the southwest monsoon (redrawn from Villanoy et al. 2006). (c) Occurrences of *Nodularia spumigena*; please note that this map is by no means complete; only those with clear evidence for *N. spumigena* reported in peer-reviewed English language journals are depicted; most reports stem from the past 35 years; historical evidence for *N. spumigena* blooms exists for the Baltic Sea, Australia, New Zealand, as well as inland salt lakes in the USA and Canada



**Fig. 8.4** Conceptual model of *Alexandrium fundyense* cyst and motile cell dynamics in the Gulf of Maine. Areas enclosed with dashed lines denote cyst seedbeds that provide inoculum cells. The shaded areas represent regions with growth and transport of motile cells, with darker shading denoting areas with the most dense cell accumulations. Black arrows show major currents within the eastern Gulf of Maine, and grey arrows show alternative current pathways. Modified from Anderson et al. (2014a)

Unlike *A. fundyense*, *P. bahamense* cysts are not known to occur in offshore seedbeds, but similar accumulations within inshore embayments are well documented. Within the Philippines, spatial and vertical surveys have documented highest concentrations of cysts in the innermost parts of Manila Bay, Sorsogon Bay, Malampaya Sound, and Juag Lagoon, areas where the sediments are mostly muddy and where mangrove stands are present (Corrales and Crisostomo 1996; Azanza et al. 2004; Siringan et al. 2008). The cysts that lie in the shallow areas where seedbeds do occur are susceptible to displacement by the high energies experienced during the NE monsoon. The newest of these displaced cysts, however, likely cannot germinate because of their obligatory maturation dormancy period of 2.5–3 months, approximately the same duration as the summer/inter-monsoon period that follows the SW monsoon, the periods when blooms typically occur and produce new cysts (Azanza 1997, 2013). Trends in *Pyrodinium* cyst and cell concentrations and a summary of physicochemical conditions in Manila Bay and

Sorsogon Bay during the different seasons have been previously reported, but relationships between cyst abundance and the timing and magnitude (if they exist) remain to be shown (Azanza 2013).

The physical resuspension of *P. bahamense* cysts contributes to the initiation of planktonic blooms, especially when resuspension events coincide with periods when *P. bahamense* is able to germinate. In the absence of such physical resuspension, germlings may also emerge directly from the near surface of the ocean bottom. Direct observation of such cyst emergence from cyst seedbeds has been difficult and remains an area for which new observational methodologies are needed. In situ cyst germination rates for *A. fundyense* have been estimated using various techniques like plankton emergence traps (PETs), but average excystment percentages are 10–20 times lower than laboratory-derived rates (Ishikawa et al. 2007). Presumably this difference reflects challenges in re-creating the chemical and physical conditions that cysts experience in sediments (e.g., a tortuous path through sediment particles for germling cells to reach the water column). Germling cells reared in the dark (similar to seedbeds at 100–150 m in the GOM) have been shown to have relatively poor survival (28% after 7 days, the estimated time of reaching the euphotic zone in a 100 m water column; Vahtera et al. 2014). Combined, the PET and germling results suggest that only a small fraction of resting cysts progress to the vegetative stage of the life cycle but also indicate a need for further study of these critical processes.

Similar to the case of *P. bahamense*, initiation of *A. fundyense* blooms may rely in part on physical resuspension of cysts. In the GOM and many other regions, substantial numbers of resting cysts occur within benthic nepheloid layers (BNLs). BNLs form through the action of near-bottom currents and are characterized by high concentrations of resuspended sediments, detritus, and organisms, sometimes in layers tens of metres thick. *A. fundyense* cyst abundance is enriched within BNLs but also quite patchy, varying spatially by three orders of magnitude, features that make surveys of BNLs for *A. fundyense* cysts challenging (Pilskaln et al. 2014). Still, cyst fluxes recorded by near-bottom sediment traps, maps of cyst abundance within surface sediment, and estimated BNL cyst inventories suggest that the residence time of cysts within sediments varies across the GOM, such that cysts in the eastern gulf have shorter residence times than those in the western gulf. The latter finding has significant implications especially for understanding the initiation of blooms that occur in the southern GOM/Georges Bank region, areas that are downcurrent from the primary GOM seedbeds within the Bay of Fundy and off the mid-Maine coast.

