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The case of the diatoms and the muddled mandalas: Time to recognize diatom adaptations to stratified waters

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ABSTRACT

Models used to predict future ocean ecosystem and biogeochemical behaviour depend on simplified ecological frameworks allowing the definition of plankton functional types. Foremost among such frameworks has been the mandala of Margalef. His 1978 paper has been increasingly referred to in the past decade as simplified ecological schemes have been sought to help predict the effect of climate change on phytoplankton. However, the mandala is based on an understanding of the subject that is over 40 years old, when observational studies were largely limited to the coastal ocean and to near surface waters. Furthermore, most recent reproductions of the mandala are significant oversimplifications of Margalef's original. In these simplified mandala-type constructs, diatoms, in particular, have commonly been cast as a single plankton functional type that thrive in turbulent waters and decrease in abundance with increasing stratification. On this basis, it is widely predicted that diatom productivity and hence the effectiveness of the marine biological carbon pump will decrease with climate change that is driving increased stratification of the oceans. But Margalef's original took a more refined approach and depicted diatom genera that were adapted to more stratified conditions such as those characteristic of the subtropical oligotrophic gyres. If we now draw on the vast advances in observational oceanography of recent decades it is evident that diatoms may thrive, bloom and generate significant export even in the most intensely stratified and apparently oligotrophic conditions. Indeed, some diatom species have unique adaptations to such environments. We therefore suggest that it is time to abandon oversimplified schemes and recognize the diverse ecology of diatoms.

1. Introduction

Diatom algae are a dominant phytoplankton of the world ocean. They form the base of marine food chains, they are responsible for around 40% of total marine primary production and are widely regarded as key drivers of the marine biological carbon pump (Sarthou et al., 2005; Treguer et al., 2018). An understanding of their ecology is therefore key to predicting how climate change will affect the workings of marine ecosystems and the carbon cycle. Yet the orthodox view of diatom ecology stems from a conceptual framework now almost 40 years old – the mandala of Ramon Margalef, first published in 1978 (Margalef, 1978) (Fig. 1).

Margalef's mandala or modified and simplified versions of it have been used as a basis for the tenet that diatoms chiefly thrive in turbulent upwelled, nutrient-rich waters and give way to other phytoplankton with the onset of stratification. The simplification of the mandala has diminished the richness that Margalef embedded in the original formulation. Research over the last 10–15 years has revealed the evolutionary adaptiveness of phytoplankton hypothesized by Margalef to be fundamental to the mandala's application. In particular, diatoms are not limited to the high turbulence-high nutrient (HT-HN) end of the continuum but have specific adaptations that allow them to episodically dominate both production and export in stratified conditions (Dore et al, 2008; Karl et al., 2012; Kemp and Villareal, 2013). Certainly, diatoms dominate under HT-HN conditions, but they may also flourish at the opposite end of the continuum.

Climate change is driving increasing water column stratification through warming and localised freshening of the ocean (Rhein et al., 2013) that results in reduced mixing of nutrients to surface waters. Following the "mandala" view, the resulting decline in turbulence and nutrient supply to the surface waters is predicted to favour picophytoplankton at the expense of diatoms and other large phytoplankton and thus reduce the effectiveness of the biological pump (Bopp et al., 2005; Steinacher et al., 2010; Laufkötter et al., 2016). The theoretical

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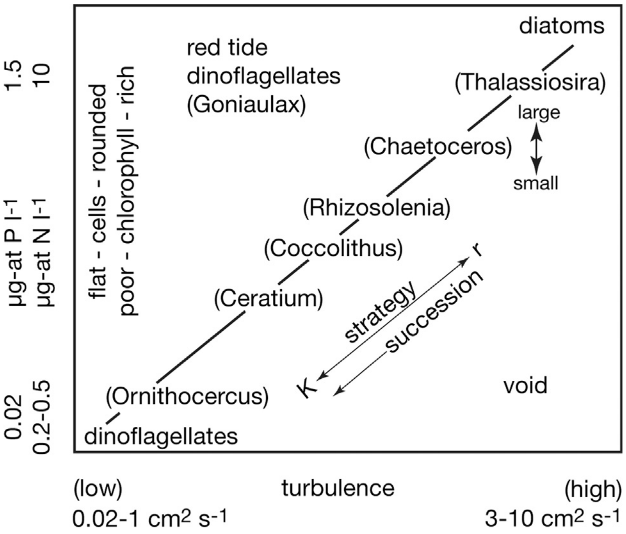

Fig. 1. The original mandala reproduced from Fig. 1 of Margalef, R. (1978) “Life-forms of phytoplankton as survival alternatives in an unstable environment”. Oceanologica Acta, 1 493–509.

and model studies that forecast such change rely on the prevailing views of phytoplankton ecology, which have largely rested on the mandala concepts. Commonly these models depict diatoms as a single plankton functional type (PFT).

The motivation for this article is driven by the increasing reference to the mandala over the past 15 years during which time research has increasingly questioned the viability of the mandala model. Although moderately cited last century, the original publication (Margalef, 1978), has collected the bulk of its 1000+ Web of Science citations (> 740) in the past 15 years with over 350 in the last 5 years (Fig. 2).

These increasing citations reflect the widespread and continued adoption of the mandala as a paradigm for characterising phytoplankton functional types despite criticisms of shortcomings (Villareal et al., 1993; Smayda and Reynolds, 2001; Boyd et al., 2010; Kemp and Villareal, 2013). Our aims are (1) to demonstrate that many recent “adaptations” of the mandala oversimplify and do a disservice to Margalef’s original construction, and (2) to highlight the implications of recent advances in the understanding of diatom ecology that supersede many of the now dated aspects of the original that have been perpetuated by these “muddled mandalas”. More broadly, we highlight that adoption of the simplified mandala view of diatoms as a single functional type leads to potentially misleading views of the effects of increasing stratification on ocean ecosystems and the carbon cycle. It is not our intent to single out specific papers for criticism but rather to illustrate a type of generalization that has become embedded in the received wisdom of the field.

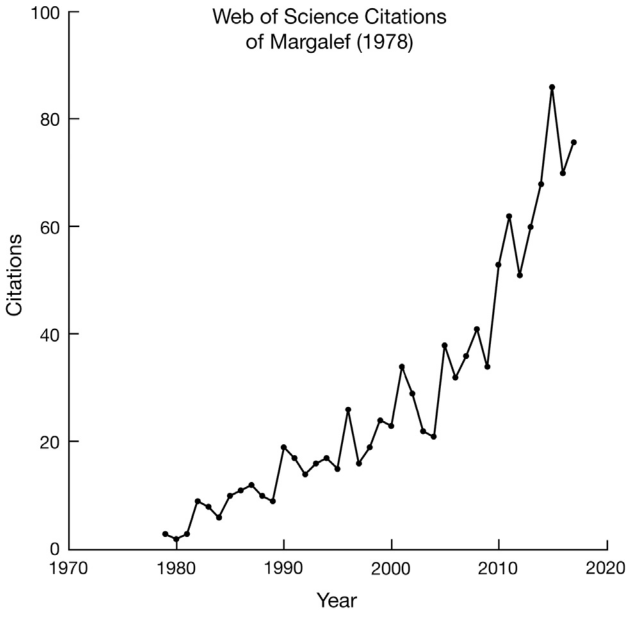

Fig. 2. Annual citations of Margalef (1978) in the Web of Science (all data bases) since publication up to and including 2017, showing rapid increase in citations in the last 15 years.

