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Margalef revisited: A new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology

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ABSTRACT

Building on the classic depiction of the progression from a diatom to a dinoflagellate bloom as a function of nutrients and turbulence, known as the "Margalef mandala", a new conceptual model or mandala is presented here. The new mandala maps twelve response or effects traits, or environmental characteristics, related to different phytoplankton functional types: (1) relative preference for chemically reduced vs chemically oxidized forms of nitrogen; (2) relative availability of inorganic nitrogen and phosphorus; (3) adaptation to high vs low light and the tendency to be autotrophic vs mixotrophic; (4) cell motility; (5) environmental turbulence; (6) pigmentation quality; (7) temperature; (8) cell size; (9) relative growth rate; (10) relative production of bioactive compounds such as toxins or reactive oxygen species (ROS); (11) r vs K strategy; and (12) fate of the production in terms of grazing. The new mandala serves to highlight the differences and trade-offs between traits and/or environmental conditions, and illustrates some traits tend to track each other, a concept that may be helpful in trait-based modeling approaches and in understanding environmental factors associated with harmful algal blooms. It is hoped that this new mandala captures some of our recent insight into phytoplankton physiology and functional traits, and has contemporary relevance in light of anthropogenic changes in nutrient form and ratio.

1. Introduction

There is currently keen interest in trait-based modeling of phytoplankton (e.g., Follows et al., 2007; Litchman and Klausmeier, 2008; Zwart et al., 2015). Trait-based models have demonstrated an emergent community structure and biogeography that predict well the global patterns of different phytoplankton functional types. Such an approach makes the assumption that phytoplankton functional types have inherent traits or characteristics that provide them an advantage in given conditions. Trade-offs between and among traits, costs and benefits of adaptations of differing species and functional types, together with those of their grazers, ultimately yields plankton dynamics that characterize the diversity of life both in the oceans and on land (Grover, 1995; Tilman, 2004; McGill et al., 2006; Bruggman and Kooijman, 2007). Understanding traits and trade-offs of different species and functional types may give us clues to understanding when and why certain types of algal blooms, including harmful algal blooms (HABs), may form and the environmental factors associated with them. Trait characteristics can be considered to be those characteristics that predict a species' fitness in response to an environmental parameter, i.e. a response trait, or those that may affect the species' contribution to ecosystem function, i.e., effect traits (Zwart et al., 2015). Both types of traits are applied herein. There is a growing body of evidence-based approaches for characterizing and developing trait-based models (e.g., Follows et al., 2007; Litchman et al., 2007; Litchman and Klausmeier, 2008; Hillebrand et al., 2013; Edwards et al., 2013a,b; Zwart et al., 2015). What is presented here is an attempt to update our conceptual depiction of the relationship between such traits.

Trait-based understanding of plankton distribution is far from a new concept. Hutchinson (1961) posed the paradox of the plankton, raising the question of how it is possible for a number of species to co-exist in a relative unstructured environment all competing for the same resource. Of course, the oceans are not nearly as "unstructured" as once thought. Margalef (1978; Margalef et al., 1979) captured the essence of much of the importance of the balance of physical forces and nutritional forces

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in his now-classic "mandala", in which he related the life forms of diatoms and dinoflagellates to turbulence and nutrients (Fig. 1). The mandala highlighted the distinction in distribution between organisms that thrive under turbulent, nutrient-rich conditions, i.e., the diatoms, and those that tend to thrive under more nutrient-poor, low-turbulent environments, i.e., the dinoflagellates. Such a simple – but elegant – conceptual model also allowed for a general understanding of the formation of HABs, or red-tides, through a seasonal succession that is driven by a change in turbulence and nutrient supply from depth (Fig. 1).

Recognizing that no model can capture all of the properties, trade-offs, and adaptive strategies of cells, there is nevertheless value in using conceptualizations such as the mandala to compare, contrast, relate, and thus simplify how different phytoplankton functional types cope with their environment. A mandala is, after all, a conceptual and spiritual symbol of the cosmic truths of the Universe (www.newworldencyclopedia.org), a representation of recurring order. The term mandala has recently been used to represent a chart or diagram that captures such concepts, and normally uses shapes such as squares and circles in a geometric pattern.

Over the past decades there have been many attempts to advance the application of Margalef's mandala and to improve either the representation of different phytoplankton taxa or different features on the mandala. As examples, Cullen et al. (2002, 2007) provided a revised view that includes the picoplankton, Balch et al. (2004) suggested a revision that included coccolithophores, while Allen and Polimene (2011) suggested that the addition of a gradient of reactive oxygen activity provided an important link between physiology and ecology. All are simplifications, of course, as is, indeed, this effort at revision. No

