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Modelling regional responses by marine pelagic ecosystems to global climate change

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[1] Current coupled ocean-atmosphere model (COAM) projections of future oceanic anthropogenic carbon uptake suggest reduced rates due to surface warming, enhanced stratification, and slowed thermohaline overturning. Such models rely on simple, bulk biogeochemical parameterisations, whereas recent ocean observations indicate that floristic shifts may be induced by climate variability, are widespread, complex, and directly impact biogeochemical cycles. We present a strategy to incorporate ecosystem function in COAM's and to evaluate the results in relation to region-specific ecosystem dynamics and interannual variability using a template of oceanic biogeographical provinces. Illustrative simulations for nitrogen fixers with an off-line multi-species, functional group model suggest significant changes by the end of this century in ecosystem structure, with some of the largest regional impacts caused by shifts in the areal extent of biomes. *INDEX TERMS:* 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4805 Oceanography: Biological and Chemical: Biogeochemical cycles (1615); 1620 Global Change: Climate dynamics (3309)

1. Introduction

[2] The ocean carbon cycle modulates global climate by acting as a source and/or sink for atmospheric carbon dioxide [*Siegenthaler and Sarmiento*, 1993], and climate in turn impacts the functioning of the ocean via alteration of the magnitude and sign of physico-chemical and biotic carbon sinks [*Woodwell et al.*, 1998]. Experiments using COAM's provide a method for assessing marine biogeochemical responses to and feedbacks on future climate change [*Sarmiento et al.*, 1998; *Joos et al.*, 1999]. Predicted changes in ocean physics—higher sea surface temperatures (SSTs), enhanced upper ocean stratification, and slowed deep water formation [*Houghton*, 2001] tend to lower estimated ocean carbon uptake due to the solubility pump and circulation. Physico-chemical carbon sinks are readily incorporated into COAM's as the dependence of surface pCO_2 on temperature [*Joos et al.*, 1999] and carbonate chemistry [*Kleypas et al.*, 1999] are well known. The likely effects of global warming on oceanic biota, and hence the biological pump, are more problematic [*Falkowski et al.*, 2000]. COAM's use simple biogeochemical parameterisations [*Sarmiento et al.*, 1998; *Joos et al.*, 1999] or rudimentary biological (PZND) models [*Cox et al.*, 2000], and a major challenge is to determine the biological complexity required for numerical models to accurately capture climate change impacts and subsequent biotic feedbacks [*Doney*, 1999].

[3] The response of oceanic biota to climate change may be divided into two components, changes in the magnitude of bulk rate processes, and shifts in ecosystem structure [*Falkowski et al.*, 1998]. Model simulations under warmer and more stratified conditions produce 5% decreases in global oceanic productivity, a balance between reduced nutrient availability in low and mid-latitudes (up to 10%) and shallower mixed layers in high latitudes, [*Cox et al.*, 2000; *Bopp et al.*, 2001]. An assessment of how global oceanic production is altered by recent climate variability—using remote-sensing—suggests a 10% increase over 36 months [*Behrenfeld et al.*, 2001]. The impact of floristic shifts such as to more calcifiers have yet to be incorporated into COAM's but have the potential to both alter elemental stoichiometry and concurrently impact multiple biogeochemical cycles [*Denman et al.*, 1996]. Such ecological processes are highly dynamic [*Field et al.*, 1998] and not well understood [*Falkowski et al.*, 2000].

2. Methodology

[4] Climate-induced changes in ocean physics are estimated from the NCAR Community Climate System Model [*Boville and Gent*, 1998]. The CCSM model is integrated in two configurations, a control simulation with atmospheric forcing (i.e., greenhouse gases) set at 1870 values and a historical/future simulation using observed trends in climate forcing up until 1990 then switching to the IPCC SRES A1 scenario. Ten year average monthly climatologies are produced for the period 2060–2070 for both the Future and Control integrations.

[5] These climatologies are then used to drive an off-line, global marine mixed-layer ecosystem model where the biology is simulated independently at each grid point and then composited to form global fields [*Moore et al.*, 2002a]. Sub-surface nutrient fields and atmospheric iron deposition are obtained from climatological databases. This approach captures the seasonal to interannual response of the ecosystem to physical forcing (e.g., mixed layer depth and temperature, surface irradiance). To account for the effect of multi-decadal to centennial trends in upper thermocline nutrient fields, the subsurface nutrient fields are reduced uniformly by 10% after *Bopp et al.* [2001]. Note, that accurate predictions of the biotic response to reduced nutrients require data on algal uptake kinetics in relation to changing nutrient concentrations.

