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Consequences of increased temperature and CO_2 for phytoplankton community structure in the Bering Sea

Clinton E. Hare[1], Karine Leblanc[1,2], Giacomo R. DiTullio[3,4], Raphael M. Kudela[5], Yaohong Zhang[1], Peter A. Lee[3], Sarah Riseman[3], David A. Hutchins[1,6,*]

[1]College of Marine and Earth Studies, University of Delaware, 700 Pilottown Road, Lewes, Delaware 19958, USA
[2]CNRS–Laboratoire d'Océanographie et de Biogéochimie (UMR 6535), OSU/COM, Campus de Luminy, Case 901, 13288 Marseille Cedex 09, France
[3]Hollings Marine Laboratory, College of Charleston, 331 Fort Johnson, Charleston, South Carolina 29412, USA
[4]Grice Marine Laboratory, College of Charleston, 205 Fort Johnson, Charleston, South Carolina 29412, USA
[5]Ocean Sciences Department, University of California at Santa Cruz, 1156 High Street, Santa Cruz, California 95064, USA
[6]Department of Biological Sciences, University of Southern California, 3616 Trousdale Parkway, Los Angeles, California 90089, USA

ABSTRACT: Global climate change is predicted to have large effects on the ocean that could cause shifts in current algal community structure, major nutrient cycles, and carbon export. The Bering Sea is already experiencing changes in sea surface temperature (SST), unprecedented algal blooms, and alterations to trophic level dynamics. We incubated phytoplankton communities from 2 Bering Sea regimes under conditions of elevated SST and/or partial pressure of carbon dioxide (pCO_2) similar to predicted values for 2100. In our 'greenhouse ocean' simulations, maximum biomass-normalized photosynthetic rates increased 2.6 to 3.5 times and community composition shifted away from diatoms and towards nanophytoplankton. These changes were driven largely by elevated temperature, with secondary effects from increased pCO_2. If these results are indicative of future climate responses, community shifts towards nanophytoplankton dominance could reduce the ability of the Bering Sea to maintain the productive diatom-based food webs that currently support one of the world's most productive fisheries.

KEY WORDS: Phytoplankton dynamics · Carbon dioxide · Temperature · Community structure · Bering Sea · Continuous culture

INTRODUCTION

Currently, little is known about the effects of future anthropogenic CO_2 and temperature increases on marine phytoplankton productivity and species composition. Subarctic regions such as the Bering Sea are predicted to be especially affected by climate change, including a decrease in sea ice cover and an increase in surface seawater temperature (SST) (Chapman & Walsh 1993). The Bering Sea has already exhibited changes that are being attributed to climate change, including warmer temperatures (Stabeno et al. 2001), blooms of temperate species such as coccolithophorids (Stockwell et al. 2001), and shifts and declines in upper trophic levels (Brodeur et al. 1999, Stockwell et al. 2001).

The global average surface temperature of the ocean has increased 0.6 ± 0.2°C over the last century (IPCC 2001). Models predict an increase of 1 to 4°C over the next 100 yr (Bopp et al. 2001). Shifts in phytoplankton community structure may occur in response to increasing temperature (Noiri et al. 2005), as well as potentially in response to other changing climate variables, such as partial pressure of carbon dioxide (pCO_2)

*Corresponding author. Email: dahutch@usc.edu

(Tortell et al. 2002, Kim et al. 2006) and changes in the mixed layer depth (Arrigo et al. 1999).

While studies have shown that elevated pCO_2 might enhance algal growth rates (Wolf-Gladrow et al. 1999, Hutchins et al. 2007), the direction and magnitude of changes in the algal community are still not well understood. Riebesell et al. (2000) and Wolf-Gladrow et al. (1999) reported decreases in calcification rates in coccolithophores with increasing CO_2 levels. Tortell et al. (2002) reported that high pCO_2 concentrations (750 ppm) during semi-continuous bottle experiments in the tropical Pacific resulted in a shift away from *Phaeocystis* sp. and toward diatoms.

