Integrating functional diversity, food web processes, and biogeochemical carbon fluxes into a conceptual approach for modeling the upper ocean in a high-CO_2 world

Louis Legendre
Villefranche Oceanography Laboratory, BP 28, Villefranche-sur-Mer, France

Richard B. Rivkin
Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland, Canada

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[1] Marine food webs influence climate by channeling carbon below the permanent pycnocline, where it can be sequestered. Because most of the organic matter exported from the euphotic zone is remineralized within the "upper ocean" (i.e., the water column above the depth of sequestration), the resulting CO_2 would potentially return to the atmosphere on decadal timescales. Thus ocean-climate models must consider the cycling of carbon within and from the upper ocean down to the depth of sequestration, instead of only to the base of the euphotic zone. Climate-related changes in the upper ocean will influence the diversity and functioning of plankton functional types. In order to predict the interactions between the changing climate and the ocean's biology, relevant models must take into account the roles of functional biodiversity and pelagic ecosystem functioning in determining the biogeochemical fluxes of carbon. We propose the development of a class of models that consider the interactions, in the upper ocean, of functional types of plankton organisms (e.g., phytoplankton, heterotrophic bacteria, microzooplankton, large zooplankton, and microphagous macrozooplankton), food web processes that affect organic matter (e.g., synthesis, transformation, and remineralization), and biogeochemical carbon fluxes (e.g., photosynthesis, calcification, respiration, and deep transfer). Herein we develop a framework for this class of models, and we use it to make preliminary predictions for the upper ocean in a high-CO_2 world, without and with iron fertilization. Finally, we suggest a general approach for implementing our proposed class of models.

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1. Introduction

[2] The ocean makes up about 70% of the Earth surface and has an average depth of 4000 m. The light-dependent production of organic matter, which takes place in the illuminated surface layer (called the "euphotic zone"; typically ~100 m or less, i.e., <2.5% of the ocean's volume), supports most life in the ocean. The waters below the euphotic zone and down to 1000 m are the most important ocean area for the decomposition, recycling and transformation of this organic matter. Most global climate change research programs and models have considered state variables and processes occurring primarily in the euphotic zone [e.g., *Fasham*, 2003; *Boyd and Doney*, 2003], and have thus sometimes neglected crucial feedbacks to the regulation of global primary production and ocean-atmosphere interactions.

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[3] There are various terms used to describe the different depth strata in the ocean, each corresponding to different criteria. The upper 1000 m of the water column can be divided based on either metric depths, i.e., the epipelagic layer (0–150 m) and the mesopelagic layer (150–1000 m), or photic depths, i.e., the euphotic zone (down to 1% of surface irradiance, corresponding to the zone in which net photosynthesis takes place) and the disphotic zone (in which irradiance is too low for net photosynthesis, but sufficient to influence vision by animals). In recent years, the term "twilight zone" has used to identify the water column below the euphotic zone, from ~100 to 150 m down to about 1000 m. An important depth horizon for climate issues is the maximum depth of the winter mixed layer, also called permanent pycnocline (see below). The depth of the permanent pycnocline, which is typically within the mesopelagic layer, generally varies with latitude being shallower at lower latitudes [e.g., *Oschlies and Kähler*, 2004, Table 4a]. In middle and high latitudes from spring through autumn, a

seasonal pycnocline develops above the permanent pycnocline. In this paper, we refer to the layer between the surface and the permanent pycnocline as the "upper ocean."

[4] Remineralization of organic compounds within the mesopelagic layer and the subsequent upward reflux of dissolved inorganic nutrients are critical in controlling primary production on global change timescales. Remineralization is difficult to quantify, especially in the mesopelagic layer, and remains poorly characterized throughout the entire water column. The depth dependence of nutrient remineralization and its controlling factors for various nutrients are important components of biogeochemical models. Global models do not yet adequately represent remineralization processes. Linkages between the euphotic zone and the underlying waters have important roles in regulating the rates of degradation and the remineralization length scales of the organic material that is transported to depth. Differential remineralization of nutrients may lead to decoupling the cycles of C, N, P, Si and Fe in the water column. This, in turn, could lead to changes in the distributions of growth-limiting nutrients and to subsequent ecosystem shifts [e.g., *Karl*, 1999]. The relation of remineralization depth to the vertical scales of stratification, circulation, and isopycnal ventilation to the surface or the ocean's interior determines the timescales of nutrient sequestration and reflux.

