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REVIEW AND SYNTHESIS

The biogeography of marine plankton traits

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Abstract

Changes in marine plankton communities driven by environmental variability impact the marine food web and global biogeochemical cycles of carbon and other elements. To predict and assess these community shifts and their consequences, ecologists are increasingly investigating how the functional traits of plankton determine their relative fitness along environmental and biological gradients. Laboratory, field and modelling studies are adopting this trait-based approach to map the biogeography of plankton traits that underlies variations in plankton communities. Here, we review progress towards understanding the regulatory roles of several key plankton functional traits, including cell size, N_2-fixation and mixotrophy among phytoplankton, and body size, ontogeny and feeding behaviour for zooplankton. The trait biogeographical approach sheds light on what structures plankton communities in the current ocean, as well as under climate change scenarios, and also allows for finer resolution of community function because community trait composition determines the rates of significant processes, including carbon export. Although understanding of trait biogeography is growing, uncertainties remain that stem, in part, from the paucity of observations describing plankton functional traits. Thus, in addition to recommending widespread adoption of the trait-based approach, we advocate for enhanced collection, standardisation and dissemination of plankton functional trait data.

Keywords

Biogeochemistry, biogeography, diazotroph, microbe, mixotrophy, ocean, phytoplankton, predator–prey, trait, zooplankton.

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INTRODUCTION

From individual plankton to global processes

Marine plankton communities play active roles in, and are also subject to, global biogeochemical cycles and climate variability. Key community functions – including the export of carbon (C) from the ocean surface, the transfer of energy and organic matter to higher trophic levels and the drawdown of nutrients essential for primary production – determine the exchange of C and other elements between the surface ocean and the atmosphere and ocean depths (Falkowski *et al.* 1998). Environmental conditions, in turn, feedback on the relative abundance and diversity of species in marine plankton communities (Finkel *et al.* 2007; Barton *et al.* 2010; Edwards *et al.* 2013). An essential component to understanding this complex, two-way interaction is the ability to assess and predict how marine plankton communities respond to environmental change.

Climate change over the next century is projected to alter the environmental conditions experienced by plankton, including temperature, pH, light, water column stratification and turbulence, the supply of nutrients to the ocean surface, and the concentration and speciation of dissolved inorganic C (see Box 1 for overview of projected climate impacts). Model projections of how plankton communities will respond to environmental conditions over the next century vary substantially, but the general trajectory is towards greater stratification of the water column, weaker nutrient delivery to the surface and acidification (Sarmiento *et al.* 2004; Caldeira & Wickett 2005). Even within the relatively recent observational record, there is some evidence that the oligotrophic zones of the ocean (i.e. those with low nutrients and chlorophyll) may be expanding (Irwin & Oliver 2009), yet we do not fully understand why these changes have occurred or how community structure has varied. This uncertainty arises because we have limited knowledge of the ecological niches for the vast number of plankton that make up plankton communities.

Here, we demonstrate, using compelling examples for both phytoplankton and zooplankton, a tractable way forward that focusses on how functional traits determine how and why plankton communities change across space and time. We review laboratory studies that identify relationships between traits and species or functional groups (that is, groups of species with similar traits), as well as observational and modelling studies that identify the temporal and spatial distribution of functional traits and their environ-

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Box 1 Key impacts of climate change on marine plankton habitats

The marine environment is expected to change markedly over the next century in response to anthropogenic greenhouse gas emissions. There is significant regional and intermodel variability in projections of climate change (e.g. Rykaczewski & Dunne 2010), and untangling the ecological and biogeochemical ramifications of these changes is an ongoing challenge (for review of climate impacts on marine ecosystems, see Doney *et al.* 2012). We summarise here several pattern changes that are likely to impact marine plankton communities, and revisit these pattern shifts in our discussion of how plankton traits may redistribute in response to changing climate.

Circulation. Ocean circulation, and consequently the horizontal and vertical transport of heat, salt, nutrients and plankton themselves, will adjust to changing surface wind and buoyancy forcing, and with it redefine the physical boundaries of large marine biomes (Sarmiento *et al.* 2004; Rykaczewski & Dunne 2010). Latitudinal shifts in wind stress curl patterns, for example, would imprint on the extent and strength of the wind-driven subpolar and subtropical gyre circulations.

Stratification. In an average sense, it is anticipated that ocean temperatures will increase, particularly at the surface, and that this will lead to decreases in sea ice cover and increases in the thermal stratification of the water column (Sarmiento *et al.* 2004; Bopp *et al.* 2005). Imprinted on this pattern are changes in salinity. Increased precipitation and ice melting at high latitudes will further enhance stratification, while increased evaporation at lower latitudes will decrease stratification (Curry *et al.* 2003). However, the general pattern is towards greater stratification. The warmer temperatures and increased stratification (which leads to enhanced light exposure) may lead to a longer phytoplankton growing season at higher latitudes.

Nutrient Availability. The general increase in stratification limits the vertical supply from deep waters of essential nutrients, but also increases the average light exposure of cells in the ocean surface layers. This, in effect, may lead to a poleward expansion of oligotrophic, subtropical regions of the ocean (Sarmiento *et al.* 2004; Bopp *et al.* 2005).

Acidification. Seawater will become increasingly acidic as anthropogenic carbon dioxide is taken up at the surface and subsequently redistributed by ocean circulation (Caldeira & Wickett 2005; Doney *et al.* 2012). Barring rapid adaptive evolution (Lohbeck *et al.* 2012), the growth and distribution of marine calcifiers, such as coccolithophores, and other taxonomic groups may be impacted.

mental covariates. In essence, we seek to identify and understand the underlying ecophysiology of the biogeography of plankton traits, rather than of plankton species. We define biogeography generally to include temporal and spatial plankton distributions. Where and when, for example, is it advantageous for a phytoplankter to be a mixotroph, a diazotroph, or a large cell? Where and when is ambush feeding or large body size favoured among zooplankton? Conversely, where and when are these traits not advantageous?

Trait-based plankton ecology

A plankter's functional traits are characteristics that mediate growth, reproduction and survival (Violle *et al.* 2007), and determine its fitness for given biotic and abiotic conditions (Westoby & Wright 2006; Litchman & Klausmeier 2008). The fitness of a particular species, therefore, varies along environmental and biological gradients, producing its characteristic temporal and spatial distribution, or biogeography, and distinct trait combinations are favoured in particular regions and periods. In some cases, traits can be linked to specific genes; for example, phytoplankton N_2-fixation requires the *nifH* gene (N_2-fixation is the biologically mediated conversion of dinitrogen gas into ammonia). In other cases, traits are controlled by many genes and may evolve independently in multiple groups. This makes it possible to treat the presence of traits independently from species or phylogeny. Traits can emerge from the interaction of multiple, finer-level traits and the environment an organism encounters. Meta-traits (for example, organism size) can determine physiological traits and trade-offs across traits as well as important ecological properties (for example, predator and prey identity for zooplankton), yet they arise from the more atomic traits that govern life history.

Recent progress in plankton trait biogeography

Although terrestrial plant ecologists have long considered how traits vary along environmental gradients (Westoby & Wright 2006; Moles *et al.* 2011), in marine plankton ecology this perspective is rapidly developing. Key phytoplankton traits and trait trade-offs are now being revealed, often by analysing compilations of laboratory and field data from many species (Edwards *et al.* 2012; Irwin *et al.* 2012). As many of these traits are constrained by cell or body size (e.g. Fig. 1), it is possible to make inferences about the distribution of traits based on variations in the size spectra, or the relative abundance of different size classes of plankton (Cermeño *et al.* 2006). At the same time, molecular methods can now identify phytoplankton traits in the field in a manner not previously possible. For example, recent studies have identified the spatial distribution in the expression of the *nifH* gene, which encodes for the iron (Fe) protein of nitrogenase required for N_2-fixation (Zehr 2011).