2. The original Margalef mandala

In a pioneering work of fitting phytoplankton to behavioural patterns, Margalef published the mandala in 1978 (Fig. 1). This grew from his research predominantly on the coastal seas and rias of Spain, in the western Mediterranean, and parts of the Caribbean (Peters, 2010). Derived largely from his understanding of how environmental changes are linked to successional characteristics of the phytoplankton, the mandala cannot be viewed in isolation from Margalef’s concepts of the stages of succession (Margalef, 1967). We first highlight the key aspects or “properties” of the mandala.

2.1. Key aspects of the mandala 1: the role of turbulence

The presence of turbulence in the water column was central to the mandala as Margalef clearly summarises: “In water of low turbulence, non-motile cells sink fatally and the population disappears.” (Margalef, 1978). This classical view, that without turbulence non-motile phytoplankton will sink, remains well embedded, not least in modelling studies: “if turbulent diffusion is low, sinking phytoplankton species may tumble downwards and are lost in the dark” (Huisman and Sommeijer, 2002). This orthodoxy also features in recent reviews such as in “Nature Reviews Microbiology”: “when nutrient concentrations and turbulent mixing are low, small cells are more likely to be selected” (Falkowski and Oliver, 2007). As turbulence decreases and stratification becomes stronger, the mandala depicts the increasing primacy of smaller and/or motile groups such as dinoflagellates and coccolithophores (Fig. 1).

2.2. Key aspects of the mandala 2: nutrients and their relation to turbulence

In the original mandala figure, Margalef (1978) used typical phosphate and nitrate concentrations on the nutrient axis whilst also referring more generally to “nutrient concentration” in some related figures. He saw nutrient supply and turbulence as “the most important factors shaping cells through evolution and the only reason for proceeding to a functional interpretation of morphology.” (Margalef, 1978, p. 502). He associated nutrients strongly with turbulence and viewed species adapted to high nutrient concentrations (high uptake rates) as also being adapted to turbulence. On the other hand, “Species adapted to thrive and persist under low concentration of nutrients may also be manifestedly adapted to low turbulence, which allows and even requires some motility from the part of the organisms.” (Margalef, 1978, p. 502). From a community perspective, energy input dominated: “Primary production appears simply as a function of the external energy supplied to the system and degraded in it” (Margalef, 1978, p. 498).

2.3. Key aspects of the mandala 3: r/K selection

When Margalef was conceptualising the mandala in the 1960s and early 1970s, the theory of r- and K-selection (MacArthur and Wilson, 1967; Pianka, 1970) emerged as one of the first predictive models for life-history evolution and was adopted widely by the ecological community. In the r/K model, r refers to the maximum growth rate and K to the carrying capacity of the environment so that “r-selected” species are characterised by small size, high reproduction rates, short generation time, high dispersal and can exploit empty niches or unstable environments. In contrast, the characteristics of "K-selected" species include larger size, slower growth rates, longer life and primacy in stable environments. Within textbooks, typical r-selected organisms are cited as small rodents, bacteria and diatoms with typical K-selected examples including elephants, whales and dinoflagellates.

Phytoplankton ecologists used differences in growth and loss rates, nutrient uptake rates and storage capacity to place phytoplankton along a r- K-continuum and this came to be regarded as a "unifying concept" in phytoplankton ecology (Kilham and Hecky, 1988). In applying the r/K model to marine plankton, Margalef also used the background of seasonal succession from the rapidly changing spring to the stably stratified summer water column so that species characteristic of the spring bloom were typically r-selected and those of the summer stratification were K-selected (Fig. 1).

2.4. Key aspects of the mandala 4: a species-based approach depicts ecological plasticity

While the original mandala does refer to groups (diatoms, dinoflagellates) it also takes a species- or at least genus-based approach. This is explicit in Margalef's concept of the stages of succession where he clearly identified diatom genera such as *Rhizosolenia* that are typical of highly stratified conditions (Margalef, 1967; Margalef, 1978). Thus, the diatoms do not just appear at one corner, but rather, different diatom genera populate a line extending from high turbulence and high nutrients towards the low turbulence and low nutrients corner (Fig. 1). This ecological plasticity across different diatom groups was inherent in Margalef's writings. In contrast, many of the simplified mandalas redrawn in recent publications only portray "diatoms" as being at one corner; at the r-selected extreme, representing the highest turbulence and highest nutrient end member.

3. Examples of oversimplification in modified mandalas

To illustrate our point, we reproduce three recent examples of "adaptations" of the mandala, all of which are from rather different perspectives, but which collectively illustrate current usage across conceptual, theoretical and modeling scenarios, and also spanning geological time scales. They also demonstrate the range of simplifications of the original.

3.1. Typical recent depiction of a mandala adaptation

The first mandala "adaptation" that we illustrate was published in a commentary paper in the Proceedings of the National Academy of Sciences (Kudela, 2010) and described how major groups organize along the turbulence axis (Fig. 3). The focus of the commentary was a study by d'Ovidio et al. (2010) that used an innovative satellite ocean color method combined with altimetry to identify the distribution of major groups of phytoplankton in ephemeral niches originating from stirring by mesoscale turbulence. The critical difference here is that the ecological plasticity of diatoms shown in Margalef's original is gone, a simplification common in the current literature. There is no reference to different diatom genera and diatoms are shown only to occupy one corner at the "r-selected" extremity and at the end of the continuum in the highest nutrient, highest turbulence space.

3.2. A modeler's mandala

One of the key targets of recent biogeochemical modelling efforts has been the prediction of the future operation of the marine biological carbon pump in increasingly stratified oceans. Most models have followed a simplified mandala approach and defined diatoms as a single plankton functional type (PFT) (Le Quéré et al., 2005) dependent on turbulence and high nutrients and so it is no surprise that they predict decreases in diatom abundance: for example, reductions of 10–60% (Bopp et al., 2005). Such models generally predict the replacement of diatoms by other phytoplankton groups (Litchman et al., 2006). Similarly, coupled carbon-cycle climate models with diatoms as a single PFT show decreases in primary production and export with increased stratification (Steinacher et al., 2010; Laufkötter et al., 2016). The development of PFT has been central to marine biogeochemical modelling, yet PFT definition is fraught with controversy (Anderson, 2005; Flynn, 2005; Flynn, 2006; Le Quéré, 2006; Franks, 2009; Anderson, 2010; Shimoda and Arhonditsis, 2016). A recent "mandala-type illustration" (Fig. 4) serves to illustrate the common representation in models that diatoms conform to a single functional group (Allen and Polimene, 2011).