Less is known about the effects of temperature change on algal community structure. Increased temperatures might shift communities away from diatoms due to decreased nitrate reductase activity at elevated temperatures (Lomas & Glibert 1999). This trend towards non-silicified species is possibly occurring in the Bering Sea, where recent unprecedented coccolithophore blooms have coincided with unusually warm temperatures (Stockwell et al. 2001). Shipboard experiments by Noiri et al. (2005) showed shifts from diatoms towards coccolithophores with increasing temperature in the subarctic Pacific. Behrenfeld et al. (2006) recently suggested that global increases in SSTs may have a negative effect on marine primary production. Phytoplankton are sensitive to climatic changes such as temperature and may respond by quickly expanding or contracting their ranges (Hays et al. 2005) or by shifting size and/or community composition (Kudela et al. 2006). Responses to increasing SSTs may not be consistent between different algal functional groups and trophic levels (Edwards & Richardson 2004).

The aim of the present study was to examine how phytoplankton community structure in the Bering Sea changes when temperature and pCO_2 are increased to levels predicted for the year 2100. We found that changes in these climate variables could have large effects on the composition of the phytoplankton community and their photosynthetic capabilities.

MATERIALS AND METHODS

In August 2003, we collected near-surface seawater from 2 sites in the Bering Sea: one in the deep-water central basin ('Offshore', 55° 1.339' N, 179° 1.828' W) and one in the middle of the broad southeastern continental shelf ('Shelf', 56° 30.899' N, 164° 43.799' W). The 2 temperature/pCO_2 manipulation experiments were incubated for 9 to 10 d using shipboard continuous culture incubation systems or 'ecostats' (Hutchins et al. 2003, Hare et al. 2005, 2007). Near-surface water (10 to 15 m) for the experiments was collected using a trace metal clean Teflon pump system (Bruland et al. 2005). For each experiment, 50 l reservoirs were filled with 0.2 µm-filtered seawater to supply continuous addition of fresh medium to the incubation bottles. Incubation bottles (2.5 l) were initially filled with unfiltered water containing the intact plankton communities.

In the Offshore experiment, carried out in the iron-limited, high nutrient, low chlorophyll (HNLC) waters in the central basin (Leblanc et al. 2005), 1 nM $FeCl_3$ was added to all treatments. In the Shelf experiment, 0.5 nM $FeCl_3$ was added, and the seawater was also supplemented with low levels of major nutrients (4 µM nitrate, 1 µM phosphate, and 8 µM silicic acid) due to very low initial concentrations present in the collected seawater. Iron was added to all of the treatments in both experiments as a precaution to prevent possible differential contamination of individual bottles, which could complicate the interpretations of the responses to changing temperature and carbon dioxide. The effects of global change on iron supply to the ocean are not totally understood, but are likely to vary regionally and may have large effects on primary production and nutrient cycles. Takeda & Tsuda (2005) suggested that future expansion of the desert areas in the Asian continent may increase the atmospheric iron supply to the western North Pacific, and thus, this region may be likely to experience more iron-replete conditions than is the case today.

Two systems were used for each experiment: a flow-through deckboard incubator at ambient summertime SST (~10.4°C) and an incubator maintained at ~4.7 ± 0.5°C above ambient seawater temperature, as predicted for high latitude ocean regimes by the year 2100. Incubator light levels were adjusted to 34% of incident intensity. Within each temperature treatment, triplicate incubation bottles were kept equilibrated at present-day pCO_2 (~370 ppm) by gentle bubbling (~3 ml min^{-1}) with uncontaminated outside air. Another set of triplicate bottles was adjusted to pCO_2 projected for 2100 (750 ppm, IPCC 2001) by bubbling with a commercially prepared air/CO_2 mixture (Tortell et al. 2002, Fu et al. 2007, Hutchins et al. 2007). CO_2 equilibration was verified throughout the experiments using pH measurements. This experimental design allowed us to compare the biological and biogeochemical effects of elevating temperature alone (High temperature treatment), CO_2 alone (High CO_2 treatment), and both together (Greenhouse treatment) in relation to controls incubated at present-day temperature and CO_2 (Ambient treatment).

