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Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models

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Abstract

Ecosystem processes are important determinants of the biogeochemistry of the ocean, and they can be profoundly affected by changes in climate. Ocean models currently express ecosystem processes through empirically derived parameterizations that tightly link key geochemical tracers to ocean physics. The explicit inclusion of ecosystem processes in models will permit ecological changes to be taken into account, and will allow us to address several important questions, including the causes of observed glacial–interglacial changes in atmospheric trace gases and aerosols, and how the oceanic uptake of CO_2 is likely to change in the future. There is an urgent need to assess our mechanistic understanding of the environmental factors that exert control over marine ecosystems, and to represent their natural complexity based on theoretical understanding. We present a prototype design for a Dynamic Green Ocean Model (DGOM) based on the identification of (a) key plankton functional types that need to be simulated explicitly to capture important biogeochemical processes in the ocean; (b) key processes controlling the growth and mortality of these functional types and hence their interactions; and (c) sources of information necessary to parameterize each of these processes within a modeling framework. We also develop a strategy for model evaluation, based on simulation of both past and present mean state and variability, and identify potential sources of validation data for each. Finally, we present a DGOM-based strategy for addressing key questions in ocean biogeochemistry. This paper thus presents ongoing work in ocean biogeochemical modeling, which, it is hoped will motivate international collaborations to improve our understanding of the role of the ocean in the climate system.

Keywords: carbon cycle, climate change, ecosystem, functional types, glacial–interglacial cycles, modeling, ocean, plankton

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Introduction

Of the 450 Pg C emitted through fossil fuel emissions and deforestation during 1750–2000, 40% was absorbed by the land biosphere and 26% by the oceans (House *et al*., 2002). The land CO_2 sink is thought to be mostly caused by CO_2 fertilization and the response to land-use change, whereas the ocean CO_2 sink is thought to be mostly a physical–chemical response to the increased concentrations of atmospheric CO_2. Models of the land and of the ocean are able to reproduce roughly the time evolution of these sinks for the past two centuries (Prentice *et al*., 2001). Yet, when projected into the future, the response of the land and ocean models differs radically: land models show much larger uncertainty than their oceanic homologues (Fig. 1). The reason for such different behaviors may lie in the fact that the ocean is more predictable than the land because of its large buffering capacity. Alternatively, it may be that oceanic models do not include the essential complexity in ecological responses that is present in terrestrial models. The fact that global carbon models cannot reproduce glacial–interglacial variations in atmospheric CO_2 (Sigman *et al*., 2000) is a strong incentive to explore alternative avenues in ocean biogeochemical modeling.

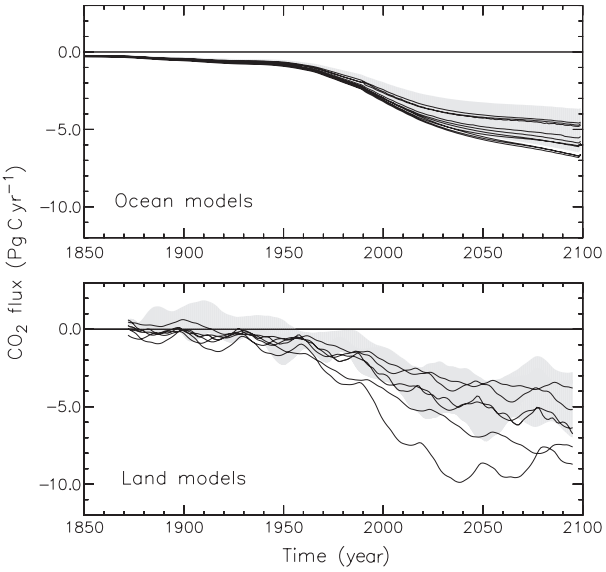

Fig. 1 Ocean and land CO_2 sinks as estimated with Ocean Biogeochemical Models (top) and Terrestrial Ecosystem Models (bottom). The black lines are estimates from different models when atmospheric CO_2 increases but the climate remains the same. The shaded area is model estimates when both atmospheric CO_2 increases and the climate is allowed to change. Model simulations are summarized in Prentice *et al*. (2001) and include results from ocean models (Maier-Reimer *et al*., 1996; Sarmiento *et al*., 1998; Joos *et al*., 1999; Matear & Hirst 1999; Bopp *et al*., 2001; Dutay *et al*., 2002) and terrestrial models (Cramer *et al*., 2001).

The first generation of ocean biogeochemical models (OBM) defined biological rates based on geochemical observations (Maier-Reimer & Hasselmann, 1987; Najjar *et al*., 1992; Maier-Reimer, 1993). This strategy has several disadvantages: it cannot take into account the fact that rates may differ under different climatic regimes, it does not take advantage of the information available on the physiology of the marine plankton, and it uses geochemical observations to parameterize the model, thus making these observations unusable as a validation tool.

The amount of data on biological rates was limited at the time the first OBMs were conceived. This is no longer true. In the past 20 years, information has been gathered regarding the rate of growth, mortality, and remineralization of different plankton groups, and some of this information has been recently synthesized (e.g. Rivkin & Legendre, 2001; Hirst & Kiørboe, 2002; Hirst & Bunker, 2003; LaRoche & Breitbarth, 2005; Sarthou *et al*., 2005; Veldhuis *et al*., 2005; Schoemann *et al*., 2005). There is currently enough information available to develop a new generation of global OBMs more closely based on the physiology and ecology of marine organism, which we call Dynamic Green Ocean Models (DGOMs).

The development of DGOMs is inspired by parallel developments of terrestrial Dynamic Global Vegetation Models (DGVMs, Cramer *et al*., 2001). Although there are important differences between terrestrial and marine ecosystems (notably in the pace of succession, the turnover time of primary producers, the relative importance of herbivory, and the transport of plankton), there are also enough similarities for DGVMs to provide a successful precedent for modeling ecosystem–climate interactions. DGVMs have demonstrated that it is possible to reduce biological complexity to a level that is manageable in the modeling context through application of the concept of functional types (see e.g. Steffen (1996); Smith *et al*. (2001)). DGVMs successfully reproduced the observed variability in land CO_2 sinks over the past two decades, including part of the large sink that followed the eruption of Mount-Pinatubo (Prentice *et al*., 2000; Lucht *et al*., 2002). DGVMs estimate that climate-induced changes in ecosystem composition have a large impact on both the magnitude and the spatial distribution of land CO_2 sinks (Cramer *et al*., 2001), and can lead to a large positive feedback with atmospheric CO_2 and climate (Cox *et al*., 2000).

In contrast, ocean carbon models are unable to reproduce year-to-year variability in observed surface chl*a* (Prentice *et al*., 2004) and in glacial–interglacial CO_2 variations, which must be of oceanic origin (Sigman

et al., 2000). Developments toward more complex processes in ecosystem models were first criticized as being far less important than physical processes (Broecker, 1991), and were later readvocated with the publication of new modeling (Sarmiento & Le Quéré, 1996; Doney, 1999; Boyd & Doney, 2002) and experimental results (Falkowski *et al.*, 2003), and following an increased understanding of feedback processes (Denman *et al.*, 1996; Boyd & Doney, 2003). The debate remains unchanged mostly because no satisfactory answer has been given as to the role of marine ecosystems in climate. Although the physical circulation clearly plays an important role in ocean biogeochemistry (Doney *et al.*, 2004; Sarmiento *et al.*, 2004; Gnanadesikan *et al.*, 2004) major model developments of the representation of ecosystems are also needed, and have already begun (Baretta *et al.*, 1995; Blackford & Burkill, 2002; Moore *et al.*, 2002; Aumont *et al.*, 2003; Gregg *et al.*, 2003). Such developments need an increased mechanistic understanding of which environmental factors exert control on marine ecosystems, and how to preserve such mechanisms in global models. In this commentary, we advocate that such developments must be pressed further and must be better coordinated. We report efforts to develop a DGOM based on the representation of 10 plankton functional types (PFTs) to investigate biogeochemical processes in the ocean.

The paper is structured as follows: In the next section, we discuss some of the fundamental scientific questions that can best be addressed using a DGOM, and thus motivate this initiative. In 'Model developments and parameterization', we discuss the basis for model construction, focusing particularly on (a) identifying the list of functional types, (b) defining the processes controlling the growth and mortality of functional types, and (c) characterizing the biological processes that control the fate of organic matter in the ocean. In the fourth main section, we discuss theoretical considerations that could help improve the model parameterizations. In the fifth main section, we develop an evaluation strategy. Although completion of a DGOM is likely to take some years, initial developments have produced some interesting results, which are discussed in the penultimate section. In the final section, we discuss immediate research priorities to complete model development, and in the conclusion section we discuss the expected implications of the use of a DGOM to address issues related to the role of marine ecosystems in climate.

Research Questions

Life regulates the composition of the atmosphere. In the absence of life, the concentration of atmospheric gases such as O_2, CO_2, and their isotopes would be very different. As DGOMs take into account the interactions between climate and marine ecosystems, it will enable us to revisit a number of outstanding questions about the functioning of the earth, including the following:

- What controlled the regular variations in atmospheric CO_2 content over the Quaternary ice age cycles as observed in the Vostok (Barnola *et al.*, 1987; Petit *et al.*, 1999) and EPICA (EPICA Community Members, 2004) ice core records?
- What determined the atmospheric CO_2 concentration during the preindustrial Holocene and its subsequent evolution during the industrial era (Joos *et al.*, 2004)?
- How is the ocean uptake of anthropogenic CO_2 likely to evolve over time, taking into account influences of different CO_2 emission pathways, changes in climate, sea-ice distribution, oceanic stratification and circulation, and changes in the external input of nutrients via rivers and aeolian dust (Boyd & Doney, 2003)?
- On time scales from months to hundreds of thousands of years, what role is played by the ocean in regulating the atmospheric content of reactive trace gases and aerosols by providing sources and sinks for compounds such as N_2O (reactive in the stratosphere), dimethylsulfide (DMS), and halogenated organic species?
- On time scales from months to hundreds of thousands of years, what regulates the abundance of measurable atmospheric tracers of the global carbon cycle such as O_2 $^{13}CO_2$, $O^{18}O$, and $O^{17}O$ (Bender, 2003)?
- On time scales from months to hundreds of thousands of years, what role is played by marine biology in regulating oceanic temperature and stratification, and what are the regional and global feedbacks on climate (Denman *et al.*, 1996)?
- What might be the combined impacts of climate change and potential changes in fisheries management on sustainable fisheries harvest at the regional to global scale (Beaugrand *et al.*, 2002)?
- How effective are the technologies proposed to sequester CO_2 in the ocean, including deep injection of CO_2 and large-scale Fe fertilization, and what additional impacts would they have on the marine ecosystems and the environment (Gnanadesikan *et al.*, 2003)?

