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Contribution to the Themed Section: Scaling from individual plankton to marine ecosystems

HORIZONS

Small bugs with a big impact: linking plankton ecology with ecosystem processes

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As an introduction to the following Themed Section on the significance of planktonic organisms to the functioning of marine ecosystems and global biogeochemical cycles we discuss the ramifications size imparts on the biology of plankton. We provide examples of how the characteristics of these microscopic organisms shape plankton population dynamics, distributions, and ecosystem functions. Key features of the marine environment place constraints on the ecology and evolution of plankton. Understanding these constraints is critical in developing a mechanistic understanding and predictive capacity of how planktonic ecosystems function, render their capacities in terms of biogeochemical cycling and trophic transfer, and how planktonic communities might respond to changing climate conditions.

KEYWORDS: Plankton Ecology; Scales; Biogeochemistry; Motility; Behavior

INTRODUCTION

Global scale biological processes in the open ocean are driven by microscopic plankton. Marine microbes are the biological engines behind most of the oceanic geochemical processes, including vertical material transport and carbon sequestration, and plankton biomass provides resource for higher trophic levels that support fisheries. Collectively, marine plankton fix as much

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carbon as the terrestrial biosphere (Field *et al.*, 1998). Thus, these small bugs have big impacts.

Given the dominance and large impact of small organisms in the open ocean, it is particularly relevant to understand the world plankton inhabit and how microscopic organisms affect ecosystem functioning. The vast range of scales involved, from microscopic organisms interacting on truly microscopic scales (μm and seconds), in to the ramifications of these interactions on macroscopic scales provides a formidable challenge both logistically and analytically. To gather insight into current, novel plankton research that overcomes the significant challenges associated with their study, we organized special sessions at two ASLO (Association for the Sciences of Limnology and Oceanography) meetings (Hawaii, February 2014 and Granada, February 2015) to explore the implications of the physiology and behavior of marine plankton for their population dynamics, community composition, and distribution and ultimately to large-scale, long-term ecosystem processes, including biogeochemical cycles, response to climate change, and opportunities for management strategies. Participants in the sessions were invited to contribute to the following theme section of this journal.

As an introduction to the Themed Section we first highlight size as a structuring factor of planktonic communities and food webs, describe examples of adaptation of planktonic organisms to some of the key features of their microscopic world, and how processes on the planktonic scale may scale up to impact population-level ecology and ecosystem processes, before we leave the word to the authors of the Themed Section contributions.

COMMON CHARACTERISTICS OF PLANKTONIC COMMUNITIES

Planktonic primary producers are miniscule in size

While plants in terrestrial systems occur in almost any size, from photosynthetic microscopic protists to giant trees that are taller than 100 m, the vast majority of primary producers in the open ocean are unicellular and only a few μm in diameter. In fact, the most abundant phytoplankton in the oceans are photosynthetic picoplankton that measure less than a micrometer (Chisholm *et al.*, 1988). The small size and consequently high turnover rate of phytoplankton compared to most terrestrial plants gives rise to the fact that the primary production per unit area on land and depth integrated in the oceans are of similar magnitudes on average, differing only by a factor of about 2, even though the terrestrial plant biomass is orders of magnitude higher.

Resource supply puts constraints on phytoplankton cell size. Inorganic nutrients and light are the primary limiting factors of phytoplankton growth rates and the distribution of these resources are spatially heterogeneous. The vertical gradient in light intensity is intuitively appreciated, as is the fact that nutrients are taken up by phytoplankton in the illuminated surface layer, but dead cells and other particles containing organic material, especially fecal pellets, sink to below the pycnocline, where the nutrients may be remineralized. Rapid turnover of nutrients in the surface layer fuels 'regenerated production' although this recycling does not prevent a steady drain of nutrients from the surface layer, especially since nitrogen fixation only supplies nitrogen, not phosphorus and other essential nutrients.

