From mice to elephants: overturning the ‘one size fits all’ paradigm in marine plankton food chains

Daniel G. Boyce,1,2* Kenneth T. Frank2 and William C. Leggett1

Abstract
It is widely believed that consumer control is a weak regulator of marine phytoplankton communities. It remains unclear, however, why this should be the case when marine consumers routinely regulate their prey at higher trophic levels. One possibility is that the weak consumer control of phytoplankton communities results from the inability of field researchers to effectively account for consumer–prey trophic relationships operating at the scale of the plankton. We explored this issue by reviewing studies of trophic control in marine plankton. Experimental studies indicate that size is a critical determinant of feeding relationships among plankton. In sharp contrast, of the 51 field studies reviewed, 78% did not distinguish among the sizes or species of phytoplankton and their consumers, but instead assumed a general bulk phytoplankton–zooplankton trophic connection. Such an approach neglects the possibility that several trophic connections may separate the smallest phytoplankton (0.2 μm) from the larger zooplankton (~1000 μm), a remarkable size differential exceeding that between a mouse (~10 cm) and an elephant (~2500 cm). The size-based approach we propose integrates theory, experiments and field observations and has the potential to greatly enhance our understanding of the causes and consequences of recently documented restructuring of plankton communities.

Keywords
Consumer control, marine plankton, resource control, size-based predation, trophic control.

INTRODUCTION
It is a common belief that over most of the ocean, annual trajectories of marine phytoplankton biomass are primarily regulated by resource availability rather than by consumers (Margalef 1978; Aebischer et al. 1990; Di Lorenzo et al. 2013). This view is largely based on statistical analyses of annual time series that generally indicate strong climate-driven resource regulation of phytoplankton (Behrenfeld et al. 2006), and weak grazer regulation (Micheli 1999; Shurin et al. 2002). This perspective shapes our view of how marine ecosystems will respond to ongoing climate change, and of the factors driving observed changes in phytoplankton standing stock (Boyce et al. 2010, 2014) and phytoplankton community restructuring (Polovina et al. 2008; Morán et al. 2010; Polovina & Woodward 2012) over decadal to multi-decadal scales. For example, resource-driven models suggest that phytoplankton concentrations at high latitudes will increase with warming, due to reduced upper ocean mixing (Mora et al. 2013). However, this contrasts sharply with experimental evidence that indicate phytoplankton concentrations at these latitudes will decline, due to increased consumer control by grazers as temperature increases (O’Connor et al. 2009; Lewandowska et al. 2014).

Notwithstanding the current widely accepted bottom-up view of phytoplankton dynamics, mechanistic explanations of why consumer control should be the dominant regulator of heterotrophs but not of phytoplankton is lacking. It has been hypothesised that ecosystem traits such as the degree of prey switching, or the levels of zooplankton diversity or omnivory may buffer against strong consumer regulation of phytoplankton (Sommer 2008). Another viable possibility is that the widely accepted hypothesis of weak consumer control of phytoplankton communities is an artefact resulting from the widespread inability of field-based studies to adequately resolve predator–prey trophic connections within marine microbial communities.

Here, we use published studies to document the extent to which trophic connectedness has been unaccounted for in field studies of plankton trophodynamics. We then revisit the importance of size-based predation in trophic ecology and review recent advances that enable the estimation of phytoplankton size and community dynamics at macroecological scales. Finally, we employ longstanding and well-established experimentally derived size-based predation relationships to advance an alternate approach to the estimation of trophic connectedness, trophic control and food chain structure in marine plankton. Our objective is to facilitate a more accurate resolution of the trophic controls that regulate plankton communities at large scales, and thereby to improve our understanding of the causes and consequences of recently observed
large-scale changes in marine plankton communities (Polovina et al. 2008; Boyce et al. 2010, 2014; Morán et al. 2010; Polovina & Woodworth 2012).