[6] The ecosystem model, detailed by *Moore et al.* [2002a], incorporates both multi-nutrient limitation (N, P, Si, Fe) and community structure through planktonic geochemical functional groups, i.e. diatoms (export flux and ballast), diazotrophs (nitrogen fixation), and calcifiers (alkalinity and ballast). The standard ecosystem run is forced with modern climate data from an uncoupled ocean general circulation model and observations. Direct model—data evaluations have been conducted for nine detailed, local data sets from JGOFS and historical process studies and time-series stations [*Kleypas and Doney*, 2001] and against global fields (SeaWiFS Ocean Color, satellite primary and new productivity estimates, NODC nutrients).

3. Results and Discussion

[7] Predicted changes in ocean physical forcing for 2060–2070 are presented in Figure 1. The projected patterns are spatially complex and concentrated regionally, with the largest impacts for SST and mixed layer depth in the temperate to high latitudes, and

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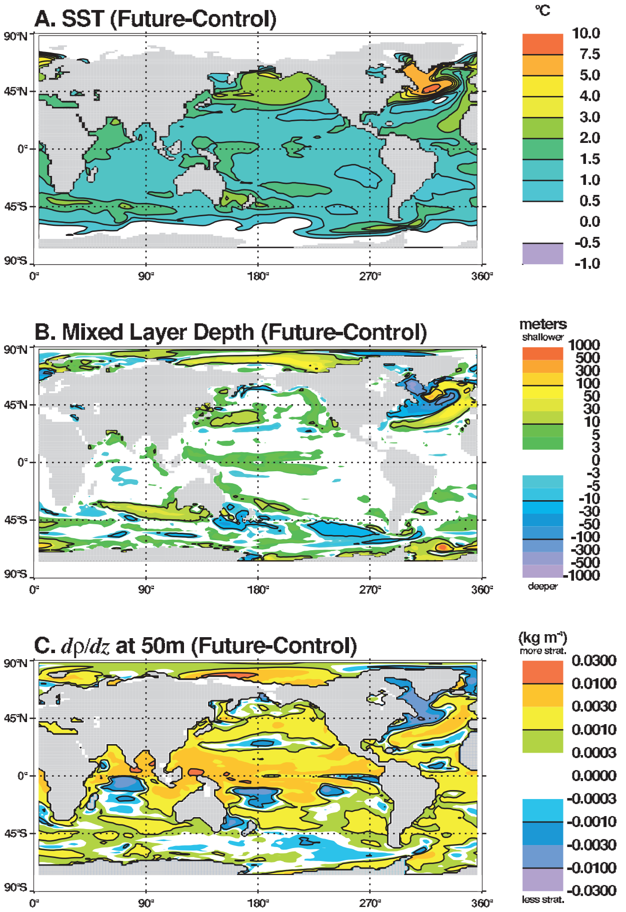

Figure 1. Projected climate-mediated changes in ocean physical forcing (Future-Control, i.e., 2060–2070 minus present) from the NCAR CCSM for (a) SST, (b) mixed layer depth, and (c) upper ocean (50 m) stratification.

for stratification in the tropics and subtropics. These broad patterns are quite similar to those of other COAM's but in general the magnitude falls toward the lower end of the envelope for climate sensitivity [J. Sarmiento, personal communication]. COAM's are least well constrained at regional scales [*Houghton*, 2001], and any model-specific results should be assessed in the context of an ensemble of COAM's.