### 8.2.2.3 Bloom Development and Transport

*Alexandrium fundyense* blooms tend to occur in two major habitats: inshore embayments and in open coastal waters. The dynamics of blooms in these distinct habitats have been explored through development of spatially explicit models that incorporate hydrography and physical forcing in addition to biological models of

germination, cell division, grazing, and other loss processes. Results from these studies have demonstrated the ways in which inshore and open coastal blooms differ with respect to the life cycle processes and behaviours that are principally responsible for their observed dynamics.

Within inshore areas like the Nauset Marsh system (Cape Cod, MA, USA), retention of bloom populations occurs behind shallow sills and other bathymetric barriers to dispersal (Anderson and Stonzenbach 1985; Crespo et al. 2011). This retentive behaviour arises from surface avoidance by vegetative stage cells during their daily vertical migrations and is reinforced by strong salinity- and temperature-driven density gradients that limit wind-driven vertical mixing and dispersal of cells. The timing of blooms and their harmful impacts is most strongly driven by temperature, which controls the rate of *A. fundyense* division. Unlike *P. bahamense* blooms in Manila Bay or coastal *A. fundyense* blooms (described below), the intensity and timing of inshore blooms are not dependent on cyst distribution or abundance (Ralston et al. 2015).

In more open, coastal systems like the GOM, cyst distributions, freshwater plumes, meteorological conditions, and circulation patterns all play significant roles in determining the intensity of harmful impacts, which are felt most strongly when expansive offshore blooms are concentrated near the coast by downwelling favourable conditions (Franks and Anderson 1992; Fauchot et al. 2008). For example, cells germinated from the two GOM cyst beds are advected in the alongshore direction from east to west in a coastal current. Growth of the vegetative cells is limited primarily by temperature from April through June throughout the GOM, whereas nutrient limitation occurs in July and August in its western areas. Thus, an observed seasonal shift in the bloom's centre of mass from west to east can be explained by changing growth conditions: early in the season, growth is more rapid in the west due to warmer temperatures there and then later more rapid in the east due to increasing nutrient limitation in the west (McGillicuddy et al. 2005).

Further explorations of GOM bloom dynamics have applied a coupled physical-biological model that is parameterized using data from several decades of observations and experiments (Stock et al. 2005; McGillicuddy et al. 2005; He et al. 2008; Li et al. 2009). The model is a nested hydrodynamic model of the GOM that includes a biological submodule. Realistic simulations of bloom development are possible using observed cyst distributions, cyst germination rates (Anderson et al. 2005), vegetative cell growth rates, and continuous real-time river flow and hydrographic data (e.g., He et al. 2008).

A large driver of the GOM model's success is the system's dependence on cyst abundance and behaviour. By virtue of their endogenous germination rhythm, the timing of bloom inoculation is well constrained, especially in comparison to more variable inshore blooms. Total cyst abundance (measured in the fall or winter) appears to be a first-order predictor of GOM bloom magnitude the following year (McGillicuddy et al. 2011). This is supported by correlations between annual cyst abundance and the geographic extent of PSP closures along the GOM coast in subsequent bloom seasons, a relationship that may be related to diminished vegetative division in these populations relative to inshore blooms (Anderson et al.

2014a). Physical and chemical processes are still likely to modulate bloom development in the GOM and may override the cyst-PSP relationship, as happened in 2010 when an anomalously warm and freshwater mass entered the GOM and likely suppressed development of that year's *A. fundyense* bloom (McGillicuddy et al. 2011).

In a similar manner, *Pyrodinium* cell and cyst movements follow wind velocity directions and cyclonic trends associated with the circulation of Manila Bay (Fig. 8.3b). Blooms form via two primary mechanisms: (1) an inoculum from cyst beds in the west that is advected along the west-northwest coast, and (2) a second inoculum from cyst beds in the southeast that spreads across the east-southeast area (Villanoy et al. 2006; Azanza 2013). Numerical models of *Pyrodinium* blooms in Manila Bay (Philippines) have been developed from physicochemical and biological data sets collected from 1994 to 2002 as well as from laboratory experiments examining *P. bahamense* behaviour (Villanoy et al. 1996, 2006; Azanza et al. 2004). Three-dimensional and spatially explicit models have been used to explore the role of *Pyrodinium* life cycle processes including reproduction, mortality, encystment, and excystment in Sorsogon Bay (Yñiguez et al. 2012). Forced by seasonally varying heat, freshwater (precipitation, runoff), and momentum fluxes (wind), temperature, salinity, nutrient, and velocity fields are simulated, which, combined with turbulent mixing and convection, affect the distribution, transport, and behaviour of *P. bahamense* cells (Villanoy et al. 2006; Azanza 2013). The model output mirrors features of *Pyrodinium* blooms in this area, which generally develop at the onset of SW monsoon and end with the onset of the NE monsoon.