QUANTIFICATION OF TROPHIC CONTROL

The relative importance of resource availability vs. consumer control in structuring ecosystems has been difficult to resolve because these types of trophic control are not directly observable in situ and must instead be estimated. In short-term or small-scale studies, trophic control can be quantified using gut content or biochemical tracer analyses, electronic tagging or dilution experiments. However, these methods are impractical when attempting to assess trophic control for the complete spectrum of species, over large spatial areas or over multiple years. Moreover, small-scale experimental approaches may not accurately reproduce the complexity and realism of natural systems. Consequently, observable patterns such as the interaction strength between spatial or temporal gradients in the abundance of predators and their prey are commonly and extensively used as state indicators of trophic control in natural systems (Fig. 1). While many such state indicators of trophic control have been used, perhaps the most common is the correlation coefficient (r_{TC}), which has been used extensively to quantify the type and strength of trophic control in marine (i.e. Frank et al. 2006), terrestrial (i.e. Post et al. 1999) and freshwater (i.e. Carpenter & Kitchell 1993) studies and is commonly featured in contemporary ecological textbooks (Moloney et al. 2011). The validity of this and other state indicator approaches relies on two critical assumptions:

(1) Trophic connectedness: There is an implicit assumption that the predator and prey species are trophically coupled in space and time.

(2) Causality: The interaction between predator and prey arises due to a causative trophic effect, rather than in response to an independent factor (sensu the Moran effect; Moran 1953).

These assumptions are interdependent: species must be trophically connected to have a causative trophic effect. Application of the method to non-trophically coupled species could therefore obscure the detection of consumer control, leading the researcher to overestimate the prevalence of resource control (Fig. 1). For this reason, accurate estimation of the degree of trophic connectedness is a critical prerequisite to the establishment of causality and to quantifying trophic control. How to establish this connectedness is the primary focus of our review.

The trophic connectedness of species and topology of food webs has been successfully estimated using the stochastic theoretical cascade model (Cohen & Newman 1985). Within the cascade model, the structure of the food web is determined by the trophic position of the component species: species of higher trophic position may consume only those occupying a lower position. The theoretical cascades model has been adapted by empiricists, and it is now common and widespread to use species trophic positions to estimate food web structure and trophic connectivity. In turn, the trophic position of an individual species requires detailed knowledge of the diet preferences of the consumer and the trophic position of the prey. Accordingly, we use ‘trophic positioning model’ to refer to the use of estimated trophic levels to determine food chain structure and feeding connectivity. The trophic position, or fractional trophic level, of any consumer species can be estimated as

\[ TL_i = 1 + \Sigma_j TL_j \times DC_{ij}, \]

where \( TL_i \) is the fractional trophic level of the prey \( j \), and \( DC_{ij} \) is the fraction of species \( j \) in the diet of \( i \) (Pauly & Palomares 2005). While larger-bodied species are easily identified, are often extensively harvested, and their diets determined through dissection, detailed diet information for small-bodied species such as microscopic plankton are difficult to obtain. Moreover, planktonic species may exhibit frequent prey-switching behaviour (Stibor et al. 2004; Sommer & Sommer 2006), and can be mixotrophic (Zubkov & Tarran 2008). Therefore, trophic levels for plankton species may be less reliably estimated, and are likely to vary in space and time (Sommer et al. 2002; Sommer & Sommer 2006). Indeed, the trophic positioning model may be more data-intensive and difficult to apply in aquatic systems, because ontogenetic changes in diet are much more common in these than in terrestrial systems. Thus, many marine species are likely to possess a different fractional trophic level at each ontogenetic stage, thus reducing the usefulness of a species-level trophic estimate.

Notwithstanding these complexities, researchers have, and continue, to commonly employ the trophic positioning model when studying trophic control in marine ecosystems and have thereby made the implicit assumption that all phytoplankton (trophic level 1) are identical in their trophic suitability, and that all grazing zooplankton (trophic level 2) are identical in their prey preferences (i.e. Smith 1982; Aebischer et al. 1990; Daskalov et al. 2007).

It is now well-understood that plankton food chains are complex, with several trophic transfers potentially separating the smallest phytoplankton cells from the largest zooplankton (Pomeroy 1974; Azam et al. 1983; Stibor et al. 2004). For example, small phytoplankton cells (0.2 \( \mu \)m) cannot be efficiently grazed by larger zooplankton (~1000 \( \mu \)m) of the size that are typically retained by commonly used zooplankton sampling platforms. Instead, phytoplankton cells in this size range may be grazed by smaller heterotrophic nanoflagellates or ciliates within a microbial food chain (Fig. 2a), which, due to their small size, are rarely retained by sampling instruments and almost never considered in measures of total zooplankton biomass.

This convenient, but in many ways misleading conceptual model leads to a misrepresentation of food chain structure and to ‘top-heavy’ food chains, in which the trophic relationships between higher trophic level consumer species are much better represented and understood than is the case for plankton, which are often simplistically and unrealistically represented as bulk biomass pools of phytoplankton and zooplankton (Fig. 2b). This approach neglects the complex predator and prey dynamics of plankton food webs and has at best obscured, and at worst biased the understanding of the trophic controls operating on plankton communities at macroecological scales. We therefore argue that an alternate, size-based approach to the assessment of trophic connectivity
and control in the phytoplankton would be a substantial improvement over the current trophic positioning model.

