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A comparison of future increased CO_2 and temperature effects on sympatric *Heterosigma akashiwo* and *Prorocentrum minimum*

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Abstract

Very little is known about how global anthropogenic changes will affect major harmful algal bloom groups. Shifts in the growth and physiology of HAB species like the raphidophyte *Heterosigma akashiwo* and the dinoflagellate *Prorocentrum minimum* due to rising CO_2 and temperature could alter their relative abundance and environmental impacts in estuaries where both form blooms, such as the Delaware Inland Bays (DIB). We grew semi-continuous cultures of sympatric DIB isolates of these two species under four conditions: (1) 20 °C and 375 ppm CO_2 (ambient control), (2) 20 °C and 750 ppm CO_2 (high CO_2), (3) 24 °C and 375 ppm CO_2 (high temperature), and (4) 24 °C and 750 ppm CO_2 (combined). Elevated CO_2 alone or in concert with temperature stimulated *Heterosigma* growth, but had no significant effect on *Prorocentrum* growth. P_{Bmax} (the maximum biomass-normalized light-saturated carbon fixation rate) in *Heterosigma* was increased only by simultaneous CO_2 and temperature increases, whereas P_{Bmax} in *Prorocentrum* responded significantly to CO_2 enrichment, with or without increased temperature. CO_2 and temperature affected photosynthetic parameters α, $\Phi_{\max}$, E_k, and $\Delta F/F'_m$ in both species. Increased temperature decreased and increased the Chl *a* content of *Heterosigma* and *Prorocentrum*, respectively. CO_2 availability and temperature had pronounced effects on cellular quotas of C and N in *Heterosigma*, but not in *Prorocentrum*. Ratios of C:P and N:P increased with elevated carbon dioxide in *Heterosigma* but not in *Prorocentrum*. These changes in cellular nutrient quotas and ratios imply that *Heterosigma* could be more vulnerable to N limitation but less vulnerable to P-limitation than *Prorocentrum* under future environmental conditions. In general, *Heterosigma* growth and physiology showed a much greater positive response to elevated CO_2 and temperature compared to *Prorocentrum*, consistent with what is known about their respective carbon acquisition mechanisms. Hence, rising temperature and CO_2 either alone or in combination with other limiting factors could significantly alter the relative dominance of these two co-existing HAB species over the next century.

Keywords: *Heterosigma akashiwo*; CO_2; HAB; Global change; Dinoflagellates; Raphidophytes

1. Introduction

The frequency and intensity of harmful algal blooms (HABs) have increased, coinciding with a global surge in population density in the coastal zone (Mudie et al., 2002; Hallegraeff, 1993) due to cultural eutrophication

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in recent decades (Anderson et al., 2002). In response to these observations, a great deal of the HAB research effort has focused on the influence of eutrophication and nutrient availability on bloom establishment and growth of species such as *Aureococcus*, toxic dinoflagellates and raphidophytes (Anderson et al., 2002; Popels et al., 2003; Pustizzi et al., 2004; Gobler et al., 2005; Zhang et al., 2006).

Eutrophication is however only one of multiple global anthropogenic biogeochemical impacts. In addition to human disturbance of natural nutrient cycles, we are also causing a massive perturbation of the global carbon cycle. Atmospheric CO_2 will more than double by 2100 due to ever-accelerating rates of fossil fuel burning (IPCC, 2001). Consequently, ocean pH will decrease by as much as 0.77 units within the next several centuries (Caldeira and Wickett, 2003). At the same time, over the next 50–100 years greenhouse warming will increase average sea surface temperatures by as much as 4–5 °C (Bopp et al., 2001; Sarmiento et al., 2002).

These changes in the coming decades will drive massive changes in the biology and chemistry of the oceans. For instance, changes in CO_2 availability can exert a strong control on algal physiology, nutrient cycling and ecological interactions. Experiments with natural phytoplankton communities suggest that one response to elevated CO_2 could be increased phytoplankton primary production in the open ocean (Hein and Sand-Jensen, 1997), or that CO_2 concentrations could affect competition among major marine phytoplankton groups (Tortell et al., 2002). A recent model suggests that the growth of marine phytoplankton will increase by 40% between current CO_2 levels and 700 ppm CO_2 (Schippers et al., 2004). Laboratory studies have shown that altered CO_2 can result in species-specific changes in cellular carbon acquisition pathways (Raven, 1997; Tortell et al., 2000; Burkhardt et al., 2001) and elemental ratios (Burkhardt et al., 1999; Tortell et al., 2000; Fu et al., 2007; Hutchins et al., 2007). Important cyanobacterial functional groups such as *Synechococcus*, *Trichodesmium* and *Prochlorococcus* will all respond differently to elevated CO_2 (Fu et al., 2007; Hutchins et al., 2007). How major HAB groups such as dinoflagellates and raphidophytes will react to globally increasing CO_2 concentrations is, however, just now beginning to be examined (Rost et al., 2006).

Many algal groups, including dinoflagellates, have evolved carbon concentrating mechanisms (CCMs) to elevate the concentrations of CO_2 near the active site of Rubisco. These mechanisms include an active transport system for bicarbonate uptake (Sukenick et al., 1997), as well as a catalyzed dehydration of bicarbonate to CO_2 by the enzyme carbonic anhydrase (CA, Badger and Spalding, 2000). However, active inorganic carbon transport and CA activity is not ubiquitous throughout all algal groups. In algae, CO_2 is the preferred carbon substrate for the principle carbon-fixing enzyme Rubisco. However, Rubisco efficiencies can differ between different groups (Badger et al., 1998; Tortell, 2000) and hence carbon fixation could be stimulated by rising CO_2 for some species but not for others.

Notably, the toxic raphidophyte *Heterosigma*, which produces devastating blooms in Delaware and around the world (Whereat, 2003; Honjo, 1992), does not appear to utilize CA (Nimer et al., 1997). This suggests that *Heterosigma* and possibly other raphidophytes may be especially favored by rising CO_2 levels. Many dinoflagellates possess a form II Rubisco that has a lower affinity for carboxylation and is extremely inefficient at processing CO_2 compared to the form I Rubisco found in all other algae (Whitney and Yellowlees, 1995). However, several studies have documented effective carbonic anhydrase activity in some dinoflagellates, including *Prorocentrum micans* and *Prorocentrum minimum* (Nimer et al., 1999; Rost et al., 2006). Other species however appear to have very limited HCO_3^- uptake capabilities (Dason and Huertas, 2004), thus there is likely a potential for carbon limitation in some dinoflagellates.

Increases in sea surface temperature may also impact carbon utilization, resulting in shifts in species composition and diversity. Likewise, temperature can differentially impact growth rate, pigment content, light harvesting capacity and photosynthetic carbon fixation in microalgae and cyanobacteria (Sosik and Mitchell, 1994; Coles and Jones, 2000; Anning et al., 2001; Fu et al., 2007). It has been suggested that climate change-driven temperature increase is the main factor stimulating HAB blooms in the Pacific and Atlantic regions of Canada over the past 50 years, based on pre-industrial sedimentary cyst records of red tide histories (Mudie et al., 2002).

Global warming trends are likely to have large consequences for HAB dominance (Eppley, 1972; Raven and Geider, 1988), however, how a combination of simultaneously rising temperature and CO_2 will affect their growth is completely unknown. To our knowledge only two laboratory studies have examined potential effects of rising temperatures on HAB species (Peperzak, 2003, 2005), and none have examined interactions with CO_2.