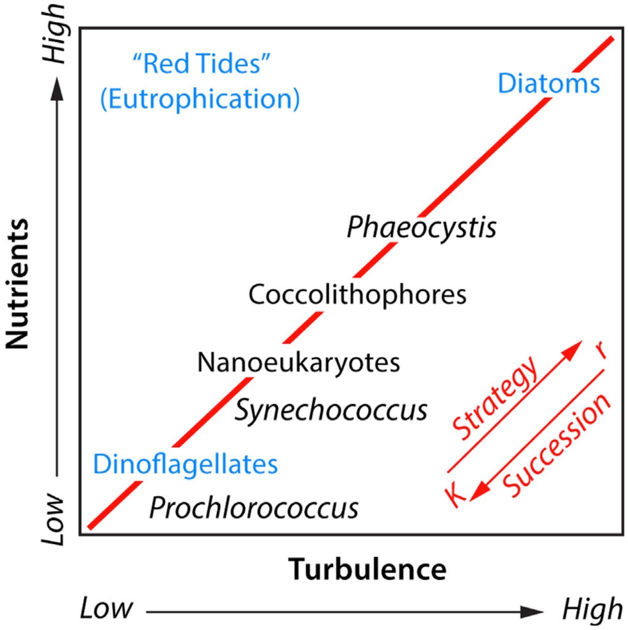

Fig. 3. A representative example of recent simplified mandala depictions, reproduced from Kudela, R.M. "Does horizontal mixing explain phytoplankton dynamics". Proceedings of the National Academy of the United States of America, 2010. 107 (43), 18235–18236, with permission of the author.

We acknowledge the challenges of incorporating additional PFT within these already complex models. However, models are only useful within the framework they are coded for. We suggest that important outcomes for the future ocean are precluded by the omission of stratified-adapted diatoms. Some recent modeling approaches do acknowledge this greater complexity by varied approaches. These include the adoption of two diatom PFT with distinct characteristics (Stukel et al., 2014); the introduction of trait-based diatom functional diversity within an existing PFT model (Terseleer et al., 2014) and the development of flexible PFT models (Smith et al., 2016). These new approaches are discussed in more detail in Section 5.4, below.

3.3. An extension of the mandala to geological timescales

A series of similar mandala-variants that incorporate the original characteristics of turbulence, nutrient availability and r/K selection with the additional aspects of resource acquisition strategies and a geological evolutionary perspective have been published by Falkowski et al. (2004), Katz et al. (2004), Tozzi et al. (2004) (Fig. 5).

These papers stress diatom dependence on turbulence – and place diatoms at one end of the r/K line without the plasticity of the original mandala. In extending their version of the mandala to geological time, they argue that the more stable stratified oceans of the Cretaceous favoured coccolithophores and dinoflagellates over diatoms. Falkowski

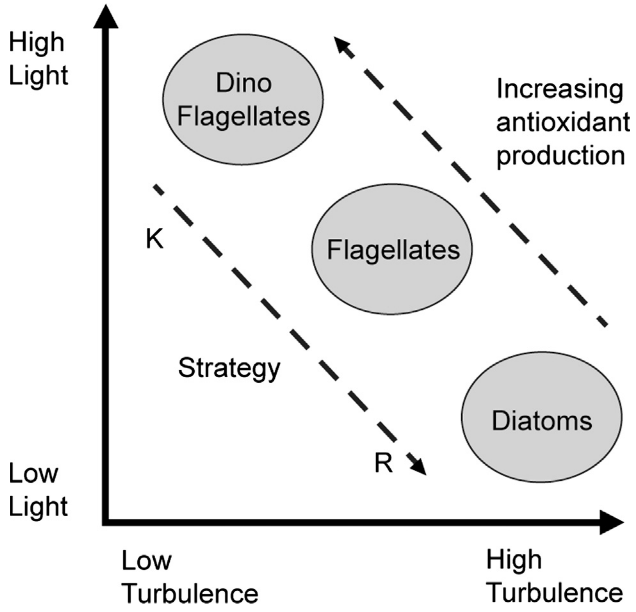

Fig. 4. A "modeler's mandala", "a mandala-type illustration of the relationship between light, turbulence, phytoplankton type and antioxidant production." Reproduced from: Allen, J.I. and Polimene, L. "Linking physiology to ecology: towards a new generation of plankton models", Journal of Plankton Research, 2011, 33 (7), 989–997, with permission of Oxford University Press.

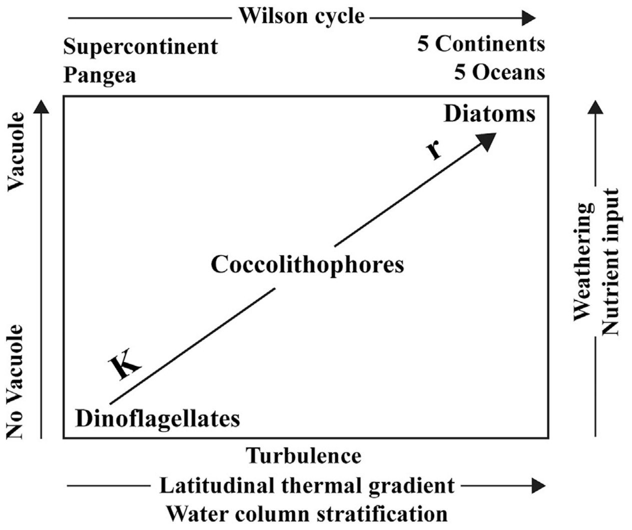

Fig. 5. An extension of Margalef's mandala to geological timescales. Reproduced from Katz, M. E. et al., "Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton" Annual Review of Ecology, Evolution and Systematics, 2004, 35, 523–556, with permission of Annual Reviews. This proposes that long-term changes in turbulence and nutrient concentration in the world ocean can force a shift from r-strategists to K-strategists.

et al. (2004) further state: "the diatoms found in Cretaceous marine deposits almost uniformly belong to extinct stem taxa", which is incorrect. Following major diatom radiation during the Cenomanian/Turonian, about 94 million years ago, many of the Late Cretaceous genera including *Rhizosolenia* and *Hemiaulus* and even some morphospecies (e.g. *Stephanopyxis palmeriana*) continue to the present (Harwood and Nikolaev, 1995; Damste et al., 2004). Furthermore, the extensive diatomite deposits of the Late Cretaceous provide geological evidence for the rise to prominence of diatoms in ocean productivity during this time (Harwood et al., 2007; Witkowski et al., 2011). Many of the dominant diatoms of this period including rhizosolenids and hemiaulids attest to massive diatom productivity and flux from the stratified oceans of the late Cretaceous "greenhouse" world (Harwood et al., 2007; Davies et al., 2009; Davies and Kemp, 2016).

