HORIZONS

The effects of changing climate on microzooplankton grazing and community structure: drivers, predictions and knowledge gaps

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Microzooplankton dominate trophic interactions and biogeochemical processes at the base of pelagic marine food webs and so their responses to a changing ocean environment have potentially large implications for ocean ecosystem functioning. This diverse array of mostly protistan species constitutes an important source of phytoplankton and bacterial mortality, and contributes significantly to the food available to higher trophic levels by packaging minute prey into larger particle sizes that can be consumed by metazooplankton. Microzooplankton are pivotal species in oceanic food webs and nutrient remineralization and so it is essential that we understand the effects that changing climate may have on the biomass, species composition and trophic activities of these assemblages. Yet, our present understanding of this topic is derived from experimental studies of relatively few species subjected to specific environmental variables (e.g. changes in temperature, CO_2, pH) in isolated culture. Most experiments and models employed to predict

the effects of climate change have focussed on primary productivity and phytoplankton community structure, with less attention paid to microbial heterotrophy. Here we outline some of the major direct and indirect changes in environmental variables that are anticipated to accompany global climate change, and our present state of knowledge regarding their potential impacts on natural microzooplankton assemblages. We highlight a few specific areas for studies to address glaring omissions in our knowledge regarding how global change influences microzooplankton abundances and activities, and hypothesize that their ecological and biogeochemical roles may become even more prominent due to expected future shifts in marine chemistry and climate.

INTRODUCTION

Ecosystem services, broadly defined, are correlated with biodiversity and the interactions supported by complex assemblages of species (Díaz *et al.*, 2006; Duffy and Stachowicz, 2006). This relationship has been demonstrated most clearly as reductions in the number and diversity of large animals and plants as a consequence of human-induced climate change, harvesting, habitat loss and purposeful or accidental species introductions. Losses of biodiversity in assemblages of top predators in ecosystems have been shown to cause dramatic restructuring of food webs, changes in energy production and/or flow and even loss of ecosystem function (Estes *et al.*, 2011). These changes in community structure and their accompanying impacts on food webs and biogeochemistry are expected to continue and accelerate in coming decades due to global climate change (Wohlers *et al.*, 2009).

The effects of climate change on species that form the base of aquatic food webs is much less clear than our perceived understanding of changes that will take place among animal and plant communities (Falkowski and Oliver, 2007). This gap exists because of our presently poor knowledge of the breadth and depth of microbial diversity, our limited ability to assess the diversity of these assemblages in nature and, consequently, our rudimentary understanding of the factors that control the structure and function of microbial communities. Considerable interest and research is now being focussed on understanding the effects of global climate change on phytoplankton community composition and primary productivity (see "Indirect Effects" below). This interest is well deserved because phytoplankton production constitutes roughly one-half of global primary production, and forms the base of pelagic food webs in aquatic ecosystems. At present,

however, there has been little research on the impact that climate change will have on the microbial consumers that play important ecological roles near the base of these food webs.

Nanoplanktonic and microplanktonic consumers (2–20 and 20–200 μm phagotrophic protists and micrometazoa, respectively; hereafter referred to as "microzooplankton" for simplicity) comprise an incredible diversity of forms and functions in pelagic ecosystems (Fig. 1). These consumer assemblages are dominated by a wide array of primarily protistan taxa that exhibit a range of phagotrophic behaviors and nutritions from pure heterotrophy to nearly pure phototrophy, as well as a variety of symbioses (Caron *et al.*, 2012). Indeed, many heterotrophic protists (aka "protozoa") exhibit some degree of phototrophic nutrition via symbiont or chloroplast retention, and many "phytoplankton" consume a variety of prey in addition to carrying out photosynthesis.

Microbial consumers were recognized decades ago as key participants in microbial food webs *sensu lato* Pomeroy (Pomeroy, 1974), and in more recent conceptualizations (Azam *et al.*, 1983; Sherr and Sherr, 2002). Bacterivorous forms, through their grazing activities, facilitate the recovery of dissolved and particulate organic matter lost through excretion and other processes into "classical" food chains, and also contribute significantly to nutrient remineralization (Caron and Goldman, 1990; Strom, 2000). Microzooplankton herbivory constitutes a major source of mortality for phytoplankton in the ocean (Sherr and Sherr, 2002; Calbet and Landry, 2004), and microzooplankton are themselves important prey items for larger zooplankton (Calbet and Saiz, 2005).

Our view of the diversity of microbial eukaryote communities that conduct these processes has changed rapidly in the past decade due to the application of genetic tools for assessing microbial diversity (Guillou
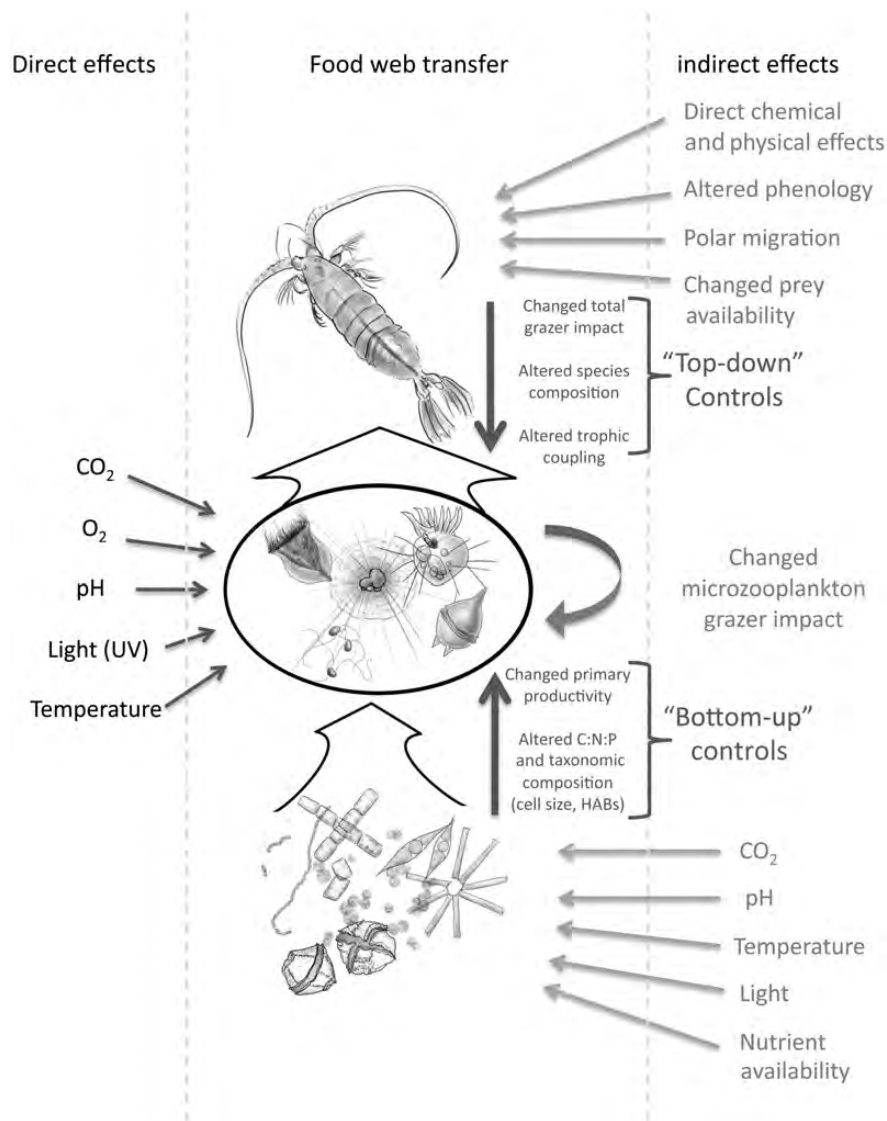
Fig. 1. Schematic overview of the trophic position of nano- and microzooplankton in planktonic food webs (center circle), and the potential direct effects and indirect effects of climate change on these assemblages. Changes in chemical and physical factors may alter the species composition and standing stocks of nano- and microzooplankton directly (left side). However, changes in environmental factors may also cause shifts in the standing stocks, species composition or productivity of prey (bottom) or changes in the standing stocks, species composition and/or top-down grazing impact of larger zooplankton that could indirectly affect the nano- and microzooplankton (right side).