Similarly, recent developments have spurred appreciation for the trait-mediated roles of zooplankton in marine food webs. For example, the maximum ingestion rate of prey by zooplankton decreases with body size, at least within taxonomic groups (Hansen *et al.* 1997), while optimum prey size generally increases with body size, although there is substantial variation between groups (Hansen *et al.* 1994). Zooplankton traits describing their feeding behaviours – whether they are ambush, filter or cruise feeding, and for how much of the time – are increasingly being implicated in structuring marine ecosystems (Kiørboe 2011; Mariani *et al.* 2013).

Plankton community models also play an integral role in understanding the distributions of plankton traits. Traditionally, these models have represented the biomass of one or a few primary producers and zooplankton with fixed traits, or perhaps even a larger range of key functional groups (LeQuéré *et al.* 2005). Models are

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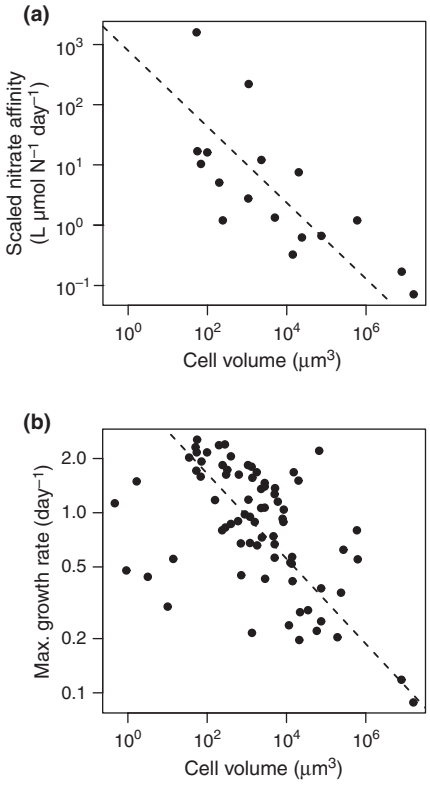

Figure 1 Scaled nitrate (N) affinity (a) and maximum specific growth rates (b) for marine phytoplankton spanning > 4 orders of magnitude in volume (data from Edwards *et al.* 2012). Scaled nitrate affinity is the nitrate uptake affinity normalised by the minimum cellular nitrogen quota. The dashed black line shows the line of best fit. In general, smaller phytoplankton cells have greater scaled nutrient affinity and maximum specific growth rates.

growing in complexity by simulating the defining traits of additional species, size classes, or taxonomic groups (Ward *et al.* 2012), physiologies (Ward *et al.* 2011), behaviours (Mariani *et al.* 2013) and interactions. These trait-based models capture the complexity of communities in a simple way by describing individuals in terms of a few key traits, and may also provide spatial context by embedding ecological interactions in ocean circulation models (Figs 2 and 3). One such approach by Follows *et al.* (2007) populated the ocean with many phytoplankton types within two size classes, with traits chosen stochastically from size-dependent ranges, and allowed competition for limited resources, predation and the environment to select for 'fit' phytoplankton at each location and time. Using the same model, Dutkiewicz *et al.* (2009) partitioned the ocean into regions dominated by 'gleaners' (small cells with high specific affinity for nutrients) and 'opportunists' (cells that grow fast with high nutrient concentration). The increased focus on modelling traits, rather than species or groups of species, helps reveal, on a resolution previously not possible, the mechanisms that regulate community ecology.

Overview

The trait biogeographical approach has several important benefits (Box 2). First, it allows for enhanced understanding of the underlying mechanisms regulating the community ecology of marine plankton in today's ocean. Second, because trait variation within and across communities leads to variation in the rates of processes such as C fixation and export, mapping out the biogeography of functional traits will allow us to better understand ecosystem functioning and biogeochemical processes. Third, plankton trait biogeography helps to inform the creation of mechanistic, trait-based community models, but also provides a useful constraint for model hypotheses and projections. Lastly, this approach enables mechanistic projections for how plankton communities may respond to future environmental change, and how these ecological changes may translate into variability in community function.

We focus on significant advances that have been made towards understanding the spatial and temporal variation in several key phytoplankton and zooplankton functional traits. The traits considered are important in the regulation of biogeochemical cycles, and will likely play a role in determining how ecosystems respond to global change. For both phytoplankton and zooplankton, we discuss the biogeography of cell or body size. For phytoplankton, we also consider mixotrophy (that is, combining autotrophic and heterotrophic nutrition) and N_2-fixation. For zooplankton, we also consider ontogeny and feeding behaviours. We have selected these traits to demonstrate the feasibility and power of the trait biogeography approach, but acknowledge that many other traits and processes are critically important. Implicit in our discussion of how trait biogeographies may shift in response to climate change is the notion that the timescales of plankton dispersal and community change are rapid relative to the rates of climate change (Provan *et al.* 2009). In other words, plankton ecological changes generally track environmental variability. We acknowledge that plankton dispersal limitation can, in certain cases, become important.

PHYTOPLANKTON

Cell size and size-linked traits

The size of phytoplankton cells constrains many of their physiological rates (e.g. nutrient uptake and growth rates), biotic interactions (e.g. grazing) and behaviour within the fluid environment (e.g. sinking speed). Therefore, cell size plays a key role in determining the diversity and relative abundance of competing phytoplankton species, as well as the transfer of elements between the surface and deeper layers in the ocean and from phytoplankton to higher trophic levels (Smetacek 1985; Cushing 1989). Our approach to discussing phytoplankton community size structure is complementary to previous work (Finkel 2007; Finkel *et al.* 2010), but is biogeography-centric; we first ask how size structure varies in space, and then consider how size-linked functional traits help bring about the spatial variations in size structure.

Phytoplankton abundance (A; cells m^{-3}) typically decreases with increasing cell volume (V; μm^3), such that $A = cV^{\xi}$, where c is a constant and the scaling exponent ξ is approximately -1 but varies from roughly $-2/3$ to $-5/3$ (Cermeño *et al.* 2006; Finkel 2007; and references therein). Although small cells are generally more abundant than larger ones, the scaling exponent varies across environmental conditions. Compilations of *in situ* observations (e.g. Irigoien *et al.* 2004) and global satellite measurements (Uitz *et al.* 2006) indicate that smaller phytoplankton cells are generally present in a range of nutrient concentrations, whereas larger cells become more common under higher nutrient supply common in regions of upwelling

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Box 2 Why plankton trait biogeography?

Regulation of community structure

Mapping the biogeography of functional traits will help reveal the mechanisms underlying variations in marine plankton communities because the dominant structuring factors should alter trait distributions in predictable ways. For example, temporal variation in light and nitrate leads to corresponding changes in the relative advantage of traits related to nitrate competition, low light tolerance and maximum growth rate (Edwards *et al.* 2013). This kind of analysis can be applied to broader spatial scales by integrating data on community abundance, functional traits and environmental variables. For example, summer nutrient depletion in the subpolar North Atlantic Ocean has been found to favour smaller over larger diatoms (Barton *et al.* 2013).