Although we focus here on the role of marine ecosystems, ocean physics plays a central role in determining the environmental conditions that regulate

the composition of the ecosystem at a given time and space (e.g. temperature, nutrient supply, light availability) and the changes in these conditions (Boyd & Doney, 2003), and to transport carbon and other passive tracers (Doney *et al*., 2004; Sarmiento *et al*., 2004). Similarly, the transport of passive tracers is closely related to marine ecosystems, as they largely determine the vertical gradients of tracers in the surface ocean, thereby modifying any impact of the physical transport. Ocean physics and marine ecosystems are closely related, and the development of a DGOM must consider physical transport and should be developed in the context of state-of-the-art physical models.

Model developments and parameterization

The first steps in the development of a DGOM are as follows: (1) to define the set of PFTs that need to be included, (2) to determine the processes controlling their growth and mortality, and (3) to determine the processes controlling the fate of organic matter in the ocean.

Definition of PFTs

Biogeochemical processes are closely linked to PFT assemblages (Falkowski *et al*., 2003), which requires their explicit representation in a model. Many PFT classifications are possible depending on the scientific question being addressed (Claustre, 1994; Falkowski *et al*., 1998; Bouman *et al*., 2003). In arriving at a definition of the key PFTs, it is important to balance the need for sufficient complexity to be able to address specific scientific questions against the current limitations of the observational basis for parameterizing and validating each class of PFT. Our criteria for distinguishing a PFT were (a) that the PFT should have an explicit biogeochemical role, (b) that the PFT should be defined by a distinct set of physiological, environmental, or nutrient requirements controlling its biomass and productivity, (c) that the behavior of the PFT should have distinct effects on the performance of other PFTs, for instance, through selective depletion of nutrients or grazing, and (d) that the PFT should be of quantitative importance in at least some region of the ocean. As a result of these considerations, we defined a set of 10 key PFTs, listed here from the smallest to the largest (Table 1).

1. *Pico-heterotrophs (e.g. heterotophic bacteria and archea)* remineralize dissolved and particulate organic matter. Remineralization prevents the export of organic matter to the deep ocean because it converts organic matter in to its inorganic form, and releases CO_2, which can be outgassed back to the atmosphere.
2. *Pico-autotrophs (e.g. Pico eukaryotes and non N_2-fixing photosynthetic bacteria such as Synechococcus and Prochlorococcus)* make a substantial contribution to primary production, but a negligible contribution to export. They have high affinities for nutrients and light because of their high surface to volume ratio. They are found everywhere, and constitute an important fraction of phytoplankton biomass in High Nutrient Low Chlorophyll (HNLC) and oligotrophic regions.
3. *Phytoplankton N_2-fixers (e.g. Trichodesmium and N_2-fixing unicellular prokaryotes* (Zehr *et al*., 2001)) can use N_2 from the atmosphere and thus control the total ocean inventory of reactive N (Falkowski, 1997; Tyrrell, 1999). N_2-fixation requires more energy than the acquisition of other dissolved organic or inorganic nitrogen forms. It is inefficient at low temperatures (Staal *et al*., 2003). Thus, N_2-fixers are advantageous in warm, nutrient poor waters, but outcompeted elsewhere. Although the true Fe demand of these organisms is not firmly established (Sañudo-Wilhelmy *et al*., 2001; Kustka *et al*., 2002), it has been suggested that aeolian Fe input may play an indirect role in determining fixation by the phytoplankton and total ocean new production over millennial time scales (Falkowski, 1997; Broecker & Henderson, 1998). The requirement of N_2-fixers for P is also the basis for a proposed mechanism by which P supply (Mills *et al*., 2004) tightly regulates the oceanic N inventory (Tyrrell, 1999).
4. *Phytoplankton calcifiers (e.g. coccolithophorids)* produce more than half of the marine carbonate flux (Schiebel, 2002). They influence atmospheric CO_2 on millennial time scales through the effect of calcification on ocean alkalinity and carbonate chemistry. Phytoplankton calcifiers also produce the densest ballasts observed in sinking particles (Klaas & Archer, 2002). They have the ability to use organic P (Riegman *et al*., 2000) but they die after 1 day in the dark (R. Geider, unpublished data), which suggests that they would be destroyed in regions where the mixing depth of the ocean is below the euphotic zone. Their calcification rate is reduced at high CO_2 concentration (low pH) (Riebesell *et al*., 2000). Low Zn concentrations influence their relative growth and calcification rates (Schulz *et al*., 2004).
5. *Phytoplankton DMS-producers (e.g. Phaeocystis and small ($<20\,\mu m$) autotrophic flagellates)* produce dimethylsulfoniopropionate (DMSP) and convert it into DMS using an extracellular enzyme (DMSP-lyase). Thus, they affect the atmospheric sulfur cycle

Table 1 Biomass and size distribution of Plankton Functional Types (PFT)

Size class	Biomass (Pg C)	PFT name	Cell Size (μm)
Bacteria			
Pico	0.35*	Pico-heterotrophs	0.3–1.0
Phytoplankton			
Pico	0.28†	Pico-autotrophs	0.7–2.0
		Phytoplankton N_2-fixers	0.5–2.0‡
Nano	0.39†	Phytoplankton calcifiers	5–10
		Phytoplankton DMS-producers	5§
		Mixed-Phytoplankton	2–200
Micro	0.11†	Phytoplankton silicifiers	20–200
Zooplankton			
Proto	0.16¶	Proto-zooplankton	5–200
Meso	0.10‖	Meso-zooplankton	200–2000
Macro	Unknown	Macro-zooplankton	>2000

*Independent values of 0.34 and 0.36 Pg C were estimated by Rivkin & Legendre (2002) and Whitman *et al*. (1998), respectively.
†The chlorophyll biomass associated to the micro- (>20 μm), nano- (2–20 μm), and pico(<2 μm)-phytoplankton size classes is estimated from the combination of the statistical analysis of an high performance liquid chromatography (HPLC) pigment database and monthly composite ScaWiFS scenes of the year 2000 (Uitz *et al*., 2005). These biomasses are then converted to carbon equivalent using C : chl*a* ratios of 50 g C g^{-1}Chl for the micro-phytoplankton and 125 g C g^{-1} Chl for other phytoplankton. Part of the mixed-phytoplankton PFT should be accounted for in the micro-phytoplankton.
‡Form colonies of 2000–5000 μm.
§Form colonies of 100–500 μm.
¶Gasol *et al*. (1997), includes only micro-zooplankton size class.
‖Our estimate based on data from O'Brien *et al*. (2002); Finenko *et al*. (2003), and Beaugrand *et al*. (2002).

(Stefels *et al*., 1995). Other nano- and pico-plankton also produce DMSP but lack the enzymatic reaction that makes DMS-producers more effective (Liss *et al*., 1997). DMS-producers have a high requirement for P. They are particularly abundant in coastal areas (Schoemann *et al*., 2005), where they are often observed in colonies. Calcifiers are also important for the DMS cycle but they are treated independently.

6. *Phytoplankton silicifiers (e.g. diatoms)* dominate micro-phytoplankton (20–200 μm) assemblages, and contribute to most of the primary production and biomass during the spring bloom in temperate and polar regions. Silicifiers contribute to carbon export far more effectively than smaller plankton through direct sinking of single cells, key-grazing pathways, and through mass sedimentation events at the end of the spring blooms when nutrients are depleted. Silicifiers require and deplete Si. They require more Fe and P than most of the smaller nano- and pico-phytoplankton (Sarthou *et al*., 2005) (Table 2). They respond to enhanced Fe input in HNLC regions as long as Si is available (Boyd *et al*., 2004). They produce little DMSP compared with most other phytoplankton (Table 2).
7. *Mixed-phytoplankton (e.g. autotrophic dinoflagellates and Chrysophyceae)* represent phytoplankton of heterogeneous size (2–200 μm) and taxonomic composition for which no distinct biogeochemical role is defined. This PFT constitutes the background biomass of phytoplankton, which do not bloom in the open ocean, have low seasonality, and no direct impact on the cycles of S, Si, or $CaCO_3$.
8. *Proto-zooplankton (e.g. ciliates, heterotrophic flagellates)* are unicellular heterotrophs (5–200 μm) that dampen bloom formation of small phytoplankton. They graze preferentially on small phytoplankton (1–20 μm), such as the pico- and nano-phytoplankton PFTs. Their growth rates are similar to that of phytoplankton in the pico- and nano-size range, and their ingestion rates are closely coupled to the production rates of their prey.
9. *Meso-zooplankton (e.g. copepods, appendicularians, amphipods)* produce large and fast-sinking fecal pellets and are an important source of food for fishes. They graze preferentially on larger plankton (20–200 μm), such as proto-zooplankton and phytoplankton silicifiers. Their grazing and reproductive rates are slower than that of proto-zooplankton.
10. *Macro-zooplankton (e.g. euphausids, salps, pteropods)* also produce large fecal pellets, which sink much faster than those of meso-zooplankton. Furthermore, macro-zooplankton graze across a wide spectrum of sizes (filter feeding), including the