et al., 2008; Not *et al.*, 2009; Cheung *et al.*, 2010; Countway *et al.*, 2010; Scheckenbach *et al.*, 2010; Stoeck *et al.*, 2010; Caron *et al.*, 2012). As a consequence, we are gaining a better understanding of the complex structure of these assemblages, and an appreciation for the swiftness with which these assemblages can respond to changes in environmental conditions and food web structure (Caron and Countway, 2009; Kim *et al.*, 2011). It is highly likely that these species will be responsive to both direct effects of changing ocean chemistry and physics, as well as indirect factors precipitated by global

climate change that might affect the availability of prey and/or the activities of consumers of microzooplankton. Both direct and indirect effects of environmental change have the potential to also interact with other anthropogenic stressors such as overharvesting, invasive species introductions and habitat modification and loss. We presently understand few of the details of these responses. Moreover, the ramifications of changes in microzooplankton community structure and/or activity can be expected to reach far up into pelagic food webs. This situation may be especially true for polar

ecosystems where water temperature and the seasonal retreat of sea ice strongly affect the magnitude and timing of primary production and trophic coupling (Hunt *et al.*, 2002; Jin *et al.*, 2009), and where many global change impacts including warming (Sarmiento *et al.*, 2004) and acidification (Orr *et al.*, 2005) are especially pronounced.

What are the potential direct and indirect impacts of global climate change on microzooplankton, and what are the most conspicuous gaps in our understanding? Below we briefly summarize our state of knowledge on these topics, highlight some controversial or speculative suggested future trends and discuss some of the obstacles that impede a better understanding of how global climate change might affect these assemblages.

DIRECT IMPACTS OF CLIMATE CHANGE ON MICROZOOPLANKTON

Climate change entails shifts in multiple environmental factors, some of which can be expected to co-vary. Predicting how planktonic communities will respond to these interconnected variables is not straightforward. The direct impacts of global climate change on the taxonomic composition and activities of microzooplankton assemblages will be the sum of the physiological responses of these species to a number of varying chemical and physical parameters, including temperature, pH and irradiance (Fig. 1, left side).

Temperature

The most conspicuous and well-documented consequence of global climate change is a slow rise in ocean temperature on the order of $>1°C$ per century that has been recorded in recent decades and that is predicted to continue and accelerate in the future (Hansen *et al.*, 2006). The geographical distributions of some plankton species including copepods (Richardson, 2008) and dinoflagellates (Hallegraeff, 2010) are undergoing poleward migrations as a consequence of ocean warming. This response is also possible for microzooplankton species. Thermal tolerances of many protists are quite high, however, in the range of $≥40°C$ (Martinez, 1980; Sittenfeld *et al.*, 2002). Temperatures in the proximal ocean would therefore be unlikely to approach the thermal limits for most species *sensu stricto*, so complete elimination of fundamental niches by increasing temperature seems unlikely in tropical or temperate ecosystems. Nevertheless, relatively modest changes in

temperature could still have significant direct effects on local microzooplankton species composition, abundances, feeding activities and growth efficiencies. At present, the response of most microzooplankton species to the direct effects of temperature is poorly characterized.

A dramatic, direct effect of ocean warming on microzooplankton assemblages might be expected in polar regions, in part because present information indicates the most significant warming in these ecosystems (Meredith and King, 2005; Hansen *et al.*, 2006). Additionally, extremely low environmental temperatures exert a strong constraint on the trophic activities, metabolic activities and growth rates of microzooplankton (Caron *et al.*, 2000; Rose and Caron, 2007). Rose *et al.* (Rose *et al.*, 2009a) observed a 43% increase in microzooplankton abundance in a Ross Sea plankton community incubated for 1 week at $4°C$ above the ambient temperature $(0°C)$. More generally, Rose and Caron (Rose and Caron, 2007) conducted an analysis of growth rate data that indicated that the maximal rates of growth for herbivorous and bacterivorous protists at low temperature were less than the rates attained by phytoplankton. This relationship was reversed at warm environmental temperatures $(>10°C)$. The authors argued that the higher potential maximal growth rates of photosynthetic protists at polar temperatures could be a partial explanation for the existence of massive phytoplankton blooms that are observed in some polar ecosystems (Smith and Gordon, 1997). That conclusion was based on an analysis of hundreds of data points obtained for protists growing in culture, but studies that have examined the growth rates of assemblages or individual species of microzooplankton in nature are still rare, and are needed to test that conclusion. Moreover, the applicability of this relationship to certain types of protists has been questioned (Sherr and Sherr, 2009), leaving an additional question that must be addressed.

The underlying reason that low environmental temperature appears to exert greater control over heterotrophic processes among protists relative to phototrophy has been attributed to differences in the activation energies of these processes. This relationship has been recognized as a component of the metabolic theory of ecology (Brown *et al.*, 2004; López-Urrutia, 2008). Enhancements in heterotrophic processes relative to phototrophic processes as a consequence of warming have been observed in mesocosm experiments, implying a loss of energy and material transfer to higher trophic levels (Wohlers *et al.*, 2009). One recent modeling study concluded that a warming climate could alter the balance between phytoplankton growth and microzooplankton herbivory in the ocean (Chen *et al.*, 2012). Such findings indicate that even a modest increase in

temperature in polar environments could alter the fundamental relationship between microzooplankton and their prey, allowing microzooplankton growth rates and, consequently, community grazing pressure to keep pace with phytoplankton production.