4. Why it is time to move on from the mandala

We now revisit the key aspects of the mandala articulated above and summarise their limitations. Specifically, we identify how subsequent research has fostered entirely new perspectives on the roles of turbulence and nutrient cycling in diatom ecology. At the time of the mandala's conception, open ocean observational programmes were rudimentary and open ocean time series rare. Sampling was primarily from the surface 10 m or so and the deep chlorophyll maximum in particular, and the subsurface, in general, were rarely sampled. Vertical migration of giant diatoms and diatom mats was unknown. Little was known of the intracellular, nitrogen fixing symbioses that are now understood to fuel extensive oceanic diatom blooms in oligotrophic oceans. The world of *Prochlorococcus, Synechococcus,* the microbial loop and the implications for size structure in the ocean were largely undiscovered. These new data do not negate the mandala. Rather, they extend Margalef 's concepts to oceanic life-spaces unknown when the mandala was conceived. The mandala's great contribution was the organization of phytoplankton along an energy gradient, a concept still valid today. However, we cannot freeze that concept in 1978 nor should we accept the oversimplifications of more recent generalized representations.

4.1. Turbulence is not required to keep non-motile phytoplankton suspended

4.1.1. Diatoms can regulate their buoyancy

Central to the mandala is the assumption that non-motile phytoplankton require turbulence to prevent them sinking. While diatoms as a group do sink (Smayda, 1970), this is observationally coupled to life-history characteristics (Smetacek, 1985) of early-mid successional stage species near the HT, HN end of the mandala. However, there is abundant field and laboratory evidence that large diatoms regulate their internal ion pool (Woods and Villareal, 2008 and references therein), organic solute composition (Boyd and Gradmann, 2002) and possibly water transport (Raven and Doblin, 2014). Cellular energy is tightly coupled to buoyancy regulation (Waite and Harrison, 1992; Waite et al., 1997) with near neutral buoyancy evident in many taxa across a wide cell size range, perhaps down to cells as small as 200 μm^3 (Waite et al., 1997; Erga et al., 2015; Vega and Villareal, 2016; Villareal, 2016). As a result, nutrient replete diatoms can be essentially neutrally buoyant (Richardson and Cullen, 1995; Waite et al., 1997). Large oceanic diatoms are positively buoyant in both field samples and laboratory cultures at rates of $m\,h^{-1}$ (Moore and Villareal, 1996; Villareal et al., 1996) and common coastal diatoms can be positively buoyant in life cycle stages as well (Waite and Harrison, 1992). Ascending behaviour of *Hemialus hauckii*, a typical open ocean diatom containing a diazotrophic symbiont, was seen in conjunction with positively buoyant transparent exopolymer particles (TEP) in laboratory cultures (Hoppe, 2013; Villareal et al., in preparation). While ascent rates were $< 1\ m\,d^{-1}$, the upwards motion was contrary to expectations for bloom forming diatoms. However, when suitable *in situ* field experimental methods are used, a shift from sinking to neutral buoyancy and ascending behaviour is observed at the onset of the spring diatom bloom (Acuña et al., 2010).

While sinking rates are usually represented as a bulk property common to all the component cells, they are actually a cell-specific property with a range of rates within a single population (O'Brien et al., 2006; Aumack and Juhl, 2015; Gemmell et al., 2016). A diversity of intra-population sinking rates may have been the result of high evolutionary pressure to eliminate parasitoids (Raven and Waite, 2004). The extreme regulation of cellular density can be seen in large diatoms such as *Coscinodiscus wailesii* that can modulate sinking rates from near maximum to near-zero at a time scale of 10^2 ms (Gemmell et al., 2016).

Thus, sinking is a property selected for by diatoms that is under immediate metabolic control but is not obligate, most particularly for the largest diatoms (Villareal et al., 2014). It does appear to be an essential component of early successional stages, but is not a requirement for oligotrophic-adapted or nutrient replete diatoms. This has been mechanistically incorporated into allometric models that demonstrate that large cells can have a competitive advantage even under calm conditions if energy/nutrient supplies are adequate (Wirtz, 2013). The persistent presence of a characteristic diatom community in the mixed layers of oligotrophic seas (Guillard and Kilham, 1977; Venrick, 1988; Venrick, 1990; Malviya et al., 2016) argues strongly that sinking losses are insufficient to remove these populations.

4.1.2. *Water column structure may delay or arrest sinking and promote formation of persistent diatom thin-layers*

Density interfaces in the coastal ocean are the common location of thin layers of phytoplankton and associated transparent exopolymer particles (TEP) that may persist for several days (Dekshenieks et al., 2001; Alldredge et al., 2002). These are commonly diatom-rich and may include large porous flocs often dominated by chain-forming diatoms such as *Thalassiosira, Pseudo-nitzschia,* and *Chaetoceros* (Macintyre et al., 1995; Alldredge et al., 2002; McManus et al., 2003; Greer et al., 2013; Timmerman et al., 2014). Settling in such density interfaces may be delayed by both diffusion-limited retention and entrainment of lighter fluid (Prairie et al., 2013). Settling is reduced further within sharper density gradients (Macintyre et al., 1995; Prairie et al., 2015) so that the strongest interfaces such as the main seasonal thermoclines may foster the most intense and persistent thin layers. Experimental evidence also suggests that TEP may also form neutrally- and positively buoyant aggregates (Azetsu-Scott and Passow, 2004; Mari et al., 2017).

4.2. *Diatoms do not require high surface nutrient concentrations to "bloom"*

In the next sections, we summarize the adaptations that enable diatoms to subsist, grow and bloom in stratified waters (Fig. 6). These include the ability of diatoms to: (1) grow in low light conditions at depth thus tapping the nutricline; (2) regulate buoyancy enabling them to mine nutrients from depth and migrate upwards to higher light levels; (3) develop symbioses with nitrogen-fixing cyanobacteria; (4) undertake luxury uptake and storage of nutrients in their vacuole. Diatom adaptations to the subtropical gyres are also considered. We adopt the recent qualitative definition of a bloom of Behrenfeld and Boss (2018) as a high concentration of phytoplankton (mg C m^{-3}) and note, as they do, that there is otherwise no objective and quantitative definition of a bloom. We distinguish between the scenarios above, in which the high biomass concentrations are all driven by growth from instances of high biomass that may have originated partly by horizontal or vertical advection, due to planetary waves (Cipollini et al., 2001) or fronts (Yoder et al., 1994; Kemp et al., 2006).

4.2.1. *Diatoms may bloom in subsurface chlorophyll maxima*

Observations of the subsurface ocean in the past two decades have highlighted the importance of production in deep- or subsurface chlorophyll maxima (DCM or SCM). A higher tempo of fieldwork and increasing use of towed undulators and AUVs including gliders have documented the widespread extent of SCM in coastal and shelf seas during summer stratification, and in many cases these are diatom-dominated. SCM are dominant summer features in settings ranging from mid latitude shelves such as those of the NE Pacific (Anderson, 1969; Perry et al., 2008) or NW Europe (Weston et al., 2005; Hickman et al., 2012) to the Arctic (Martin et al., 2010) and constitute biomass maxima. Such subsurface biomass peaks also generate major flux events (Sancetta et al., 1991; Kemp et al., 2000; Smetacek, 2000).