Incubations were allowed to grow in batch mode without dilution for 2 (Shelf) to 3 d (Offshore), after which medium was supplied from the reservoirs to the incubation bottles using peristaltic pumps at a dilution rate of

0.4 d^{-1} for another 8 (Shelf) or 6 d (Offshore). Cells were kept suspended by gentle mixing of the bottles by hand every hour, and gravity driven outflow was collected in collection bottles. Incubation bottles were monitored daily for dissolved inorganic nitrogen (nitrate plus nitrite), orthophosphate, and silicic acid (Bruland et al. 2005), and chlorophyll *a* (chl *a*) (Hare et al. 2005, 2007). Daily sampling directly from the bottles was limited to ~10% of bottle volume to avoid significant perturbations of the continuous culture system. Continuous removal of cells through a gravity-fed outflow avoided excessive biomass accumulation. Statistical analysis was performed using 1-way ANOVA with SPSS software.

Microscopic cell enumeration samples (50 ml) were preserved on the final days and counted as in Hare et al. (2005). Initial phytoplankton samples were taken for microscopic enumeration at each location, but due to poor preservation of nanophytoplankton and overall low cell abundance, these data could only provide a qualitative approximation of the starting communities. High performance liquid chromatography (HPLC) analysis was as described in DiTullio & Geesey (2002). Samples for taxon-specific pigments were measured from the initial water and the daily continuous culture outflow collections. Photosynthesis vs. irradiance (P/E) curves were assessed using ^{14}C-$NaHCO_3$ uptake in 30 min incubations at the appropriate temperature (11 or 15°C, ±0.2°C) in a photosynthetron over an irradiance range of 0 to 850 µmol photons m^{-2} s^{-1} (Fu et al. 2007, Hutchins et al. 2007). P/E experiments used water pooled from the replicate treatments at the final timepoint of each experiment. The fitted curves represent the best-fit (iterative non-linear curve fitting with Marquardt least-squares analysis) using the 3-parameter model of 44SigmaStat (SPSS) and GraphPad Prism statistical packages.

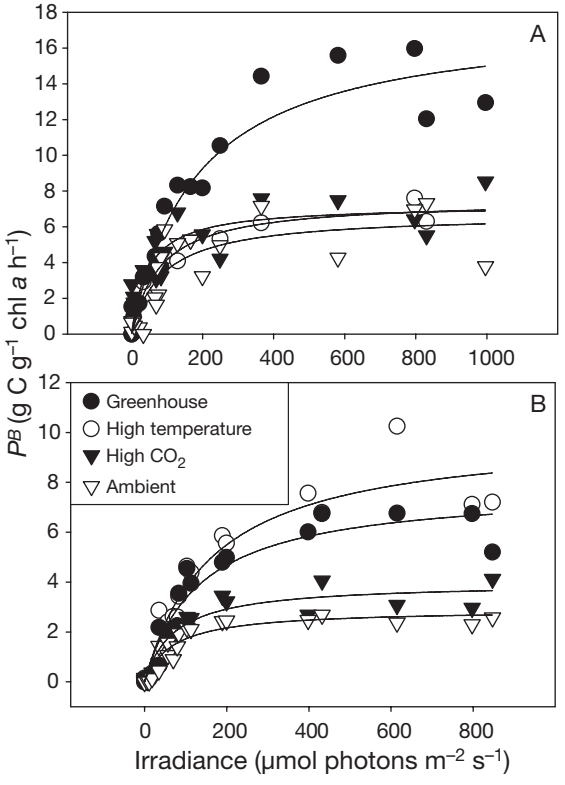

Fig. 1. Photosynthesis vs. irradiance (P/E) curves from the end of the Bering Sea incubations at the (A) Shelf and (B) Offshore locations, showing the effects of increased temperature and pCO_2 on phytoplankton community chl *a*-normalized carbon fixation rates (P^B_{max}). P/E experiments were conducted with water samples pooled from the 3 replicates in each treatment. R^2 values for the goodness-of-fit of the curves range from 0.68 to 0.93 (Shelf) and 0.89 to 0.93 (Offshore)

RESULTS

Seawater pCO_2 equilibration at projected year 2100 levels (750 ppm; High CO_2 and Greenhouse treatments) resulted in a reduction of 0.2 to 0.3 pH units relative to the initial values and compared to the present-day pCO_2 treatments (370 ppm; High temperature and Ambient treatments). Initial pH values were 7.94 in the Offshore experiment and 8.09 in the Shelf experiment. There was also a smaller increase in pH (~0.05 U) due to reduced CO_2 solubility at higher temperature treatments relative to the bottles incubated at the same pCO_2 at the lower temperature.