#### 8.2.2.4 Sexual Induction and Cyst Formation

Historically, investigations of resting cyst production by *A. fundyense*, *P. bahamense* (Corrales et al. 1995), and many other dinoflagellates have been culture based and have relied on nutrient starvation to induce sex. Specific limiting nutrients that induce resting cyst formation by *A. fundyense* include nitrogen (N), phosphorus (P), and iron (Anderson et al. 1984; Doucette et al. 1989). These approaches are consistent with a prevailing paradigm in the study of microbial eukaryotes that transitions from asexual reproduction to sexual fusion are only advantageous when a population's environment no longer supports continued cell division (Margulis and Sagan 1985). However, evidence that nutrient limitation induces field populations to encyst is limited.

Studies of localized, inshore *A. fundyense* blooms often report the occurrence of sexual stages (gametes and planozygotes) when measured nutrient concentrations would be expected to support continued division by vegetative cells (e.g., Anderson et al. 1983; Anglès et al. 2012; Brosnahan et al. 2015). Linkage of nutrient stress and sexual induction in offshore blooms has been similarly challenging. A simple nutrient-based induction model was able to replicate the cyst deposition zones in the Bay of Fundy and western GOM (McGillicuddy et al. 2005). However, direct

linkage of sexual induction and nutrient stress was not supported in the only direct observation of encystment in this system, a remarkable red water event that occurred in 2009. Concentrations of N and P during that event should have been sufficient to support continued division (Townsend et al. 2014), but instead, the population was dominated by planozygotes, dissipated within 1 week, and was successfully linked to a major deposition of new resting cysts during a subsequent benthic survey (McGillicuddy et al. 2014).

An alternative stimulus for sexual induction may be high cell concentrations. Recent intensive investigations of *A. fundyense* blooms in the Nauset Marsh system (Cape Cod, MA USA) have shown that growing degree days, a simple temperature-based metric, can collapse interannual and spatial variability in the timing of both the development and peak of Nauset blooms (Ralston et al. 2014). This metric relies on the linear response of *A. fundyense* population growth rate to increasing temperature, a relationship that has been shown through both observed accumulation rates within the Nauset ponds and through deployments of an Imaging FlowCytobot (IFCB), a submersible imaging-in-flow cytometer that enables direct estimation of in situ division rates [Brosnahan et al. 2015; see also Chap. 18, Glibert et al. (2018)]. Nauset bloom peaks occur at accumulations of growing degree days that translate to peak concentrations of a few million cells  $L^{-1}$ , very similar to the concentrations observed during encystment by the 2009 GOM population described by McGillicuddy et al. (2014). High-frequency sampling with an IFCB has shown that conversions from vegetative stage cells to gametes occur en masse at these concentrations and further that encystment is likely the dominant process leading to the termination of these blooms (Velo-Suárez et al. 2013; Brosnahan et al. 2015; Choi et al. 2017). Thus, the success of the growing degree metric in predicting Nauset bloom peaks may arise from its skill in predicting the accumulation of cells to concentrations in excess of several million cells  $L^{-1}$ , a threshold at which blooms shift from continued division to sexual fusion. It remains to be shown whether *A. fundyense* in other environments and regions behave similarly. If so, it may be that *A. fundyense* recognize and exploit ephemeral physical and/or biological conditions in order to return to the benthic resting cyst stage rather than wait for growth limitation as an encystment cue. Still other factors known to induce encystment by other dinoflagellate species include the presence of parasites (Toth et al. 2004) and grazers (Rengefors et al. 1998). Both of these factors have the potential to decimate natural HAB populations, particularly when they reach such high cell concentrations. Future field investigations of *A. fundyense*, *P. bahamense*, and other dinoflagellate HAB species should further explore the role of these and other species-species interactions as triggers of encystment, a process that is known to also occur within populations that are far less dense than those observed during Nauset blooms and the 2009 GOM event.