In the oligotrophic Mediterranean, diatoms are now known to form a major component of extensive summer DCM in "bloom-magnitude" concentrations (Crombet et al., 2011). In open oceanic settings, diatoms often dominate the DCM, for example, in the Southern Ocean, seasonally recurrent diatom-dominated DCM constitute up to 50% of total water column production (Kopczynska et al., 2001; Parslow et al., 2001; Gomi et al., 2010; Queguiner, 2013). Extensive DCM diatom blooms also occur in the outwardly oligotrophic Sargasso Sea, stimulated by eddy-driven doming of isopycnals (McGillicuddy et al., 2007). Eddy input of nutrients also leads to subsurface diatom blooms in the Pacific Ocean (Brown et al., 2008; Landry et al., 2008). These scenarios are further discussed in Section 4.2.4, below. Goldman documented rapid growth of large Sargasso Sea diatoms at low light levels typical of the DCM in multiple diatom species (Goldman et al., 1992; Goldman and McGillicuddy, 2003). In summary, as Goldman et al. (op. cit.) state: "… there is no physiological constraint on these large diatoms from growing fast enough at very low light levels to meet the new production estimates resulting from eddies". In keeping with the energy regulation of sinking rates (Waite et al., 1997), such deep populations are sustained due to negligible sinking rates even in these large diatoms.

4.2.2. *Diatoms mine nutrients from depth through buoyancy regulation*

Giant diatoms (10^7 + μm^3) regulate their buoyancy to engage in multi-day migrations to mine nitrate (and probably also phosphate) from the nutricline and return to the near surface (Richardson et al., 1996; Villareal et al., 1996; Villareal et al., 1999; Woods and Villareal, 2008). Ascent rates can be up to 7 m h^{-1} (Moore and Villareal, 1996). Vertical migration (VM) permits exploitation of spatially separated light and nutrient resources (Villareal et al., 1993; Villareal and Carpenter, 1994; Singler and Villareal, 2005), a characteristic Margalef explicitly considered a property of dinoflagellates but not diatoms. In fact, vertical migration appears to be common in large non-motile phytoplankton from diverse families (Villareal et al., 2014) suggesting convergent evolution has provided a common solution at one end of the mandala. Vertically migrating diatoms can contribute to or account for several geochemical features including preformed nitrate anomalies and oxygen excesses in the subsurface oxygen maximum just below the mixed layer at HOT and BATS (Letscher and Villareal, 2018; HOT – Hawaii Ocean Time-Series; BATS – Bermuda Atlantic Time-series Study). In addition to permitting *Rhizosolenia* growth, vertical migration contributes substantially to nitrate supply to the surface mixed layer (Villareal et al., 1996; Richardson et al., 1998) and may provide up to 27% of the surface nitrate pool through nitrate release (Singler and Villareal, 2005). Such nitrate release likely contributes to the substantial diatom blooms of the North Pacific Subtropical Gyre (Wilson and Qiu, 2008). Buoyancy regulation permits this migration over several 10 s of meters, but a full transit from nutricline depths to the surface may not be required for all species. We are unaware of any global models that permit ascending behaviour by a generalized diatom group either to migrate, for depth-regulation, or as a life history characteristic. Sinking of diatoms has generally been considered a uni-directional flux rather than the nuanced, highly regulated buoyancy regulation seen in a variety of biogeochemically significant diatoms.

4.2.3. *Symbiotically-derived nitrogen fuels massive diatom blooms*

The most biogeochemically significant symbioses involve the cyanobacterium *Richelia intracellularis* and the diatom genera *Hemiaulus* and *Rhizosolenia* in Diatom Diazotroph Associations (DDAs) (Venrick, 1974; Villareal, 1992). Margalef (1967) explicitly noted these genera as part of the late succession (stratification) stages, although the significance of the *Hemiaulus* association was not recognized until much later (Villareal, 1994). DDAs form extensive blooms in the North Pacific Subtropical Gyre (Dore et al., 2008; Villareal et al., 2011), the tropical North Atlantic (Carpenter et al., 1999; Subramaniam et al., 2008), the eastern Equatorial Atlantic (Foster and Zehr, 2006) and South China Sea (Grosse et al., 2010). Symbiont fuelled diatom blooms may also generate significant carbon flux, for example at the ALOHA site, where *Hemiaulus/ Richelia* blooms lasting a maximum of 30 days generate 20% of the total annual export in a recurrent annual export pulse (Karl et al.,