All dissolved nutrients reached relatively stable levels and did not significantly change for the last 3 d of each experiment ($p < 0.05$, data not shown). Nitrate was depleted, but phosphate was not, by the end of the experiments for all treatments. Silicic acid was completely used in the Offshore experiment, while it was not depleted completely in the Shelf experiment in any of the treatments. In the Offshore experiment, the algal community became apparently co-limited by the rate of both nitrate and silicic acid supply, while in the Shelf experiment, the algal community was only limited by the input rate of nitrate.

P/E curves from the end of the Shelf experiment demonstrated that maximum chl *a*-normalized photosynthetic rates (P^B_{max}) in the Greenhouse treatment increased 2.6 times compared to the other 3 treatments ($p < 0.05$, Fig. 1A, Table 1). Similar trends were seen when maximum carbon fixation rates were normalized to particulate organic carbon (POC-specific rates) or to volume, although differences between treatments were somewhat smaller when using these normalizers (Table 1). In the Offshore experiment, chl *a*-normalized P^B_{max} increased significantly in both the Greenhouse and High temperature treatments (2.7 and 3.5 times,

respectively, $p < 0.05$) relative to the Ambient and High CO_2 conditions (Fig. 1B, Table 1). Again, POC- and volume-normalized values followed similar trends but differences were somewhat less pronounced (Table 1). Thus, either increasing temperature alone, regardless of CO_2 (Offshore), or elevating temperature and CO_2 together (Shelf), resulted in a doubling or tripling of the potential carbon fixation rates of these 2 Bering Sea algal communities.

In the Shelf experiment, total phytoplankton biomass measured as chl *a* increased 2 to 3 times during the batch growth phase and remained relatively consistent until Day 5 during dilution. After Day 5, there was a separation between treatments, with the highest chl *a* in the Ambient treatment and the lowest in the Greenhouse treatment. Chl *a* in the Ambient treatment stabilized at approximately double the concentration in the other treatments for the last 2 d of the experiment (Fig. 2A, $p < 0.05$). In the Offshore experiment, chl *a* increased in all treatments for the first 6 d of the experiment, with the largest increase in the High temperature treatment by Day 6 (Fig. 3A). On the final day (Day 9), the highest biomass was seen in the Greenhouse treatment, while all other treatments returned to around the same levels as on Day 4. In both experiments, the treatments with the 3 lowest chl *a* levels declined nearly to that of the initial concentration. A limited number of POC measurements suggested that the trends in POC were in general similar to those seen for chl *a* (data not shown).

The pigments fucoxanthin (typically from diatoms), 19-hexanoyloxyfucoxanthin (19-hex, haptophytes) and 19-butanoyloxyfucoxanthin (19-but, typically from pelagophytes) demonstrated taxon-specific responses to temperature and pCO_2 changes. In the Shelf experiment, changes in fucoxanthin were similar to changes in chl *a*, with high levels in the Ambient treatment but declines to near-initial values in the High temperature and/or High CO_2 treatments after a brief initial increase (Fig. 2B). On the last 2 d of this experiment, fucoxanthin was significantly higher in the Ambient treatment than all the other treatments (Fig. 2B, $p < 0.05$). The nanophytoplankton groups (haptophytes and pelagophytes, Fig. 2C,D) showed a strong stimulation by increased temperature alone. Although there were significant differences between the High temperature and the rest of the treatments for 19-hex or 19-but on Day 7 ($p < 0.05$), this difference was not significant at most timepoints due to large standard deviations between replicates.