**IMPORTANCE OF SIZE**

Organism size is an critical determinant of many ecological processes including metabolism, energy use, mobility, production and mortality (Woodward et al. 2005). In the trophic context, organism size sets first-order constraints on feeding behaviour, and thus regulates food web structure and the pathways and efficiencies by which primary production flows through ecosystems (Ryther 1969; Sheldon et al. 1972; Cohen et al. 1993; Sommer et al. 2002; Barnes et al. 2010). For vertebrate consumers, feeding relationships are well-described by

---

**Figure 1** Statistical state indicators of trophic control. Simulated time-series of abundance of trophically coupled food web components (species or functional groups) are used to infer the type and strength of trophic control at macroecological scales for a three trophic level food web. (a) Trophic connections between species within the food chain are developed. (b) Simulated time-series of relative biomass for different trophic levels are plotted over the last century (1900–2010). (c) The interaction between abundance time-series of trophically coupled food chain components provides an index of trophic control. In this case, the interaction metric is the correlation coefficient and is shown on each plot. *Application of the method to food web components that are not trophically coupled does not prevent the detection of resource control or weak trophic control, but may lead to the incorrect conclusion that consumer controlled systems are actually resource control (bottom left panel in c). For all plots, colours depict the food web components. Green denotes trophic level 1, yellow denotes trophic level 2 and red denotes trophic level 3. Columns denote simulations of consumer (left) and resource control (right).
predator–prey body size relationships that explain a large fraction of the variability in feeding interactions within freshwater (Fig. 3a), and marine (Fig. 3b) ecosystems (Reuman & Cohen 2004; Brose et al. 2006; Barnes et al. 2010). These size-based relationships appear to be broadly general, existing both within, and across different habitats and ecosystems, and for species spanning multiple taxonomies and body sizes. Such predator–prey size relationships are believed to arise primarily due to gape-size constraints (Bremigan & Stein 1994), for which body size is a more easily measured and reliable proxy. Body size is also incorporated into some ecosystem food web models. For instance size has been used to parameterise predator attack rates within a newly developed general end-to-end ecosystem model (Harfoot et al. 2014), and appears to closely align to niche space within widely used niche models. Indeed, niche models using organism size alone to form the niche axis are capable of correctly predicting 57–68% of the trophic connections in the food web (Petchey et al. 2008; Williams et al. 2010).

The importance of size-based predation has also been demonstrated experimentally in plankton food chains. Consistent with the conceptual model of the microbial food chain (Fig. 2a), an early freshwater experiment by Burns (Burns 1968) found a strong linear relationship between the carapace length of a filter-feeding zooplankton (Cladocera) and the

Figure 2 Food web structure. (a) Qualitative model depicting the flux of primary production through the microbial marine food chain. The number of trophic transfers, and hence the efficiency of energy transfer, between primary producers and fishes depends on the size structure of the community. Arrows depict the energy flow and blue circles show trophic transfers through the food chain. Colours depict the different pathways by which primary production flows up the food chain. Figure was adapted from Azam et al. (1983). (b) Visual representation of the estimated trophic structure obtained from a published food web model of the Icelandic marine ecosystem (Buchary 2001). Circles represent different species or species groups, semi-transparent lines represent feeding relationships between components. Top consumers are represented as dark circles and are at the top of the diagram, light blue circles are lower trophic level consumers, cannibalistic species are orange and phytoplankton are green.

Figure 3 The size of vertebrate consumers and their prey. (a) The average size (mm) of vertebrate predators and their prey from freshwater ecosystems (data from Brose et al. 2006). (b) The average size of predators and their prey from more than 27 marine ecosystems (Brose et al. 2006; Barnes et al. 2010). Colours depict the habitat from which the measurements were collected. Lines and shaded areas depict the model I OLS linear regression line and 95% confidence limits about the mean respectively. The dashed line in (a) is a generalised additive model regression fitted to the data. None of the relationships involve phytoplankton.
length of spherical plastic beads (1–80 μm diameter) that served to simulate their prey. Using a collection of experimental and field observations derived from aquatic foodwebs, Warren (1987) found that organism length could explain 90% of the variability in predator–prey feeding relationships among invertebrates ($P < 0.0001; n = 28$). In a series of mesocosm experiments, Stibor et al. (2004) demonstrated contrasting food web configurations and food chain length that were highly dependent on the initial size structure of the phytoplankton community. An ecosystem supported mainly of large-sized phytoplankton ($105 \mu m^3$) resulted in a three-level food chain (large phytoplankton–copepods–predators) and strong predator effects on phytoplankton. Alternatively, an ecosystem supported primarily of smaller phytoplankton ($52 \mu m^3$) led to a four-level food chain (small phytoplankton–ciliates–copepods–predators) and weak predator effects. The pooled results from these experiments yielded a neutral response of the phytoplankton community to predator manipulation. These findings further emphasise the importance of accounting for size structure in trophic ecology.