Variation in community function

Key community processes like carbon export, N_2-fixation and productivity of higher trophic levels vary in space and time, and understanding the causes of this variation is a significant challenge. Plankton functional traits have a dual role in this context: they determine the success of species as a function of environmental conditions, and then the traits of dominant species determine the rate and magnitude of ecosystem processes, thereby feeding back to modulate environmental conditions. Mapping the biogeography of functional traits will thus allow trait distributions to be linked to variation in ecosystem functions.

Validating and refining plankton community models

Plankton community models are increasingly representing the traits of additional species, organism sizes or functional groups to simulate community structure and function (Follows *et al.* 2007; Mariani *et al.* 2013; Ward *et al.* 2012). These models benefit from plankton trait biogeography in two primary ways. First, increased understanding of how traits vary and co-vary across species will aid in developing realistic but tractable model representations of functional diversity. Second, model predictions must be evaluated against empirical patterns of distribution for traits, species or functional groups.

Projecting future ecosystem processes under global change

All of the above challenges will need to be met to successfully predict how the ocean ecosystems may respond to global environmental change. Current controls on large-scale variation in community structure and function must be better understood to anticipate how ecological patterns will change under new environmental regimes. Models will need to capture the ecology of diverse plankton communities and assess how community structure varies across the globe to make accurate predictions of the consequences of different degrees of anthropogenic change.

or enhanced mixing. Using a global ocean model with a size-structured phytoplankton community, Ward *et al.* (2012) demonstrated that phytoplankton size spectra vary regionally, with large cells relatively rare in oligotrophic seas and relatively more common in areas of strong upwelling or in subpolar gyres (Fig. 2, points 'A' and 'B' respectively).

The co-regulation of phytoplankton populations by bottom-up (nutrient limitation) and top-down (predation) processes provides a compelling explanation for the maintenance of phytoplankton community size spectrum at a given location, and also for its global-scale variations (Armstrong 1994; Ward *et al.* 2012). Cell size influences a cell's uptake rate of dissolved nutrients by modifying the surface area available for uptake transporters and the diffusive flux of nutrients towards the cell (Aksnes & Egge 1991). Within taxonomic groups, smaller cells typically have higher scaled nutrient affinities (defined as the clearance rate at low nutrient concentrations, normalised by cell nutrient content) than do larger cells (Fig. 1), and therefore may maintain positive growth at lower nutrient concentrations than larger competitors (Edwards *et al.* 2012). In the subtropical gyres, which are characterised by consistent stratification and weak nutrient delivery to the surface, smaller phytoplankton cells are able to draw down ambient nutrient concentrations to critically low levels at which larger cells cannot survive, and the size spectra slope is steeply negative (Fig. 2, Point 'A').

In the subpolar gyres, coastal upwelling zones, and regions of enhanced turbulent mixing, nutrient delivery is greater (Fig. 2, Point 'B'). The population of small phytoplankton cells increases in response to the additional nutrients, but is subject to intense grazing pressure by their predators, who themselves are relatively small and quick to respond to changes in prey density (Hansen *et al.* 1994, 1997). This top-down control keeps the smaller phytoplankton cells from consuming all available nutrients, and allows successively larger, less competitive size classes of phytoplankton to grow, each in turn grazed down by their successively larger, more slowly growing predators (Armstrong 1994; Ward *et al.* 2012). This mechanism is thought to underpin the positive correlation between total primary productivity or nutrients and average phytoplankton cell size, as well as the broadening of the cell size distribution with additional nutrients (Irigoien *et al.* 2004; Schartau *et al.* 2010). Certain taxonomic groups, such as the diatoms, have evolved to have higher growth and nutrient uptake rates than others (Edwards *et al.* 2012), and may thus modify the conceptual picture we have developed here.

Imprinted onto this mechanism may be other size-dependent factors that impact phytoplankton fitness, including light (see review by Finkel *et al.* 2010 for others). All else being equal, larger cells absorb fewer photons per pigment than smaller cells of the same shape, due to increased self-shading of pigment with increasing cell volume (Duysens 1956). As a result, larger phytoplankton cells tend to have lower intracellular pigment concentrations than smaller cells under any given irradiance regime, which should cause smaller cells to have a growth advantage under low light conditions that often occur in deep mixed layers in temperate and high latitude waters (Finkel *et al.* 2004). Alternatively, the high levels of self-shading caused by larger cell volume can be advantageous in stratified water columns when photon flux densities and ultra-violet light doses are high (Key *et al.* 2010). One goal for future work should be to quantify the relationship between light conditions and size spectra across

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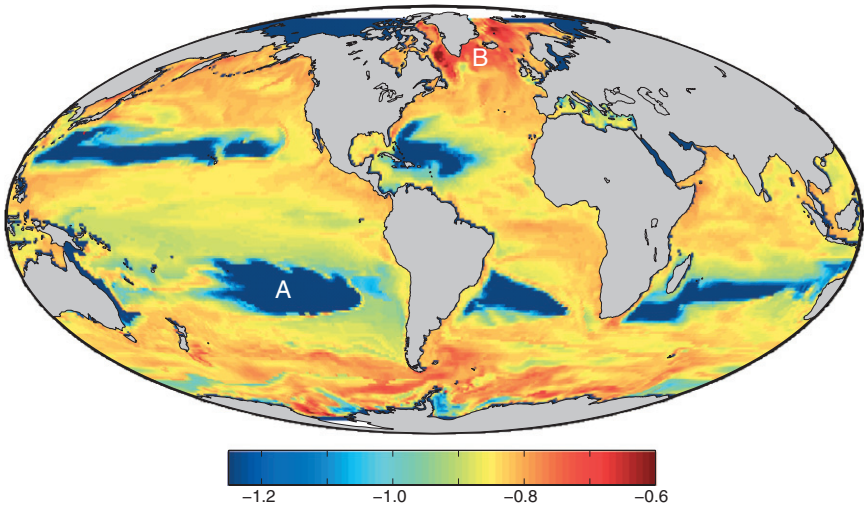

Figure 2 Size-spectral slope in a global size-structured plankton community model (data from Ward *et al.* 2012). 'A' indicates a subtropical location with relatively few large cells present (more negative slope), whereas 'B' indicates a subpolar location with a greater representation of large cells in the community (less negative slope).

the ocean, which will require disentangling the effects of light conditions from the effects of nutrient supply.

Various other size-dependent mechanisms may be important under certain conditions, including phytoplankton sinking and swimming speeds, the impact of turbulence on nutrient uptake, and the effect of fluctuating nutrient supplies (Kiørboe 2008). Recent studies have also argued that increasing temperature may reduce phytoplankton cell volume (e.g. Hilligsøe *et al.* 2011), although the mechanistic link remains unclear (Atkinson *et al.* 2003). We also note that many phytoplankton form aggregates of cells, such as diatom chains, that modify their effective sizes and thus their interaction with the physical environment and predators. The costs and benefits of aggregation are an area of active research (Pahlow *et al.* 1997). Lastly, the range of photosynthetic pigments deployed by phytoplankton determines, in part, their distribution and community structure (Stomp *et al.* 2004), and represents an important regulatory set of traits.

Observations suggest that as oligotrophic conditions expand, so too do ecosystems dominated by smaller phytoplankton (Irwin & Oliver 2009), and coupled climate and ecosystem models indicate that warmer, more stratified future oceans may favour smaller phytoplankton (Bopp *et al.* 2005). Similar shifts in phytoplankton size structure due to changing nutrient availability appear in the geological record (Finkel *et al.* 2007). The greater extent of oligotrophic seas may weaken the ocean's biological carbon pump, or its biologically mediated export of carbon from the surface layer to deeper waters (Falkowski *et al.* 1998). It should be stressed, however, that the complex and sometimes competing effects of temperature, nutrient availability, turbulence, ocean acidification, grazing and light on phytoplankton fitness remain to be fully quantified.