[8] Insight into the likely spatial scales, magnitude and sign of ecosystem responses to climate change are available from synthesis of the decade-long JGOFS and the increasing global chlorophyll archives (SeaWiFS). A three-stranded approach—remote-sensing/vessel surveys, perturbation experiments and time-series observations—provides detailed biogeographical distributions of algal groups, rigorous tests of how environmental factor(s) and their interplay control ecosystem structure, and observational evidence of transient changes in ecosystem structure that are linked to interannual climate variability, respectively (Table 1). Figure 2 displays the observed floristic shifts due to both the direct and indirect effects of mixed layer shoaling, widely predicted under future climate scenarios. Marked differences in the biotic response occur by region, characterised by floristic shifts leading to both negative and positive feedbacks on carbon uptake (and alteration of other biogeochemical cycles). In mid- and low latitudes, nitrogen-fixers increase dramatically under more stratified conditions [*Karl et al.*, 1997] (negative feedback) whereas in the Ross Sea, a shift from *Phaeocystis* to diatom blooms may result in a concomitant decrease in carbon fixation per unit nitrogen [*Arrigo et al.*, 1999] (positive feedback). In the Equatorial Pacific, shoaling of the upper-ocean thermocline results in increased upwelling of iron and inorganic carbon rich water, and a community shift to large diatoms with subsequent greater export [*Chavez et al.*, 1999] (both positive and negative feedback).

[9] Dynamic responses by oceanic ecosystems—in longer-term studies referred to as regime or domain shifts [*Karl et al.*, 1997]—have been widely reported in terrestrial systems [*Wuethrich*, 2000]. These shifts may yield insights into the effects of sustained environmental changes not possible with mesoscale perturbation

Table 1. A Summary of Datasets Collated for the Pacific Ocean From JGOFS and Other Archives

Region	Biogeography	Mechanistic understanding	Oceanic forcing	Feedbacks
Bering Sea	SeaWiFS and ship surveys[a]	Lab perturbation experiments[b], (pCO_2), modelling[c]	Warming event and mixed layer shoaling[a]	Increased areal extent of calcification
HNLC Subarctic Pacific (West and East)	SeaWiFS and ship surveys (west and east)[d]	Shipboard perturbation experiments[d] (Fe)	Atmospheric dust inputs and ENSO events[d]	Episodic shifts to diatoms; potential increase in POC export
North Subtropical Pacific Gyre	Ship surveys and HOT[e]	Shipboard perturbation experiments[f,p] (light/P/Fe)	Climate variability, ENSO events[e]	More nitrogen fixers—altered nutrient stoichiometry
Equatorial Pacific	SeaWiFS, TAO mooring array ship surveys[g]	Mesoscale perturbation experiments[h] (Fe)	Climate variability El Nino/ La Nina[g]	Floristic shift to diatoms and increased POC export during La Nina
Sub/Tropical Pacific	SeaWiFS, and ship surveys[i]	Lab perturbation experiments[i] (Fe)	NA	NA
Subantarctic Pacific	SeaWiFS[j], and ship survey[k]	Deckboard perturbation experiments[k] (light/Fe/silicic acid)	NA	Episodic Fe/light mediated shifts to diatoms
Polar open Southern Ocean	SeaWiFS[j] and ship surveys[l,m]	Mesoscale and deckboard perturbation experiments[m] (Fe and light)	NA	Fe-mediated shifts to diatoms, CO_2 drawdown, elevated DMS
Ross Sea	SeaWiFS and shipboard surveys[n]	Deckboard perturbation experiments[o]	Seasonal changes in upper ocean physics[n]	Altered nutrient uptake stoichiometry (*Phaeocystis* vs. diatoms)

For justifications for province-wide extrapolation from time-series sites see individual studies [e.g., *Karl et al.*, 1997]. A similarly extensive suite of datasets exist for other basins such as the Atlantic [*Lipschultz and Owens*, 1996; *Sanudo-Wilhelmy et al.*, 2001; *Behrenfeld and Kolber*, 1999]. NA denotes no available data.

[a] *Napp and Hunt Jr.*, 2001. [b] *Riebesell et al.*, 2000. [c] *Tyrrell and Taylor*, 1995. [d] *Harrison et al.*, 1999. [e] *Karl et al.*, 1997. [f] *Sanudo-Wilhelmy et al.*, 2001. [g] *Chavez et al.*, 1999. [h] *Coale et al.*, 1996. [i] *Behrenfeld and Kolber*, 1999. [j] *Moore et al.*, 1999. [k] *Boyd et al.*, 1999. [l] *Smith Jr. et al.*, 2000. [m] *Boyd et al.*, 2000. [n] *Arrigo et al.*, 1999. [o] *Olson et al.*, 2000. [p] Conducted in the Atlantic but reported to be applicable to the Pacific. POC denotes Particulate Organic Carbon.