Despite the demonstrated importance of size in structuring ecological food chains, our literature review revealed that the potential influence of size-based predation is rarely incorporated into the design or analysis of field-based studies of trophic control in the marine plankton (see Supporting information for details of literature search). Only ~20% (10 of 51) of field-based and non-experimental studies involving plankton trophic dynamics we reviewed evaluated the roles of organism size or species composition in determining trophic connectedness. This proportion declined to 12.5% (3 of 24) when only studies conducted at macroecological scales (spatial scales greater than ‘station’ and temporal scales greater than 5 years) were considered. Overall, the proportion of studies that evaluated organism size or species composition was greatest for short term, small-scale studies, and least for macroecological studies. Of the studies evaluated, zooplankton abundance was commonly obtained using plankton nets or the continuous plankton recorder (CPR), from which the minimum zooplankton size can be easily inferred from the mesh size of the instrument. In contrast, phytoplankton abundance was most frequently assessed using measurements of total chlorophyll-a concentration (mg m$^{-3}$), ocean colour (‘greenness’) or primary production (mg C m$^{-2}$ D$^{-1}$) – methods that subsume the entire phytoplankton assemblage and lump species spanning several orders of magnitude in size (~1–1000 μm). Incredibly, this size differential is approximately proportional to that between a mouse and an elephant (~10–2500 cm or ~0.05–15 000 lbs).

Zooplankton grazing on phytoplankton was assumed in all 51 studies we reviewed. However, the reality is that by neglecting to consider the potential effects of size-based predation (Fig. 2a), it is possible that no direct trophic connectedness existed between zooplankton and phytoplankton in ~80% of the studies reviewed. Equally relevant, in those studies in which plankton size was reported, the average minimum size of the zooplankton retained by the sampling instrumentation was 331 μm. This contrasts dramatically with evidence that microzooplankton between 20 and 200 μm are the dominant grazers in the world oceans, consuming between 60 and 75% of daily primary production (Calbet & Landry 2004; Landry & Calbet 2004). This difference between the minimum size of zooplankton retained by sampling instrumentation (331 μm) and the size of the dominant grazers (20–200 μm), suggests that there may be at least one trophic transfer between the sampled zooplankton assemblage and phytoplankton. Hence, the assumption of direct trophic connectedness between zooplankton and phytoplankton in the majority of the 51 published field studies we reviewed is inappropriate.

As an alternative to assuming that all phytoplankton are grazed by all zooplankton, as many studies currently do, we propose that estimates of plankton size may be used to more accurately resolve trophic connectedness in plankton food chains. The idea of size-based food chains is not new. Size is a directly observable and measureable trait, and is directly related, through theory and observation, to the trophic dynamics of all organisms. The size-based approach has proved successful in predicting trophic connectedness in ecosystem food web models (Petchey et al. 2008; Williams et al. 2010), and several studies have found that body size is interchangeable with the trophic position of an organism (Elton 1927; Trebliko et al. 2013).

### Estimating Plankton Size at Macroecological Scales

The quantification of phytoplankton cell size or species composition has historically been a difficult and painstaking process requiring microscopic enumeration, flow cytometry, size-fractionated filtration, various particle size distribution techniques or other time consuming methods (Table 1 contains full summary of available methods and Table S1 contains references). This may explain why size-based predation information is rarely incorporated into plankton trophic studies. Obtaining continuous time-series of phytoplankton size measurements over regional spatial scales using such methods has been virtually impossible given limitations linked to vessel and personnel cost and availability and the expense of sampling remote ocean areas. The few decadal (~10 year) time-series of phytoplankton size or community composition that do exist, originate from fixed station locations, such as the Hawaiian Ocean Time-Series (HOTS) and Bermuda Atlantic Time-Series (BATS). The one exception is the continuous plankton recorder (CPR) time-series which has been sampling the northeast Atlantic Ocean more or less continuously since ~1940. However, the CPR uses a 270 μm mesh that may not accurately sample the entire zooplankton or phytoplankton size spectrum (Dippner & Krause 2013). For example, microphytoplankton (<2 μm diameter) comprise more than 90% of the phytoplankton biomass in some oligotrophic regions of the north Atlantic (Tarran et al. 2000) and elsewhere (Li et al. 1983), and an even greater proportion of primary production (Stockner & Anita 1986).