[5] The production of organic carbon by phytoplankton and calcification by planktonic organisms, followed by transport of organic matter and carbonates to the ocean's interior and by diffusion of atmospheric CO_2 in the surface ocean is known as the "biological carbon pump" [*Volk and Hoffert*, 1985]. In order to predict the interactions and feedbacks between the biological pump and climate, we must quantify the vertical transport of biogenic carbon to the depth of sequestration. Sequestration typically occurs when carbon sinks (or is advected) below the depth of the permanent pycnocline, where it would be prevented (for centennial timescales) from being ventilated or mixed back to the surface where it could reequilibrate with the atmosphere. This means that the relevant process for climate change is not only the downward export of carbon from the euphotic zone, but its sequestration below the permanent pycnocline. Hence the downward transport and remineralization of carbon and nutrients must be considered over the layer that extends from the surface to the depth of sequestration, rather than the more traditional approach that focuses on the downward flux out of the euphotic zone. Although the depth of the permanent pycnocline varies with ocean basin and latitude, for simplicity, we use here the bottom of the mesopelagic layer at (1000 m) as the global average depth of sequestration.

[6] Food web structure controls the flows of energy and chemical elements, and food webs may be described in terms of individual species or functional groups of taxa with similar roles. Ecosystems respond to external forcing factors, such as changes in ocean physical and chemical regimes, and the indirect and direct impacts of human activity, e.g., types and concentrations of nutrients and contaminants, release of climate active gasses, types of fishing and exploitation of living resources, and changes in biodiversity [e.g., *Beaugrand et al.*, 2002; *Chavez et al.*, 2003]. Ecosystem changes will in turn influence the biogeochemical cycling of carbon and nutrients, and ultimately have a strong feedback on the atmosphere and the climate.

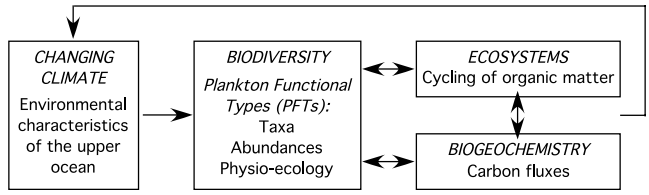

Figure 1. Climate-related changes in the environmental characteristics of the upper ocean will influence the biodiversity (i.e., taxonomic composition, abundances, and physioecological characteristics) of key groups of pelagic organisms (i.e., plankton functional types (PFTs)). To predict interactions between the changing climate and biology in the upper ocean, we propose here a conceptual modeling approach that considers the interactions among the PFTs, ecosystem functioning (i.e., food web processes that affect the cycling of organic matter), and the accompanying biogeochemical fluxes of carbon. Direct effects of environmental characteristics on biogeochemistry (e.g., effects of temperature and CO_2 concentration on carbonate chemistry) are not illustrated in this figure.

[7] In this paper, we propose that the environmental characteristics of the upper ocean determine the taxonomic composition, abundances and physioecological characteristics of the key groups of pelagic organisms (i.e., plankton functional types, PFTs (section 2.1)). The PFTs in turn control both the food web processes that affect the cycling of organic matter (OM (section 2.2)) and the accompanying biogeochemical fluxes of carbon in the upper ocean (section 2.3). On the basis of this general assumption, we develop a conceptual framework for models that combine PFTs, food web processes that affect OM and biogeochemical carbon fluxes, in the upper ocean (section 2.4), to assess the effects of the changing climate on biologically mediated ocean processes (Figure 1). Using this model framework, we discuss the possible effects of climate change–driven modifications in environmental characteristics of the upper ocean in a high-CO_2 world, without and with Fe fertilization, on PFTs, food web processes, and biogeochemical carbon fluxes (section 3). We conclude by discussing studies that are needed to further resolve the most pressing issues, and by reporting ongoing efforts in the direction we propose (section 4).