Size-dependent constraint on nutrient uptake rates is the fundamental reason that the primary producers in the ocean are small. In the oligotrophic ocean, it is often assumed that small size is a competitive advantage because smaller, spherical organisms, have relatively larger surface areas to better facilitate nutrient uptake. However, when nutrients are limiting, the surface area does not limit the uptake rate, as there are vastly more uptake sites are available than necessary to process the limiting nutrient. Instead, uptake is a function of the organisms' substrate affinity. At low nutrient concentrations diffusive delivery increases in proportion to the radius (not the area) of the cell (Berg, 1992), which implies that the volume-specific uptake rate scales inversely with the cell radius squared. This is a much more severe constraint than the surface area limitation. The most oligotrophic parts of the oceans are dominated by the smallest plants, the cyanobacteria, that are approaching the smallest possible size of a cell (Raven, 1994), while the selective pressure for size is relaxed under eutrophic conditions, where cells may be larger. Thus, it is the vertical separation of the uptake and remineralization of inorganic nutrients and the consequent nutrient limitation of the surface dwelling oceanic primary producers that leads to the small size of primary producers and to the dominance of small heterotrophic organisms in the combustion of organic matter in the oceans. Interestingly, recent modeling and observational efforts have shown that vertical transport of matter and energy by motile organisms is an important conduit in the biological pump, and can provide a biologically mediated reversal of the physically imposed separation of nutrient sources and sinks (Steinberg *et al.*, 2000; Stemmann *et al.*, 2004; Iversen *et al.*, 2010).

Planktonic food webs are size structured

Typically, the (almost) consistently small size of primary producers in the oceans implies that their consumers are also small. Although there are exceptions (e.g. tunicates

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Lombard *et al.*, 2013; dinoflagellates, Jacobson and Anderson, 1993), the typical size ratio between herbivores and their phytoplankton prey is 10:1 (Hansen *et al.*, 1994; Kiørboe, 2008). This producer–consumer size ratio implies that planktonic food webs are highly size structured with the majority of production occurring at the low end of the size spectrum. In addition, the low transfer efficiency of matter and energy across trophic levels (~10–20%) implies that, for consumers in the 1 mm size range, <1% of primary production remains available. Remarkably, mixotrophic plankton may constitute an important enhancement of trophic transfer efficiency and carbon export from the surface ocean (Ward and Follows, 2016). Dissolved organic material derived from primary producers and other organisms (e.g., leaking, 'sloppy feeding') is consumed by sub-micron sized bacteria and processed in the microbial loop (Hobbie *et al.*, 1972; Azam *et al.*, 1983), reinforcing the idea that small organisms consume a high percentage of the organic carbon, leaving only a small fraction for higher trophic levels or export production. Interestingly, these constraints are relaxed when planktonic communities receive external nutrient inputs that relax the advantages of small primary producers. Thus, the small size of primary producers, combined with low trophic transfer efficiency results in predictable, highly size structured food webs with the smallest organisms being the most abundant.

Predation pressure is constant

Predation is another, important structuring factor in plankton. Hairston *et al.*, (1960) argued convincingly that herbivores on land are subject to intense predation pressure by carnivores, relieving the predation pressure on the plant-prey of the herbivore. Subsequent intentional and accidental large-scale experiments have verified Hairston's hypothesis (see Smetacek, 2012). However, in the ocean, predation pressure on phytoplankton is constant and immediate. It is well documented that, out of the myriad of mechanisms that can induce phytoplankton mortality or remove phytoplankton biomass (e.g. sinking, mixing, viral lysis and herbivorous predation), predation has consistently been found to be quantitatively dominant (Calbet and Landry, 2004; Banse, 2013). Overall, the vast majority of primary production does not appear to accumulate and there is a surprisingly tight coupling between the rates of primary production and herbivory (Banse, 2013). The unicellular herbivores, key predators of phytoplankton, can reproduce asexually and rapidly match increases in resource abundance (Strom, 2008), yet withstand long (~weeks) periods of starvation (Menden-Deuer *et al.*, 2005; Calbet *et al.*, 2013). Predation pressure by these organisms does not necessarily vary seasonally. Simultaneous to protistan predation, metazoan predators with much longer lifespans also exert considerable predation pressure on phytoplankton (e.g. Campbell *et al.*, 2009). One implication of this seasonally, near constant, high predation pressure is that the biomass ratios of primary producers to herbivores are often low, and can even be less than unity (e.g. Sherr and Sherr, 2009). Given this constant predation pressure, it is therefore not surprising that predation is a significant factor in shaping the ecology and evolution of phytoplankton (Smetacek, 2001). Thus, research that seeks to attribute phytoplankton population dynamics to bottom up conditions alone inevitably excludes the major loss factor of phytoplankton production. Predictions of plankton population dynamics are likely improved with formulations where cell division rates are a function of bottom up forces while subsequent biomass accumulation rates scale with top down predation pressure. The latter in comparison has received vastly less attention in investigations of plankton ecology, with notable exceptions (Verity and Smetacek, 1996; Ward *et al.*, 2012; Behrenfeld and Boss, 2014).