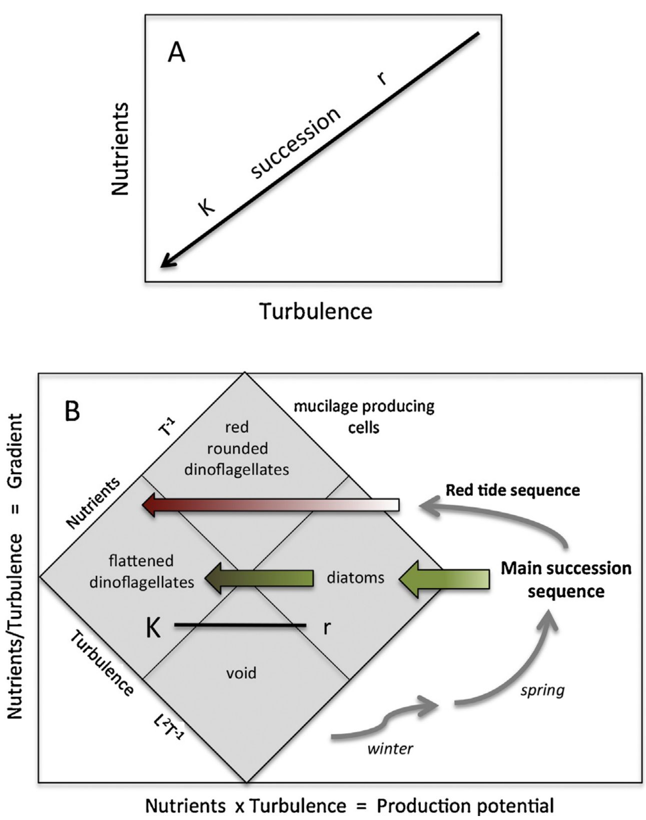

Fig. 1. Margalef's mandala. The mandala (B) was developed from the original conceptual understanding of the trajectory of phytoplankton responses to nutrients and turbulence (A). Note that the mandala illustrates both a generalized winter-spring bloom sequence and a "red tide" sequence. (A) Redrawn from Margalef et al. (1979); (B) reproduced from Smayda and Reynolds (2001) with permission of the *Journal of Plankton Research.*

conceptualization of the sort of the mandala can capture the full spectrum of adaptations, from life history to nutritional and behavioral strategies that we now know exist within the phytoplankton, in contrast to what was known to Hutchinson (1961). Well noted by Wyatt (2014), a simple turbulence scale fails to capture the dynamics in the vertical and fails to incorporate fine-scale structures such as thin layers. Wyatt (2014) also stated that many adaptive strategies also cannot be incorporated. For example, Wyatt (2014) noted that, "If we add a few simple shapes (say spheres, discs, rods, needles), some spines, threads or trichocysts, motility, gas vesicles, colony formation, whether cells are rigid or flexible, EPS formation, bioluminescence, functional properties (specific production rates, nutrient uptake rates, half saturation coefficients, internal stores, pigment suites), some demographic features, the spectrum of responses obviously gets out of hand very rapidly...".

In spite of its limitations, one of the important strengths of the original mandala was the incorporation of the ecological concept of r vs K strategies, the trade-off between growth and productivity on the one hand, and maintenance and efficiency of resource acquisition on the other. The mandala appropriately recognizes the diatoms as the r strategists, and the dinoflagellates as K strategies. Smayda and Reynolds (2001), based on Grime (1977), extended this concept in their adaptation of a conceptual representation of various life forms using a 3-compartment, rather than a 2-compartment, differentiation of life forms. This approach differentiated the colonists (C-strategists), the stress-tolerant, large cells from the slow growing (S-strategists) and the ruderal cells (R-strategists) that can cope with high nutrients, high light, and high turbulence.

Since the publication of Margalef's mandala not only have there been massive advances in our understanding of phytoplankton cell functioning, but there have also been grand-scale global changes in environments due to anthropogenic activities. What follows is an attempt to update the mandala, capturing recent insight into phytoplankton physiology and functional traits, as well as the complex changes of nutrient enrichment due to our increasing and changing nutrient footprint. This mandala adds a visual tool to our current "compelling evidence for this trait linkage from environmental conditions to ecosystem function for aquatic systems..." (Zwart et al., 2015, p. 2261).

2. The new mandala

The new mandala maps twelve effect or response traits (Fig. 2): (1) relative preference for chemically reduced vs chemically oxidized forms of nitrogen; (2) relative availability of inorganic nitrogen and phosphorus; (3) adaptation to high vs low light or the tendency to be purely autotrophic vs mixotrophic; (4) cell motility; (5) environmental turbulence; (6) relative pigmentation quality, from higher relative proportion of carotenoids (brown) to higher relative proportion of phycobiliproteins and chlorophylls (blue-green or green); (7) temperature; (8) cell size; (9) relative growth rate; (10) relative production of bioactive compounds such as toxins or reactive oxygen species (ROS); (11) ecological strategy, as r vs K; and (12) fate of the production in terms of grazing. Viewing these axes from the inner square out, it places key importance on nutritional strategies, and modes of motion. The next set of axes superimposes physical constraints or variability, namely turbulence, and temperature, acting in opposite directions; high turbulence is associated with low temperatures and vice versa. Pigmentation is a response axis. Other emergent properties are shown on the largest box, including cell size, growth rates, potential to produce toxin, and overall ecological strategy. The overarching circle represents the fate of the production in the food web and the relative strength of macro vs micro-grazing control.