2. Proposed Framework for Model Development

[8] Existing conceptual and numerical models of the upper ocean generally focus on biodiversity, ecosystem functioning, or the fluxes of chemical elements and associated feedbacks. Because the climate related changes in the upper ocean will influence the diversity and functioning of plankton functional types, relevant models must take into account the roles of functional biodiversity (i.e., species or taxa grouped together based on their ecological or biogeochemical functions) and pelagic ecosystem functioning in determining the biogeochemical fluxes of carbon, in order to predict interactions between the changing climate and the ocean's biology. Models belonging to this class should

Table 1. Size Characteristics of Five Aggregate Plankton Functional Types (PFT), Their Food Resources, and the Primary Contributions That Each PFT Makes to the Food Web Processes That Affect Organic Matter (OM) and the Concomitant Biogeochemical Fluxes of Carbon in the Upper Ocean[a]

PFTs	Groups of Organisms	Sizes of Organisms	Sizes of Food Resources	Food Web Processes That Affect OM	Biogeochemical Carbon Fluxes
Phytoplankton	procaryotic phytoplankton	0.6–1 μm	0.4–0.5 nm	synthesis	photosynthesis
	eucaryotic phytoplankton	1.0–200 μm (2000 μm)	0.4–0.5 nm	synthesis	photosynthesis calcification, deep transport
Heterotrophic bacteria	heterotrophic bacteria	0.2–1.2 μm	0.5–0.7 nm (30 m)	transformation, remineralization	heterotrophic respiration
Microzooplankton	protozoa and larvae of invertebrates	1.5–700 μm	0.2–25 μm	transformation, remineralization	calcification, heterotrophic respiration, deep transport
Large zooplankton	mesozooplankton	1.5–15 μm	5–500 μm	transformation, remineralization	heterotrophic respiration, deep transport
	fish larvae	1–50 mm	0.05–4 mm	transformation, remineralization	heterotrophic respiration
	macrozooplankton	20–200 mm	>200 μm	transformation, remineralization	heterotrophic respiration, deep transport
Microphagous macrozooplankton	microphagous macrozooplankton	10–150 mm	1–500 μm	transformation, remineralization	calcification, heterotrophic respiration, deep transport

[a]Sizes adapted from *Legendre and Rassoulzadegan* [2004]. Abbreviations are as follows: PH, phytoplankton; HB, heterotrophic bacteria; μZ, microzooplankton; LZ, large zooplankton; MM, microphagous macrozooplankton.

consider the interactions among functional biodiversity, ecosystem functioning, and the fluxes of elements and associated feedbacks (Figure 1).

[9] Most existing models of biogeochemical fluxes and marine pelagic ecosystems consider a three-layer water column (i.e., the euphotic zone, the mesopelagic layer or twilight zone and the ocean's interior), variable numbers of plankton functional types or food web processes and/or various biogeochemical carbon fluxes. We propose an approach for a class of models that is based on the integration of a two-layer water column (i.e., above and below the sequestration depth) with recent concepts in food webs, biodiversity and ocean biogeochemistry. Such models should include a minimum of: five plankton functional types (functional biodiversity, i.e., phytoplankton, heterotrophic bacteria, microzooplankton, large zooplankton and microphagous macrozooplankton), three classes of food web processes that affect OM (ecosystem functioning, i.e., synthesis, transformation and remineralization) and four biogeochemical carbon fluxes (fluxes and feedbacks, i.e., net photosynthesis, calcification, respiration by heterotrophs and transport of carbon compounds below the sequestration depth). These are described in the following paragraphs. Our proposed framework provides the bases for developing models for the whole upper ocean.

[10] Numerical models based on the framework we propose will be depth resolved for all variables, including physical (e.g., vertical distributions of temperature and salinity, and vertical movements) and chemical (e.g., vertical distributions of chemical species and rates) properties. As noted above, biogeochemical and food web models generally consider a two-layer or a three-layer water column. In three-layer water column models, food web processes and/or biogeochemical carbon fluxes are represented explicitly for the euphotic zone, whereas general equations are applied to describe vertical changes in food web and/or biogeochemical properties below, i.e., in the mesopelagic layer and the ocean's interior (e.g., the equation of *Betzer et al.* [1984], describing the decreasing particle flux with depth). In other words, three-layer models do not explicitly represent processes and/or fluxes below the euphotic zone. In two-layer water column models, food web processes and/or biogeochemical carbon fluxes are explicitly represented from the surface down to the depth of sequestration, and possibly below in the ocean's interior. The present papers advocates using a generic two-layer model.