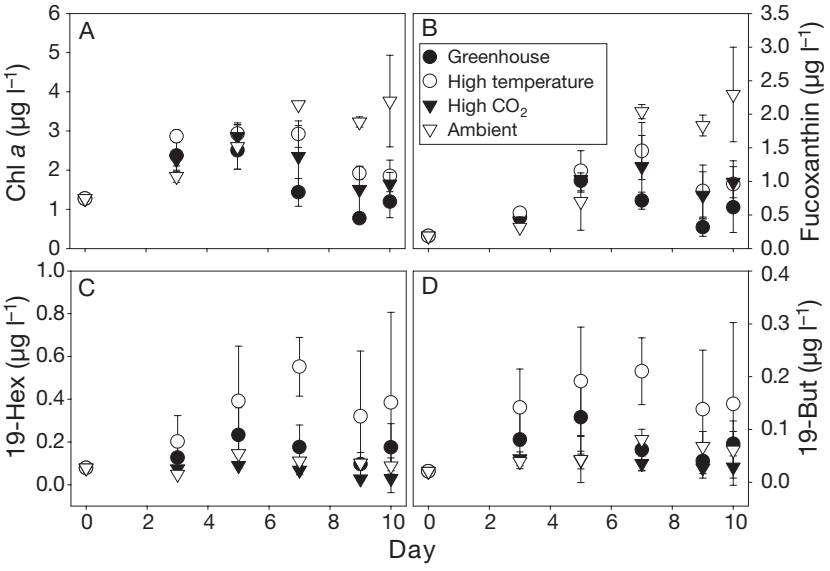

Fig. 2. Concentrations of algal photosynthetic pigments in the 4 temperature and pCO_2 treatments during the Shelf experiment: (A) chlorophyll *a*; (B) fucoxanthin, mostly diatoms, (C) 19-hexanoyloxyfucoxanthin (19-hex), haptophytes, and (D) 19-butanoyloxyfucoxanthin (19-but), pelagophytes. Symbols are the means, and error bars are the standard deviations of triplicate bottles

In the Offshore experiment, only fucoxanthin concentrations in the High CO_2 treatment were significantly higher than the 2 treatments with increased temperature ($p < 0.05$, Fig. 3B). 19-hex and 19-but were highest in the Greenhouse and the High temperature treatments throughout most of the experiment (Fig. 3C,D). Due to variability among replicates, however, the levels of these 2 pigments in the 4 treatments were not significantly different from each other on the final day.

Despite the lack of consistently significant differences in nanophyto-

Table 1. Final maximum light-saturated chl *a*-normalized photosynthetic rates (P^B_{max}, g C g^{-1} chl *a* h^{-1}), specific rates normalized to POC ($P^B_{max\ (POC)}$, h^{-1}), and normalized per unit volume (P_{max}, g C l^{-1} h^{-1}) in the 4 temperature and pCO_2 treatments in both Bering Sea experiments

Treatment	Shelf			Offshore		
	P^B_{max}	$P^B_{max\ (POC)}$	P_{max}	P^B_{max}	$P^B_{max\ (POC)}$	P_{max}
Ambient	6.7	0.056	1.59×10^{-5}	2.9	0.033	3.42×10^{-5}
High CO_2	7.2	0.042	7.56×10^{-6}	4.0	0.052	4.88×10^{-5}
High temp.	7.5	0.048	1.31×10^{-5}	10.0	0.104	8.03×10^{-5}
Greenhouse	17.7	0.122	1.96×10^{-5}	7.8	0.083	7.18×10^{-5}

plankton pigments, the general trends in these pigments were confirmed by microscopic cell counts. Total algal abundances were highest in the Ambient treatment in the Shelf experiment and in the Greenhouse treatment in the Offshore experiment (Table 2). In the Shelf experiment, diatoms appeared to dominate the initial community (data not shown). The final ratio of diatom:nanophytoplankton (D:N) cells counted in the Ambient treatment was more than double the ratio in any of the treatments with either elevated CO_2 or temperature, though this result was not significant for any of the treatments due to large error bars (Table 2). The trend in the final D:N ratio suggests that the Ambient treatment resembles the original community composition, while the other treatments shifted towards nanophytoplankton dominance relative to the in *situ* community, as was seen for pigments.