Table 2 Traits that characterize different Plankton Functional Types

	Max growth rate at 0 °C* (day^{-1})	Max mortality rate† (day^{-1})	Light		Half–saturation				DMSP/C‡‡ (mol/;mol)
			Affinity‡	Stress§ 0 to 1	P¶ (nM)	Fe‖ (aM)	Si** (μM)	Other nutritional source††	
Bacteria									
Pico-heterotrophs	2.1	No data						5 (DOM)	**0.000**
Phytoplankton									
Pico-autotrophs	0.6	0.05	3.2	0	19	No data			**0.010**
Phytoplankton N_2-fixers	0.04	0.05	1.6	No data	75	120		0 (N_2)	**0.000**
Phytoplankton calcifiers	0.2	0.05	1.6	1	4	20		**1.9 (DOP)**	**0.012**
Phytoplankton DMS producers	0.6	0.05	1.6	No data	700	20			**0.012**
Phytoplankton silicifiers	0.6	0.05	5.1	0	**75**	120	4		**0.002**
Mixed-phytoplankton	0.6	0.05	1.6	0.5	19	20			**0.012**
Zooplankton									
Proto-zooplankton	0.6	1e¶-proto						18	
Meso-zooplankton	**0.24**	**0.058**						**0.29**	
Macro-zooplankton	No data	No data						No data	

Bold numbers are based on a data compilation. DOP, dissolved organic phosphorous; DOM, dissolved organic matter. Empty boxes mean that the information is not applicable to this PFT.

*Based on data from Eppley (1972), Thingstad & Lignell (1997), Rivkin *et al*. (1996), Kustka *et al*. (2003), Le Vu (2005), and Hirst & Bunker (2003).

†Excluding grazing. Based on data from Brussaard *et al*. (1997) and Hirst & Kiørboe 2002.

‡chl*a*-specific initial slope of the photosynthesis light curve (α) in $10^{-7}\ \frac{m^2\ molC}{gChl\ \mu mol\ photons}$. Data from Geider *et al*. (1997).

§R. Geider, unpublished data.

¶Based on data from Riegman *et al*. (2000), Sañdo-Wilhelmy *et al*. (2001), Veldhuis & Admiraal (1987), and Sarthou *et al*. (2005).

‖Based on data from Sañdo-Wilhelmy *et al*. (2001) and Sarthou *et al*. (2005).

**Based on data from Sarthou *et al*. (2005).

††Based on dala from Riegman *et al*. (2000), Stihl *et al*. (2001), and Hirst & Bunker (2003). The half-saturation for N_2 is 0 because N_2 is never limiting.

‡‡Archer *et al*. (2002).

DMSP, dimethylsulfoniopropionate.

smallest phytoplankton, thus their fecal pellets provide an indirect route by which even small phytoplankton biomass can be transferred to the deep ocean. They can achieve very high biomass locally, but they tend to have a patchy distribution. The environmental conditions that control their standing stocks, physiology, and life cycles are poorly documented. Meso- and macro-zooplankton such as foraminifera and pteropods also produce $CaCO_3$ and are thought to contribute to up to half of the marine carbonate flux (Schiebel, 2002).

It will certainly be necessary to subdivide these PFTs at a later stage to include processes and rates not recognized in our current classification, or for which sufficient information is lacking. Similarly, some PFTs may not be needed because of revised evidence or because their traits may be too difficult to define. For example, many PFTs produce DMSP (Table 2), but our current understanding of the DMS cycle suggests that the DMS-producers differ in the efficiency with which DMSP is converted to DMS. It may be possible to resolve the DMS cycle without isolating DMS-producers. Further theoretical developments may allow us to reduce the number of PFTs by considering for instance size spectra as a proxy for a number of rates.

PFT traits and input data

In order to represent PFTs in biogeochemical models, more physiological data are required. Some of the estimates presented in Table 2 are based on a single report, or on measurements of a single group that may not be representative of the range of behavior within a PFT. An effort to compile the available data on a global scale for all PFTs or to determine experimentally the factors exerting control on each PFT, and for multiple members of any one PFT, is required.

Each PFT can be characterized by a specific set of physiological traits (i.e. a measurable or observable property of individual PFT). There are a number of difficulties inherent in deriving PFT-specific values for each of the relevant traits. When trait values are based on laboratory experiments, they are usually conducted on individual species easy to culture and that are not necessarily characteristic of the PFT as a whole. When trait values are based on empirical observation, the sparse measurements may not represent average responses adequately, and some of the parameters required for the formulation of a model are not measured directly but have to be derived from the measurements of proxies or related parameters. Table 2 shows examples of PFT-specific values for the traits that were initially proposed for Nutrient–Phytoplankton–Zooplankton–Detritus (NPZD) models (Fasham *et al.*, 1993; Six & Maier-Reimer, 1996; Aumont *et al.*, 2002), and that have been extended to characterize PFTs in recent models (Gregg *et al.*, 2003; Moore *et al.*, 2002; Aumont *et al.*, 2003). Quantitative values have been obtained from the literature. These data are only indicative, and will require refinement as more observations become available.

Under ideal conditions of light and nutrient availability, the maximum growth and mortality rate of each PFT is finite for a given temperature and, for those taxa that can be cultured, can be measured in the laboratory. A generic growth rate value of $0.6\,day^{-1}$ at $0\,^{\circ}C$ is widely used for phytoplankton (Eppley, 1972; Banse, 1991). The information available for individual PFTs is mostly qualitative. Laboratory experiments suggest that under ideal conditions of light and nutrient availability, calcifiers (Le Vu, 2005) and N_2-fixers (Kustka *et al.*, 2003) grow more slowly than the generic rate, whereas bacteria grow faster (Rivkin *et al.*, 1996; Thingstad & Lignell, 1997). Field studies suggest that proto-zooplankton can grow at about the same rate as phytoplankton and hence, the time lag between increases in phytoplankton and increases in proto-zooplankton is only a few days. Based on direct observations and allometry, proto-zooplankton generally grow faster than meso-zooplankton (Hirst & Bunker, 2003).

Zooplankton mortality is generally considered as density dependent, and is parameterized as the square of the concentration. This formulation accounts for the increasing pressure on zooplankton as density increases both as a result of grazing by zooplankton of similar size and mortality caused by diseases and parasites (Ohman & Hirche, 2001).

When light and/or nutrients are limiting, PFTs compete for resources. For light limitation, the growth rate increases asymptotically from zero at a threshold light level to its maximum growth rate when sufficient light is available for growth (Fig. 2). The slope representing the growth rate as a function of light level is called the affinity for light (Table 2), and it is a function of the Chl/C ratio. The relation between the affinity and the Chl/C ratio, the affinity dependence, is PFT specific (MacIntyre *et al.*, 2002), although few data are available to estimate a value for each PFT.

The light environment and its effect on growth rates are difficult to represent in models because of the physical dynamics of the surface ocean. Under the effect of winds, the ocean surface is well mixed up to a depth of 50 m on average, and between 10 and 500 m regionally. Because of mixing, phytoplankton cells experience subdaily variability in light intensity. The growth of a PFT depends on its capacity to adapt to fast variability in light levels, and their ability to survive in

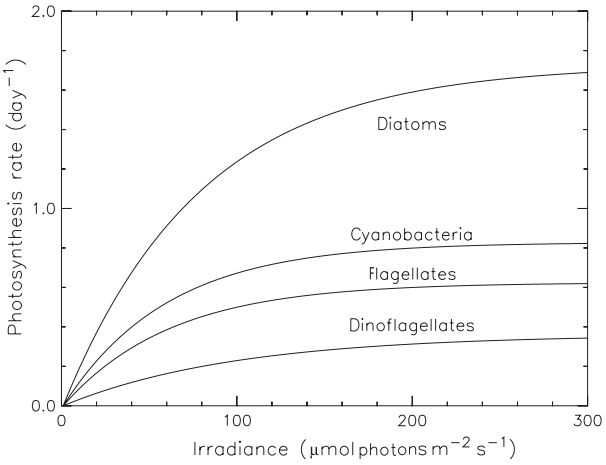

Fig. 2 Example of productivity vs. irradiance at 15–25 °C for different phytoplankton groups (Geider *et al*., 1997). The diatoms include *Phaeodactylum tricornutum, Skeletonema costatum, Thalassiosira pseudonana,* and *Thalassiosira weissogii*. Cyanobacteria include *Microcystis aeruginosa, Oscillatoria agardhii,* and a marine *Synechococcus*. Autotrophic flagellates include *Emiliania huxleyi* and *Isochrysis galbana*. Autotrophic dinoflagellates include *Gonyaulax tamarensis, Gymnodinium galatheanum, Gyrodinium aureolum, Prorocentrum micans,* and *Pyrocystis noctiluca*. The standard deviation in the measurements is roughly 50% of the absolute values (for 9–32 species and conditions examined), which highlights the need for repeated measurements on different plankton species and conditions.

the dark (Berges & Falkowski, 1998). Laboratory experiments have shown that silicifiers can survive for weeks in the dark, while calcifiers begin to die after 1 day (R. Geider, unpublished data). Thus, some of the calcifiers would die in fall and winter when the mixing depth is deeper than the euphotic zone, whereas silicifiers would have reduced productivity (because of the low light level) but would maintain relatively high biomass over the winter months, which also contributes to their early spring bloom.

The response of PFTs to nutrient conditions determines their competitive ability. This can be quantified in terms of the half-saturation for a specific nutrient. A PFT with a high half-saturation for a nutrient requires a high concentration of that nutrient to grow. All autotrophic PFTs need P and Fe, but silicifiers and N_2-fixers have a stronger requirement for these two elements compared with other autotrophs (Sañudo-Wilhelmy *et al*., 2001; Sarthou *et al*., 2005). Calcifiers have a low requirement for P because they have many receptors for P. In addition to the inorganic sources of nutrients, the use of nutrients from organic matter has been shown for several PFTs such as the N_2-fixers (Stihl *et al*., 2001), other pico-autotrophs (Li *et al*., 1998), and calcifiers (Riegman *et al*., 2000).