Nitrogen fixation

Diazotrophs are organisms that convert nitrogen gas from the atmosphere (N_2) into bioavailable ammonia, providing a globally significant source of N to the ocean. Because of this ability to fix nitrogen and their distinct cellular elemental ratios (Quigg *et al.* 2011), or elemental stoichiometry, the distribution of N_2-fixers influences oceanic N : P ratios (Weber & Deutsch 2012). Diazotrophs impact the structure and function of marine ecosystems in the current ocean, as well as on much longer timescales (Tyrrell 1999).

Diazotrophs include both photoautotrophic cyanobacteria (members of the phytoplankton) and heterotrophic bacteria. Among the cyanobacteria, both colonial (*Trichodesmium*) and unicellular species (*Crocosphaera*) contribute to N_2-fixation (Capone *et al.* 1997). Some heterocystous filamentous cyanobacteria also occur as symbionts of other organisms, such as diatoms, and the widely distributed but poorly understood UCYN-A group appears to be photoheterotrophic and may occur as a symbiont (Zehr 2011). N_2-fixation is also carried out by some heterotrophic γ-proteobacteria (Halm *et al.* 2012), but much less is known about their ecology and distribution. Although these diverse N_2-fixers exhibit a range of functional traits, they all use the nitrogenase enzyme complex to catalyse the conversion of N_2 gas into ammonia. Therefore, we consider the ability to fix N as an ecologically and biogeochemically important functional trait, and discuss the underlying causes of its spatial distribution.

Diazotrophs are most conspicuous in warm, oligotrophic waters from *c.* 30°S to 30°N, although there appears to be substantial variation between regions (Luo *et al.* 2012; Fig. 3). Observed N_2-fixation rates are higher in the North than the South Atlantic and Pacific basins, and diazotrophs appear to be common in the Baltic and Mediterranean Seas. Different diazotrophs have distinct spatial and temporal distributions (Church *et al.* 2008), but in the following discussion we focus on the larger scale pattern of integrated diazotroph biomass and N_2-fixation rates (Fig. 3).

Understanding what drives the large-scale biogeographical patterns of diazotrophs is challenging due to the fact that temperature, light and nutrients co-vary across latitude. *Trichodesmium* possess a high optimal temperature, a high light requirement and low susceptibility to photoinhibition (Capone *et al.* 1997), which may constrain their distribution to low latitudes. It has also been proposed that diazotrophs such as *Trichodesmium* and *Crocosphaera* are restricted to warm waters due to temperature-dependence of respiration and flux of O_2, which inhibits nitrogenase (Staal *et al.* 2003).

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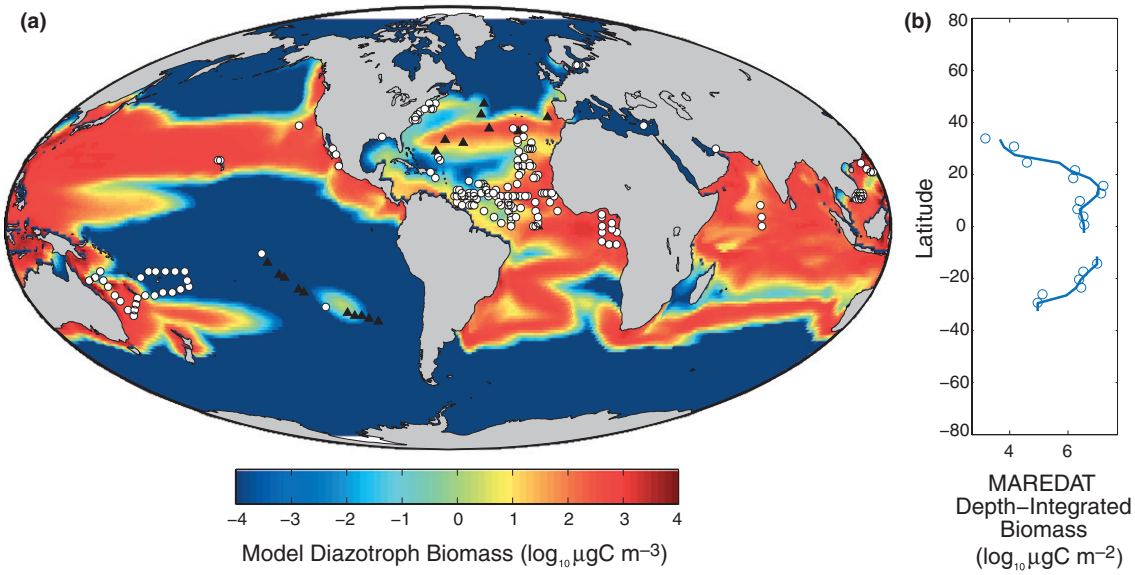

Figure 3 (a) Annual mean biomass of model diazotrophs in top 50 m (data from Dutkiewicz *et al.* 2012). Observed cyanobacterial diazotroph abundances have been estimated from qPCR assays targeting *nifH* genes and compiled by Luo *et al.* (2012); black triangles and white circles indicate observations of zero and greater than zero diazotroph biomass respectively. (b) Latitudinal variation in observed depth-integrated diazotroph biomass. Depth-integrated diazotroph observations from Luo *et al.* (2012) were averaged onto a 3° × 3° grid and zonally averaged (open circles), and then smoothed with a 5-point running mean (solid line). Model data courtesy of Stephanie Dutkiewicz.

Recent modelling studies suggest that the availability of N and Fe, in addition to temperature and light, regulate the global-scale distribution of diazotrophs, with the availability of phosphorus (P) playing an additional, regional regulatory role (Monteiro *et al.* 2010; Dutkiewicz *et al.* 2012). At higher latitudes with greater availability of bioavailable N, models show that diazotrophs are outcompeted by non-diazotrophs because of their relatively slow maximum specific growth rates, which may stem from the energetic cost of breaking the N_2 gas triple bond (Monteiro *et al.* 2010). At lower latitudes, diazotroph distribution appears to be constrained by the relative availability of N and Fe. Because of their relatively high demand for Fe due to the Fe-rich nitrogenase enzyme complex, in a global model diazotrophs were numerous in the subtropical North Pacific, where Fe was relatively high but N was low, and rare in zones where both N and Fe were low (Dutkiewicz *et al.* 2012). These studies are supported by observations that show an inverse correlation between the abundance of nitrogenase reductase genes and nitrate concentrations in the Pacific (Church *et al.* 2008), but a positive correlation with Fe concentrations along the Atlantic Meridional Transect (AMT; Moore *et al.* 2009). An additional constraint on the distribution of diazotrophs is the bioavailability of P. For example, in low N and high dissolved Fe conditions in the tropical and subtropical North Atlantic, N_2-fixation has been found to also closely track concentrations of bioavailable P (Sanudo-Wilhelmy *et al.* 2001). Diazotrophs have a high P requirement relative to non-diazotrophs (Quigg *et al.* 2011), and are thus sensitive to P limitation of growth.