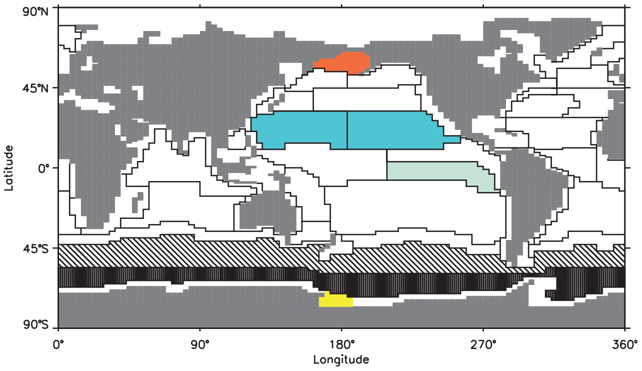

Figure 2. A map of recently observed floristic shifts mediated by shoaling of mixed layer depth, stratification and thermocline adjustment. These shifts are the result of direct and/or indirect effects of stratification, as indicated. A scheme of oceanic biomes [*Longhurst*, 1998] has been superimposed. Red denotes a persistent coccolithophore bloom (Bering Sea) [direct/indirect, *Napp and Hunt Jr.*, 2001] blue – a shift to more nitrogen fixers attributed to ENSO (El-Nino-Southern Oscillation) events in subtropical waters [indirect/direct, *Karl et al.*, 1997]; green – floristic shifts to diatoms during ENSO transitions [indirect, *Chavez et al.*, 1999]; yellow – shifts from *Phaeocystis* to diatom blooms due to seasonal shoaling of mixed layer depth [direct, higher light levels, *Arrigo et al.*, 1999]. Shaded bands in the Southern Ocean denote where there is observational [*Blain et al.*, 2001] or experimental [*Boyd et al.*, 1999; *Boyd et al.*, 2000] evidence of the indirect role of shoaling of the mixed layer depth on algae community structure; diatom growth in deep mixed layers may be co-limited by light and iron supply.

experiments [*Coale et al.*, 1996]. As such they may be appropriate historical analogues to climate change, since modes of longer-term climate change are thought to project onto those of shorter-term, natural climate variability [*Corti et al.*, 1999]. Other factors to consider include shifts in the biogeographical extent of species [*Parmesan*, 1996], foodweb effects [*Wuethrich*, 2000], external perturbations such as dust supply [*Falkowski et al.*, 1998], and the length of the algal growth season [*Reid et al.*, 1998]. Coupled models now are being developed that link terrestrial ecosystem processes with climatic systems [*Cao and Woodward*, 1998] often with explicit dynamic vegetation models [*Cox et al.*, 2000]. More effort is required to incorporate climate-mediated shifts in marine ecosystems—driven on regional scales by biogeography, the interplay of environmental factors, and oceanic forcing—to assess the cumulative magnitude and sign of biotic feedbacks.

[10] Presently, it is ill-advised to proceed directly from simple marine PZND models to the level of biological detail in Table 1. One alternative is to build generic, multi-species models around plankton functional groups, where each species is potentially omnipresent, and regional patterns emerge in the model prognostically from a simple set of rules and physico-chemical forcing (“universal-distribution, local-selection”). Exploratory results are shown in Figure 3 using CSSM physics and reduced subsurface nutrients (10%) (Figure 1). The chlorophyll difference field (future-control, Figure 3a) shows regional patterns of both higher and lower stocks at temperate to high latitudes and in coastal upwelling zones associated with the interplay of subsurface nutrients and light limitation. The magnitude of these differences are significant relative to the annual mean chlorophyll levels in the control (0.5 mg m^{-3} or less). Globally primary and new production decrease by 5.5% and 8%, respectively, mostly due to the reduced subsurface nutrients.

[11] Modelled spatial patterns of nitrogen fixation (Figure 3b) in the control agree well with the limited information available from in situ [*Capone et al.*, 1997] and geochemical [>100 Tg N/y, *Gruber and Sarmiento*, 1997] studies. In the future (Figure 3c), nitrogen fixation strengthens by 27% (94 Tg N/y) with higher rates in the oligotrophic subtropical gyres and eastern tropical boundaries, and poleward expansion due to warming and stratification, suggesting that the boundaries of the subtropical biomes for nitrogen fixers have altered on the centennial time-scale. Sensitivity studies show that the elevated nitrogen fixation is due mostly to changes in physics, not subsurface nutrients, consistent with observations that the diazotrophs are light and iron (mostly from dust) limited in both cases.