Fate of dissolved and particulate matter

The transformation of organic to inorganic material, the depth at which this occurs, and the sinking of organic matter are influenced by many processes (see sections on 'Aggregation and sinking of particles,' 'Remineralization of organic matter,' and 'Dissolution of inorganic matter' for a discussion of the biological processes). Several authors (Jackson, 1990; Riebesell & Wolf-Gladrow, 1992) have developed models that represent the particle formation and sinking in surface water based on discrete particle size classes. Unfortunately, the values of model parameters are often unknown and computational costs of these types of models are very high. To circumvent this problem, simplified aggregation models with few variables have been developed (Kriest & Evans, 1999; Ruiz *et al*., 2002). One main drawback in the use of particle aggregation models lies in the lack of parameters based on field observations. It is also not yet clear whether such models improve the representation of POC sinking in models (L. Bopp, unpublished model simulations).

Theoretical considerations

The number of PFTs that are required for a fully functional DGOM is not known at present. Even with the 10 we identified here, there are still poorly constrained or unknown trait values. There is need for an assessment of our mechanistic understanding of the environmental factors that exert control over PFTs in the ocean. In some PFTs such as Silicifiers, our understanding is relatively good. In other PFTs such as calcifiers, it is poor and is based on statistical analysis rather than experimental evidence (see Iglesias *et al*., 2002). The number of required traits could be minimized based on theoretical foundations. For example, the diffusion of elements across a membrane is a physical process controlled by well-determined environmental factors; chemical reactions consume or produce energy in given quantities and dense particles sink fast. In the following sections, we highlight processes for which a small gain in our understanding of underlying processes would lead to major improvements in the reliability of DGOMs.

Growth of phytoplankton functional types

On land, theoretical foundations exist to relate photosynthesis to the intercellular CO_2 concentration, temperature, and available radiation (Farquhar *et al*., 1980). The Farquhar model is based on a treatment of the CO_2 and O_2 dependencies of photosynthetic carbon fixation in C-3 plants. Whereas CO_2 concentration is one of the

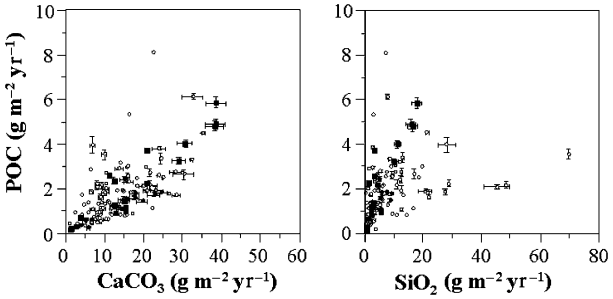

Fig. 3 Relationship between the flux of particulate organic carbon (POC) and that of $CaCO_3$ (left) and SiO_2 (right) observed in sediment traps below 2000 m (from Klaas & Archer, 2002).

main factors limiting photosynthesis by C-3 plants, CO_2 is usually not a limiting factor for phytoplankton photosynthesis because phytoplankton possess a CO_2-concentrating mechanism, whereas C-3 plants do not. The CO_2-concentrating mechanism largely removes the CO_2 dependence of photosynthesis in algae, except at very low dissolved inorganic carbon levels.

In the ocean, the size of the phytoplankton sets theoretical boundaries to maximum growth rate (Raven & Kübler, 2002). The plankton size and shape determine its surface-to-volume ratio. Although the exchange of nutrients between the plankton cell and its environment occurs only at the surface of the cell, the entire mass of the plankton, contained in the given volume, has to be maintained. Small plankton have a higher surface-to-volume ratio than larger cells and can use nutrients more efficiently. The relationship between size and growth works well within a PFT (Sarthou *et al*., 2005). However, it does not necessarily apply across PFTs (Table 2) because phytoplankton taxa have evolved different adaptive strategies to varying environmental conditions and can partly overcome the limitations as simply predicted by nutrient diffusion (e.g. variations in the number of N transporter genes and expression (Hildebrand & Dahlin, 2000), changes in cell quotas for nutrients (Geider *et al*., 1998), use of alternative enzymes of pathways (Laroche *et al*., 1999), and even strategies to improve their defenses against grazing by zooplankton (Strom *et al*., 2002)).

As an example, nutrient limitation can lead to wide variability in the ratio of the limiting nutrient concentration (N, P, Fe, and Si) and of C. Deviations from the average stochiometry of water occur between individual plankton samples (Redfield, 1934), between identifiable water masses (Copin-Montégut & Copin-Montégut, 1983) and through time at a given location (Karl, 1999). Culture studies and bioassays show about a 50-fold variability in C : P, and about a 20-fold variability in N : P in phytoplankton and bacteria between nutrient-replete and P- or N-limiting conditions (Geider & La Roche, 2002; Makino *et al*., 2003). The internal nutrient concentration thus depends not only on the environmental conditions but also on the specific characteristics of the PFT, and can vary in time and space.

Growth of zooplankton functional types

Part of the organic material that comes out of the mixed layer is first ingested by zooplankton and then repackaged in fecal pellets. Thus, we recognize the feeding habits, growth, and mortality of zooplankton as some of the important processes that influence biogeochemical cycles. The growth rate and size range of food ingested by the zooplankton can be expressed in first order as related to size (Armstrong, 2003b; Gentleman *et al*., 2003). Proto- and meso-zooplankton graze mostly on plankton and particles whose sizes are 10–100% and 2–6% of their own body size, respectively (Hansen *et al*., 1994). Some of the larger zooplankton ingest organic material of all sizes (filter feeding) using a mucous filter, which collects small particles. The ingested food influences the size and composition of the fecal pellets, and this determines their sinking speed.

Aggregation and sinking of particles

The size of a particle is a key parameter in determining its sinking speed. Phytoplankton cells of a few micrometers in diameter sink at less than 1 m day^{-1}, whereas particles several mm in diameter may sink several hundred meters per day (Berelson, 2002). Thus, the aggregation of the organic material influences its sinking speed. The aggregation is a function of the size, relative density of the particles (or their encounter rate), and stickiness of the organic material. The sinking speed is a function of the size, density, and morphology of the particles. Size, density, stickiness, and morphology result from the characteristics of the PFTs. Thus the PFTs that contribute most to sinking aggregates are

larger, bloom-forming organisms, and those that produce either dense hard shells, transparent exopolymer particle (TEP) (Passow & Alldredge, 1995; Engel *et al*., 2004), or dense fecal pellets.

The mineral content of the particles also influences biogeochemical cycles. An analysis of sediment-trap material has shown that the mineral content of the particle determines how much C is transported out of the mixed layer compared with other nutrients such as nitrogen and phosphorous (Fig. 3). The $CaCO_3$ and lithogenic contents of particles effectively carry more carbon to the deep ocean than opal (Francois *et al*., 2002; Klaas & Archer, 2002; Armstrong, 2003a), although the absolute role of lithogenic particles is small. The mechanism behind this 'ballast' effect and how it changes with depth is not yet fully resolved.

Remineralization of organic matter

Incubation experiments on aggregates and fecal pellets have shown that bacterial degradation of particle organic matters (POM) by microorganisms follows a first-order kinetics (Grossart & Ploug, 2001; Ploug, 2001). The influence of zooplankton activity on POM degradation at depth has not yet been quantified, although it is probably significant (Stemmann *et al*., 2004). Furthermore, different elements have different length scales of remineralization, and the activity of some PFTs can influence this length scale by preferentially remineralizing organic matter with high nutrient to carbon ratios, or by dissolving the protective shells (e.g. Bidle & Azam, 1999). Although a quantitative understanding of processes affecting POM degradation at depth is still lacking, results of sediment trap experiments provide empirical relationships for the description of POM fluxes as a function of the depth from which remineralization rates can be derived (Antia *et al*., 2001). This approach is, however, not adequate for studying the whole range of feedbacks between the biology and biogeochemical cycles in the ocean, and a better understanding of the underlying processes needs to be incorporated.

The degradation of POM by bacterial and zooplankton activity leads to the release of dissolved organic matter (DOM) and CO_2. DOM can also be generated through exudation by phytoplankton, in particular, under nutrient stress conditions. The rates for DOM release are poorly constrained and are usually assumed to be constant (Six & Maier-Reimer, 1996; Aumont *et al*., 2003). Over 70% of the DOM in the ocean is resistant to biological utilization (Benner, 2002). This large fraction corresponds to the refractory, slowly cycling pool of DOM, which can be remineralized by ultraviolet degradation near the surface.

Dissolution of inorganic matter

The dissolution of $CaCO_3$ is determined by the carbonate saturation state of surrounding waters, which is indirectly controlled by atmospheric CO_2 concentration (Feely *et al*., 2004). Because only the deep ocean is undersaturated, carbonate dissolution should occur in waters that are generally deeper than 3000 m. However, as much as 60–80% of the $CaCO_3$ dissolution occurs in the upper 1000 m (Buitenhuis *et al*., 1996; Milliman *et al*., 1999; Feely *et al*., 2002; Sabine *et al*., 2002). The action of pelagic organisms, in particular, zooplankton grazing and bacterial activity in aggregates and fecal pellets, has been proposed as a mechanism for shallow $CaCO_3$ dissolution. Model studies of calcium carbonate dissolution in the acidic gut of zooplankton (Jansen & Wolf-Gladrow, 2001) and in aggregates (Jansen *et al*., 2002) do not support such high rates of shallow $CaCO_3$ dissolution. The dissolution of aragonite could also account for an important fraction of carbonate dissolution above 1000 m depth (Feely *et al*., 2002; Jansen *et al*., 2002; Sabine *et al*., 2002). Pteropods are the main producers of aragonite but their ecology, distribution, and abundance are poorly known.