Irradiance

Increased thermohaline stratification in many regions due to warming and freshening of the surface ocean is expected to result in increased mean irradiance exposures for populations inhabiting the upper mixed layer. Higher rainfall, ice melting, warming, and changing wind patterns under altered climate regimes can all contribute to mixed layer shoaling and stratification with potentially important indirect effects on microzooplankton (see the section "Indirect effects"). Increased irradiance and exposure to UV radiation in particular may also have significant direct effects on the growth and behavior of some heterotrophic protists (Macaluso *et al.*, 2009), and consequently affect the structure of marine food webs as a result of species-specific differences in UV sensitivity (Belzile *et al.*, 2006). Mostajir *et al.* (Mostajir *et al.*, 1999) noted an adverse impact of UV-B on a natural ciliate assemblage in mesocosm experiments. Decreases in ciliate abundances were coupled to increases in small phytoplankton and small heterotrophic flagellates. There is little understanding of the magnitude of this effect at present, or how the other factors that co-vary with increases in irradiance can be integrated to provide an overall understanding of its effects on marine food webs or microzooplankton specifically.

pH and CO$_2$

Direct effects of decreasing pH and increasing CO$_2$ in the ocean on microzooplankton also have not been adequately addressed, with one notable exception. Changes in ocean chemistry can have negative impacts on calcification by planktonic foraminifera. These large protists produce calcium carbonate (calcite) skeletons that are important indicators of water quality, and have been extensively employed in paleoclimatological reconstructions (Hemleben *et al.*, 1988). Moy *et al.* (Moy *et al.*, 2009) noted an apparent link between increased atmospheric CO$_2$ concentration and decreased calcification in planktonic foraminiferal fossil records. Measurements of the effects of increased CO$_2$ and lower pH on calcification among these species are still rare, but a few reports indicate that changes in ocean chemistry will negatively affect calcification in these species within the next century (Russell *et al.*, 2004; Lombard *et al.*, 2010, 2011).

Although other types of direct acidification effects on non-calcifying heterotrophic protists are usually not anticipated to be remarkable, there is a lack of actual information to either support or refute this assumption. For instance, it has been shown that bacterial flagellar motion depends on the maintenance of a transmembrane proton gradient (Manson *et al.*, 1977). If the activity of protistan flagellae depends on a similar mechanism, changes in pH could well affect motility in some microzooplankton species. Future acidification could also lead to more variable proton concentrations in the cell surface boundary layers of marine plankton (Flynn *et al.*, 2012), which could affect numerous cellular processes that rely on proton pumps. Whether such direct physiological effects of changing pH will be significant for microzooplankton is an open question that will require more research.

Oxygen

One of the most widely predicted consequences of ocean climate change is worldwide expansion of oxygen minimum zones (OMZs) (Oschlies *et al.*, 2008; Gruber, 2011). A global shift toward lowered seawater oxygen concentrations could increase the relative importance of micrograzers in marine food webs because most macrozooplankton cannot permanently occupy OMZs of <0.29 mg L^{-1}, while many protistan grazers survive even in completely anoxic water through anaerobic respiration (Marcus, 2001). For instance, the biomass of unidentified ciliates in the oxygen-depleted, sulfidic OMZ of the Baltic Sea can sometimes exceed that of the more diverse microzooplankton assemblage in the overlying aerobic water column (Setala, 1991). Thus, projected future increases in ocean suboxia and hypoxia could favor trophic interactions dominated by protistan micrograzers tolerant of low O$_2$ levels, but to date there has been no experimental or modeling work to address this possibility.

INDIRECT EFFECTS OF CLIMATE CHANGE ON MICROZOOPLANKTON

A myriad of factors affecting the amount and quality of microzooplankton prey ("bottom-up" controls) and the abundances and activities of microzooplankton predators ("top-down" controls) are expected to co-vary with changes in ocean chemistry and physics accompanying global climate change (Boyd *et al.*, 2010). Characterizing and predicting the overall effect of this complex array of interactions on microzooplankton assemblages

constitutes a formidable task. These indirect effects can be broadly grouped into the effects of changing climate on the productivity of microzooplankton prey populations (phytoplankton and bacteria), the taxonomic and cellular composition of prey assemblages and the abundances and trophic activities of microzooplankton predators (Fig. 1, right side).

Primary productivity and bacterial productivity

The most significant indirect effects of climate change on microzooplankton abundances, activities and community composition will probably result from the response of the phytoplankton community to changing environmental conditions. Phytoplankton constitute the food source for herbivorous microzooplankton, and directly or indirectly affect the magnitude and composition of the dissolved and particulate material entering the microbial food web (i.e. the substrate available for bacterial growth). Therefore, understanding the response of photosynthetic assemblages to the changing ocean environment is paramount to understanding how microzooplankton assemblages will be affected.

Experimental, observational and modeling studies have been carried out to illuminate the response of phytoplankton to global climate change. Based on first principles, changes in thermal warming and wind-induced turbulent mixing of the upper mixed layer of the ocean, and their cascading effects on the light regime and nutrient concentrations to which phytoplankton are exposed, are believed to be of paramount importance in determining the effects of global climate change on total primary productivity. These changes could affect the magnitude, timing or duration of spring phytoplankton blooms in temperate regions (Sommer and Lengfellner, 2008; Sommer and Lewandowska, 2011) but the direction and magnitude of this effect may be different for different algal groups. Edwards and Richardson (Edwards and Richardson, 2004) used a long-term phytoplankton data set to argue that the timing of abundance increases of dinoflagellates were more affected by a warming ocean than for diatoms. The temporal stability of diatom blooms was explained by a stronger dependence of growth on photoperiod relative to temperature, while dinoflagellates bloomed earlier in the year because of a direct influence of temperature on growth rates of these species, and also earlier stratification of the water column which presumably gave motile dinoflagellates a competitive advantage in acquiring nutrients.

The overall predicted impact of climate change on total primary productivity in the global ocean is controversial. Studies examining warming and stratification have predicted decreases (Behrenfeld *et al.*, 2006), while work investigating CO_2 enrichment often demonstrates a stimulation of the growth rates of some photosynthetic groups (Hutchins *et al.*, 2007; Riebesell *et al.*, 2007). Increased concentrations of CO_2 and decreased pH alter the availability of CO_2, bicarbonate and carbonate ions in the water column. Preferences for these carbon constituents exist among algal groups (Rost *et al.*, 2008; Beardall *et al.*, 2009), and it is anticipated that there will be "winners" and "losers" among phytoplankton taxa in their competition for inorganic carbon in the future ocean (see next section).