[12] These ecosystem results are illustrative since other potential climatic impacts have been omitted (e.g., altered dust deposition; reduced surface pH). But the present solutions do highlight that regional floristic shifts may be as or more important than alterations in bulk integrated global productivity.

[13] Over-laying a template of biogeographical provinces or biomes [*Longhurst*, 1998] enables direct comparison with the observed unique regional responses to oceanic physical forcing (Figure 2). The province boundaries should be thought of as fuzzy and dynamic on the time-scales of COAM simulations, due to alteration of ocean physics and subsequent changes in biomes (Figure 3c). Regional biogeochemical models and remote-sensing classification schemes, containing province-specific biological

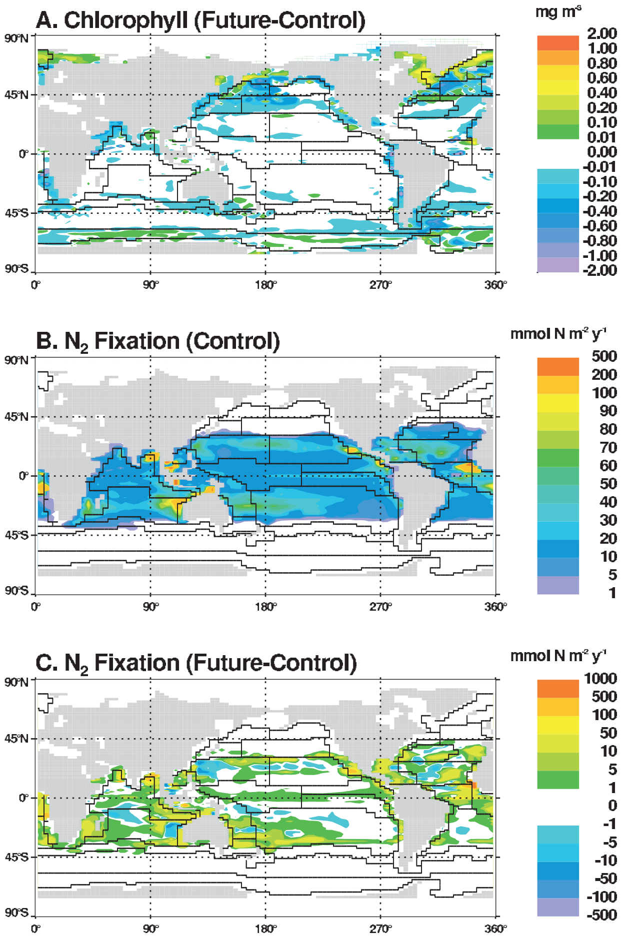

Figure 3. Simulations using the CSSM (Figure 1) with an off-line, multi-species pelagic ecosystem model for (a) chlorophyll (Future-Control), (b) N$_2$ fixation (Control), and (c) N$_2$ fixation (Future-Control). Each panel is overlaid with the template featured in Figure 2. Note that while the estimate of elevated N$_2$ fixation reflects reduced phosphorus levels, more field data are needed to assess the impact of nutrient limitation on N-fixers [*Sanudo-Wilhelmy et al.*, 2001].

parameters, species and foodwebs, would provide a framework to synthesise and accommodate the many and sometime disparate findings from field (Table 1) and lab [*Riebesell et al.*, 2000] studies. Climate response could then be better estimated by mapping the predicted regional patterns of ocean forcing (Figure 1) into changes in the spatial boundaries of biogeochemical provinces.

4. Conclusions

[14] Here, we highlight the key role that floristic shifts at a regional level will play in determining the global marine ecosystem response to future climate change. Two complementary approaches are advocated—one global (incorporation of greater biological complexity) and one regional (data interpretation based on a scheme of provinces). Both approaches are based on the concept that planktonic community dynamics are largely governed by bottom-up physical forcing [*Margalef*, 1978]. The selection of functional groups and definition of provinces depends on the questions we wish to answer [*McGowan*, 1999], and the strengths and weaknesses of these approaches need to be rigorously explored in more detail against observations. Especial focus should be paid to the dynamic response of marine ecosystems to natural interannual-decadal climate variability and skill of models should routinely be assessed against the historical record using hind-casting experiments.

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