In contrast to *A. fundyense*, *P. bahamense* blooms are often composed of mixtures of different life stages, i.e., vegetative cells, dividing cells, gametes, temporary cysts, and resting cysts, suggesting that vegetative division and encystment occur concurrently in these populations (Azanza 2013; Azanza et al. 2004). This conclusion is further supported by model-based studies of *Pyrodinium* blooms

in Manila Bay and Sorsogon Bay for which sensitivity experiments concerning sexual responses to light, temperature, salinity, and nutrient conditions have been carried out (Villanoy et al. 2006; Yñiguez et al. 2012; Cayetano et al. 2013). Future investigations like those described for *A. fundyense* that document the relative distribution of sexual stages in time and space during *P. bahamense* blooms will likely shed further light on the role of encystment in limiting bloom intensity and promoting bloom decline. Still, the dominant factor leading to the termination of *P. bahamense* blooms in the Philippines appears to be the altered hydrographic conditions associated with the NE monsoon season. Mixed investments in cell division and encystment by these populations may reflect adaptation to this type of abrupt habitat change which is uncoupled in its timing from normal bloom progression. It is noteworthy that for both *P. bahamense* and *A. fundyense*, the onset of sexual processes does not coincide with conditions that would be expected to inhibit further vegetative division. This is in contrast to conclusions drawn from culture studies and underscores the importance of new cyst formation for the survival and persistence of these organisms.

### 8.3 Diatoms: *Pseudo-nitzschia* spp.

*Pseudo-nitzschia* are marine planktonic diatoms belonging to the raphid lineage, the most recent one in the evolutionary history of diatoms (Kooistra et al. 2007). About 35 species are presently included in this genus (Lelong et al. 2012; Teng et al. 2014; Lim et al. 2013), and up to 18 are known to produce the neurotoxin domoic acid (DA), responsible for amnesic shellfish poisoning (ASP) syndrome. Like the PSP toxins produced by *P. bahamense* and *A. fundyense*, DA is accumulated by filter feeders and thus enters marine food webs. Consumption of this toxin causes a range of human health impacts including gastrointestinal distress, neurological disorders, and, in more severe cases, coma and death (Lefebvre and Robertson 2010). It has also been linked to broader ecosystem impacts including mortality of sea lions, birds, and whales (Lefebvre et al. 2002). Blooms of *Pseudo-nitzschia* species occur worldwide in both coastal seas and open oceanic waters where closure of aquaculture installations for prolonged periods can cause severe economic losses (Trainer et al. 2012).

#### 8.3.1 Life Cycle

Like the majority of diatoms described, *Pseudo-nitzschia* species undergo progressive cell size diminution during vegetative growth, due to the distinctive structure of the siliceous frustule and the modality of cell division (Montresor et al. 2016). To

escape from this miniaturization trap, large-sized cells must be produced, and this “rejuvenation” occurs within the sexual phase. Sexual reproduction has been illustrated in various details for 14 *Pseudo-nitzschia* species (Lelong et al. 2012). The majority of *Pseudo-nitzschia* has been shown to have heterothallic mating systems and allogamous sexual reproduction. Species are dioecious, i.e., sexual fusion only occurs between cells of opposite mating type (MT+ and MT−) and vegetative clones are fully self-sterile.

One fundamental requirement for *Pseudo-nitzschia* sex to start is that cells of opposite mating type should be below a species-specific sexualization size threshold (Chepurnov et al. 2005; Scalco et al. 2014). Round, non-motile, and morphologically undistinguishable haploid gametes are produced by meiosis in separate gametangia. They are however behaviourally different, because gametes produced within the MT− gametangium are sessile, while gametes produced by the MT+ gametangium slide towards the sessile ones and conjugate, thus restoring the diploid phase (Scalco et al. 2015), which in turn transforms into an auxospore (Fig. 8.1e, f). It is within the auxospore—a stage that lacks a rigid siliceous frustule—that a cell of the maximum size is produced. Exceptions to this general scheme have been reported for *P. subcurvata* and *P. brasiliensis*, which have a homothallic mating system in which gametes of opposite mating types are produced by single clonal strains (Fryxell et al. 1991; Quijano-Scheggia et al. 2009).