These mechanisms indicate several potentially conflicting paths by which diazotroph distributions may shift under global environmental change. Rising temperatures and CO_2 concentrations in the ocean surface may facilitate increased N_2-fixation and/or growth rate of N_2-fixers and expand their geographical distribution (Hutchins *et al.* 2007; Stal 2009). Changes in the hydrological cycle in a warmer climate may reduce the atmospheric deposition of Fe into the ocean and limit the range and abundance of diazotrophs (Berman-Frank *et al.* 2001). Although rising temperatures are expected to increase the extent of oligotrophy (Sarmiento *et al.* 2004), we have a poor understanding of how the supply ratio of N, P, and Fe will change. If changes in nutrient availability lead to increased P limitation, this may restrict N_2-fixers due to their high P requirements. Alternatively, if N limitation is increased, N_2-fixers may have a competitive advantage over non-N_2-fixers and increase their dominance and range. Unravelling which, if any, of these possibilities may play out will require incorporation of diazotrophs with realistic physiology and nutrient requirements into trait-based plankton community models (e.g., Monteiro *et al.* 2010; Dutkiewicz *et al.* 2012) that are run with environmental forcing consistent with expected future changes. Although we have focussed on diazotrophs in particular, phytoplankton exhibit a range of N : P requirements, and this trait is likely to be crucial for interpreting how plankton communities respond to, and feed back on, global change (Finkel *et al.* 2010; Weber & Deutsch 2012).

Mixotrophy

Mixotrophs are organisms that combine both autotrophic and heterotrophic nutrition, and this blending may be a much more common strategy than previously imagined (Hansen 2011). This trait is particularly common among the dinoflagellates, but is found in a wide range of microbes (Hansen 2011). Mixotrophs have been shown to increase the efficiency of nutrient drawdown in aquatic systems (Tittel *et al.* 2003), and can account for much of the bacterial grazing in pelagic and coastal zones (Havskum & Riemann 1996; Zubkov & Tarran 2008). Despite their importance, there are no quantitative estimates of the global importance of mixotrophy with regard to primary production and nutrient cycling. Thus,

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improved understanding of mixotroph ecology and the resulting implications for marine food webs and biogeochemical cycles is an important goal.

Mixotrophy has the advantage of broadening the pool of available resources (Tittel *et al.* 2003), but there are also certain physiological 'trade-offs' associated with maintaining two trophic machineries. In comparison with obligate photoautotrophs such as diatoms, the dinoflagellates, many of whom are mixotrophic, are typically associated with slow maximum specific growth rates and a low affinity for inorganic nutrients (Edwards *et al.* 2012). In a similar fashion, growth and grazing rates in some mixotrophs have been shown to be slower than in similar, heterotrophic specialists (Jeong *et al.* 2010). Given these relatively uncompetitive traits, how is it that mixotrophs are able to coexist with, or even outcompete, their apparently superior competitors?

Competition between specialists and mixotrophic plankton can be thought of in terms of the principle of opportunity costs (Stephens & Krebs 1987). Strictly autotrophic and heterotrophic plankton are able to exploit certain resources more efficiently through specialisation, but to do so they reduce their resource opportunities. Mixotrophs increase their resource opportunities by consuming both inorganic and organic resources, but in doing so they are less efficient. In oligotrophic environments, where resources are relatively scarce, there is less advantage in specialisation. Mixotrophs are able to thrive in these regions (Havskum & Riemann 1996; Zubkov & Tarran 2008), because they are able to take advantage of both inorganic and organic resource encounters (Ward *et al.* 2011). Specialists, in contrast, gain an advantage in eutrophic conditions, where resources (either dissolved inorganic nutrients or prey) are so abundant that they can afford to be selective. Thus, it is conceivable that this oligotrophic niche for mixotrophs may expand poleward as stratification increases and nutrient delivery to the surface decreases under climate warming scenarios (Sarmiento *et al.* 2004).

Mixotrophic generalism can also be thought of as a 'bet-hedging' strategy, through which the mixotrophs experience less risk because they do not rely on just one resource (Stoecker 1998). In a changing environment, mixotrophs are able to bridge the gap between bloom periods, where inorganic resources are abundant, and post-bloom periods, where inorganic resources are scarce, prey are abundant, and production is driven by grazing and recycling of organic matter. This bet-hedging mechanism yields a succession of trophic strategies, from autotrophs, through mixotrophs, to heterotrophs, as has been observed in the North Atlantic Bloom Experiment (Sieracki *et al.* 1993) and Continuous Plankton Recorder data (Barton *et al.* 2013).

We currently have limited understanding of mixotroph biogeography, but there are at least three ways this uncertainty can be decreased. First, field studies should quantify mixotrophic distribution, but also prey ingestion and photosynthetic rates as a function of environmental conditions such as temperature, light, nutrients and prey availability. Second, knowledge of the distribution of mixotrophic taxa can be paired with laboratory and field-based estimates of the prevailing trophic strategy for each taxa to make predictions about the spatial and temporal distribution of mixotrophs in the ocean (Barton *et al.* 2013). Third, trait-based plankton community models that allow for a range of trophic strategies (Ward *et al.* 2011) should be implemented on a global scale and employed to quantify the affects of mixotrophy on marine food webs and biogeochemical cycles. In each approach, it should be recognised that organisms may acquire essential nutrients independently through different trophic pathways: photosynthesis, uptake of organic nutrients, assimilation of organic detritus, or grazing or predation on other living organisms. The traditional definition of plankton as either heterotrophs or autotrophs needs to be broadened to include such trophic plasticity. Ultimately, mixotrophs may be considered an important plankton group distinct from either phytoplankton or zooplankton in terms of their functional traits, ecology and biogeochemical functions.

ZOOPLANKTON

A natural division among the zooplankton is between heterotrophic microbes (e.g. ciliates, amoebae, some nanoflagellates and dinoflagellates) and metazoa, including copepods, jellyfish (cnidarians and ctenophores) and chaetognaths. Our discussion of trait biogeography will focus on the metazoan plankton, both because of their ecological importance but also to draw a contrast with the microbial phytoplankton. Furthermore, the copepods will play a prominent role in our discussion of the metazoan plankton. Copepods are ubiquitous and a strong contender for the most numerous metazoan class.

Body size and size-linked traits

As with the phytoplankton, size is the major structuring trait among zooplankton. For example, body size influences swimming speeds, lipid storage, prey and predator size, and almost all vital rates (growth, fecundity, metabolism, feeding, etc.; Kiørboe 2008). However, size is not a simple trait in metazoa. Due to development, an individual zooplankter will go through many sizes during its life, and traits and processes that are linked with size will thus change as it develops.

Zooplankton communities are strongly size-structured, mainly because size determines a zooplankter's predators and prey. Zooplankton feed on prey that are generally smaller than themselves, and the average predator : prey size ratio in plankton is about 10 on a linear scale (Hansen *et al.* 1994). This typically leads to a relationship between the size of the herbivorous zooplankton and the size of the primary producers. For example, the oligotrophic subtropical gyres are dominated by small phytoplankton (as discussed in the previous section on phytoplankton) that are grazed by small herbivorous zooplankton, such as flagellates and ciliates (Calbet & Landry 2004). These, in turn, are eaten by larger zooplankton. Conversely, large herbivorous zooplankton (mainly copepods of the *Calanus* genus) dominate the strongly seasonal subpolar and arctic oceans that are characterised by spring blooms of large diatoms. In accordance with this general pattern, the average zooplankton body size along the AMT decreases in the oligotrophic seas and increases in more nutrient-rich regions (San Martin *et al.* 2006). Thus, it is reasonable to predict that a climate-mediated shift towards more oligotrophic seas with smaller phytoplankton and a more prominent microbial loop would favour smaller omnivorous zooplankton.

An important deviation from the general relationships between zooplankton functional traits, prey preference and body size is the presence of gelatinous plankton characterised by a high water content, or 'jelly factor'. In addition to the cnidarians and ctenophores, gelatinous forms include the pelagic tunicates, and are also found among pteropods, protists and pelagic polychaetes. The hallmark of gelatinous zooplankton is their inflated size relative to their mass.