It is likely that changes in total primary productivity as a consequence of changes in CO_2 availability will be overshadowed by the indirect effect of climate change on nutrient availability as a consequence of increased thermal stratification and thus reduced rates of nutrient replenishment to surface waters. Decreases in estimates of global net primary production have been noted and linked to increases in sea surface temperature and stratification (and its presumed effect on nutrient availability) (Behrenfeld *et al.*, 2006). Recent analyses indicating a global decline in phytoplankton have generated attention and also some controversy (Boyce *et al.*, 2010; Mackas, 2011; McQuatters-Gollop *et al.*, 2011). Changing climate regimes can also be expected to affect continental dust inputs to the surface ocean and so alter the delivery of the limiting micronutrient iron to phytoplankton communities, but the magnitude and even the sign of these changes in iron supplies are presently uncertain (Boyd *et al.*, 2010).

If changes in the ocean temperature lead to a reduction in global primary productivity, this effect is expected to vary regionally, resulting in considerable spatial heterogeneity. Hansen *et al.* (Hansen *et al.*, 2006) proposed that the uneven warming on the east and west sides of the Pacific will increase the likelihood of strong El Niños events in the Pacific. These events have both direct effects (substantially warmer surface waters) as well as important indirect effects on primary production. Enhanced stratification of the water column due to warming of surface water could prevent upwelling events that are important mechanisms for transporting nutrients into photic zone communities. Region-specific changes in the phytoplankton community structure, rates of primary productivity and microzooplankton herbivory in these situations are anticipated. Chen *et al.* (Chen *et al.*, 2012) predicted increases in microzooplankton herbivory in eutrophic environments but not in oligotrophic regions based on modeling of microzooplankton herbivory and phytoplankton growth information from dilution experiments.

It is also possible that region-specific outcomes to global warming may be non-intuitive or contrary to generalized responses. For example, Rykaczewski and Dunne (Rykaczewski and Dunne, 2010) noted that primary productivity in the California Current System may increase in response to global warming, as a consequence of decreased ventilation of the North Pacific and concomitant changes in processes leading to increases in nitrate. Modeling of the Barents Sea predicted a slight increase (8%) in primary productivity in this region as a consequence of ocean warming and particularly due to effects on productivity in the northern Barents Sea (Ellingsen *et al.*, 2008).

A "non-intuitive" effect of ocean warming on primary productivity may also occur at the poles. Reduced mixing due to warming and freshening of surface waters may increase thermohaline stratification of the water column, thereby reducing the deep vertical mixing that often constrains productivity due to light limitation in these waters (Doney, 2006). The overall effect may be to retain phytoplankton more effectively in the photic zone of the water column, thereby increasing rather than decreasing primary productivity. However, this effect might be counter-balanced by relative increases in microzooplankton grazing mortality due to ocean warming (see "Direct Effects", above). These potentially counteracting effects on food web structure and function point to the importance of regionally based field observations and experimental studies.

Bacterial biomass constitutes an important prey assemblage for a large number of microzooplankton species, but there is little information regarding the impact that changing ocean temperature and chemistry will have on global bacterial production and the many carbon and nutrient cycling pathways that prokaryotes control. It has been argued that major biogeochemical processes may not be dramatically affected, based on the fact that these processes have continued fairly unabated through major cataclysms in Earth's history, and also from observations across a wide spectrum of modern environments including many extreme environments (Joint *et al.*, 2011). In contrast to this viewpoint, some experimental work suggests the possibility of substantial global change-mediated shifts in ocean biogeochemical cycles, including decreased nitrification, enhanced nitrogen fixation and large shifts in the chemical speciation and availability of key nutrients such as ammonium and iron (Hutchins *et al.*, 2007; Shi *et al.*, 2010; Beman *et al.*, 2011). A postulated future coupling of lowered ammonium oxidation rates with global stimulation of nitrogen fixation has been suggested to lead toward reduced levels of nitrate-supported new production and increased reliance of primary producers on regenerated nitrogen species. This scenario would likely foster a greatly expanded microbial food web and increase the abundance of pico- and nanophytoplankton at the expense of larger nitrate-utilizing groups such as diatoms (Hutchins *et al.*, 2009), thus setting the stage for a much larger role for protistan grazers in future marine trophodynamics.

Similarly, intensified nutrient limitation of primary producers in a high-irradiance, more-stratified ocean may increase the amount of dissolved organic matter released by phytoplankton (Wetz and Wheeler, 2007), thereby stimulating heterotrophic bacterial production. It is probable that changes in phytoplankton productivity, taxonomic composition and trophic coupling will all affect the amount and quality of dissolved and particulate organic matter available as substrate for bacteria. The net influence of these factors on overall bacterial productivity requires study and resolution.

Taxonomic composition of the phytoplankton

Environmental factors that co-vary with global climate change are anticipated to result in significant changes in the taxonomic composition of phytoplankton assemblages, and examining these responses has become a rich topic for observational and experimental science in recent years. The ramifications for the microzooplankton assemblages that prey on the phytoplankton should also be significant, but there is presently little consensus on the specific changes that will occur in phytoplankton assemblages beyond a few broad generalities, and therefore limited ability to predict the response of microzooplankton to one of the primary potential driving forces resulting from global climate change. Examination of the changes in these trophic linkages as a consequence of climate change is a research area that is ripe for study.

One of the few experimental studies using a natural plankton community to examine the effects of increased temperature and CO_2 (individually and together) on microzooplankton demonstrated a significant effect on microzooplankton abundance and taxonomic composition (Rose *et al.*, 2009b). To a large extent, these shifts were driven by temperature, although interactions between warming and CO_2 also led to the development of a distinct assemblage in the combined "greenhouse" treatment. The authors concluded that the changes in the phytoplankton assemblage as a result of these environmental perturbations probably had a greater impact on microzooplankton than any direct effect of either CO_2 or temperature (Rose *et al.*, 2009b). An increase in

the dominance of unpalatable phytoplankton during the experiment affected microzooplankton abundances and grazing activities. Less obvious responses of the microzooplankton community to increased CO_2 levels in mesocosm experiments were reported by Suffrian et al. (Suffrian et al., 2008). These experiments exemplify the difficulty of carrying out experiments of these types and assigning the cause of observed changes to direct or indirect aspects of climate change.