The dissolution of opal occurs everywhere because the entire ocean is undersaturated in silicic acid. In addition to silicic acid concentrations, several factors equally affect opal dissolution in the water column: temperature, specific surface area, Al concentrations, and organic material coating (van Cappellen *et al*., 2002). The effect of temperature seems well constrained (Rickert *et al*., 2002), and is responsible for both depth-dependent and geographical variations in silica dissolution. Other effects should depend on species-specific characteristics, which are not well known nor described.

Iron sources and sinks

Fe availability strongly influences the abundance and types of phytoplankton in HNLC regions (de Baar & Boyd, 2000). Fe concentration in the deep ocean hardly varies compared with other nutrients (Johnson *et al*., 1997). Fe concentration does not increase between the Atlantic and the Pacific, which is an indication of bacterial remineralization in other nutrients. Fe concentration does not decrease with depth, which is an indication of scavenging in other metals. The constant Fe concentration at depth has been interpreted as being a result of complexation by strong Fe-binding ligands such as marine DOM (Buffle, 1988; Johnson *et al*., 1997). It is unclear as to which DOM molecules bind ligands, and how they are related to the original PFT that formed the organic matter. However, the high Fe

concentration of the deep ocean adheres to between 20% and 80% of the Fe demand of plankton, with the lowest estimate based on the geochemical analysis of Fung *et al*. (2000) assuming 10% solubility for the Fe from dust sources, and the highest estimate based on model simulations (Archer & Johnson, 2000; Moore *et al*., 2002; Aumont *et al*., 2003).

Evaluation strategy

The key test of a DGOM is related to whether it can reproduce the mean state and variability of the fluxes of CO_2, O_2, N_2O, and DMS under modern conditions (Table 3). These fluxes integrate all biological, physical, and chemical processes and thus provide information on the overall performance of the model. A good representation of the well-observed mean state is essential. A good representation of the variability provides additional information to test whether the model is responding correctly to climate variability. Many processes could be optimized to obtain a good representation of the mean state, but it is more difficult to optimize a model in such a way as to reproduce variability correctly.

There are also a number of less stringent tests of the model that would be helpful to evaluate processes individually. One such test is related to whether the model can reproduce observed patterns of PFT distribution and abundance under modern climate conditions (Fig. 4). Another important challenge is to reproduce the outcome of *in situ* experiments, e.g. Fe fertilization carried out in the open ocean (e.g. Coale *et al*., 1996, 2004; Boyd *et al*., 2000; Buesseler *et al*., 2004), and mesocosm experiments where blooms are artificially triggered in a natural but controlled environment (Passow & Alldredge, 1995). Although the upscaling of these experiments to the global context cannot be evaluated, the local response of the models can nevertheless be constrained. Such experiments parallel tests of DGVMs to reproduce the vegetation response to the eruption of Mount Pinatubo (Lucht *et al*., 2002) and the artificial fertilization of land vegetation by CO_2 (T. Hickler, unpublished results).

It is not enough for a DGOM to reproduce modern mean state and variability. Understanding the long-term evolution of the climate system underpins many of the questions that motivate the development of DGOMs. Thus, it is important to ensure that the model is capable of reproducing past states of the ocean. Climate modelers have long realized that the ability to simulate the different conditions of the past is a key test of model performance (Mitchell, 1990; Grassl, 2000; Joussaume & Taylor, 2000; Harrison *et al*., 2002). This is also true for OBMs, which can be validated with geological records of paleooceanographic conditions. The geological past provides instances when both the physical and biological parameters of the ocean were in a radically different state from that at present. During the Last Glacial Maximum (LGM, ca. 21 000 year BP), the tropical oceans were 2–3 °C cooler than at present (Sonzogni *et al*., 1998; Mix *et al*., 1999; Rosell-Melé *et al*., 2004), Arctic and Antarctic sea ice was more extensive than at present, at least seasonally (Weinelt *et al*., 1996; Crosta *et al*., 1998; de Vernal *et al*., 2000), and the thermohaline circulation was different, with shallower and less strong deep water formation in the North Atlantic (Labeyrie *et al*., 1992). River inputs to the ocean were reduced (Hartmann 1994; Farrera *et al*., 1999), while aeolian (mineral dust) inputs were increased (Petit *et al*., 1999; Kohfeld & Harrison, 2001). Simulating ocean biology and biogeochemistry under these different conditions would provide a stringent test for a DGOM.

Modern simulations would allow us to evaluate the model mean fields, as well as its seasonal and interannual variability. LGM simulations would allow us to evaluate the long-term climate impact. To address the full range of questions posed in the introduction, however, a DGOM needs to be fully coupled to an Earth System model so that both impacts and feedbacks can be considered. With this evaluation strategy in mind, we present below the possible sources of evaluation data for modern and paleosimulations of the ocean.

Present conditions

Air-to-sea flux. Ultimately, the model must simulate the observed mean, seasonal cycle, and variability of the air-sea fluxes of CO_2, O_2, N_2O, and DMS to answer the questions posed in the introduction. Data are available for the mean fluxes of CO_2 and DMS (Kettle & Andreae, 2000; Takahashi *et al*., 2002) and for the variability in some regions of the world (Feely *et al*., 1999; Sciare *et al*., 2000; Bates, 2001; Brix *et al*., 2004). Interannual variability of CO_2 flux at high latitudes is poorly constrained. Regional patterns of N_2O fluxes are constrained only by assuming that they are closely linked to heat flux. However, N_2O fluxes are large and poorly constrained in the coastal zone (Naqvi *et al*., 2000).

Biomass. Ocean color sensors provide an estimation of the surface chl*a* content of the world ocean. Thus, they are a very useful tool for the survey of the phytoplankton biomass on synoptic scales. Estimates of chl*a* from SeaWiFS satellite since 1997 provide chl*a* mean values as well as its seasonal cycle and interannual variability for the open ocean (Behrenfeld

Table 3 Minimum set of evaluation data

	Modern			
Model component or process	Direct observations	Processed observations	Indirect observations	L–M indirect observations
Air-to-sea fluxes				
CO_2	No data	pCO_2 analysis*; ocean inversions	Atmospheric inversions	Atmospheric CO_2
DMS	No data	DMS analysis		Atmospheric MSA
O_2	No data	pO_2 analysis; atmospheric APO; ocean inversions	APO inversions	
Biomass				
Total	chl*a* from SeaWiFS (1997–2005); WOA[‡]; POC database[§]	HPLC[†]		
Pico-heterotrophs	Database[¶]			
Pico-autotrophs	Database[‖]			
Phytoplankton N_2-fixers	No database		Bloom frequency**	
Phytoplankton calcifiers	Database[‖]	HPLC[†]	Bloom frequency[††]	% Ca in sediments
Phytoplankton DMS producers	No database			
Phytoplankton silicifiers	Database[‖]	HPLC[†]		% Si in sediments
Mixed-phytoplankton	Database[‖]	HPLC[†]		
Proto-zooplankton	No database			
Meso-zooplankton	WOA[‡]; CPR[‡‡]			
Macro-zooplankton	No database			
Surface-to-depth flux				
POC	Sediment traps[§§]	Ocean inversions[¶¶]	Satellite chl*a*	Database[‖‖]
$CaCO_3$	Sediment traps[§§]		Alkalinity analysis***	
Si	Sediment traps[§§]			
Ocean-to-sediment flux				
POC, $CaCO_3$, Si, sediment composition, O_2 flux	Database[†††,‡‡‡]			Database[‡‡‡]
Global cycles				
N, P, O_2, Si	WOA[‡]			
DIC, TALK	Database[§§§]			
Fe	Database[‖]			

DIC, dissolved inorganic carbon; TALK, total alkalinity; APO, atmospheric potential oxygen is a measure of the oceanic contribution to atmospheric O_2 variations.
*Takahashi *et al*. (2002).
[†]Statistical analysis using a database of high performance liquid chromatography (HPLC) and ScaWiFS data (see text) (Uitz *et al*., 2005).
[‡]World Ocean Atlas 2001 (Conkright *et al*., 2002).
[§]Schneider *et al*. (2003).
[¶]Rivkin & Legendre (2002).
[‖]Based on ~300 data points distributed globally (Gregg *et al*., 2003).
**Subramaniam *et al*. (2002).
[††]Brown *et al*. (2000).
[‡‡]Continuous Plankton Recorder (Beaugrand *et al*., 2002).
[§§]Global compilation of over 100 sediment traps (Klaas & Archer, 2002; Francois *et al*., 2002).
[¶¶]Global estimate based on inversion of geochemical tracers (Schlitzer, 2000).
[‖‖]Bopp *et al*. (2003), and Kohfeld *et al*. (2005).
***Indirect estimates based on alkalinity (Lee, 2001; Sarmiento *et al*., 2002).
[†††]Jahnke (1996).
[‡‡‡]Catubig *et al*. (1998).
[§§§]Key *et al*. (2004).