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This may allow partial escape from predators and a large prey capture area, with consequently large clearance rates relative to other zooplankton of a similar mass (Acuña *et al.* 2011). The inflated size also implies a prey : predator size ratio that deviates dramatically from the typical 10 : 1. For example, salps feed primarily on bacteria and small phytoplankton (Sutherland *et al.* 2010), which is thought to explain their prevalence in oligotrophic environments characterised by small primary producers.

The 'jelly factor' trait encompasses a specific trade-off between large volume relative to mass and vulnerability to predation and mechanical disturbance. The latter characteristic means that gelatinous species are fragile and not well preserved in standard zooplankton nets, making it difficult to characterise their distribution. Overharvesting of small pelagic fish, which are the principal predators of zooplankton, has been followed by increases in zooplanktivorous jellies in several locations (Lynam *et al.* 2006). Jellyfish are also associated with conditions that favour non-silicified phytoplankton over diatoms, including high N : Si ratios and increased stratification (Richardson *et al.* 2009). Coupling overfishing with the impacts of climate change have led some to suggest that we may be heading towards 'a more gelatinous future' (Richardson *et al.* 2009), although this prediction is a subject of debate (Condon *et al.* 2012).

Ontogeny

Ontogeny describes the structural development of an organism through its life. For zooplankton, there are a wide variety of ontogenetic patterns, but a general model begins with the egg, progresses through a series of developmental stages, and terminates with the reproducing adult.

A first order trait associated with ontogeny is development time, that is, the time to develop from an egg to a reproducing adult. This trait plays a critical role in the life history as it has direct importance to their rate of population growth. The timing of maturity can be particularly important to semelparous species (that is, those species that reproduce once in a lifetime) or species that rely on a seasonal bloom, such as *Calanus finmarchicus* in the North Atlantic. The timing of key morphological changes, such as the development of swimming or feeding appendages, can be similarly important. Through its influence on grazing rates, zooplankton development time also plays a key role in structuring phytoplankton communities, and consequently biogeochemical cycles, as discussed previously (Section Phytoplankton).

A key ontogenetic trade-off impacting zooplankton fitness exists between body size, generation time and fecundity. Zooplankton tend to either mature early at a small size with consequently low egg production, or mature later at a larger size with higher egg production (Fig. 4; Kiørboe & Hirst 2008). Thus, in comparison to a late maturation strategy, early maturation yields a short generation time and a greater chance of reaching adulthood, but fewer eggs. A large size may also be advantageous depending on the predator regime.

Development rate depends primarily on temperature for a wide range of taxonomic groups, particularly in non-food-limited conditions (Mauchline 1998). The sensitivity to temperature of development time is represented by E_D, or the activation energy required for the metabolic processes involved in development (Maps *et al.* 2011; Table 1). Assembling temperature sensitivity trait data, as we have done here, may help determine future zooplankton community changes. For example, taxa with the highest temperature sensitivity

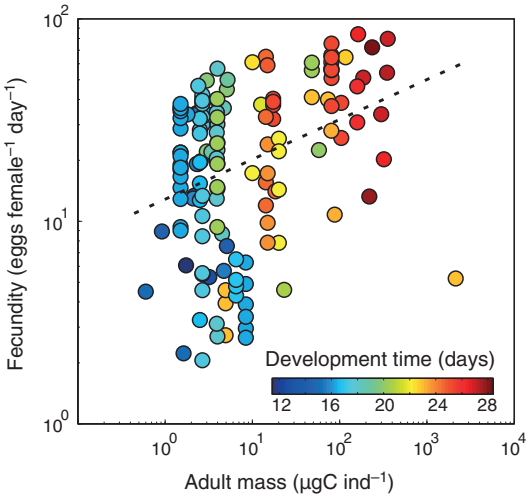

Figure 4 Zooplankton fecundity as a function of adult body mass, with colours showing development time (data are from Kiørboe & Hirst 2008). The dashed black line shows the line of best fit.

may experience the greatest changes in development rates under climate warming scenarios, which will also have consequences for phytoplankton communities.

Growth and development rates are not strongly coupled and the disproportionate influence of temperature on development produces a strong negative relation between temperature and adult body size, both within and between species (Forster *et al.* 2011). For example, longer development times are generally associated with polar and subpolar systems, as typified by genera such as *Calanus*, *Eucalanus*, *Neocalanus* and *Rhincalanus*, while tropical and subtropical copepod species have shorter development times (Fig. 5). The genus *Calanus* provides an example of the strong temperature-size pattern. The largest members of this genus are polar, with *C. hyperboreus* (7 mm total length) occurring in the Arctic and *C. propinquus* (5 mm) occurring in the Southern Ocean. As one moves towards equator, the characteristic size of the local species decreases. In the North Atlantic, *C. hyperboreus* gives way to *C. glaciallis* (4 mm), then *C. finmarchicus* (3 mm), which dominates the subpolar gyre and coastal seas. In the eastern North Atlantic, *C. finmarchicus* is replaced by *C. helgolandicus* (2 mm) in warmer waters, and the distribution of this species is expanding poleward due to warming (Beaugrand 2009). However, the overall association between copepod size and temperature is not as clear as for this particular genus. Large species occur in warm waters (for example, *Euchaeta* spp. and *Pleuromamma* spp. are in the same size range as *C. finmarchicus*), while *Oithona* spp. (0.3 mm) are found nearly everywhere (Gallienne & Robins 2001).

The development of overwintering strategies in many zooplankton represents second order ontogenetic traits with important biogeographical implications. For example, many copepod species have dormant stages with reduced metabolic rates and slowed development, and these stages allow them to survive periods of unfavourable conditions such as reduced food or high mortality (Johnson *et al.* 2008). Such copepods either produce resting eggs that may survive for decades in the sediment (Mauchline 1998), or they diapause as juveniles that persist on stored wax ester lipids. Other taxonomic groups, such as ctenophores, appear to accumulate lipids

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Table 1 Functional traits and biogeographies for some common marine and estuarine copepods

Genus	Species	E_D (eV) (Record *et al.* 2012 Table 1)	Diapause (Mauchline 1998 Tables 40, 60)	Generations (year^{-1}) (Mauchline 1998 Table 58)	Feeding mode*	Biogeography
Acartia	*clausi*	0.64	E, N?	2.0–7	A/F	SP/CS
Acartia	*grani*†	0.82	E		A/F	SP/CS
Acartia	*steueri*	0.8	N?		A/F	SP/ST/CS
Calanus	*finmarchicus*	0.75	C5 (C4?)	1.0–3	F	SP
Calanus	*glacialis*	0.74	C3, C4, C5	0.33–3	F	P/SP
Calanus	*helgolandicus*	0.7	C5?	0.2	F	ST
Calanus	*hyperboreus*	0.77	C5	0.25–0.5	F	P
Calanus	*marshallae*	0.85	C5	1.0–4	F	P/SP
Calanus	*pacificus*	0.74	C5	1.0–3	F	SP/ST
Calanus	*sinicus*	0.72	NR	1.0–3	F	SP/ST
Centropages	*abdominalis*	0.8	E	6	C/A	P/SP
Centropages	*furcatus*	0.85	E		C/A	ST/T
Centropages	*hamatus*	0.85	E	5.0–8	C/A	SP/ST/T
Centropages	*typicus*	0.86	E	4.0–7	C/A	SP/ST/T
Eurytemora	*hirundoides*	0.86	NR		C	SP
Metridia	*longa*	0.64	NR	1.0–2	C	P/SP/ST
Metridia	*pacifica*	0.7	C4, C5	1.0–4	C	P/SP
Neocalanus	*cristatus*‡	0.82	C3, C4, C5	1		P/SP
Oithona	*colcarva*§	0.63	NR		A	ST/T
Paronychocamptus	*nanus*	0.65	NR			SP
Parvocalanus	*crassirostris*§	0.77	NR		F	ST/T
Pseudodiaptomus	*hessei*§	0.44	NR			ST
Pseudocalanus	*minutus*	0.7	C4, C5	1.0–2	F	C
Pseudocalanus	*newmani*	0.65	NR	3.0–5	F	P/SP
Pseudocalanus	*elongatus*	0.67	NR		F	SP/ST
Sinocalanus	*tenellus*§	0.83	E			ST/T
Tachidius	*discipes*	0.61	NR			SP
Temora	*longicornis*	0.87	E	2.0–6	F	SP/ST
Tortanus	*discaudatus*	0.98	E		C	SP