The fossil record has provided a few clues that have been integrated into our thinking of how global climate change will affect phytoplankton communities. For example, ocean warming during the past 65 million years resulted in a significant decrease in the frustule size of marine diatoms over this same period (Falkowski and Oliver, 2007). Shifts from more to less silicified forms, or from large-to-small phytoplankton cell sizes, might be expected due to enhanced competition for nutrients and decreased buoyancy in areas experiencing increased thermal stratification due to ocean warming.

Some generalities regarding the success of different classes of phytoplankton (e.g. diatoms versus dinoflagellates versus coccolithophorids) are also emerging from ecological modeling, informed by observational and experimental results, that provide some broad guidelines or expectations of the consequences of climate change (Litchman et al., 2006; Beardall et al., 2009). Modeled scenarios are often contrary to the outcomes of physiological studies examining the response of individual phytoplankton species to specific factors associated with climate change. These contradictory outcomes may result from inter-specific or even intra-specific variations in the physiological susceptibility among algae to changing environmental parameters affected by climate change. As a consequence, predicting how the taxonomic composition of phytoplankton assemblages might respond to climate change is not straightforward at this time.

Moline et al. (Moline et al., 2004) reported shifts in the phytoplankton community composition off the Antarctic Peninsula from diatom-dominated assemblages to cryptophyte-dominated ones, and in the size structure of the phytoplankton community to smaller average cell size as a consequence. This shift was attributed to lower salinities in the coastal environment as a consequence of increased glacial melting. A recent study proposed a somewhat different scenario in which no consistent trend in the size structure of the phytoplankton was observed, but rather a more heterogeneous response of the ecosystem due to mesoscale changes in the extent of sea-ice and in circulation patterns (Montes-Hugo et al., 2008). A shipboard manipulative study in the Bering Sea tested the individual and combined effects of increased temperature and CO_2

and documented large shifts in the algal community away from diatoms and toward nanoflagellates, with warming rather than CO_2 being the prime driver of these taxonomic changes (Hare et al., 2007). Shifts from dinoflagellate-dominated to diatom-dominated phytoplankton communities have been reported for the northeast Atlantic and North Sea based on a 50-year data set provided by the Continuous Plankton Recorder (Hinder et al., 2012). These data are somewhat in contradiction to model predictions that generally indicate shifts toward dinoflagellates and away from diatoms, and indicate that the "devil is in the details" with respect to predicting regional competitive outcomes among phytoplankton taxa in the face of changing climate.

The specific response of the phytoplankton community to climate change will almost certainly cause changes among the herbivorous microzooplankton. For example, shifts in phytoplankton composition away from diatoms and toward small flagellated and non-motile forms should enhance the success of tintinnids and naked oligotrichous ciliates which play important roles as consumers of picoplankton- and nanoplankton-sized cells in pelagic marine ecosystems (Dolan, 1991; Sherr and Sherr, 1994, 2002; Kim et al., 2011). This shift in the community structure could also dramatically reduce the success of heterotrophic dinoflagellates that prey on diatoms (Jacobson and Anderson, 1986; Strom and Buskey, 1993).

A general shift toward harmful algal bloom (HAB) species has been predicted by some investigators [reviewed in Fu et al. (Fu et al., 2012)]. A global increase in the frequency and severity of HAB events during the past several decades has been documented, although the relationship of these increases to global climate change is confounded by changing land use and coastal eutrophication (Glibert et al., 2005; Anderson et al., 2008). For example, a shift toward an increased frequency of HABs in Chesapeake Bay is anticipated based on a review of historical data and present understanding/prediction of how changes in precipitation, nutrient inputs, etc. might act in concert with the direct effects of climate change (Najjar et al., 2010).

Warmer temperatures have been strongly implicated in the increased frequency of the dominance of cyanobacterial species in freshwater (Paerl and Huisman, 2008; Paerl and Huisman, 2009; Paerl and Paul, 2011), but stimulation of certain marine cyanobacterial taxa has also been reported (Fu et al., 2007). Cyanobacteria tend to have excellent tolerance to warm water temperatures and water column stratification (e.g. many can accumulate into dense "surface scums" that can shade phytoplankton living in the water column below them)

that make them highly successful competitors in climate warming scenarios. In addition, many cyanobacteria are poor food items for planktonic consumers, and some are outright toxic. Interestingly, microzooplankton biomass may play a role in improving the nutritional composition of the nano- or microplankton in situations where the phytoplankton community is dominated by toxic or unpalatable cyanobacteria (Park et al., 2003).

A shift toward less palatable or toxic phytoplankton species could result in major changes in microzooplankton taxonomic composition, abundance or trophic coupling. Prey selectivity of microbial herbivores and its relationship to phytoplankton species composition and bloom development are well known (Strom et al., 2003; Tillmann, 2004). Heterotrophic dinoflagellates and ciliates employ mechano- and chemoreception to determine the suitability of potential prey (Flynn et al., 1996; Hansen et al., 1996; Buskey, 1997; Buskey et al., 1997). In turn, many algae are capable of using chemical defenses to retard or inhibit the grazing activities of microzooplankton (Wolfe et al., 1997). Leão et al. (Leão et al., 2012) noted changes in the taxonomic composition of the cyanobacterial and protistan assemblages in lake water following additions of cyanobacterial allelopathic compounds, and some compounds produced by phytoplankton act specifically to retard growth or impair reproduction of zooplankton (Ianora et al., 2004). Some bloom-forming species of harmful algae produce exopolymer secretions (EPSs) that can deter protistan herbivores (Liu and Buskey, 2000), or other substances that render them unpalatable to many microbial consumers (Caron et al., 2000; Calbet et al., 2011). Stimulation of phycotoxin production under high CO_2 conditions has also been reported for some HABs, including two diatom species in the genus *Pseudo-nitzschia* (Sun et al., 2011; Tatters et al., 2012). The estuarine mixotrophic dinoflagellate *Karlodinium veneficum* synthesizes much more virulent karlotoxin congeners when seawater CO_2 is elevated (Fu et al., 2010). Since karlotoxins function to both deter predation on the dinoflagellate (Adolf et al., 2008) and facilitate the capture of its prey (Sheng et al., 2010), this could have implications for multiple levels of trophic interactions in estuaries where blooms of *K. veneficum* occur.

Other "generalized" effects of climate change that are anticipated include the selective inhibition of the growth of phytoplankton that do not possess UV-retarding compounds, or species that produce calcareous structures such as the coccolithophorids. However, the magnitude and the specific outcomes of these effects are poorly known and require continued study to accurately predict response. For example, moderate amounts of UV-A (315–400 nm) can be stimulatory to algal photosynthesis and repair of damaged DNA, while intense UV-B radiation (280–315 nm) generally has opposite and highly deleterious effects (reviewed in Gao et al., (Gao et al., 2012)). Decreased pH is anticipated to have a strong negative impact on coccolithophorids (Delille et al., 2005; Doney et al., 2009), but there are new reports that decreasing pH may not necessarily lead to a decrease in calcification by all of these taxa (Smith et al., 2012). The fate of calcifying phytoplankton in particular may have direct implication for the flux of carbon from surface waters into the deep ocean (Hutchins, 2011) as well as implications for microzooplankton herbivory.