Nanophytoplankton cells could not be unambiguously classified under the microscope, but pigment data suggested that they included haptophytes, pelagophytes and prasinophytes. Nearly all diatoms were pennate species, with very few centric species present. The small pennate *Cylindrotheca* sp. was the main diatom species present, and counts of this species were significantly higher on the final day in the Ambient treatment than in all other treatments ($p < 0.05$). The abundance of this diatom decreased on the final day for all increased temperature and CO_2 treatments, similar to the trend for chl *a*, suggesting that the decline in chl *a* on Day 10 was driven by the decline in *Cylindrotheca* sp.

Despite differences in community structure, the Offshore community responded in an analogous manner. Though a minor component of the final community, both dinoflagellates and centric diatoms were present in significantly greater numbers in the Greenhouse treatment than in the other treatments ($p < 0.05$). The final D:N ratio was significantly higher in the Ambient treatment than in any of the 3 treatments with increased temperature and/or CO_2 ($p < 0.05$) and lowest in the High temperature and Greenhouse treatments (Table 2). In this experiment, the large pennate *Pseudo-nitzschia* sp. was the main diatom species present. In the initial collected water, the original community appeared to be dominated by nanophytoplankton (data not shown). Diatoms appeared to increase in final abundance in all treatments compared to the initially collected water, which had extremely low diatom cell abundance. This was likely due to the addition of iron to all bottles in this iron-limited regime, alleviating the iron stress on larger cells, such as diatoms (Leblanc et al. 2005). Interpretation of the Offshore experimental results must be made in the context of a future offshore Bering Sea regime where iron inputs and availability are likely to increase, as suggested by Takeda & Tsuda (2005).

Table 2. Microscopic phytoplankton cell counts (cells ml^{-1}) in the 4 temperature and pCO_2 treatments in the Shelf and Offshore Bering Sea experiments. Values are mean ± SD of triplicate bottles. D:N, diatom to nanophytoplankton ratio

	Total diatoms	Nanophytoplankton	D:N
Shelf			
Ambient	16505 ± 6553	7550 ± 262	2.17 ± 0.79
High CO_2	1544 ± 1247	1987 ± 616	0.92 ± 0.91
High temp.	4807 ± 2865	11412 ± 6431	0.60 ± 0.49
Greenhouse	1242 ± 421	1080 ± 555	1.31 ± 0.62
Offshore			
Ambient	8542 ± 1380	6600 ± 990	1.29 ± 0.02
High CO_2	5754 ± 1109	7300 ± 2500	0.83 ± 0.20
High temp.	7778 ± 1049	19600 ± 8773	0.46 ± 0.20
Greenhouse	6475 ± 1561	27200 ± 37206	0.32 ± 0.36