Planktonic communities are diverse

Long known and appreciated (Hutchinson, 1961), the molecular revolution has revealed that planktonic communities harbor immense phylogenetic diversity. This characteristic strongly influences the methodological and analytical approaches utilized in studying plankton ecology. Despite the amazing observable biodiversity on land, terrestrial plants and animals are phylogenetically relatively homogeneous, representing only two branches on the tree of life (Falkowski *et al.*, 2004), whereas in the ocean, plankton occupy almost all of the known phylogenetic diversity (Rynearson and Palenik, 2011). The vast size range (discussed above) and physiological and behavioral diversity of planktonic organisms poses important challenges in their study, as life history patterns, biochemistry and physiology can vary significantly due to ancestral lineages in seemingly similar species. Recent investigations have shown that not only is there a great deal of diversity among the smaller oceanic eukaryotes (de Vargas *et al.*, 2015; Worden *et al.*, 2015), but that even within species, there can be significant intra-specific variation in elemental composition, morphology, physiology and behavior (e.g., Moal *et al.*, 1987; Boyd *et al.*, 2013; Fredrickson *et al.*, 2011; Rynearson and Armbrust, 2004; Harvey *et al.*, 2013; Kiørboe, 2013; Menden-Deuer and Montalbano, 2015). Model simulations suggest that this intra-specific variation may be adaptive (Menden-Deuer and Rowlett, 2014).

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SCALING UP: FROM INDIVIDUAL ADAPTATIONS TO PROPERTIES OF POPULATIONS AND ECOSYSTEMS

What are the characteristics that provide opportunities for extrapolating our understanding of plankton ecology to predicting large-scale features and processes? The behavior and physiology of individual planktonic organisms are adapted to the environment in which plankton live and their microscopic size places constraints on their biology. These adaptations and constraints have implications for the dynamics of populations as well as to the distribution of species, as exemplified below. However, often the relationships between individual behaviors and population and community ecology are not (yet) fully, or even well understood, motivating the organization of the themed sessions at ASLO meetings.

The environment of microscopic plankton is characterized by being viscous and nutritionally dilute. These are characteristics that require adaptations in foraging behaviors (Paffenhőfer *et al.*, 2007), as image formation is only possible for organisms exceeding several millimeters in size (Martens *et al.*, 2015), thus constraining microscopic foragers to use chemical and hydromechanical cues to search for food. Not only do inorganic nutrients occur in very dilute and limiting concentrations in the open ocean, the availability of food for zooplankton and other heterotrophs is also very low compared to terrestrial systems. The biomass per unit surface area of plants in terrestrial systems is on average about 100 times the average biomass of plants in the ocean (Falkowski *et al.*, 1998). This difference is due to the fact that terrestrial plants need supportive structures to stay suspended in air while marine primary producers are near neutrally buoyant and can float without the need for such structures or to expend energy to control buoyancy and vertical position. In addition, the biomass of primary producers in the ocean is distributed in an approximately 100 m water column, rather than on a two-dimensional surface. Thus, compared to terrestrial systems, the availability of food to herbivores in the open ocean is extremely low. Many terrestrial herbivores, with ruminants as a well-known example, are adapted to process huge amounts of easily accessible plant material with a low nutrient content (e.g. Nie *et al.*, 2015), conversely pelagic herbivores are adapted to clear enormous volumes of viscous water to ingest small volumes of microscopic cells of a high nutritional quality. Thus, zooplankton, herbivorous, carnivorous and omnivorous, must daily clear a volume of water to concentrate prey particles that corresponds to 10^6 times their own body volume (Hansen *et al.*, 1997; Kiørboe, 2011).