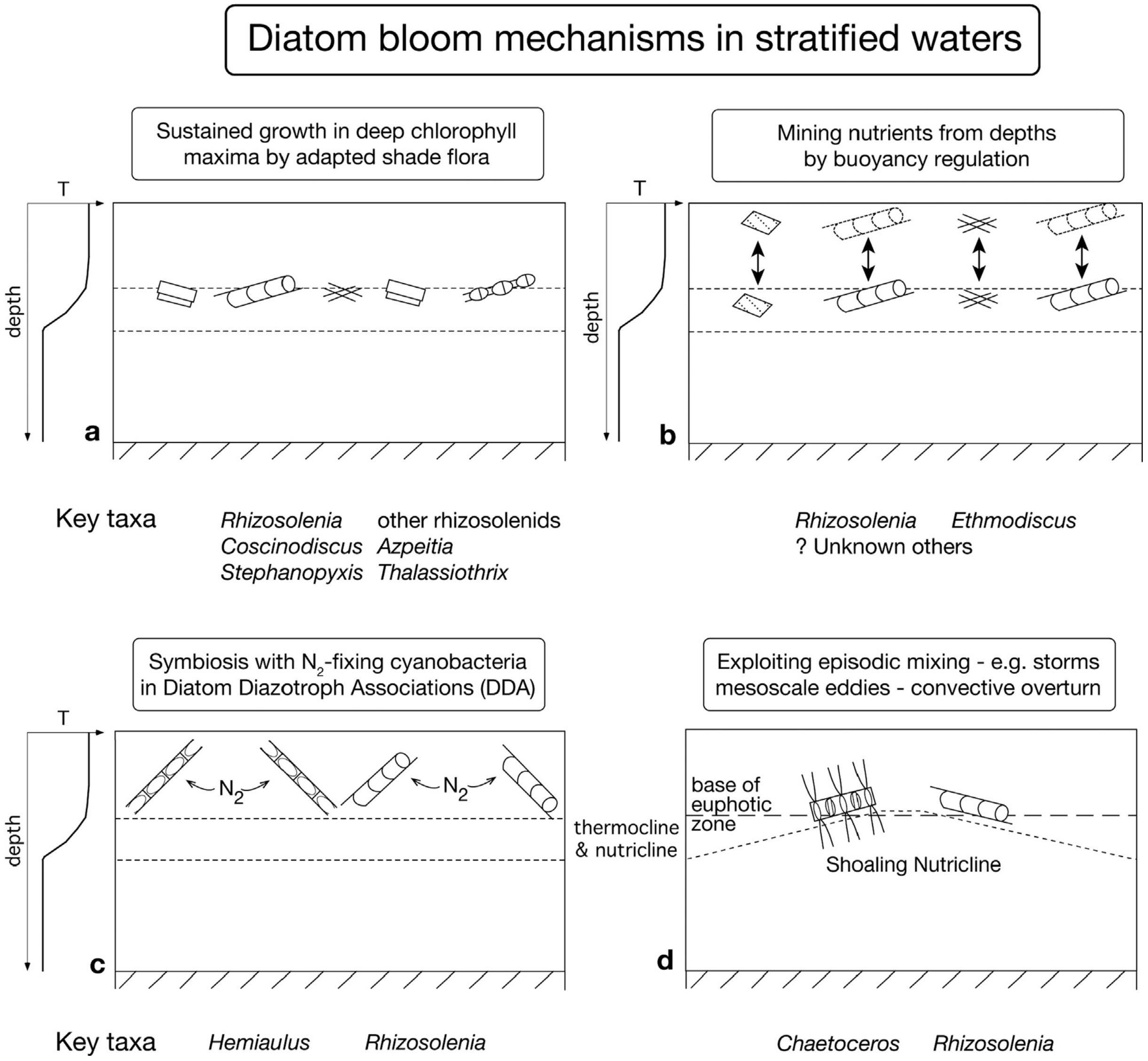

Fig. 6. Diatom adaptations to bloom in stratified waters include the ability to: (a) grow in low light conditions at depth, (b) mine nutrients from depth and migrate to higher light levels, (c) engage in symbioses with nitrogen-fixing cyanobacteria, (d) exploit episodic mixing events. The vertical axis represents depth in the water column with schematic thermoclines shown to the left. The dotted lines represent the upper and lower boundary of the nutricline. In panel d, the heavy dashed line represents the base of the euphotic zone in an episodically mixed water column. All of these scenarios are capable of generating bloom concentrations that can result in massive flux (Sancetta et al. 1991, Kemp et al., 2000, Kemp and Villareal, 2013).

2012). Based on satellite imagery, such summer chlorophyll blooms are more common farther north in the Pacific, deeper into the oligotrophic gyre (30–32°N) than at Sta. ALOHA (22.45° N) (Villareal et al., 2012). In some cases *Hemiaulus/ Richelia* are minor components of the diatom flora in these blooms, which may be dominated by small pennate diatoms that may exploit the DDA-sourced nitrogen (Villareal et al 2012). Such small diatom taxa are frequently overlooked (Guillard and Kilham, 1977) due to both their small size and frequent tendency to aggregate (Fryxell, 2000). Leblanc et al. (2018) observed that nanoplanktonic diatoms can sediment rapidly to depth, thus suggesting how a complex floristic interdependence between symbiotic and asymbiotic diatoms can lead to significant carbon transport.

4.2.4. *Nutrient storage capacity places diatoms in "pole position" to exploit episodic nutrient supply through mixing stimulated by storms, mesoscale eddies or deep convective mixing*

Observations over the past 10–15 years have highlighted the biogeochemical significance of storms and larger scale eddies in generating significant but time-limited diatom production in the major stratified oceanic regions. Cyclonic features south of Hawaii and mode water eddies in the Sargasso Sea have triggered exceptional diatom blooms, generally in the subsurface (McGillicuddy et al., 2007; Brown et al., 2008; Landry et al., 2008) while shorter lived storms may generate intense diatom blooms lasting just days (Krause et al., 2009; Lomas et al., 2009). These relatively short-lived diatom blooms may generate a large portion of annual organic carbon export (Krause et al., 2009). Elsewhere, convective overturn resulting from intense surface cooling generates diatom-dominated blooms in the otherwise oligotrophic Eastern Mediterranean (Pedrosa-Pamies et al., 2016). It is no surprise that diatoms dominate such blooms as they have adaptations that allow them to subsist in greater numbers than their competitors when nutrients are scarce, thus placing them in "pole position" to exploit episodic nutrient supply. Diatoms are unique among the dominant phytoplankton in possessing a large central vacuole that facilitates luxury uptake and storage, particularly of nitrate, where internal concentrations can reach mM (Dortch, 1982; Dortch et al., 1984). This enables the diatom cell to divide up to four times when competing phytoplankton would be nutrient limited, thus bridging periods of nutrient scarcity and represents a key adaptation to environments characterised by episodic nutrient availability (Raven, 1997; Kooistra et al., 2007). Furthermore, the restraint of diatom production by Si limitation is also fundamentally different to limitation by N, P or Fe because diatom silicification is independent of the carbon metabolism in the diatom cell cycle (Martin-Jezequel et al., 2000). Thus, cessation of production by Si limitation leaves diatoms replete in other nutrients (C, N, P) and therefore physiologically well-placed to respond to a reintroduction of nutrients in an episodic mixing event (Harrison et al., 1977; De La Rocha et al., 2010). Some diatom species are also able to store Fe (Marchetti et al., 2009). A further adaptation, derived from exosymbiont gene transfer, is the presence of the urea cycle, lacking in green algae and higher plants, facilitating rapid recovery from sustained N-limitation, that would further contribute to their head start over competitors (Allen et al., 2011).

4.2.5. *High diatom growth with low nutrients*

The mandala, for all its usefulness, was derived largely from work in coastal systems and during a period when the spring bloom seasonality of the North Atlantic Ocean and its shelf seas dominated conceptual approaches to oceanic rhythms. Subsequent work on diatom isolates to generate nutrient and growth rates relationships to provide mechanistic explanations have focused on laboratory-accessible species including such atypical forms as *Phaeodactylum* to represent all diatoms. While understandable, this oversimplifies and has limited the portrayal of diatoms in models, since batch culture techniques were typically used where continuous culture methods are more appropriate. An example often overlooked is the pivotal work of Goldman and McCarthy (1978) where chemostat experiments showed clearly that near maximum growth rates ($\sim 2.9\,\mathrm{div\,d^{-1}}$; $\mu{:}\mu_{max} = 0.94$) of the diatom *Thalassiosira pseudonana* (clone 3H) could be sustained at ammonium concentrations below the detection limit ($0.03\,\mu\mathrm{M}$).

4.2.6. *Si-uptake shows diatom adaptation to the subtropical gyres with distinct bloom mechanisms*