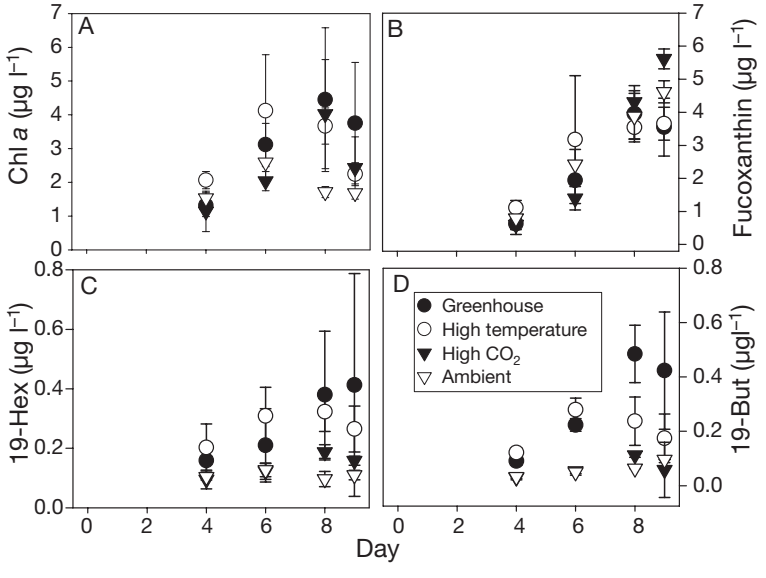

Fig. 3. As for Fig. 2, but during the Offshore experiment

DISCUSSION

Increased temperature either alone or in concert with elevated CO_2 led to substantial increases in potential algal carbon fixation rates by Bering Sea phytoplankton. These increases were documented for both biomass-normalized rates (POC and chl *a*) and also for bulk productivity per unit volume. The sensitivity of the enzymatic dark reactions of photosynthesis to temperature has long been recognized (Geider & Osborne 1992). Noiri et al. (2005) were the first to

show that temperature can have a large influence on phytoplankton community composition in bottle experiments during the Subarctic Pacific Iron Experiment for Ecosystem Dynamics Study (SEEDS). Future surface ocean warming effects on *in situ* phytoplankton communities are still not well understood, although similar physiological trends to those seen in our study have also been seen in laboratory cultures (Fu et al. 2007, Hutchins et al. 2007). Our results suggest that as long as photosynthesis is not limited by other factors such as nutrients or light, maximum carbon fixation rates could potentially double with expected surface ocean warming trends over the next 100 yr. Future global change experiments should assess primary productivity changes under the experimental regimes, as well as changes in photosynthesis versus light relationships as in our experiments.

Such an increase in photosynthetic rates could potentially provide negative feedback on atmospheric CO_2 concentrations by increasing the ability of the marine biota to sequester carbon via the 'biological pump'. However, carbon export efficiency depends not only on absolute rates of C fixation, but also on community structure (Boyd & Newton 1999). If currently dominant large diatoms are replaced by smaller and less rapidly sinking nanophytoplankton species, export could be less efficient despite higher carbon fixation rates in surface waters. It has been suggested that export of sinking organic carbon may be lower under future warming scenarios (Laws et al. 2000, Bopp et al. 2001). The magnitude and even the direction of future changes in carbon sequestration will depend on the responses of both the microbial assemblage and ocean biogeochemistry.

Even though nanophytoplankton cell abundance increased in both high temperature treatments, overall final algal biomass (as chl *a*) was lower. Increased temperature enhanced maximum potential carbon fixation rates despite this overall lower chl *a* biomass. The reasons for this unexpected observation are presently unknown but could include diversion of photosynthate from particulate to dissolved organic carbon production at elevated temperatures, as has been observed in response to pCO_2 increases in other regimes (Riebesell 2004). Although we did not evaluate microzooplankton grazing pressure in our incubations, protozoan feeding rates also scale with temperature (Laws et al. 2000, Rose & Caron 2007). Community structure shifts from diatoms to nanophytoplankton could act to tighten the coupling between grazers and primary producers, resulting in decreased algal biomass. Changing top-down control could modify or even negate the effects of bottom-up global change variables, and thus affect biomass production, food web structure, and carbon sequestration.

Nutrient dynamics in the 2 experiments were quite different, due to the 2 distinct regimes within the Bering Sea where the communities were initially collected. The Shelf experiment water was initially relatively depleted of all nutrients, and therefore nutrients were added to this experiment at the ambient ratios. While the community at the Shelf site was likely experiencing little if any iron stress, the Offshore community was iron-limited as in other HNLC areas. Major nutrients were elevated, but iron concentrations were very low, as were diatom biomass and chl *a*. These 2 nutrient regimes and communities are likely the reason for the different responses we observed in P^B_{max} in the 2 experiments. However, further work will be needed to determine the exact mechanisms involved in our observation that temperature alone increased P^B_{max} in the Offshore community, but simultaneous increases in both temperature and CO_2 were needed to elicit the same response in the Shelf community.

While the Shelf experiment became nitrogen limited during continuous dilution, the Offshore experiment was eventually co-limited by both silicic acid and nitrogen. The addition of iron initially in both experiments, especially in the Offshore community, would have released diatom communities from iron stress. As noted in the 'Materials and methods', future increases in aeolian Fe supplies may tend to make this regime less iron-limited in the future (Takeda & Tsuda 2005), so this scenario may in fact be a realistic one. During the final days of the Offshore experiment, however, silicic acid limitation of the diatom community could have affected their relative dominance in the community. It is interesting to note that the Shelf community also exhibited an apparent shift away from diatoms due to our experimental treatments, although silicic acid was never depleted in this experiment (always > 6 µM).