Recently, however, remote sensing methodologies that employ spectral-, abundance-, or ecological-based methods, particle size distributions and biogeochemical models (see Table I for complete list of these methods and Table S1 for references) have dramatically increased the ability to estimate
phytoplankton size and species composition at macroecological scales. These new techniques now make it possible to approximate the phytoplankton community composition and/or size structure at daily to weekly time scales and at a near global resolution.

These new methods differ in their complexity, data requirements, accuracy and output (Fig. 4). The output products generated are either phytoplankton size classes (PSCs), the estimated spherical diameter of the phytoplankton cells, or phytoplankton functional types (PFTs). Although PFTs are primarily defined based on biogeochemical function rather than size, per se, many routinely fall into distinct size categories (Roy et al. 2013). The differences between the algorithms employed to achieve these outputs are significant and have led to international workshops and collaborations designed to compare and validate their outputs against *in situ* observations (http://pft.ees.hokudai.ac.jp/satellite/index.shtml), and a report has recently been published by the International Ocean-Colour Coordinating Group (IOCCG) on resolving PFT’s and PSC’s using space-borne technologies (Sathyendranath 2014).

### HOW EXPERIMENTS, MODELS AND OBSERVATIONS CAN BE USED TO BETTER UNDERSTAND PLANKTON TROPHIC DYNAMICS: A PRELIMINARY FRAMEWORK

Here, we provide an example of how the results of experiments conducted at smaller scales can be used in combination with estimates of phytoplankton sizes derived using newly developed remote-sensing-based techniques, together with field observations, to improve the understanding of plankton trophic dynamics.

We compiled measurements on the size of plankton predators and their prey originating from 63 published laboratory studies (Table S2), and previously assembled by three peer-reviewed studies (Hansen et al. 1994; Fuchs & Franks 2010; Wirtz 2012). These extracted measurements encompass all major marine and freshwater plankton taxa and include cell diameters ranging between 0.6 and $2 \times 10^4$ µm. This accumulated experimental evidence indicates that a relationship consistent with the well-established predator–prey body size relationships in freshwater and marine vertebrate consumers (Fig. 3) also exists for marine plankton (Fig. 5a). The observed log–log linear relationship relating the size of plankton predators and their prey is based on long-standing ecological theory, and can be formally expressed as

$$ESD_{PRD} \propto ESD_{PRY}.$$  

where $ESD_{PRD}$ and $ESD_{PRY}$ are the equivalent spherical diameters of the plankton predator and prey respectively. Extending this representation, we fitted ordinary least-squares log–log linear models to the extracted experimental measurements to derive the following predictive equations

$$ESD_{PRD} = 18.5ESD_{PRY}^{0.985} \quad (3)$$

$$ESD_{PRY} = 0.313ESD_{PRD}^{0.744} \quad (4)$$

The above equations explain 73% of the variance in the relationships on a log–log scale and can be used with confidence to estimate trophic connectivity within plankton food chains. Given the diameter of a plankton predator or prey, the equations can be used to estimate the prediction intervals within which a given proportion of future observations will fall (Fig. 5a). These intervals can be then interpreted as the probable predator–prey size limits; points falling outside these intervals are statistically unlikely to be trophically coupled. The above equations were estimated on a log–log scale, but are presented on the response scale for clarity.