Zooplankton have developed various mechanisms to examine, and extract prey from such large volumes of viscous water, each of which comes at a mortality cost (Kiørboe, 2011). Water is not easily sieved and prey are not easily approached due to viscosity, and non-visual prey perception is mostly short-ranged. Another adaptation for finding prey in a dilute environment is to move rapidly in a directed fashion, which results in enhanced resource encounter rates, but elevates the risk of predator encounter rates (Gerritsen and Strickler, 1977; Visser and Kiørboe, 2006). The various feeding behaviors that have evolved to solve these problems are associated with different predation risks and, thus, have direct implications for population dynamics and organism distributions. The foraging strategies that are the most beneficial depend on the relative availability of food and concentration of predators. Motile phytoplankton also utilize movement to acquire resources and avoid predators (Harvey and Menden-Deuer, 2012). Schuech and Menden-Deuer (2014) observed that the vertically biased movement characteristics of many single-celled plankton species provide the underpinnings of large-scale phenomena, such as diel vertical migration. Identifying such key characteristics of motility behaviors at the microscopic scale allows scaling of these important features to identify the mechanistic underpinnings of macroscopic phenomenon. Ultimately, such linkages allow predictions of cell–cell encounter rates and many derived processes, including resource uptake, cell distributions, and population dynamics. Thus, the distribution of species (and traits), is directly dependent on individual behaviors (Visser, 2007; Menden-Deuer, 2010; Mariani *et al.*, 2013).

Sexual reproduction and mate-finding represent similar problems as resource encounter because the distance between mates is vast in the 3D ocean, and random mate encounter is rarely sufficient to maintain a population in the face of high mortality. Many metazoan zooplankton have solved this problem by expanding their footprint through chemical signaling: the females produce pheromone signals that the males find using high risk searching behaviors (Doall *et al.*, 1998; Tsuda and Miller, 1998). The implications for population dynamics are evident in several ways: (i) mate encounter rate may limit reproductive rate (Kiørboe, 2007), (ii) the risk-taking behavior of the males leads to female-based adult populations in the field (Hirst *et al.*, 2010), (iii) the searching performance of the males predicts the minimum possible sustainable population density due to allee effects (Gerritsen, 1980) that can be verified by observations (Kiørboe, 2006; Choi and Kimmerer, 2008), and, finally, (iv) mate finding performance determines the ability of a species to colonize a new area,

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e.g., through ballast water introduction (Choi and Kimmerer, 2008). Thus, individual feeding and mate-finding behaviors in the dilute open ocean govern the population structure and dynamics of zooplankton to a significant extent.

Bacteria feeding on dissolved organic molecules leaking mainly from phytoplankton must collect these molecules from an even larger relative volume than zooplankton (about 10^8 cell volumes per day) and rely on molecular diffusion to come into contact with molecules. For the larger motile bacteria, chemotaxis can be used to aggregate in ephemeral patches of elevated nutrient concentration (Stocker, 2012). The ability of motile bacteria to utilize chemical gradients and trails to localize food not only makes marine snow aggregates biological hot spots in the ocean (Azam and Long, 2001) but also contributes to the degradation of sinking aggregates and alters and reduces vertical material fluxes. Thus, quantitative estimates of bacterial swimming rates and responses to sinking particles are an integral element to accurately estimating rates of export production.

The patchy distribution of resources in the ocean elicits remarkable feedback mechanisms between bacterial and zooplankton foraging behaviors and the resultant or emerging distribution of their populations. Resource-locating foraging behaviors have been observed for marine consumers at all trophic levels ranging from bacteria to zooplankton. Marine snow and other resource-derived stimuli elicit rapid responses and colonization by bacteria and in turn attract protistan bacterivores (e.g. Fenchel and Blackburn, 1999; Azam and Long, 2001; Grossart *et al.*, 2006), altering the distribution of these organisms, concentrating biomass, and likely forming desirable prey patches for higher trophic levels. Copepods have been shown to respond to prey patches in a similar manner (Tiselius, 1992; Saiz *et al.*, 1993). Likewise, herbivorous protists have evolved foraging behaviors that enhance predator–prey encounter rates (e.g. Harvey *et al.*, 2013), and enable the exploitation of phytoplankton patches (Menden-Deuer and Grünbaum, 2006). Likely as a result of prey-specific foraging behaviors, phytoplankton aggregations co-vary with protistan predator aggregations in the field (e.g. Stoecker *et al.*, 1984, Menden-Deuer, 2008). Remarkably, the spatial structure of aggregations, namely steep gradients in resource concentrations, rather than absolute biomass concentrations, appear central to eliciting predator aggregations (Menden-Deuer, 2008), a characteristic that is observed across several trophic levels in marine food webs (Benoit-Bird and McManus, 2012). Across trophic levels, heterogeneous prey distributions elicit behavioral responses in consumers that result in alterations of swimming behaviors, affect consumer dispersal rates and population distributions, and imply that patchy resource distributions are an important factor in adequately resolving population abundances. Possibly even more important, heterogeneous distributions also affect the rates of resource uptake and growth of consumers. However, although evidence based on rate measurements from the field is sparse, patchy plankton distributions have been shown to affect copepod fecundity, protistan grazing rates and phytoplankton primary production (Mullin and Brooks, 1976; Menden-Deuer and Fredrickson, 2010; Menden-Deuer 2012; Calbet *et al.*, 2015).