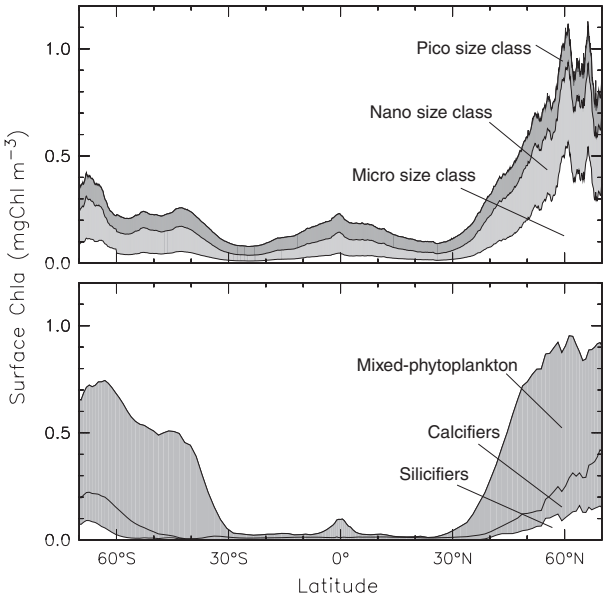

Fig. 4 Zonal average of the contribution of different phytoplankton plankton functional types to the total chl*a* (in mg Chl m^{-3}) for the (top) micro-, nano-, and pico-size classes estimated using the combination of the statistical analysis of an HPLC pigment database and monthly composite SeaWiFS scenes of the year 2000 (Uitz *et al*., 2005) and (bottom) silicifiers, calcifiers, and mixed-phytoplankton estimated using a Dynamic Green Ocean Model. The model and observation classes are not strictly equivalent, but nevertheless highlight an underestimation of the biomass of silicifiers and an overestimation of mixed-phytoplankton at high latitudes in the Dynamic Green Ocean Model.

et al., 2001; Yoder & Kennelly, 2003). In the coastal zone, the SeaWiFS data can only be used to provide an upper bound, rather than a quantitative estimate because of potential interfering signals from suspended sediment and Gelbstoff (Ladner *et al*., 2002). The MERIS satellite launched in 2002 has higher spectral and spatial resolution than SeaWiFS and includes a preprocessed biomass product for coastal waters (Doerffer & Fischer, 1994).

Satellites also provide indirect information on the distribution of some individual PFTs. Some calcifiers, after they bloom, release coccoliths that have high reflectance and can be detected from space (Brown *et al*., 2000) (Fig. 5). Exploratory work to detect Trichodesmium blooms appears promising (Subramaniam *et al*., 1999, 2002). Methods are also emerging for mapping diatoms and other PFTs from space (Alvain *et al*., 2005; Sathyendranath *et al*., 2004).

Recently, Uitz *et al*. (2005) derived the vertical profiles of the chl*a* associated with three phytoplankton size classes (i.e. micro, nano and pico) from their analysis of an HPLC pigment database, and using a combination of the approach of Morel and Berthon (1989) and the method of Vidussi *et al*. (2001). Their analysis yields relative contributions of PFTs, which can be converted into absolute concentrations using remotely sensed chl*a*. From this, a global estimation of the biomass associated with these three size classes was made (Table 1, Fig. 4). The approach developed by Uitz *et al*. (2005) can be applied to any kind of biomarker pigment, potentially leading to estimation that conform more closely to the PFTs included in the model (e.g. silicifiers from fucoxanthin).

Direct measurements of the concentration of chl*a* are also available (Conkright *et al*., 2002), which give information on the vertical distribution of biomass, and the biomass in the coastal zone. *In situ* biomass data have been synthesized only for meso-zooplankton (Beaugrand *et al*., 2002; Conkright *et al*., 2002) and for bacteria (Rivkin & Legendre, 2001).

Surface-to-depth flux. The export of POM, $CaCO_3$, and Si from the surface to the deep ocean is the most direct way that we have to test model performance, and can be constrained by both direct and indirect observations. Direct information comes from sediment-trap data (Francois *et al*., 2002; Klaas & Archer, 2002). However, the large spatial variability in the traps, and the relatively short time series of the available measurements (typically 3–10 months), make it difficult to use these data directly as a means to validate a model without first applying statistical analysis. Spatial patterns for export of POM can also be obtained from inversions of oceanic tracers (Schlitzer, 2000). These results show a large export in the Southern Ocean compared with the North Atlantic, a result that appears robust but contrasts with those deduced from satellite chl*a*. It has been proposed that the fact that the satellites do not subsurface see chl*a* may be the cause of the discrepancy, but there is little evidence of this and no real consensus as yet (Schlitzer, 2002).

Ocean-to-sediment flux. Over long time scales (>1 kyr), the amount of organic and inorganic material that reaches the ocean floor will partly determine the mass balance of the ocean for nutrients and carbon. Data from sediment traps are available (Jahnke, 1996; Catubig *et al*., 1998), although an extension to the coastal zone, where most of the sedimentation occurs (Milliman, 1993), is needed.

Global cycles. The ability to reproduce global patterns and vertical gradients of elements (C, N, P, O_2, Si, and Fe) is a stringent test of the model. Global cycles integrate all major biological, chemical, and physical processes and, thus, they magnify all possible

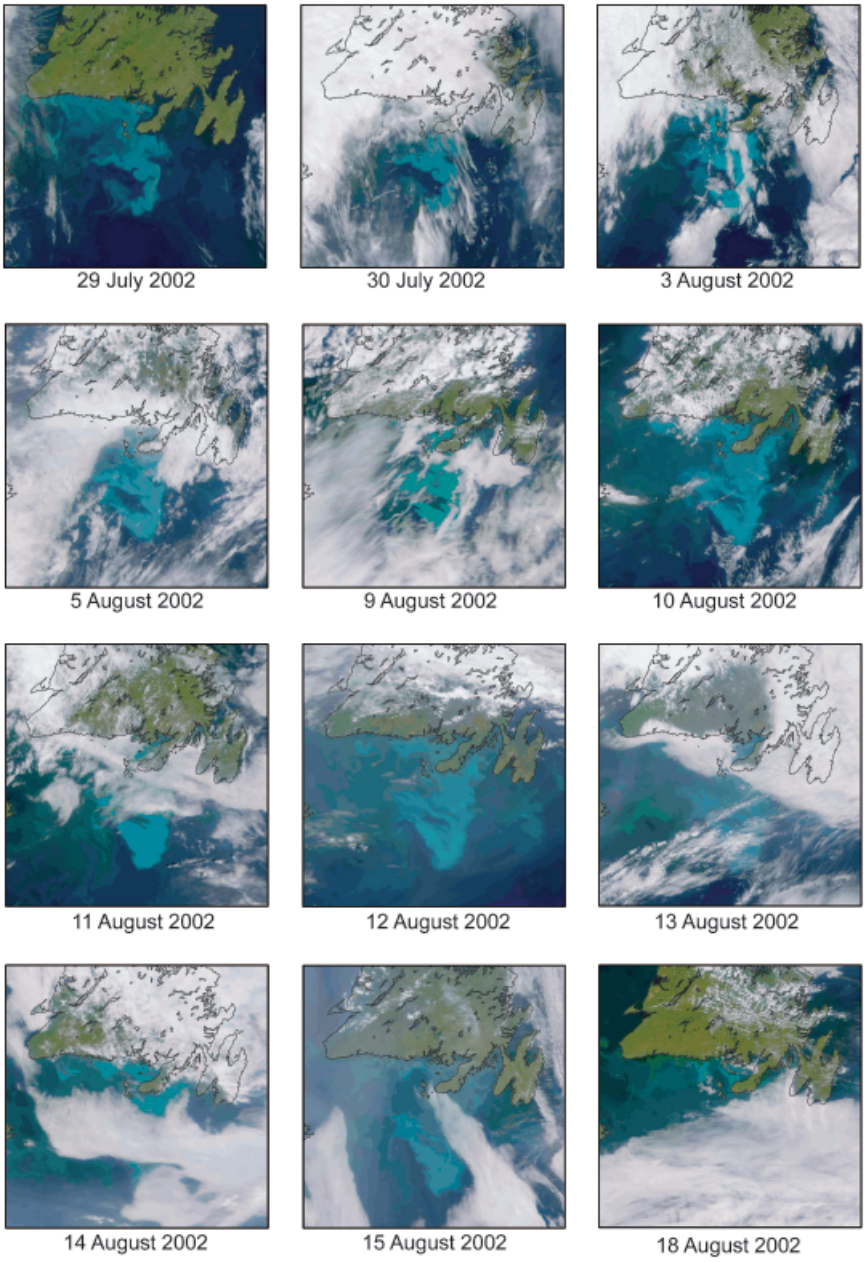

Fig. 5 Time evolution of a calcifiers bloom South of Newfoundland during the summer of 2002. The scenes are SeaWiFS images processed at the Bedford Institute of Oceanography.

uncertainties. They are also extremely useful, in particular, as indicators of the behavior of the ocean interior in the model. The remineralization length scale is shallower for N and P than for C, and Si is dissolved deeper in the ocean than $CaCO_3$. Partly as a result of these different length scales, the vertical profiles of P/N, C, TALK, and Si have maxima at depths of 1000, 2000, 3000 m, and at the bottom, respectively (Fig. 6). This influences the relative supply of Si by ocean mixing compared with that of N and P. The GEOTRACES program (http://www.ldeo.columbia.edu/res/pi/geotraces/) will yield and give rise to global data online that can be used as a validation of modern model simulations in the next few years.

Other ocean tracer analyses, such as correlations between chl*a*, sea surface temperature (SST), and sea surface height (SSH) for various time scales, have been used to determine the relative importance of physical, biological, and thermodynamic processes in controlling ocean biogeochemical cycles (Gruber *et al*., 2002; Le

Quéré *et al.*, 2002; Takahashi *et al.*, 2002). Such an analysis may be useful to ensure that the model reproduces the correct underlying process, and not only the observations.

Paleo conditions

In principle, paleooceanographic data may provide a record of the presence and relative abundance of individual PFTs through time. In practice, the paleooceanographic record represents what is delivered to the seafloor, and the surface water abundances must be reconstructed from the seafloor signal. Most analyses have focused on determining changes in the species assemblages within single functional types. It is therefore difficult to estimate how abundances of PFTs change. Information on the presence/absence of a given PFT at specific times may be useful for model evaluation. However, a comprehensive and global validation data set on PFT distributions is not currently available.