Results of laboratory experiments have shown that in *P. multistriata* successful sexual reproduction can only be achieved when parental strains are in the exponential growth phase; when crossing strains in the late- or post-exponential growth phase, only few gametes were detected, and auxospores and initial cells were not produced (Scalco et al. 2014). Moreover, the onset of the sexual phase in this species requires a threshold cell concentration to start, and it is accompanied by the arrest of growth of the vegetative parental cells. These observations suggest the presence of sex pheromones that mediate the attraction of opposite mating types and induce a cell cycle arrest in G<sub>1</sub> when cells can be committed to shift to meiosis, as has been recently shown for the benthic diatom *Seminavis robusta* (Moeys et al. 2016).

Although sexual reproduction is a fundamental phase in *Pseudo-nitzschia* life cycles, there are only two reports of sex events in the natural environment. Scarcity of reports is attributable to low sampling frequencies and limitations of the visual identifications of the sexual stages, which tend to be relatively rare and ephemeral. Sexual stages of two *Pseudo-nitzschia* species have been recorded at the LTER station MareChiara in the Bay of Naples (Mediterranean Sea), where they accounted for 9.2 and 14.3% of the total number of cells of *P. cf. delicatissima* and *P. cf. calliantha*, respectively (Sarno et al. 2010). Another massive sex event has been reported along the Washington coast (USA) involving *P. australis* and *P. pungens* (Holtermann et al. 2010). Auxospores were detected for a longer time interval (about 3 weeks) and accounted for 59% of the *P. australis* population at the end of the bloom.



### 8.3.2 Bloom Dynamics

A considerable number of studies have been carried out on *Pseudo-nitzschia* bloom dynamics in the last decades, showing that these species can be recorded both in coastal and offshore waters, in upwelling systems, as well as in more secluded environments like fjords and bays [Trainer et al. 2012; see also Chaps. 10, 11, Roy et al. (2018) and Pitcher et al. (2018)]. Intensive monitoring programmes coupled with the continued development of physical/biogeochemical models are delivering forecast capabilities that promise to better safeguard public health and local economies (e.g., Lane et al. 2009; Anderson et al. 2009; Giddings et al. 2014). However, the biological mechanisms leading to the formation and demise of *Pseudo-nitzschia* blooms are not yet fully understood. Like all unicellular microalgae, *Pseudo-nitzschia* species experience periodic increases in their cell number, often with a marked phenology (Fehling et al. 2006; Ruggiero et al. 2015). The inoculum for the bloom does not derive from the germination of benthic resting stages, which have never been reported in areas where *Pseudo-nitzschia* species are regular members of the phytoplankton community (e.g., McQuoid 2005; Montresor et al. 2013). However, in periods between subsequent blooms, cells can be present in the water column at very low, undetected concentrations or might accumulate at physical discontinuities within the water column, such as the pycnocline and/or subsurface TLs (Rines et al. 2002; Timmerman et al. 2014).

Blooms reflect increases in cell growth rates which demand ample supplies of nutrients and light, yet these factors do not fully explain variability in the timing of phytoplankton blooms. A complex signalling mediated by infochemicals between *P. multiseriata* and a species of *Sulfitobacter* has been recently discovered (Amin et al. 2015). These bacteria can convert tryptophan produced by the diatom into indole-3-acetic acid, which in turn promotes diatom cell division. Interactions between *Pseudo-nitzschia* species and their microbial consortium may also modulate the toxicity of these species and their susceptibility to attacks by algicidal bacteria (Sison-Mangus et al. 2013). Species with different levels of toxicity also differ in their bacterial communities, with toxic *Pseudo-nitzschia* hosting lower microbial diversity than nontoxic ones. Massive sinking at the demise of blooms is a distinctive trait of diatom life cycles, and in this way toxic *Pseudo-nitzschia* transport DA to the deep ocean. Considerable amounts of toxin have been recorded in sediment traps at depths greater than 800 m, where DA enters benthic food webs through filter feeders and their predators (Sekula-Wood et al. 2009).

Changes in *Pseudo-nitzschia* species composition have been observed in sediment core samples (Lundholm et al. 2010) and at sites where long-term data are available (reviewed by Trainer et al. 2012). Though these composition changes are most often thought to reflect environmental changes, disappearances of some species may also be caused by failures to complete their sexual cycles. The consequent lack of recruitment of large cells to these populations is an understudied mechanism for species extirpations in existing time series data sets.