E_D is the activation energy of ontogenetic rate (Maps *et al.* 2011). Diapause stage: E = egg; N = naupliar diapause; Ci = diapause in the *i*th copepodid stage; NR = none reported. Feeding mode: A = ambush; F = feeding current (hovering); C = cruising. Biogeography: P = polar; SP = subpolar; ST = subtropical; T = tropical; CS = continental shelf; C = cosmopolitan.

*The separation between 'feeding current' (hovering) and 'cruising' feeding modes is gradual. A neutrally buoyant zooplankter that beats its feeding appendages will cruise through the water, while a negatively buoyant individual that beats the appendages in the same way will produce a feeding current. Most species are intermediate in their feeding mode but may be more towards one end of the continuum. Some species may switch between ambush feeding and feeding-current feeding or cruise feeding.

†Guerrero *et al.* (1994).

‡Saito & Tsuda (2000).

§Peterson (2001).

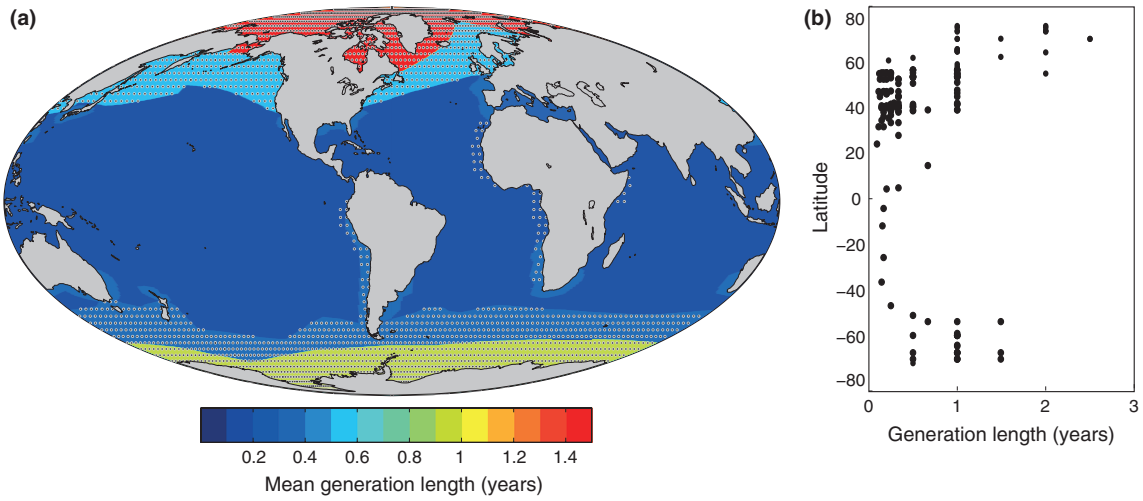

Figure 5 (a) Estimated biogeographical patterns of characteristic generation length and diapause strategy for calanoid copepods. Mean generation length was computed from Mauchline (1998; Table 58) by grouping species into six regions (Antarctic, subantarctic, warm-temperate/upwelling, warm oceans, subarctic and Arctic) and averaging the generation length within each region. Dotted areas indicate the presence of species with late-copepodid diapause strategies, estimated from Mauchline (1998; Table 60) and Lee *et al.* (2006). (b) Generation length is also plotted as a function of latitude.

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for overwintering as well (Lundberg *et al.* 2006). Diapausing species are generally large and occur in polar, subpolar, and upwelling environments (Fig. 5), and because of the immense lipid resource they provide, particularly in polar and subpolar environments, are critical to the highly productive fishery ecosystems that occur in these regions (Lee *et al.* 2006).

Feeding behaviours

Several functional traits characterise zooplankton feeding: the way in which they collect prey, the rates at which they feed and the extent to which they select between different prey. Trade-offs associated with food availability and the presence of zooplankton predators determine the spatiotemporal distribution of these feeding traits along environmental gradients, which we describe below.

Zooplankton are known to feed in three ways: some are ambush feeders that sit motionless in the water and wait for prey to pass within their capture sphere; others generate a feeding current that is passed through a filter or from which they capture entrained prey; or they may cruise through the water and capture encountered prey (Kiørboe 2011). This categorisation transcends taxonomy and life forms. For example, ambush feeders include some protozoans (e.g. helioflagellates, radiolarians), some pteropods and jellyfish, and some copepods. Conversely, different feeding behaviours may occur within the same taxonomic group (Table 1). Certain zooplankton may also employ different feeding behaviours in response to changing environmental conditions and prey abundance (Mariani *et al.* 2013; Table 1).

Ambush feeding is less efficient in terms of clearance rates than the more active feeding strategies because prey encounter rates depend on prey swimming speeds that are typically less than zooplankton cruising and feeding current velocities, and they are limited to feeding on motile prey. This lower volumetric search rate, however, comes with a lower metabolic expenditure and predation risk (Kiørboe *et al.* 2010). Such trade-offs have been used to predict the distribution of feeding behaviours along gradients of food availability, predator abundance and predator type, as well as vertical distributions of feeding behaviours (Visser 2007; Kiørboe 2011). Because of the high metabolic cost and predation risk of active relative to ambush feeding, less active feeding behaviours should prevail in oligotrophic environments or in environments with high predation risk, while zooplankton can afford a more active feeding strategy in less risky and more food rich environments.

These predictions remain to be tested against field observations, and a first step may be to categorise zooplankton species to feeding type (Table 1). However, it is difficult to translate the predictions to biogeographies in simple ways because the governing factors (predation risk, prey abundance and prey motility) may co-vary. For example, low predator concentrations that would favour an active feeding behaviour are characteristic of oligotrophic environments that, on the other hand, would favour an ambush strategy. Therefore, biogeographies of feeding types may not be distinct on ocean wide scales, but variation in the occurrence of feeding behaviours may be important on seasonal scales, where it may partly govern the seasonal succession of the phytoplankton (Mariani *et al.* 2013).

Zooplankton feeding rates are typically described by the functional response in ingestion rate to prey density and are characterised mainly by two traits, the maximum clearance rate and the maximum ingestion rate (Hansen *et al.* 1997). Both traits are tied to body size. The maximum clearance rate of zooplankton varies in proportion to body mass when compared over the entire size and taxonomic range of zooplankton, but within groups a different size scaling may apply, and there is a substantial variation between species (Hansen *et al.* 1997; Kiørboe 2011). One may predict that the maximum specific clearance rate will be high for species living in oligotrophic environments because of the need to search larger volumes of water to find sufficient prey. Conversely, in upwelling zones and subpolar regions characterised by diatom blooms and high prey density, the need for fast food processing (short gut throughput times), and hence high maximum ingestion rate, may be more pronounced. Copepods feeding on diatoms indeed have significantly higher faecal production rates and shorter gut passage times than when feeding on flagellates, with significant implications for the vertical flux of phytoplankton carbon packed in rapidly sinking faecal pellets in these regions (Besiktepe & Dam 2002).