Recent attention has focused on the potential effects of rising CO_2 and concomitant acidification on aquatic communities (Wolf-Gladrow et al. 1999, Riebesell et al. 2000, Fu et al. 2007, Hutchins et al. 2007). A model suggests that doubling atmospheric CO_2 could result in up to a 2-fold increase in photosynthetic carbon fixation by marine and freshwater algae (Schippers et al. 2004). However, field incubation experiments have shown little or no effect of CO_2 manipulations on the growth rates or primary productivity of marine phytoplankton assemblages (Tortell et al. 2002). In our experiments, increases in temperature within the range expected over the next 100 yr had effects on community composition comparable to or larger than those seen from increases in pCO_2. Doubling of maximum photosynthetic rates was indeed observed, but only when temperature was increased either alone or in combination with CO_2.

A previous study in the tropical Pacific demonstrated shifts towards haptophytes at low pCO_2 and towards diatoms at higher pCO_2 levels (Tortell et al. 2002), but temperature effects were not considered. Here, we saw somewhat different trends in temperature and CO_2 effects on community structure in the Bering Sea offshore and shelf communities. In a mesocosm experiment using a coastal phytoplankton community, Kim et al. (2006) found that increases in pCO_2 increased growth rates of the diatom *Skeletonema costatum* but not *Nitzschia* spp. The effects of rising CO_2 and temperature may be species-, community- or regime-specific, and could favor different taxonomic groups in different oceanic provinces.

Our results will require further confirmation, but may suggest that increasing temperature could be a primary driving force in future algal dominance shifts away from diatoms and towards smaller nanophytoplankton groups in the Bering Sea. In the subarctic Pacific during iron addition experiments in HNLC water, Noiri et al. (2005) found that, below a temperature threshold of 13°C, diatoms became dominant, while Prymnesiophyceae were dominant at 18°C. Although the specific mechanisms responsible for this shift are not known, diatom nitrate reductase activity declines rapidly at elevated temperatures, potentially favoring the growth of competing species (Lomas & Glibert 1999, Berges et al. 2002). Recent summertime mixed layer shoaling and surface warming events in the shelf regions of the Bering Sea have been attributed to an ongoing climate regime shift (Stabeno et al. 2001). As in our shipboard manipulative experiments, these warming events have been accompanied by unprecedented community shifts from diatoms to haptophyte nanophytoplankton (the coccolithophorid *Emiliana huxleyi*; Stockwell et al. 2001). Increases in SST can thus have large effects on both the growth rate of in *situ* species and the overall algal community structure (Noiri et al. 2005, present study).

The limited duration of our shipboard experiments cannot address questions about possible long-term evolution of community structure or algal physiology to global change. They do, however, demonstrate the likely responses of currently dominant phytoplankton groups and may provide evidence as to which ones are pre-adapted to grow best under future temperature and pCO_2 conditions. While our relatively short-term natural community manipulative study should be interpreted cautiously, marine global change perturbation experiments can provide a valuable tool to help predict potential changes in ocean communities and elemental cycles in the decades to come. Shipboard experiments yield a unique perspective that can complement insights obtained from laboratory studies, time series stations, long-term observations, and quantitative modeling efforts.

Future community shifts in the Bering Sea away from diatoms and towards nanophytoplankton groups may also direct carbon and energy flow away from productive food webs that currently produce a large fraction of the world's total fisheries harvest. A 'greenhouse' ocean may instead tend towards more microbially dominated trophic interactions that will have far less potential to produce economically desirable top predator biomass, a process that may already be underway in the Bering Sea (Hare & Mantura 2000). It still remains to be determined how this change will affect marine biological resources and uptake of atmospheric carbon in this regime and in other high latitude oceans such as the North Atlantic and Southern Ocean.

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