This approach can be used to better represent and parameterise trophic studies involving plankton. For example eqns 3 and 4 can be used in conjunction with remote sensing observations to predict the probable grazer size range, and when applied sequentially may be used to predict the average microbial food chain length at any location at any time (Menden-Deuer & Lessard 2000; Barnes et al. 2011; Polovina &
Woodworth 2012). Following the approach developed by Barnes et al. (2011), and adapted by Polovina & Woodworth (2012), the median phytoplankton cell diameter \( (M_{DS0}) \) can be derived as

\[
M_{DS0} = 2.14M_{BS0}^{0.35}
\]

where \( M_{BS0} \) is the median phytoplankton cell weight, which was estimated by Barnes et al. (2011) as

\[
\log_{10}(M_{BS0}) = 1.34 - 0.043SST + 0.929(\log_{10}(Chl))
\]

where SST is the sea surface temperature (°C) and Chl is the chlorophyll-\( a \) concentration (mg m\(^{-3}\)). Predictive eqns 5 and 6 are based on ecological theory, observations and experiments that show that increasing temperature leads to reductions in phytoplankton cell size (Daufresne et al. 2009; Morán et al. 2010). The method is based on a space-for-time (ergodic) assumption (Rosenzweig 1998) derived from 361 water samples collected from 12 ocean regions ranging from tropical to temperate, and including upwelling and oligotrophic regions (Barnes et al. 2011). The predictive model (eqn 6) explains 50% of the variance in phytoplankton cell size (Barnes et al. 2011).

To demonstrate the utility of this approach, we used eqns 5 and 6 to predict the median phytoplankton cell size globally during March of 2005 using remotely sensed monthly average SST and Chl measurements (Fig. 5b; see Supporting information for description of data). We used the above methods (eqns 5 and 6) to estimate phytoplankton cell size rather than one of the alternate approaches shown in Fig. 4 or listed in Table 1, because the method is capable of resolving the continuous cell size spectrum, rather than discrete size classes or functional types. Estimated median phytoplankton cell diameters across the global ocean during this time period ranged between 0.4 and 17 \( \mu \)m (Fig. 5b), which is consistent with the lower (0.2 \( \mu \)m; Agawin et al. 2000) and upper (> 200 \( \mu \)m) bounds of empirically derived estimates. This empirical size range is expected to be wider, since it includes sizes assessed across many times and locations, whereas the range estimated here (Fig. 4) includes sizes assessed during a single month and year.

The emergent spatial patterns of phytoplankton cell size (Fig. 5b) are primarily related to factors influencing ocean mixing, temperature and nutrient concentration, consistent with the results of independent studies (Margalef 1978; Atkin-

---

Figure 4 Climatological global spatial gradients in phytoplankton cell size or functional types. Schematic depicts how available sea surface parameters (green box) may be used to estimate phytoplankton size class from biogeochemical models (Brewin et al. 2010; red arrows), functional groups using spectral-based methods (Alvain et al. 2005, 2008; blue arrows) or spherical cell diameter using empirical methods (Barnes et al. 2011; Polovina & Woodworth 2012; green arrow). The methods used to derive these estimate are presented in Table 1 and Table S1; further details of the data used to produce this figure are in the supporting information.
Figure 5 Size-based predation in microbial ecosystems. (a) The estimated spherical diameter of marine plankton prey and their consumers derived from experiments (Table S1). Line depicts the linear regression fit. Shaded areas represent the prediction intervals about the mean for different levels of confidence; for the 95% interval, 95% of future values are predicted to fall within the interval. (b) Estimated median phytoplankton cell diameter and probable grazer size range estimated globally during March, 2005. Colours represent the size of phytoplankton cells and of grazers; white areas contain no data. (c) Same as in (a), but with colours depicting the primary feeding mode of the zooplankton consumer. Linear regression parameters were estimated within consumer feeding types.

This approach could be used to modify the design of sampling programmes aimed at resolving trophic dynamics in plankton and to determine whether trophic connectedness is probable. For instance, phytoplankton in the south Pacific gyre are among the smallest in the ocean (0.2 μm Agawin et al. 2000; Fig. 5b), and the predicted probable grazer size range of these picophytoplankton is between 0.2 and 65 μm, which is far below the retained size of most zooplankton sampling platforms (331 μm in our literature review). This knowledge could be used to estimate the number of trophic transfers separating picophytoplankton from a zooplankton assemblage of known size, or to increase the minimum size resolution of the zooplankton sampling instrument. Alternately, the probable prey size range for a zooplankton assemblage sampled with the CPR, which uses a 270 μm mesh, is predicted to fall between 1.8 and 228 μm. This knowledge could be used to estimate the average size or community composition of the contemporaneous phytoplankton assemblage and to determine whether trophic connectedness is probable. Finally, the method could also be used to estimate the number of trophic transfers and, following the ten per cent law (Lindeman 1942), the transfer efficiency of primary production up the microbial food chain. For example it has been hypothesised that the small nekton-to-primary production ratio in open ocean ecosystems (< 0.5%), relative to upwelling ecosystems (~ 1%; Iverson 1990), arises due to the small size of primary producers there (Sommer et al. 2002). The size-based model (Figs 2a and 5a), would suggest that the small size of primary producers in open ocean ecosystems leads to a longer food chain with more trophic transfers, and a reduced fraction of primary production available to higher trophic levels, and may explain the observed difference between the energetic transfer efficiencies in open ocean vs. upwelling ecosystems. The approach could be further expanded to estimate the total productivity of ecosystems or the capacity of different ecosystems to support fisheries.