Prey size selectivity in zooplankton is mainly passive in that it is governed by encounter rates and capture probabilities that, in turn, are functions of the feeding behaviours and morphology (Kiørboe 2008). Prey selection may, however, also be based on other characteristics of the prey, mainly the nutritional value or chemical composition, as has been demonstrated for copepods (Cowles *et al.* 1988). Prey detection and selection is, however, only feasible for prey cells that are large enough to produce a measurable signal, and the size threshold appears to be *c.* 10 and 50 μm for chemical and hydromechanical signals respectively (Legier-Visser *et al.* 1986). Zooplankton feeding on small prey cells, therefore, must collect food by an automatic process, such as filtering the water (e.g. tunicates) or by direct interception or diffusional deposition (e.g. most protozoans), whereas consumers of larger prey may use more active feeding processes, such as selecting prey cells that arrive in a feeding current or are encountered as the zooplankter cruise through the water (e.g. many copepods). As small phytoplankton cells dominate in oligotrophic oceans, one may predict that herbivorous zooplankton should largely feed using automatic processes here. Carnivorous copepods, on the other hand, would mainly prey on heterotrophic protozoans in these regions. In upwelling regions and seasonal, higher latitudes, blooms of large phytoplankton cells are grazed mainly by zooplankton with individual prey detection, such as copepods and dinoflagellates.

Although we may be able to make some predictions about the spatial distribution of zooplankton feeding traits, there are, as yet, few data available to test such predictions. One promising avenue for progress is species-centred databases on biogeography. If one can assign traits to individual species (as we have done for Table 1), it is possible to translate species to trait biogeographies, as exemplified by Fig. 5.

TRAIT-BASED PLANKTON ECOLOGY IN THE NEXT 10 YEARS

We have outlined a strategy for how plankton functional traits can be used to understand plankton biogeography and community structure, but also to make informed predictions about how climate change may alter marine plankton communities. Despite the significant developments discussed here, uncertainties remain. Consider, for example, that we have only a preliminary picture of where and when mixotrophic phytoplankton prosper in the ocean, and know little of how zooplankton feeding strategies vary. In general, the challenge of understanding and predicting how marine ecosystems may respond to future climate change magnifies these uncertainties.

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However, we have highlighted three promising and complementary approaches to minimizing these uncertainties. The first approach is to directly measure plankton functional traits along environmental gradients in the field; for example, field and satellite studies mapping plankton cell and body size (Cermeño *et al.* 2006; Uitz *et al.* 2006), phytoplankton expression of the *nifH* gene (Luo *et al.* 2012), and phytoplankton bacterivory (Zubkov & Tarran 2008). Some plankton functional traits, particularly morphological traits such as size, are readily observable, while others, such as maximum growth and nutrient uptake rates for phytoplankton and zooplankton feeding behaviour, are difficult to quantify in this manner. A second, but less direct, approach is to measure an organismal trait in a more controlled setting, and then map the trait back onto environmental gradients using known biogeographical distributions. Using this 'trait-to-map' strategy, Barton *et al.* (2013) described the spatial variations in seasonal succession of North Atlantic diatoms of varying size and dinoflagellates with a range of trophic strategies. We have also applied this approach to generate the trait distributions in Fig. 5. A third approach is to develop plankton community models that represent key plankton traits and trade-offs among traits in spatially explicit environmental conditions. These models can be used to formalise and test our understanding of regulatory mechanisms, identify relevant traits, predict current and future plankton community structure, and can be compared with field and laboratory observations. Understanding of zooplankton feeding behaviours (Mariani *et al.* 2013), plankton size structure (Armstrong 1994; Ward *et al.* 2012) and the distribution of N_2-fixation (Monteiro *et al.* 2010; Dutkiewicz *et al.* 2012) have benefitted from this approach.

Each approach will benefit from improved resolution of the distribution of species or functional groups and their traits. Numerous broad-scale observational and data aggregating efforts are underway to characterise the distribution of plankton species, size classes or taxonomic groups. Notable examples include the Continuous Plankton Recorder survey (Richardson *et al.* 2006), reanalyses of satellite ocean colour data (Uitz *et al.* 2006), plankton community model intercomparison data sets (O'Brian *et al.* 2012) and the Ocean Biogeographic Information System (OBIS 2012). However, similar efforts focussing on the distribution of plankton functional traits are relatively few. This is due undoubtedly to the difficulty of obtaining physiological and morphological measurements at sea and in the lab. Yet, another limitation is that there currently is no central clearinghouse for data describing how plankton functional traits vary within and across species. Thus, we advocate here for the creation of a global database of plankton traits across all species and locations.

Well-developed community database efforts are underway for the study of terrestrial plants and their functional traits, and may provide a successful model. The TRY trait database (Kattge *et al.* 2011), for example, has some three million trait entries for 69 000 of the 300 000 known terrestrial plant species in a vast range of habitats. By bringing together a range of existing regional or more trait-specific, specialty databases, the TRY database seeks to collect trait data for a broad range of species on a global scale and provide standardised data and metadata through a single data portal. In so doing, the database is poised to be a massive boost in studying the community ecology, evolutionary biology and biogeography of terrestrial plants.

A future plankton database is likely to have many similarities to TRY, but also aspects that reflect differences between terrestrial and marine habitats. Consider, for example, that plankton are generally short-lived, embedded within turbulent fluid flows, and often motile. Therefore, an essential component of the plankton database – perhaps even more so than for existing terrestrial databases – must be the collection of concomitant environmental and biotic data, including temperature, salinity, photosynthetically active radiation, pH, dissolved inorganic nutrients, and predator and prey abundances, among others. This is particularly true for parameters affected by climate (Box 1). Many regional and trait-specific databases already exist (Kiørboe 2011; Edwards *et al.* 2012; Barton *et al.* 2013), and should be brought together seamlessly. As many plankton traits co-vary (for example, phytoplankton cell size and nutrient uptake rates), it may be possible to 'fill' knowledge gaps for species and/or traits without abundant data (Bruggeman 2011; Shan *et al.* 2012). In addition to defining the relative fitness of each organism, the functional traits in such a database should also be those that can inform and validate trait-based plankton community models. Although we have not discussed adaptation, or fast micro-evolutionary changes in traits, the small size of phytoplankton and their large populations suggest that adaptation may play a role in how plankton respond to climate change (Lohbeck *et al.* 2012), though this possibility has not yet been fully assessed. The database will allow for assessment of intraspecific variability in traits in the current ocean, but also serve as an important baseline for evaluating changes in traits over time.

We hope that this review of plankton trait biogeography has served two central purposes. First, understanding of the mechanisms underpinning marine plankton biogeography, the community's role in biogeochemical cycles, and how communities may respond to future climates can be improved by adoption of the trait-based approaches outlined here. Second, the need for enhanced collection, standardisation and dissemination of plankton trait data is growing, and we hope that this collaboration will galvanise broad support for the necessary efforts.

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AUTHORSHIP

ADB, AJP and EL conceived and coordinated the review, and all authors contributed substantially to writing the manuscript.

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