Bulk elemental composition also affects the nutritional quality of phytoplankton to their consumers, and changes in elemental stoichiometry (C:N:P) of phytoplankton are expected to take place as a consequence of climate change (Finkel et al., 2010). A cascade of effects on microzooplankton is anticipated, but overall changes in phytoplankton C:N and N:P ratios as a consequence of some environmental parameters such as lower pH are not completely clear (Hutchins et al., 2009). CO_2 has been shown to affect the cellular composition of phytoplankton (Burkhardt and Riebesell, 1997; Riebesell et al., 2007), and prey C:N ratios have been shown to affect prey selectivity by some herbivorous protists (John and Davidson, 2001). Prey C:N:P stoichiometry could also alter the gross growth efficiencies and the magnitude and efficiency of nutrient remineralization by herbivorous microzooplankton (Goldman et al., 1987a; Caron et al., 1990). Information on these features of microzooplankton physiology are rarely studied any more, but are urgently needed in order to estimate the potential impact of climate change on pelagic food web structure and energy flow.

Changes in phytoplankton elemental stoichiometry could also affect the relative importance of the bacteria–microzooplankton trophic link in the plankton by altering the composition of the substrates available for bacterial growth. The C:N:P stoichiometry of bacterial substrate is a major factor controlling nutrient competition between phytoplankton and bacteria (Goldman et al., 1987b; Elser et al., 1995; Ietswaart and Flynn, 1995). In situations where bacteria compete successfully with phytoplankton for growth-limiting nutrients, bacterivorous protists play an important role in mediating nutrient remineralization, repackaging bacterial biomass into larger organisms and trophic transfer (Caron et al., 1988). Therefore, energy and elemental flow through the microbial food loop (sensu Pomeroy, 1972) might increase significantly if climate change reduces nutrient availability in the photic zone due to increased thermal stratification.

Top-down control, seasonality and trophic coupling

Changes in primary productivity and phytoplankton species composition are major indirect "bottom-up" forcing factors on microzooplankton abundances and activities, but direct (and indirect) influences of climate change on meso- and macrozooplankton assemblages must also be considered because they represent potential changes in "top-down" control of microzooplankton (Fig. 1). Recent studies have indicated apparent linkages between climate change (or other long-term climate phenomena) and fluctuations in zooplankton populations ranging from copepods to jellyfish (Beaugrand et al., 2002; Lynam et al., 2004; Hays et al., 2005). Potential direct effects include increased levels of CO_2 and lower pH that could have negative effects on pelagic calcifying molluscs (pteropods and heteropods). Many of these species are generalists that feed on minute particles collected using mucus webs (Gilmer, 1972). These taxa are important components of high latitude ecosystems, where they influence the abundances and diversity of macro- and microzooplankton.

Long-term field observations have indicated that ocean warming has resulted in the pole-ward movement of tropical and temperate zooplankton species, and the timing of appearance of various species and life stages (Richardson, 2008). However, the movement of some populations toward the equator has also been reported, presumably indicating a response to regional variances in ocean circulation resulting from global warming patterns. These changes will alter zooplankton species composition, and potentially their grazing activity, in various oceanic realms.

A fair amount of information is now becoming available on zooplankton phenology (i.e. the timing of seasonal activities), improving our understanding of the temporal mismatches that might result from the responses of different trophic levels to environmental change. For example, Edwards and Richardson (Edwards and Richardson, 2004) reported that the seasonal cycles of growth and reproduction of some copepods have shifted to earlier in the year over the past several decades, causing a loss of synchrony in the trophic transfer of primary productivity to higher trophic levels. These and other observations indicate significant shifts in the timing of life history events for a number of important meso- or macrozooplanktonic species. Changes in the timing of the appearance of zooplankton can have important implications for the success of juvenile fish populations (Richardson, 2008) and also for zooplankton grazing on microzooplankton assemblages. Collectively, changes in the geographical

distributions of zooplankton could substantially alter not only top-down control on microzooplankton populations, but also potentially alter the availability of phytoplankton prey to microzooplankton because of changes (positive or negative) in the extent of herbivory by mesozooplankton.

Changes in food web structure and phytoplankton–zooplankton trophic coupling in pelagic ecosystems may have important consequences for the vertical flux of organic matter to the deep ocean and deep-sea communities. A shift to dominance by smaller phytoplankton (due to more severe nutrient limitation in a warmer, more stratified ocean) could result in a greater percentage of primary production being consumed by microzooplankton, leading to a decrease in rapidly settling particles. Along with reduced storage of carbon in the deep ocean by the biological pump (Passow and Carlson, 2012), such decreases could also lead to potentially major changes in the deep-sea benthic fauna as a consequence of changes in food availability (Smith et al., 2008). Smith et al. (Smith et al., 2008) noted that such effects may not be linear, and therefore a drastic change in the total amount of primary production would not be necessary to bring about significant changes in food availability in the deep ocean.

FUTURE DIRECTIONS

Understanding the potential impact of global climate change on microzooplankton assemblages is essential because of the pivotal ecological roles that these species play in planktonic ecosystems. As noted above, however, climate change will affect a variety of chemical and physical features of the ocean, resulting in an array of direct effects on microzooplankton as well as a variety of indirect effects resulting from influences on trophic levels above and below these important microbial consumers (Fig. 1). As a consequence, accurate understanding and prediction of the response of microzooplankton assemblages to climate change can only be achieved by understanding how multiple environmental forcing factors will translate into emergent community-level changes in natural microzooplankton assemblages and their ecological activities. Three general approaches for investigating the effects of climate change have been, and will continue to be used to address this pressing need. These are as follows:

(i) Performance of experimental studies on individual species in the laboratory, and manipulative experiments with natural communities.
(ii) Establishing correlative empirical relationships with climate change through short-term

observations in nature and long-term ecological monitoring efforts.

(iii) Modeling efforts that incorporate existing information on the effects of climate change on ecosystem structure and function in order to predict future response to global climate change and to identify key gaps in our understanding.