Collectively, these examples show that behavioral characteristics of species and interactions at the individual level have footprints much larger than the microscopic scales on which they occur. Currently we lack the analytical ability and theoretical foundation to integrate such fine scale biological information in ecosystem level models, e.g., biogeochemical models of the global carbon cycle. Clearly, we need a mechanistic understanding of the underlying processes and trait based approaches (e.g. Barton *et al.*, 2013) are a promising means to concentrate biological variability in terms of ecological functions, processes and group characteristics. However, even the sophisticated insight promised by trait-based ecology may not be enough. Research from other fields, for example, on long distance dispersal of plants, suggests that scaling up approaches need to incorporate stochasticity at the individual level and relatively rare events at the ecosystem level (Nathan, 2006). To make progress on this important problem, we need to acquire better data that concurrently measures processes at multiple spatio-temporal scales and identifies underlying mechanisms. We also need to embrace existing, or develop novel, statistical methods that can accommodate stochasticity and variability at the individual level and link this variability to ramifications at the ecosystem level, which is subject to its own scales of variability and stochasticity. In short, the scaling up approaches our special session called for are urgently needed for a better understanding of marine planktonic communities and the globally important processes they affect.

SUMMARY OF CONTRIBUTIONS

The papers contributed to this Theme Section highlight fascinating aspects of plankton ecology and taxonomy both from laboratory and field studies. The great lengths researchers have gone to ask even the most fundamental questions is impressive, such as determining species identity. Dolan (2015) brings forth the 'inconvenient truth',

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his words, that the taxonomic duplications, such as synonyms or variants of the same species having received multiple taxonomic attributions are common, including the dinoflagellate *Ceratium ranipes*, which changes species name depending on the time of day of sampling, due to light-induced variations in morphology. Obviously, light is a major stimulus in marine ecosystems and diel changes in the elemental stoichiometry of picoplankton are reported by Lopez *et al.* (2016). Such light-driven and potentially predictable variations in cellular elemental concentrations are essential to large-scale modeling efforts to illuminate the biogeochemical footprint of these small but important phytoplankton. Along similar lines, Morris *et al.* (2016) investigated how biologically mediated removal potential of hydrogen peroxide varied with diel cycles and across phyla in the South Pacific. They found that removal potential peaked at time of highest concentration, potentially offsetting the harmful effects of this reactive oxygen intermediate. The suggested close coupling between ambient chemical conditions and organism responses offers another opportunity for gaining mechanistic insights and predictive understanding of the biogeochemistry of plankton. A study on the phototrophic dinoflagellate, *Heterocapsa triquetra* suggests that cells have the ability to distinguish different types of co-occurring particles or conspecifics as well as exhibit a high degree of sensitivity to changes in seawater viscosity, as seen through changes in motility behaviors (Orchard *et al.*, 2016). In a study off the southern California Bight that combines modeling to quantify bloom duration and transport pathways of harmful algae with statistical analysis of potential covariates of species occurrence, Bialonski *et al.* (2016) observed how well a species' ecology is embedded in the complex interplay between biotic and abiotic factors. Using the unfortunately named but otherwise amazing new observation technology, the "*In Situ Ichthyoplankton Imaging System* (ISIIS)", Greer *et al.* (2016) report observations of the differences in group-specific aggregation behaviors that underlie diverse phenomena, including patchiness, and reveal abundance and distribution patterns that are critical to assessing ecological impacts. Tiselius *et al.* (2016) analyzed an impressive 28-year time series from a coastal fjord to identify significant linkages between primary production and the likely forcing function of wind induced vertical mixing and resultant enhanced nutrient supply. Their results relied on not only inclusion of primary producers but also two higher trophic levels, demonstrating that food web studies, rather than abundance measures were necessary to identify both the large scale forcing functions (North Atlantic Oscillation) and the local scale regulators (predation and trophic cascade effects). These studies clearly continue to highlight the amazing diversity and complexity of plankton and point a way forward for overcoming obstacles in measuring the true impact of these small bugs.

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