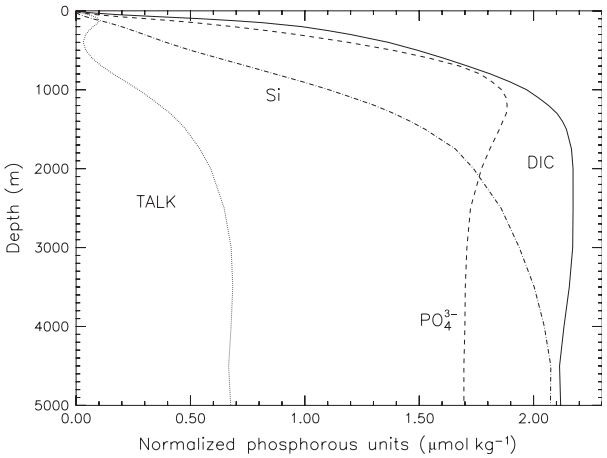

Fig. 6 Global mean profiles of PO_4^{3-}, Si, DIC, and TALK concentrations relative to surface values and normalized to P units using a P:C:Si ratio of 1:122:55. PO_4^{3-}, and Si data are from the World Ocean Atlas 2001 (Conkright *et al.*, 2002), DIC and TALK data are from Key *et al.* (2004).

Several paleooceanographic studies have reconstructed surface paleo primary productivity, based on single PFT assemblages and organic carbon contents (see Kohfeld *et al.* (2005) for an extensive list of references). However, most of these analyses have used transfer function equations to empirically relate species assemblages to single surface ocean characteristics such as temperature. In reality, sediment assemblages are controlled by multiple surface ocean conditions (including the PFT assemblage), as well as remineralization and degradation processes in the water column and sediment. Therefore, a potentially more fruitful approach would be to use a prognostic model to directly simulate the tracers for which observations are available.

A number of different measures have been used as indicators of total export, including fluxes of organic carbon, opal, carbonate, alkenones, ^{231}Pa, ^{10}Be, barium, authigenic uranium, cadmium, and benthic foraminifera (Wefer *et al.*, 1999). We have synthesized available data on changes in export (Bopp *et al.*, 2003;

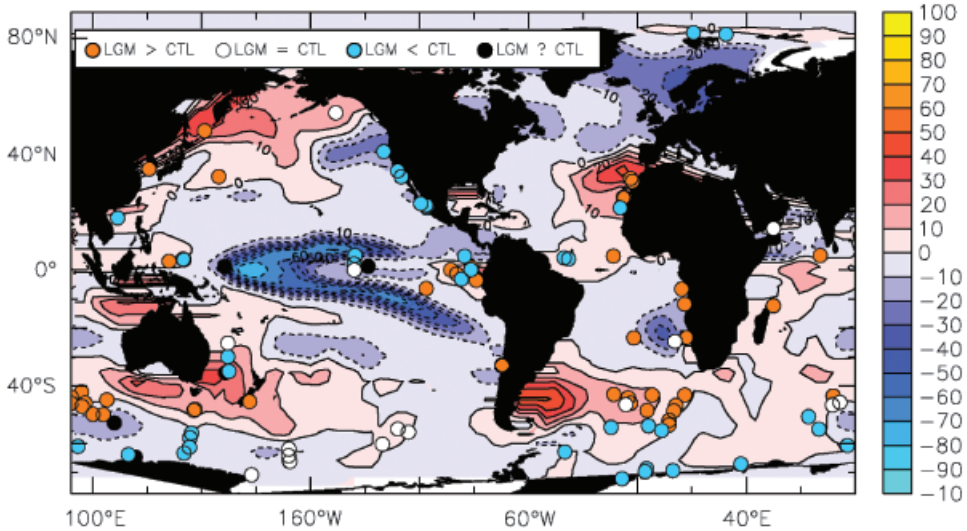

Fig. 7 Observed (superimposed circles) and modeled changes in biological export at the Last Glacial Maximum compared with the late Holocene (Bopp *et al.*, 2003). Model results are in percent. Observations are qualitative only and indicate an increase (red), decrease (blue), or similar (white) export for the two time periods.

Kohfeld *et al*., 2005) between the LGM and the Holocene based on a consensus interpretation of all the indicators measured at a given core location. The LGM data set (Fig. 7) includes 148 sites worldwide and shows consistent patterns of change. Export was globally higher during the LGM than at present, except in the Southern Ocean and parts of the North Pacific. Some regions, however, were poorly constrained, either because of an insufficient data-coverage or because of conflicting evidence between the proxies.

Model results

The current version of our DGOM is based on the PISCES biogeochemistry model (Bopp *et al*., 2003), which is a modification of the HAMOCC5 model (Aumont *et al*., 2003) adapted to the OPA general circulation model (Bopp *et al*., 2002). PISCES includes four PFTs: Silicifiers, mixed-phytoplankton, proto-, and meso-zooplankton. Phytoplankton growth is colimited by nutrient availability (P, Si, Fe) and light. PISCES simulates surface chl*a* patterns that are closer to the observations than simpler NPZD models (Fig. 8), mainly because of the explicit representation of Fe fertilization from atmospheric dust.

We used the PISCES model to simulate the impact of increased dust deposition during the LGM (Bopp *et al*., 2003). In simulations where dust was changed to the LGM value but the climate fields were kept the same as in the modern simulation, the abundance of silicifiers increased, leading to an increase in carbon export by ca. 6%, but the primary production was similar to its present value. However, when the PISCES model was rerun using SST, winds and fluxes, and sea ice extent from an LGM simulation, export decreased by 7% in response to decreased equatorial upwelling and high-latitude stratification. The model was able to reproduce the large-scale patterns of changes in export consistent with paleo-environmental evidence, although the boundaries between regions where export increased and regions where it decreased were sharper in the observations, especially in the Southern Ocean. The observations available were insufficient to evaluate the large decrease in modeled export in the western Equatorial Pacific and Northern Atlantic oceans (Fig. 7).

We modified the PISCES model to include phytoplankton calcifiers. Preliminary results from this DGOM do not affect the mean surface chl*a*, but lead to significant changes in its interannual variability (Figs 8 and 9) (Prentice *et al*., 2004). Neither model is able to reproduce the observed pattern in chl*a* variability (Fig. 9). In the observations, variability is proportional to the mean chl*a*. In the NPZD and PISCES models, chl*a* variability is generally high at low chl*a*, and nearly zero at high chl*a* concentrations. The DGOM behaves slightly differently. It has high variability in the equatorial Pacific where chl*a* is relatively high. An analysis of the DGOM simulation shows that the high chl*a* variability is related to the presence of phytoplankton calcifiers, which respond much faster to changes in P concentration than other PFTs.

In the current version of our DGOM, calcifiers grow between 40°N and 40°S but they are almost absent poleward of these latitudes. In reality, however, blooms of calcifiers are observed in the 40°–70° latitude band of both hemispheres (Fig. 10). The traits defined for calcifiers and the zooplankton that graze them (Table 2)

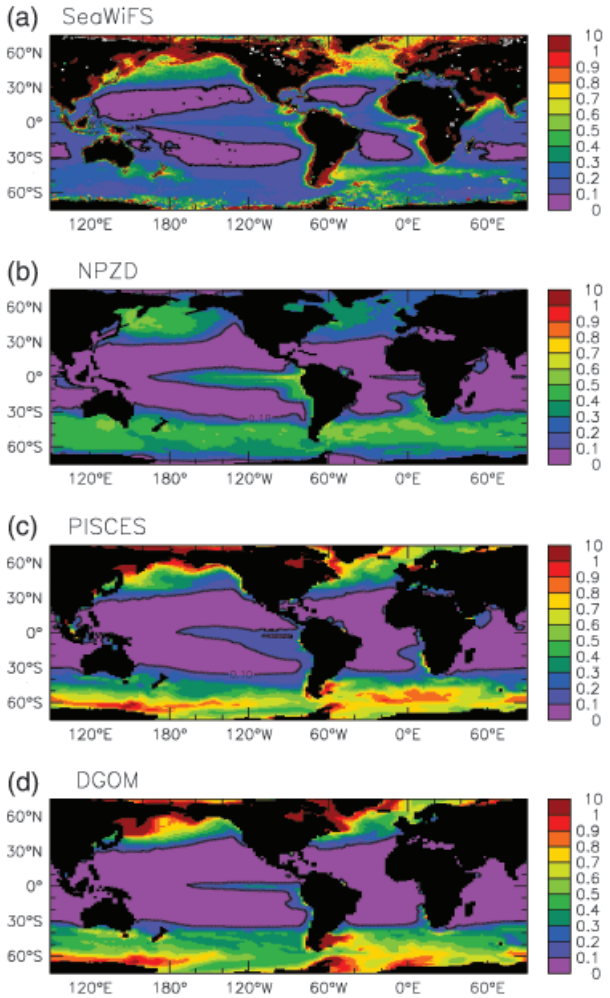

Fig. 8 Annual mean concentration of chl*a* in mg m^{-3} (a) derived from SeaWiFS satellite, and modeled by (b) an Nutrient–Phytoplankton–Zooplankton–Detritus (NPZD) model, (c) PISCES model with four plankton functional types (PFTs), and (d) a Dynamic Green Ocean Model (DGOM) with five PFTs.