Our earlier analysis (Fig. 5a) indicated that phytoplankton size explains 73% of the variability in the size of their consumer on a log–log scale. Other factors such as the nutritional content (Cebrian & Cebrain 1999), organism shape (Warren & Lawton 1987), or the defensive adaptations of phytoplankton may well explain much of the residual variability. Predator feeding modes can also influence size-based feeding relationships. For instance, small freshwater piranhas may occasionally consume much larger organisms by group feeding, and large baleen whales can consume zooplankton by filter-feeding. However, such extreme examples are uncommon (Barnes et al. 2010).
Following the approach used by Wirtz (2012), wherein predator feeding strategy and morphology are considered, we incorporated the feeding mode of the consumer (active, mixed or passive) into the simple predictive framework presented here. This produced different regression parameters and levels of uncertainty (Fig. 5c). The resulting predator–prey relationship was most variable for passive consumers that filter their prey from the water using sieve- or comb-like apparatus. Alternatively, active consumers that select food individually and are more constrained by gape-size exhibited a very strong predator–prey size relationship ($r^2 = 0.9$). Prey motility (Tisielius & Jonsson 1990) and chemical quality (DeMott 1988) may also influence the prey selection of active zooplankton consumers.

Given the limited experimental data available and the high explanatory power of the derived predator–prey relationship (Fig. 5a), we did not attempt to discriminate between different zooplankton feeding strategies when constructing empirical predator–prey size relationships (eqns 3 and 4). Incorporation of these behavioural traits, while requiring an enhanced knowledge of the zooplankton community, could, ultimately, lead to narrower prediction intervals of the predator–prey size relationships and improved accuracy and precision of the predictions (Fig. 5c). Given that experimental evidence suggests a low degree of coexistence between active and passive zooplankton consumers in marine ecosystems (Becker et al. 2004; Sommer & Sommer 2006), improved knowledge of feeding strategies may be a productive avenue of future research.

CONCLUSIONS AND IMPLICATIONS

Our analyses suggest that the trophic positioning model, currently widely employed in studies of trophic control in marine systems, may be inappropriate for resolving trophic connectedness at the level of the plankton, for which trophic position is difficult to estimate. As an alternative, we propose a trait-based approach based on organism size as a more mechanistically relevant and practical method of resolving trophic connectedness among plankton. Such size-based approaches are widely used to parameterise predator attack rates in general ecosystem models (Harfoot et al. 2014), and to define niche space within niche models. Organism size has also been shown to be an accurate indicator of trophic position (Elton 1927; Trebilco et al. 2013). In fact, organism size was used in classical ecological pyramids to denote a species’ position in the food chain (Elton 1927), and was only later replaced by the trophic level (Lindeman 1942; Odum & Brewer 1959). Recent experiments have also convincingly demonstrated that the size structure of phytoplankton communities can have strong effects on food chain length and on the detection of trophic effects (Stibor et al. 2004; Sommer & Sommer 2006).