### 8.3.3 Modelling of Life Cycle Transitions

The pattern of cell size variation over time can help to infer the timing of sex in natural diatom populations. In the Gulf of Naples, *P. multistriata* blooms in summer-autumn, and a regular alternation of uni- and bimodal cell size classes has been recorded over 11 years (D'Alelio et al. 2010). Large-sized cohorts, most likely representing the product of sexual reproduction, were recorded every second year. The population progressively reduced in size and, upon reaching the cell size threshold for sex in the bloom of the second year, produced a new cohort of large cells. Life cycle dynamics and the regular pattern of cell size reduction and restitution were simulated with an individual-based model parameterized with data on growth rates, cell size reduction dynamics, and cell size threshold for sex gained from laboratory observations. The model output reproduced the coherent pattern in *P. multistriata* population dynamics observed in nature only when a seasonal variation in the rate of cell division was imposed; a rapid acceleration of growth rate during the bloom phase was in fact mirrored by cell size reduction. Further, this fine-tuned organization of its life cycle appears to be independent from more proximate environmental conditions. The model also predicted that the species would become locally extinct if sex did not occur within 4 years.

The biovolume of *Pseudo-nitzschia* cells during the life cycle can vary about one order of magnitude between the largest and the smallest cells. This has implications for growth capability (D'Alelio et al. 2009; Amato et al. 2005), toxicity, sinking rates, and selective grazing. The inclusion of life cycle traits, such as cell size reduction and restitution, in theoretical models can provide insights on the impact of different size classes on diatom population dynamics (Hense and Beckmann 2015).

## 8.4 Cyanobacteria: *Nodularia spumigena*

Cyanobacteria are among the most prominent HAB-producing taxa and cause a variety of negative impacts including contamination of drinking water and livestock and wildlife mortalities [see also Chap. 20, Burford et al. (2018)]. *Nodularia spumigena* Mertens ex Bornet & Flahault 1888 (Fig. 8.1g) is of particular interest because this species produces nodularin, a cyclic pentapeptide hepatotoxin that affects many higher-trophic-level organisms including humans (Rinehart et al. 1988). Recent studies suggest that *N. spumigena* also produces a specific neurotoxic amino acid, but due to methodological difficulties, its relevance is still under debate (e.g., Cox et al. 2005; Kruger et al. 2010). *N. spumigena* is present worldwide (Fig. 8.3c), predominantly in brackish waters of temperate regions. Exceptionally large blooms occur in the Baltic Sea where surface rafts of this buoyant species can cover more than 200,000 km<sup>2</sup> (Kahru and Elmgren 2014). Environmental factors

like sea surface temperature play an important role in bloom formation, but bloom inoculum size is equally important and is strongly determined by life cycle dynamics.

### 8.4.1 *Life Cycle*

The life cycle of *N. spumigena* can be characterized by three different phases (Fig. 8.2b) that are synchronized with the seasonal cycle: a bloom phase, a resting phase, and a recruitment phase. The bloom phase occurs in summer when surface temperature is high ( $>20$  °C), the dissolved inorganic N pool is depleted, and wind and shear stresses are weak. During this phase, filaments consisting of photosynthetic vegetative cells and specialized N-fixing, anaerobic heterocysts accumulate to form blooms. Through N fixation, heterocysts supply their neighbouring vegetative cells with N, an energetically demanding process. At the end of summer, the growth rate decreases due to deteriorating external conditions such as lower temperature, an exhausted P pool, and/or reduced solar radiation. The resting phase begins during which some filaments hibernate in the water column (Suikkanen et al. 2010) until the return of favourable growth conditions the following summer. In addition, thick-walled cells, called akinetes, are formed that can withstand unfavourable conditions for several years (e.g., Huber 1984). These cells sink to bottom sediments where they may be lost by burial or decomposition, but others will germinate, stimulated by environmental cues. Light, in particular, is assumed to trigger germination in this recruitment phase. Exposure may be mediated by wind-driven resuspension or activity of specific benthic fauna (Karlson et al. 2012). Cells may also ascend to and recolonize the surface through production of gas vesicles during late spring and early summer. If surface temperature exceeds approximately 13 °C, the cells divide and initiate the next bloom phase. While the described succession of *N. spumigena* life cycle stages is “typical” under temperate conditions, it is not known how life cycle strategies vary in different environments and geographic regions. It is also unclear whether toxin production is influenced by life cycle dynamics (though this is often speculated to be the case; e.g., Cox et al. 2005).