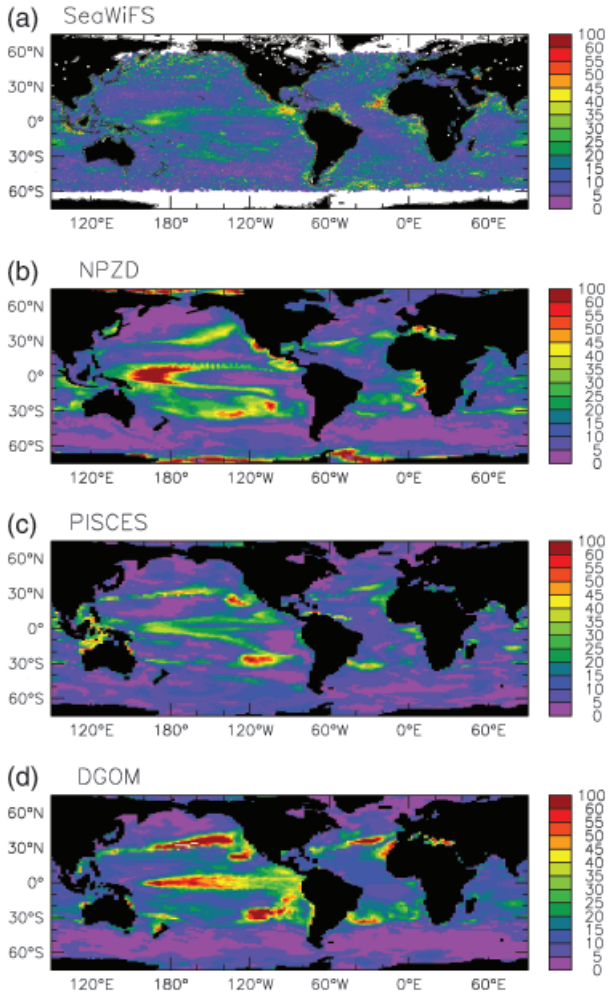

Fig. 9 Root-mean-square of chl*a* interannual variability in percent (a) derived from SeaWiFS satellite, and modeled by (b) an Nutrient–Phytoplankton–Zooplankton–Detritus (NPZD) model, (c) PISCES, and (d) a Dynamic Green Ocean Model (DGOM). The seasonal signal is removed by doing a 12-month running mean.

in the current version of the DGOM do not give calcifiers a competitive advantage at high latitudes: they have a lower maximum growth rate than other PFTs, higher light affinity, and lower resistance to darkness. Calcifiers are advantageous where P concentrations are low and where Fe is limiting, but this is not the case at least in the high latitudes of the North Atlantic Ocean. This indicates that our knowledge of the behavior of calcifiers is incomplete, which could mean that the traits of calcifiers need to be revised, or that they have protective defenses against zooplankton grazing (Strom *et al.*, 2002).

Modeling work has shown that the presence of phytoplankton biomass could warm the local temperature of the ocean by up to 4 °C (Sathyendranath *et al.*, 1991). Using the DGOM in an ocean model incorporated with reanalyzed winds and fluxes, we estimated that the presence of phytoplankton biomass at the ocean surface could account for a warming of the SST by 0.5 °C, stratify the surface ocean by 50 m, melt the sea ice by 5%, and increase surface chl *a* by 0.1 mg m^{-3} (Fig. 11, from (Manizza *et al.*, 2005)).

Sensitivity studies with the DGOM highlight parameters that have fundamental impacts on the simulated ocean biogeochemistry, and that need to be assigned a high priority. The surface biomass of phytoplankton is mostly determined by ocean physics, but the composition of the ecosystem is mostly determined by the physiological parameters of growth and loss. The difference in maximum growth rate between the PFTs is a critical parameter. A proportional change in the maximum growth rate for all PFTs only leads to small changes in the biogeochemistry. However, in our model, when the relative maximum growth rates are changed, the marine export is radically changed and all other biogeochemistry fields are affected. Likewise, a change in the zooplankton preference for the PFTs has an impact on particle size distributions and, thus, on the surface-to-depth export of carbon.

Priorities

The efforts and resources needed to develop a DGOM are large and should be pursued on a long-term basis. To aid in this task, we have identified three elements, which we consider should be treated with high priority:

- Compilation of published results to derive PFT traits on a global scale. The information for four PFTs (silicifiers, N_2-fixers, DMS producers, and picoautotrophs) was synthesized as part of the IRONAGES project (LaRoche & Breitbarth, 2005; Sarthou *et al.*, 2005; Schoemann *et al.*, 2005; Veldhuis *et al.*, 2005), but considerable scatter exists in the information. A similar effort is necessary for the other PFTs. Much more field observations are needed. Growth conditions (nutrients, light) of phytoplankton can be studied independent of zooplankton, and meanwhile, are relatively well understood. On the other hand, the grazing of phytoplankton and detritus by zooplankton is at least as important, but much more difficult to study and thus needs more attention in future investigations.
- Compilation of data to evaluate modeled PFT biomass and productivity for the present and the LGM. A database has been put together for mesozooplankton (Beaugrand *et al.*, 2002; O'Brien *et al.*, 2002; Finenko *et al.*, 2003) and bacteria (Rivkin &

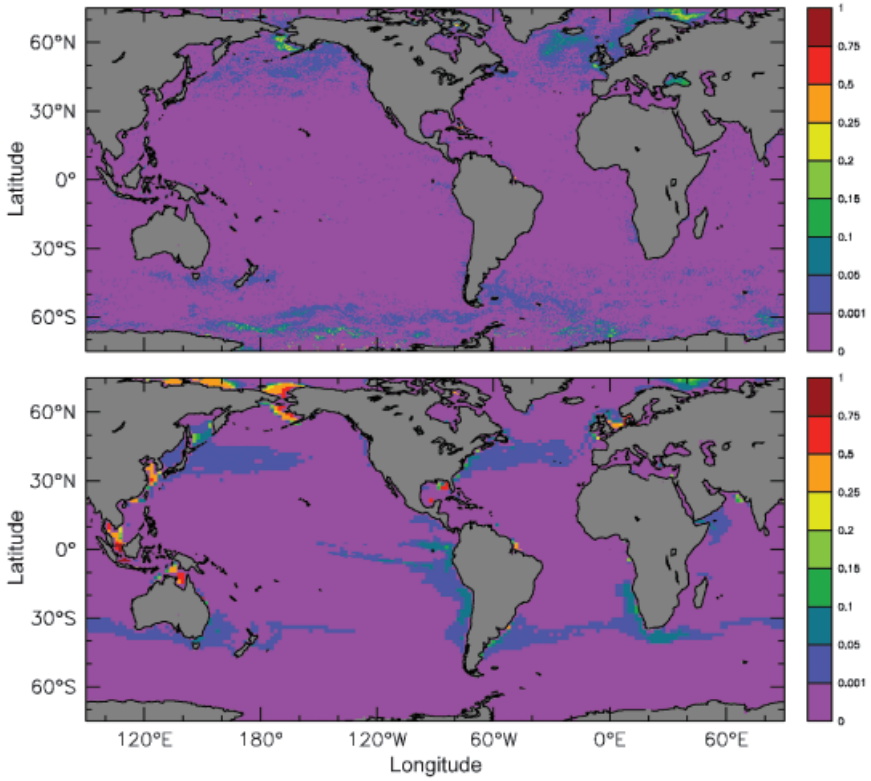

Fig. 10 Frequency of coccolithophorid blooms estimated (top) using SeaWiFS data processed by C. Brown (personal communication) based on method by (Brown & Yoder, 1994)) and (bottom) from the current version of our Dynamic Green Ocean Model (Prentice *et al.*, 2004).

Legendre, 2001, 2002). Some work has already been carried out for other PFTs, and need to be completed with more extensive data coverage (Table 3). Approaches based on satellite observations are also promising from simple size classes (Loisel *et al.*, 2002; Uitz *et al.*, 2005) up to crude classification (Alvain *et al.*, 2005), calibrated by *in situ* observations. A semi-quantitative synthesis of changes in export between the LGM and present has also been made (Bopp *et al.*, 2003; Kohfeld *et al.*, 2005). Initial analyses suggest that it may be possible to derive quantitative estimates for individual PFTs, and specifically for phytoplankton calcifiers based on alkenone measurements (T. Rosell-Mel, personal communication). However, more effort is required in this area.

- Improved theoretical understanding of the biogeochemical processes driving the growth and fate of PFTs in the ocean. This long-term effort may help to reduce the number of PFTs or traits needed to reproduce the fundamental behavior of marine ecosystems.

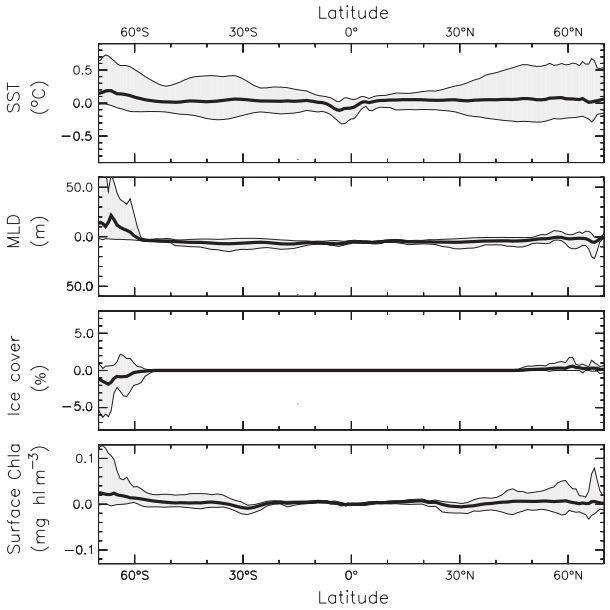

Fig. 11 Yearly (thick lines) and maximum monthly mean (shaded) change in physical properties of the ocean caused by the presence of phytoplankton biomass (Manizza *et al.*, 2005).

Conclusion

The development of a new generation of ocean biogeochemistry models based on PFTs will allow us to revisit a number of questions regarding the role of marine ecosystems in climate. The behavior of marine ecosystems in DGOMs is much more flexible than that of the current generation of ocean biogeochemistry models. The first model simulations over the past decade already show that the potential influence of marine ecosystems on greenhouse gases and aerosols could be much larger than currently assumed. The additional complexity necessary in DGOMs, however, requires a better coordination of research efforts among biologists, geochemists, and biogeochemical modelers to build a model that reproduces the right behavior of marine ecosystems for the right reasons. We argued here that this is feasible in the near future. We highlighted the current state of knowledge and some of the gaps in our understanding, and laid out a strategy to build such a model. We believe this effort will trigger international collaboration across disciplines.

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