Experimental studies of individual species subjected to changes in specific variables or combinations of variables are fundamental because they provide baseline information regarding the physiological abilities of particular microzooplankton species to acclimate or adapt to changing climate conditions. On the other end of the spectrum, correlative relationships derived from observations of the response of natural communities to climate change provide information that has been integrated across multiple forcing factors, spatial and temporal scales. Between these two extremes, modeling provides a means of attempting to extrapolate from population responses to community-level responses. Many of the outcomes of modeling efforts to date are non-intuitive, provide only the most rudimentary or generalized predictions, or yield outcomes that are often in contradiction to changes observed for natural communities. Therefore, it is presently unclear if the overall impact of direct and indirect effects will result in additive, synergistic or antagonistic outcomes on the abundances and activities of microzooplankton species. These inaccuracies and deficiencies of models point to gaps in our understanding, and indicate that a better understanding of basic physiological responses, as well as more holistic approaches and experimental studies are urgently needed to decipher the impacts of climate change on microzooplankton and their ecological activities.

A number of general areas of study that represent particularly glaring omissions in our understanding are given below.

Experimental studies of the physiological response of microzooplankton and their prey

There is presently a dearth of information on the direct effects of some climate change variables (e.g. CO_2, pH) on the physiological processes of microzooplankton, with the notable exception of temperature. As noted above, for example, concentrations of dissolved oxygen in many ecosystems may be decreased as increased thermal stratification facilitates the expansion of anoxic and hypoxic zones regionally or globally. This situation could impact the basic structure of the food web, decreasing the relative contribution of mesozooplankton which are less tolerant of these conditions and increasing the contribution of microzooplankton activities in these regions.

Indirect effects of global climate change on the phytoplankton prey of microzooplankton are expected to be the most important factors having widespread impact on the diversity, abundances and trophic activities of the consumer assemblage. There is still limited information, however, supporting the hypothesis that unpalatable or toxic phytoplankton species will increase in prevalence as the climate changes. It is conceivable that chemical warfare among algae (allelopathy) and with their consumers (grazer deterrence) will intensify, particularly in the upper water column of environments that experience intensified thermal stratification. The tacit assumption to be tested is that the taxonomic and chemical composition of the phytoplankton will select for specific microzooplankton species that are capable of feeding and growing on those phytoplankton species.

The subtle effects of changes in food quality on microzooplankton growth and nutrient cycling will be more difficult to characterize, but may be an important outcome of climate change. Gross growth efficiencies reported for herbivorous and bacterivorous protists vary tremendously (from nearly zero to >80%), and the nutritional quality of prey is believed to be a major factor controlling the portions of prey biomass converted to microzooplankton biomass, released as dissolved organic matter, or remineralized. These changes must be characterized if we are going to understand the impact of changes in phytoplankton community composition as a consequence of climate change on food web structure and trophic transfer. Additionally, the direct effect of changing temperature on growth efficiency is poorly known. Both very high and very low growth efficiencies have been reported for heterotrophic protists as a consequence of growth at low environmental temperature (Choi and Peters, 1992; Mayes *et al.*, 1997). However, one recent study of an Antarctic isolate of a bacterivorous protist indicated no effect on gross growth efficiency across a broad range of environmental temperatures when the protist was first acclimated to each temperature examined (Rose *et al.*, 2009c). More work will be required to sort out the response of this parameter to changing ocean temperature.

Studies of mineral depositing microzooplankton constitute a specific area of interest for experimentation. Direct measurements of the effects of increased CO_2 and lower pH on calcification among planktonic foraminifera are rare, yet there are predictions that these changing environmental conditions will significantly affect calcification in these species within the next century (Russell *et al.*, 2004; Lombard *et al.*, 2010, 2011). Given the low species diversity among planktonic

foraminifera and their exceptional importance in paleo-climatological studies, it is imperative that we better understand the ramifications of changing ocean chemistry on these species. Long-term measurements are essential for obtaining reasonable appraisals of changing environmental conditions, as these are very long-lived protistan species. However, these species cannot yet be cultured through successive generations in the lab, and therefore breakthroughs in culturing approaches will be necessary to make these direct measurements.

Examination of feedback interactions between multiple climate change variables is a crucially important goal for prognostic experimental studies, but a problematic one. It is patently obvious that the responses of protists to a changing future environment will integrate all of the many facets of climate change and so studies that address only a single factor in isolation have at best limited predictive value. Multiple climate change variables may exhibit non-linear synergisms and antagonisms relative to their individual biological effects. For instance, in the Ross Sea, simultaneous warming (4°C) and iron addition (1 nM) synergistically stimulated phytoplankton growth to levels >4× higher than the effects of either perturbation alone (Rose *et al.*, 2009a). It is challenging experimentally, however, to design realistic and practical multivariate experiments, since increasing complexity necessitates cumbersome factorial matrix designs and attendant logistical and interpretive problems (Boyd *et al.*, 2010).

Microzooplankton trophic activities

The currently available evidence leads us to hypothesize that the absolute and relative importance of the ecological activities of microzooplankton in plankton communities will increase in the future ocean. Microzooplankton herbivory seems likely to become a greater controlling factor of the standing stocks of phytoplankton in polar regions, in accordance with the effect of rising temperature on the relationship between the maximal growth rates of phytoplankton and microzooplankton (Rose and Caron, 2007). In addition, changing biogeochemical cycles may promote the expansion of microbial food webs (Hutchins *et al.*, 2009) and so amplify the current role of microzooplankton as consumers of fixed carbon. Oceanographers need to establish whether there are spatial (regional) or temporal generalities in how microzooplankton grazing will respond to changing ocean conditions that can be used to predict alterations in pelagic food webs (Chen *et al.*, 2012). We have barely begun to address these important topics, but they are fundamental to understanding potential shifts in energy and elemental flow in plankton communities, and predicting potential changes in

trophic coupling between primary producers and top-level consumers. Community-level studies of microzooplankton trophic activity, across a range of environments and in the face of changing climate patterns, will be necessary to address these issues.

Modeling microzooplankton responses to climate change

A major hurdle will be translating field observations and laboratory experiments into mathematical formulations that will provide predictive power regarding the response of plankton communities to climate change. Experimental studies will provide the fundamental ecological principles to support and improve these modeling efforts, but the number of environmental and biological permutations that can be addressed in any given experiment is limited. We must rely on modeling to integrate disparate behaviors and physiologies present within planktonic communities to predict trends resulting from the multiple, coupled environmental factors that will change as climate changes.

This work will require sophisticated biological–physical models, coupled to climate change models. Ecological networks that take into account the complex interactions in species-rich communities will be required to achieve some level of predictive capability (Ings *et al.*, 2009). Such work has identified the importance of the behavior of individual species, thus fortifying the need for baseline studies of how microzooplankton species respond to variables affected by climate change, and how those individual behaviors might scale to emergent patterns and processes, population distributions or activities (Harvey and Menden-Deuer, 2011).