Silicate, as a metric for diatom production, provides great insights into the flexibility of diatoms in the Sargasso Sea of the North Atlantic and in the eastern North Pacific gyre. The contrasting annual cycles of biogenic Si and Si uptake patterns reveal differences in diatom physiology and positioning on the mandala. Silicate uptake experiments, primarily in the North Atlantic, have consistently shown that Si-addition leads to enhanced uptake in oceanic gyres (Brzezinski and Nelson, 1996; Brzezinski et al., 1998). This observation has been interpreted to indicate that diatoms are Si-limited in these oceanic waters where [Si] is $< \sim 2\ \mu\mathrm{M}$. Half-saturation constants typically used in models ($\sim 1\,\mu\mathrm{M}$) based on these observations necessarily restrict diatom growth. However, direct measurements in Pacific Ocean diatom blooms show a more complicated picture. Krause et al. (2012) noted that a Pacific Ocean diatom bloom (multispecies, but dominated by *Mastogloia woodiana*) exhibited the highest Si uptake efficiency ever recorded with K_s of 0.34 ± 0.24. In addition, a reanalysis of a global data set indicated that while uptake may be Si-limited, the increased kinetic efficiency found in Pacific diatom blooms yielded higher biomass with growth-rate inhibition suggested in only 21% of the Pacific experiments. In contrast, ~69% of the experiments from the Sargasso Sea indicated that Si-limitation was supressing growth (Krause et al., 2012). Si cycling in the two oceans is fundamentally different (Brzezinski et al., 2011). Diatom blooms in both areas generally occur during a limited period, but demonstrate different seasonal patterns despite the overall similarity of an oligotrophic setting. Blooms at the Bermuda Atlantic Time-series Study (BATS) occur in spring after winter convective overturn (Steinberg et al., 2001), in response to short term mixing events driven by winter storms (Krause et al., 2009) or mesoscale eddies (McGillicuddy et al., 2007). In contrast, the major blooms at the Hawaii Ocean Time-Series (HOT) Station ALOHA occur in summer during peak stratification. The HOT blooms are the annual maximum in biogenic Si and occur during maximum stratification, low turbulence and nutrient depletion while the BATS blooms are driven by mixing. Although biogenic Si production is 4 fold lower at Sta. ALOHA (Pacific) than the more productive BATS diatom blooms, the export of biogenic Si at the base of the euphotic zone is nearly the same. This remarkable similarity is due to the much higher Si recycling efficiency at BATS (Brzezinski et al., 2011). Had Margalef worked out of Hawaii, and witnessed the HOT blooms, the mandala would likely have looked considerably different.

4.3. *Diatoms form a continuum along the r/K selection axis*

In contrast to the recent "muddled" mandala versions (Figs. 3–5), in the original, Margalef recognized that different diatoms plotted from the "r" end of the mandala to around half way along the r-K axis (Fig. 1). With the benefit of more recent oceanographic research, he would likely have extended diatoms to the "K" end. Crucially, Margalef lacked the insights from the last two decades of observational research that now demonstrate that the taxa that he observed to persist sparsely in nutrient poor seas, such as *Rhizosolenia* and *Hemaulus* are actually major bloom formers.

Not only do different diatom species populate the full extent of the r-K continuum, individual species plot on different sections at different times. For example, the rhizosolenid, *Pseudoguinardia recta* may subsist in a DCM in the highly stratified Sargasso Sea (K-strategist) but is capable of growing at rates exceeding one $\mathrm{div\,d^{-1}}$ when a passing eddy or storm generates more nutrient input (r-strategist) (Goldman, 1993; Goldman and McGillicuddy, 2003). This plasticity in diatoms echoes broader critiques of the r/K paradigm. There has been debate as to whether some of the variability is better explained through phenotypic or developmental plasticity (Stearns, 1977) and some regard the r-K paradigm to be superseded because of this (Reznick et al., 2002). We argue that the ecological plasticity of diatoms renders the r-K scheme of little relevance. A similar conclusion was reached by a recent molecular diversity analysis of the Tara Oceans study that showed unexpectedly high diatom diversity in oligotrophic regions: "as a group the diatoms are therefore likely to display a continuous spectrum of different growth strategies" (Malviya et al., 2016). Evidence for efficient diatom export from these "oligotrophic" ocean regions is further provided by the presence of ubiquitous healthy diatoms across the deep ocean (Agusti et al., 2015).

5. How do we improve understanding of the important diatoms?

The limitations of existing conceptual approaches for understanding environmental controls on phytoplankton have been considered by Boyd et al. (2010). They summarize that the mandala has too few dimensions to depict temporal changes in multiple limiting factors. With regard to the Reynolds C, R, S Intaglio model as applied to marine phytoplankton more recently by Smayda and Reynolds (2001), Boyd et al. (op. cit.) point out that individual species within a phytoplankton group may spread across the different categories; a problem we also highlight with the simplified mandalas. Instead, they advocate a new approach combining an appreciation of the effects of interlinked changes in environmental parameters and their interplay with the most "significant controls" for any specific phytoplankton group. Our purpose, here, is to convey the message that diatoms cannot be regarded as an individual phytoplankton group or PFT. In the following, we advocate approaches that are most likely to yield the "significant controls" whose identification are the key to future prediction.

5.1. *Focus on the ecology of key diatom taxa for production and export*

We do not advocate the study of every species but water column and sediment studies show that there are some key taxa that drive production and export from a stratified water column (Sancetta et al., 1991; Kemp et al., 2000; Kemp and Villareal, 2013; Fig. 6). Plankton functional types will only ever be as good as our understanding of the ecology of the key players. Two quotes place this exercise in context: the first from a pioneer of ecosystem modeling, Gordon Riley:

> *"A necessary prerequisite……. is a thorough knowledge of the physiology and ecology of particular species and ecological groups"*,
>
> (Riley, 1952)

and the second from a recent model evaluation:

> *"Because of the still poorly understood ecology, we do not have robust group-specific parameterizations that can support predictions in a wide variety of spatiotemporal domains."*
>
> (Shimoda and Arhonditsis, 2016)

A case in point would be the genus *Hemiaulus*. Previously regarded as characteristic of the sparse flora of summer stratification (Guillard and Kilham, 1977), *Hemiaulus hauckii* has now been identified as a dominant species of vast diatom-diazotroph association (DDA) blooms that may exceed 100,000 km^2 in the North Pacific with a total area-integrated biogenic silica production equivalent to the California coastal upwelling zones (Krause et al., 2013). Summer blooms of *H. hauckii* off Hawaii also export carbon rapidly to depth providing around 20% of the annual flux to the benthos in a 4–6 week pulse (Karl et al., 2012). Significantly, new modeling efforts feature the first inclusions of a distinct DDA functional type, with separate diatoms and non-symbiotic microbial diazotrophs to simulate DDA blooms in the North Pacific Subtropical Gyre (Follett et al., 2018) and the tropical North Atlantic (Stukel et al., 2014). These studies also emphasize that key traits and parameters remain unclear.

The genus *Hemiaulus* may be an especially topical and appropriate target in the light of current trends of increasing stratification in the ocean. The Late Cretaceous Epoch (100–66 Ma), when global mean sea surface temperatures (from proxies) were around 10 °C warmer than present (DeConto et al., 2000) and atmospheric CO$_2$ concentrations exceeded present values by between two and ten times, may be regarded as an analogue for future global change. There are only four *Hemiaulus* species in the modern ocean. By contrast, in the Late Cretaceous, *Hemiaulus* was one of the dominant genera with over 40 species (Harwood and Nikolaev, 1995) and generated blooms that formed massive sedimentary concentrations (Davies et al., 2009; Davies and Kemp, 2016). Will future climate change favour a re-radiation of *Hemiaulus* as a genus?