### 8.4.2 *Bloom Dynamics*

Several characteristics of *N. spumigena* blooms are best explained as the result of life cycle transitions. One of these is the rapid increase and decrease of blooms, most likely caused by transitions from or to resting stages (Hense and Beckmann 2006). Such transitions may further be associated with high year-to-year or

interannual variability in total biomass and spatial extent of *N. spumigena* blooms (e.g., Galat et al. 1990; Hense and Burchard 2010; Kahru and Elmgren 2014). Under favourable environmental conditions, resting stages may accumulate over several years before they transform into growing stages. Such dynamics may explain substantial differences in bloom concentrations observed year to year. Life cycle transitions may also be hindered by unfavourable conditions leading to low concentrations or absence of blooms. Feedback mechanisms associated with the life cycle are therefore likely to play an important role in bloom variability; e.g., intense accumulations of growing cells may tend to produce more akinetes, leading to larger inocula during subsequent blooms (Hense 2007).

### 8.4.3 *Dispersal and Future Distribution*

The survival of resting stages for several years will principally facilitate the dispersal of *N. spumigena*. Indeed, there are reports of *N. spumigena* along bird migration routes (Stoyneva 2016). There is also evidence that *N. spumigena* can be transported in ballast water over long distances (Olenin et al. 2000), but whether colonization is successful or not will strongly depend on local environmental conditions, including interactions with endemic species. Overall, a clear statement about biogeographic expansion of *N. spumigena* over the past decades cannot be given, because a higher awareness and improved tools for detection of these cells may also explain the rise in reports of *N. spumigena*.

Continued presence and spread of *N. spumigena* depends on several factors. First, global warming is predicted to favour cyanobacteria in general and *N. spumigena* in particular (Paerl and Huisman 2009; Paerl et al. 2011; Hallegraeff 2010; O'Neil et al. 2012), because their growth optimum lies at about 25 °C (e.g., Lehtimaki et al. 1997). Second, the state of eutrophication will have consequences for the development of *N. spumigena*. If both nutrient loads and inventories, notably N and P, are reduced, the intensity of cyanobacterial blooms is likely to decline, especially if other factors like temperature remain unchanged. Third, ocean acidification might affect *N. spumigena*. Despite large uncertainties, recent studies suggest that the growth rate of this species is reduced under high pCO<sub>2</sub> (Czerny et al. 2009; Eichner et al. 2014). Toxin production, however, may still rise, because toxin content has been shown to increase with temperature (Lehtimaki et al. 1997). Again, life cycle dynamics will strongly determine how *N. spumigena* responds to climate change (Hense et al. 2013). Differing environmental requirements for different life cycle stages and the two-way interaction of each stage with its environment lead to a chaotic system, in the sense that specific features in such systems remain unpredictable, even if other aspects are known. One of these features may well be specific outbreaks of *N. spumigena*.

## 8.5 Synthesis and Recommendations

HAB-causative and other phytoplankton species are confronted with a dynamic aquatic environment and must acquire resources for growth while also guarding against diverse mortality processes in order to ensure their survival. Common stressors include variations in nutrient supply, turbulence, light availability, and temperature, as well as changing diversity of other species, including competitors and predators. Here, we have described ways in which four prominent HAB-causative organisms cope with these variable stressors through the evolution of distinctive traits within their respective life cycles. Common among these are their capability to persist in the face of extended periods of species-specific poor growth conditions between blooms. Also common is the ability to initiate transitions between life cycle phases, either through direct sensing of changing environmental conditions, anticipation of seasonal changes, high cell concentrations, or other factors that facilitate successful life cycle transitions.