Effects of climate change on mixed nutrition among microzooplankton

We suggest that the direct effects of increased CO_2 may favor protistan autotrophy over mixotrophy, but indirect effects may be more complex and difficult to predict. Information on the potential impact of climate change on a few specific aspects of the biology and nutrition of planktonic protists is virtually absent at this time. Mixed nutrition (mixotrophy) and symbioses are chief among these behaviors. The common occurrence and significant ecological importance of combined phototrophic and heterotrophic nutrition among protists is now well documented (Flynn *et al.*, in press). This behavior includes many herbivorous ciliates that retain functional chloroplasts from their algal prey, as well as a wide variety of flagellated protists (e.g. many chrysophytes, dinoflagellates, cryptophytes) that possess fully integrated chloroplasts but are also capable of ingesting and digesting prey (Sanders, 1991,

2011 Dolan, 1992; Jones, 1994; Stoecker, 1998; Stoecker, 1999; Caron, 2000; Gast *et al.*, 2007). The latter taxa have the potential to both compete with co-occurring bacteria for growth-limiting nutrients, as well as consume bacteria and other prey (Thingstad *et al.*, 1996). Mixed nutrition among protists is increasingly recognized as a fundamental aspect of the structure of planktonic food webs in marine and freshwater ecosystems (Sanders, 2011; Caron *et al.*, 2012).

Many mixotrophic species exhibit considerable physiological flexibility in their ability to conduct phototrophy and heterotrophy, but it is presently unclear how environmental cues affect the ability of mixotrophic protists to switch between nutritional modes or combine them, and therefore how changing ocean temperature, pH or CO_2 might alter their behavior. For instance, the community structure of multispecies dinoflagellate blooms can be affected simultaneously by both pH/CO_2 conditions, and by mixotrophic interactions among the component species (Tatters *et al.*, in press). Changing environmental conditions may result in physiological triggers that shift the nutritional modes of these species, altering the cellular balance between photosynthetic and phagotrophic activity. For example, higher seawater CO_2 concentrations substantially reduce the energetic costs of dissolved inorganic carbon uptake, thus making photosynthetic growth "cheaper" (Raven *et al.*, 2008; Hopkinson *et al.*, 2011). It is therefore possible that this high CO_2 subsidy might tip the balance toward autotrophy rather than heterotrophy in some facultative mixotrophs. Such trade-off responses would alter food web structure and energy flow in ways that are presently unknown, and potentially affect the ecological advantage that mixotrophic behavior endows on these species.

Abundances of kleptoplastidic species (e.g. many ciliates and heterotrophic dinoflagellates that ingest photosynthetic prey and retain their functional chloroplasts) will be affected by the fate of their preferred prey vis-à-vis the response of these algae to climate change. Similarly, surface-dwelling species of many large protists (planktonic foraminifera, radiolaria, acantharia) possess photosynthetic symbiotic algae (Caron and Swanberg, 1990). These species are abundant and highly conspicuous members of oligotrophic oceanic ecosystems where they can constitute microenvironments of extremely high primary productivity (Spero and Parker, 1985; Caron *et al.*, 1995). Normal growth and ontogeny of at least some of these species is dependent on the presence and photosynthetic activities of their species-specific symbionts, which are reacquired by each generation of hosts (Bé *et al.*, 1982). These species may be indirectly affected by climate changes that affect the presence or abundances of their symbiotic algae. Additionally, these large protists consume a wide array of prey and many possess mineral skeletons that might be affected by changing environmental conditions. Thus, their fate may be affected by multiple stressors imposed by climate change.

Top-down control by zooplankton

A fundamental gap exists in our knowledge of the overall importance of "top-down" controls on microzooplankton species composition and standing stocks that transcends deficiencies relating specifically to climate change. The importance of microzooplankton to the diets of a wide diversity of larger zooplankton and micronekton has received surprisingly little attention in recent years, despite considerable work on this trophic connection in marine pelagic ecosystems for more than two decades (Stoecker and Egloff, 1987; Stoecker *et al.*, 1987; Gifford, 1988; Stoecker and Capuzzo, 1990; Gifford and Dagg, 1991; Gifford *et al.*, 1995; Lonsdale *et al.*, 2000). The long-standing mindset by many plankton researchers that "phytoplankton" constitute most (if not all) of the prey of copepods and other meso- and macrozooplankton has fostered a situation in which this trophic connection is now a significant gap in our understanding of planktonic food web dynamics.

Microzooplankton growth is dependent on the availability of suitable prey, but abundances and species composition of microzooplankton assemblages in nature are also controlled by mortality losses to higher consumers. Changes in community composition of microzooplankton as a consequence of copepod and other zooplankton grazing activity have been documented (Granéli and Turner, 2002; Calbet and Saiz, 2005), and these studies are now being fostered by new approaches for assessing microbial eukaryote community structure (Schnetzer and Caron, 2005). Lab and field experimental studies characterizing the details of this trophic connection are overdue, with one specific goal of these studies being to help elucidate how direct and indirect impacts of climate change on zooplankton assemblages might be expected to impact their "top-down" effects on microzooplankton assemblages (Fig. 1).

CONCLUDING REMARK

The marine science community interested in global change has focussed to a large degree on studies emphasizing primary producers, while often neglecting equally important but more challenging studies addressing the effects of environmental change on multiple trophic levels and overall food web structure.

There has been a considerable increase in the number of studies investigating the impact of global climate change on various aspects of marine ecosystems in recent years. Research examining the response of microzooplankton to changing climate has not kept pace with these studies. We presently have a poor understanding of the direct effects that changing ocean chemistry and physics might have on this key trophic link in marine food webs. Long-term observational and experimental studies are needed that address the structure and function of micrograzer communities that are fully adapted to the complete suite of multiple interacting global change variables, rather than just studies focussed only on short-term acclimation to single factors. Whole plankton community manipulations are already being performed using large volume mesocosm studies. These studies are useful for formulating tentative hypotheses regarding long-term responses, but have undeniable limitations. Brief experiments with today's assemblages exposed to simulated future conditions necessarily have limited durations, and so likely have limited predictive power for long-term adaptation trends (Tatters *et al.*, in press). Consequently, novel experimental techniques may need to be pioneered, such as extended, multiple-trophic level artificial community studies examining co-evolution of microzooplankton, their prey and their predators under selection by a suite of combined global change factors. It is anticipated that microzooplankton diversity, abundances and activities will be responsive to a wide variety of changes in bottom-up and top-down controls due to the effects of climate change on the prey and predators of these species. Microzooplankton play a number of pivotal ecological roles embedded near the base of planktonic food webs, therefore understanding their fate is essential to understanding the overall effects of climate change on ocean biology and biogeochemistry.

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