The advantages of the approach we propose are considerable. The accurate trophic positioning of plankton in the trophic positioning model requires identification of the organism and detailed knowledge of the organisms diet, both of which can be difficult, costly and time consuming to obtain. Moreover, given the data-intensive nature of the trophic positioning model, spatio-temporal changes in food chain structure cannot be readily accounted for. In contrast, plankton size can be directly measured (zooplankton) or estimated globally at high temporal resolution using remote sensing techniques (phytoplankton). Given knowledge of the size of the plankton predator or prey, experimentally based empirical relationships can then be used to determine trophic linkages among plankton of different sizes. The theory of size-based predation predicts that microbial food web structure is spatially and temporally dynamic. To further explore this, eqns 5 and 6 were used to estimate phytoplankton cell diameter from remotely sensed monthly averaged surface SST and Chl from 1998 to 2008 (see Supporting information for details). We then fit statistical models to these observations to assess the space and time scales of phytoplankton cell size variability, and hence microbial food chain structure across the global ocean over this time period (Fig. 4, 5b and 6). Reductions in phytoplankton cell size over the past decade (1998–2008) were apparent in the Arctic Ocean and in the major oligotrophic gyres of all oceans (Fig. 6a). These Arctic Ocean trends may be driven by ice melt, and associated freshening of the ocean there (Li et al. 2009), whereas similar trends in the gyres have been attributed to ocean warming, reduced mixing and resulting nutrient limitation (Polovina et al. 2008; Polovina & Woodworth 2012). In contrast, increases in cell sizes are evident at most coastal locations, in the Southern Ocean and in low-latitude tropical waters. It remains unclear what drives increases in size at these locations, but the trend in coastal locations is likely influenced by land-based eutrophication (Jickells 1998), which favours large-celled species. In addition to this large spatial (Figs 4 and 5b) and decadal (Fig. 6a) variability, phytoplankton cell diameter also varies at intra (Fig. 6b) and interannual (Fig. 6c) timescales, and in response to decadal and multi-decadal climate fluctuations such as El Niño (Fig. 6d). These dynamic changes in phytoplankton cell size may cause food chain length and structure to vary on seasonal, yearly, decadal and basin-scales. The existence of non-steady-state dynamics in phytoplankton cell size, food chain structure and the transfer of energy, are currently overlooked in the design of most field studies, but could be readily incorporated within the size-based approach detailed above.

The size-based approach we propose is appealingly simple, adaptable to temporal and spatial variability, and could lead to an improved understanding of plankton dynamics and of how plankton communities will respond to ongoing climate change. It is important to also highlight that the size-based approach we propose should serve to compliment and improve existing approaches, such as trophodynamic models, which often use the trophic positioning model to determine food chain structure. For example organism size could be used to estimate trophic connectivity in situations in which the trophic level cannot be adequately resolved. Food chain connections estimated from organism size could also be used to validate connections based on trophic levels. In this manner, the size-based approach may serve to increase the robustness of existing approaches.

There is mounting evidence that marine phytoplankton communities are undergoing widespread alterations in distribution, abundance and community composition. Observational studies suggest that marine phytoplankton concentrations have declined globally over the past century (Boyce et al. 2010, 2014), that the average cell size of phytoplankton communities is shrinking (Li et al. 2009; Morán et al. 2010), and that the least productive regions of the ocean...

© 2015 John Wiley & Sons Ltd/CNRS
are expanding (Polovina et al. 2008). These trends are predicted to continue over the next century (Polovina et al. 2011; Mora et al. 2013), with probable effects on climate, marine ecosystem structure, geochemical cycling and fisheries. For example, because large particles sink more rapidly than small ones, a reduction in average phytoplankton cell size will likely lead to reduced export production to the deep ocean (Rodriguez et al. 2001), the majority of which originates from phytoplankton (Ruhl et al. 2008). As export production declines, the sequestration of CO2 to the deep ocean and the oceanic drawdown of CO2 from the atmosphere may also be reduced, with effects on the global carbon cycle and climate (Falkowski 2012). Reduced export production will also have strong impacts on deep-sea ecosystems, which are almost entirely sustained by this downward flux of organic matter.

These changes in phytoplankton abundance and community composition have been largely attributed to physically based processes associated with ocean warming, such as upper ocean stratification and nutrient limitation, yet it is unclear how biological control may have driven, or responded to such changes. Such knowledge is sorely needed, as the majority of general ocean circulation models used to forecast future ocean conditions do not currently incorporate potentially important biological processes such as the influence of environmental forcing on predator–prey interactions and trophic control. An enhanced capacity to incorporate such biological information, made possible in part by an incorporation of size-based approaches, could well improve the realism and forecasting accuracy of these models. Experimental studies suggest that continued warming may lead to strengthened consumer control of phytoplankton (O’Connor et al. 2009), but this effect is also believed to be context-specific (Lewandowska et al. 2014). It is likewise unclear what effect altered phytoplankton concentration, size structure and community composition will have on consumers and on the transfer of energy through the food chain. Resolving these important questions will require a greater understanding of the structure of microbial food webs and of how environmental change will modify this structure.

ACKNOWLEDGEMENTS

We thank B. Worm, B. Li, S. Craig and T. Eddy, for providing valuable comments on this manuscript.

AUTHORSHIP

All authors contributed to the design of the study, data interpretation and manuscript editing; D.G.B. assembled the
data, performed the statistical analyses and drafted the manuscript.

REFERENCES