5.2. Sample the large diatoms more effectively to better understand their ecology

Many of the key diatom taxa that bloom in stratified seas are large and/ or chain and mat forming diatoms whose size range (individually or in colonies) is within the "*meso*-plankton" – a size class (200 µm – 2 cm) traditionally regarded by biological oceanographers as comprising "mainly zooplankton" (Miller, 2004). This orthodoxy has too often framed oceanographic experiments so that large diatoms have been inadequately sampled and/ or sampled in zooplankton nets where they have been regarded as "contamination" e.g. by the giant diatom *Trichotoxon* during the SOIREE iron enrichment experiment (Zeldis, 2001). The ecology of the large diatoms is patchily understood and many are not in culture. The diatoms of the DCM are also poorly studied due to under sampling. Such key species need to be targeted by field and laboratory observational and experimental programmes. The inadequacy of conventional oceanographic techniques for sampling large aggregates was highlighted during the first documentation of diatom marine snow (Alldredge and Silver, 1988; Alldredge and Goltschalk, 1989) yet little has been done in the three ensuing decades to systematically improve methods in oceanographic process cruises. On the one hand, there have been significant advances in observational methods, for example, deployment of Video Plankton Recorders (VPR) and other imaging devices specifically designed for marine snow or zooplankton have been very successful in identifying aggregates and large diatoms (Honjo et al., 1984; Macintyre et al., 1995; Asper and Smith, 2003; Gorsky et al., 2003; Pilskaln et al., 2005; Picheral et al., 2010; Timmerman et al., 2014). However, the essential sampling has been confined to one-off deployments of bespoke apparatus on large ROVs (Pilskaln et al., 1998) or rarely used diver observation and sampling campaigns (Villareal et al., 1996, 2011).

5.3. Target the subsurface ocean

We have already drawn attention to the importance of deep chlorophyll maxima in diatom production. These remain understudied and their often highly restricted vertical extent has militated against adequate sampling by conventional oceanographic surveys. In near-coastal areas there have been intensive high resolution studies of thin subsurface phytoplankton layers, for example the LOCO (Layered Organisation in the Coastal Ocean) programme in Monterey Bay (Rines et al., 2010; Sullivan et al., 2010), but studies of similar intensity now need to be expanded further offshore. Increasing use of towed undulators and autonomous underwater vehicles with chlorophyll fluorescence sensors are indeed detecting ubiquitous subsurface layers. These are best known in coastal and shelf seas (Weston et al., 2005; Hodges and Fratantoni, 2009; Ross et al., 2017) but such features may extend out for several hundred km beyond the shelf break over the open ocean (Perry et al., 2008; Hemsley et al., 2015). The general interpretation of the deep chlorophyll maximum layers of the perennially stratified tropics and central gyres (the classical oligotrophic settings) is that they are not a peak of biomass but are due to increased chlorophyll content of phytoplankton as a photo-physiological adaptation to low light (Cullen, 2015). However, sea gliders and towed undulators are now detecting extensive DCM layers and subsurface hotspots in both the North Pacific Subtropical Gyre (Nicholson et al., 2008) and tropical Atlantic (Stanley et al., 2017) that also represent biomass maxima.

The subsurface needs to be targeted more by observational sampling programmes and new methods need to be developed so that they may more routinely be sampled in order to characterise the phytoplankton community structure. Where these features have been sampled, it comes as no surprise that diatoms such as rhizosolenids are often key components (Weston et al., 2005; Sukhanova et al., 2006; Gribble et al., 2007).

There is also increasing evidence from mismatches between surface and deep observations that other subsurface processes are important both for diatom blooms and for export flux. These mismatches extend beyond stratified settings and are also relevant to the spring bloom period. For example in the North Atlantic spring bloom, Rynearson et al. (2013) identified a single species of diatom resting spores as a dominant flux component whereas the vegetative stage was only a minor component of the near surface assemblage.

5.4. Represent diatom diversity in ocean ecological/biogeochemical models

A general criticism of PFT models has been their omission of sufficient functional diversity by combining or aggregating many distinct ecotypes in single PFTs, not least, in the case of diatoms (Flynn, 2006; Terseleer et al., 2014). One way around this has been to adapt the PFT approach by either adding additional diatom PFT or by embedding diversity within existing PFT modules using a trait-based approach (Litchman and Klausmeier, 2008; Smith et al., 2016). The approach of Stukel et al. (2014) in developing a model of production in the Amazon plume was to define a distinct diatom-diazotroph association (DDA) PFT for *Hemiaulus* with its intracellular nitrogen-fixing symbiont, separate from a conventional diatom PFT. This enabled the model to simulate realistic separation of nitrate-driven coastal blooms and nitrogen-fixation fuelled DDA blooms in the more distal, nitrate-poor but silica-rich, Amazon plume. Using a different strategy, Terseleer et al.

(2014) modified the diatom module within the existing MIRO model to include variation in a number of size-dependent traits including growth rates, uptake rates, photosynthetic efficiency and grazer resistance. The model successfully reproduced the dominance of smaller diatoms in the spring bloom and a later bloom of larger grazer resistant species. A further approach to facilitate greater diversity uses adaptive modeling which allows communities to self-organize or self-assemble through competition amongst large numbers of ecotypes (Follows et al., 2007; Anderson and Follows, 2010). This obviates the need for parameter tuning since the model selects the fittest parameter combinations and in the context of a global ocean circulation model, will permit distinct but related PFTs (such as different diatom species) to survive in different regions (Anderson and Follows, 2010). The challenge will be to embed to ecology of stratified-adapted diatoms fully into such models.

6. Conclusions

This contribution is primarily an appeal to take account of the diversity of diatoms for studies of ocean biogeochemistry, and in particular, ocean biogeochemical modelling. Research over the past two decades shows that diatoms adapted to stratified ocean settings may develop large biogeochemically important blooms using a range of adaptations, some of which are unique to this group. These include the ability to grow in low light conditions at depth, to mine nutrients from depth and migrate to higher light levels, and to engage in symbioses with nitrogen-fixing cyanobacteria. Each of these distinct scenarios may lead to biogeochemically important production and export and need to feature in their own right in models for prediction of future ocean behaviour. To date, most ocean biogeochemical models feature diatoms as a single plankton functional type (PFT) and this leads to potentially misleading views of the effects of increasing stratification on ocean ecosystems and the carbon cycle. Parallel concerns regarding the impact of oversimplification or loss of taxonomic data on key species have been raised by McQuatters-Gollop et al. (2017) in the context of marine management and policy decision making.

We have chosen to critically examine the mandala because many of the recent discussions of phytoplankton behaviour and PFT development cite Margalef's classic 1978 paper as a rationale for casting the diatoms as a single PFT characterised by rapid growth and biogeochemical dominance only in nutrient-replete, turbulent conditions. This one-dimensional view of diatoms has led to the widespread forecast of decreased productivity in future, more stratified oceans. We have shown that many of these recent studies have relied on a simplified version of the mandala that does not take account of Margalef's original insights into the ecological plasticity of diatoms. Taken together with recent developments in observational oceanography, we advocate consideration of a scenario whereby increased ocean stratification may actually enhance overall diatom production and export. The only way to explore this properly is to develop better parameterisations in models that can effectively reproduce the diverse ecology of biogeochemically significant diatoms.

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