Modelling studies have been a particularly effective means to identify and weigh the relative importance of different life cycle behaviours for determining the population dynamics of different HAB species in response to diverse environmental factors. Among the three meroplanktonic species reviewed here (*P. bahamense*, *A. fundyense*, and *N. spumigena*), potentially long-lived, durable benthic stages figure prominently in their overall ecology. Major seedbeds of the dinoflagellates' resting cysts and akinetes of the cyanobacterium *N. spumigena* reflect dynamic interactions between hydrography and patterns of new benthic stage production, particularly in areas where these species are well established. Moreover, accumulations of cysts can persist for years even in the absence of new depositions, imposing a continued threat of HAB impacts through future bloom inoculations. Spatial and temporal records of the resulting seedbeds are useful predictors of future bloom impacts in some cases. A prime example is the development of a HAB forecast for *A. fundyense* based on annual surveys of cyst abundance across the GOM. Short time scales for transitions between benthic and planktonic stages of *N. spumigena* and *P. bahamense* appear to be integral to their bloom dynamics and enable these species to escape short periods of adverse conditions during bloom periods. Rapid downturns in dinoflagellate populations may also be explained by production of resting cysts. The latter process may be spread over the whole bloom period in some populations or may be concentrated near the end of blooms, sometimes acting as a dominant factor leading to bloom decline.

*Pseudo-nitzschia* spp. differ from the other species discussed here in that no benthic stages in their life cycles are known. Persistence of these species during periods of non-optimal growth conditions is presumed to rely on low concentrations of cells that may linger or concentrate at density discontinuities in the water column. Like all other diatoms, these species also differ from *P. bahamense*, *A. fundyense*, and *N. spumigena* in their mode of division, a basic process in the life cycle of all microbes that is integral to these species' ability to form blooms. Specifically, *Pseudo-nitzschia* spp. undergo diminution as they divide and must

undergo sexual fusion and auxospore formation to restore large cells to their population. This cell size-driven entry and exit from the sexual phase of its life cycle that occurs when cells are in exponential growth contrasts with a prevailing paradigm about sex in microbial eukaryotes, namely, that such recombination events are only likely to be favoured when abiotic conditions are limiting. Similarly, in many field populations of the dinoflagellates *A. fundyense* and *P. bahamense*, cells appear to enter the sexual phase of their life cycle prior to the onset of significant growth limitation. This suggests that biological factors (e.g., density-dependent mechanisms and/or sex pheromones) may play important roles in determining the timing and extent of sexual conversions. Continued research and observation of natural populations is needed to better characterize the history of HAB populations leading up to sexual events and to better evaluate the roles of endogenous and exogenous factors promoting these transitions, which are crucial for the recurrence of blooms.

An ongoing challenge for studies of life cycle dynamics is the characterization of stage behaviours and transitions between stages within natural populations. Though much progress towards characterizing stage-specific behaviours has been made through laboratory experiments, it is also clear that the conditions and rates of many fundamental life cycle processes differ substantially between naturally occurring and laboratory-reared cells. The factors contributing to these differences are numerous and include contributions from natural bacterial flora, differences in nutrient supply and light conditioning, and interactions with other co-occurring phyto- and zooplankton species and parasites—all factors which are exceedingly difficult to replicate in cultures. Accordingly, in situ observations are needed, but such efforts are still in their infancy in the context of life cycle transitions.

The obstacles inherent to in situ observations include the logistics of observing oceanic phenomena than can span large areas, difficulty in discriminating morphologically similar planktonic stages (e.g., planomeiocytes, vegetative cells, gametes, and planozygotes in many dinoflagellate species), and a basic inability to observe benthic processes without massive disruption of potentially informative physical associations (i.e., for resting cysts, akinetes, and other benthic stages). Automated and robotic instrumentation is beginning to address these challenges (e.g., Brosnahan et al. 2015), but more development and application of these systems is needed. Existing and future in situ approaches must be applied to a broader range of HAB taxa to elucidate natural growth and mortality processes and other factors that modulate the timing and intensity of blooms. Ongoing and future research on the roles and interactions of different life cycle stages with bacteria, viruses, and parasites are similarly expected to yield great insights into the ecological responses of these organisms. Finally, long-term data sets on the temporal and spatial occurrences of these and other plankton species need to be maintained and expanded to enable future insights into the roles that life cycle dynamics play in shaping the ecology of these species, especially as ecosystems are challenged by climatic shifts, severe weather, and anthropogenic influences (e.g., prolonged El Niño for *Pyrodinium* and anomalous warm/freshwater inputs affecting GOM *A. fundyense* blooms). Through these activities, more descriptive and predictive models can be generated that will further our understanding of HAB dynamics and better protect

society from their impacts. Global efforts, such as may be achieved through the next-generation global interdisciplinary HAB Programme, GlobalHAB, will be important to advance this understanding and to provide the necessary advanced predictive models.

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