2.1. Plankton Functional Types (PFTs)

[11] The sizes of both pelagic organisms and their food resources largely determine the food web processes that affect OM cycling, and the biogeochemical fluxes of carbon within and from the upper ocean [e.g., *Legendre and Michaud*, 1998; *Legendre and Rassoulzadegan*, 2004] (see http://www.eolss.net). Table 1 summarizes the size characteristics of PFTs and of their food resources (or substrates for osmotrophs), and identifies their major contributions to food web processes and biogeochemical carbon fluxes. The PFTs used in models are generally based on a combination of sizes and ecological functions of groups of organisms. The functions considered vary with the objectives of the specific models (e.g., food web functioning, or biogeochemical fluxes), and will therefore differ among models [e.g., *Le Quéré et al.*, 2005, and references therein]. More comprehensive descriptions of the ecophysiological and biogeochemical roles of PFTs can be found elsewhere [e.g., *Claustre*, 1994; *Falkowski et al.*, 1998, 2003; *Iglesias-Rodríguez et al.*, 2002; *Bouman et al.*, 2003; *Le Quéré et al.*, 2005].

[12] The conceptual model proposed here explores the controls exerted by planktonic organisms on food web processes (section 2.2) and biogeochemical carbon fluxes (section 2.3) in the upper ocean. In order to simplify the discussion, we grouped the planktonic marine organisms into five aggregate PFTs (first column of Table 1). Four of our aggregate PFTs concern heterotrophs, because these organisms transform the OM synthesized by phytoplankton and channel the carbon into various biogeochemical fluxes.

[13] Numerical models generally include more PFTs than our five aggregates [e.g., *Le Quéré et al.*, 2005]. PFTs in models may correspond to different size classes or trophic categories, or to groups of organisms that have specific roles in cycling nutrients or climate active gasses (e.g., dimethyl

sulfide; DMS). Defining the key PFTs for a model generally takes into account both the need for sufficient complexity to address specific questions, and the often limited information available for parameterizing the food web or biogeochemical characteristics corresponding to each PFT [*Le Quéré et al.*, 2005]. Details on the sizes and functions of pelagic organisms on which to base the definition of PFTs to be used in models are described in the following paragraphs.

2.1.1. Aggregate PFT 1: Phytoplankton (PH)

[14] Most organic matter in oceans comes from the activity of photosynthetic plankton, which transform small inorganic molecules into particulate and dissolved organic matter (POM and DOM, respectively). Phytoplankton range in size from ~0.6 to 2000 μm (most taxa are ≤200 μm); they often form chains, of sometimes hundreds of cells, and some species may develop into colonies >1 m long (i.e., chains and aggregates of *Melosira* suspended form the sea ice in polar waters). The substrates used by photosynthetic organisms to build up organic molecules are: CO_2, water, and a wide variety of dissolved inorganic (and sometimes organic) compounds. In Table 1, the lower bound of phytoplankton substrates corresponds to the size of the CO_2 molecule (0.4 nm), and the upper bound is the urea molecule (0.5 nm), although some phytoplankton can also use larger (organic) molecules. All phytoplankton can synthesize OM from inorganic compounds, and light. Concerning the biogeochemical carbon fluxes, the contributions to phytoplankton photosynthesis and calcification and to the deep transport of carbon compounds vary with taxa and morphology. Some groups produce siliceous (e.g., diatoms) or calcareous (i.e., coccolithophorids) cell walls or plates, which act as ballast of sinking particles. Phytoplankton are the main calcifying organisms in the ocean, and the calcareous plates of coccolithophorids, called coccoliths, ballast the sinking aggregates and fecal pellets of grazers in which they are incorporated [*Armstrong et al.*, 2002; *Klaas and Archer*, 2002]. The carbon of other phytoplankton groups is transported downward by various mechanisms that include sinking phytodetritus and fecal pellets, and vertically migrating grazers.

[15] Here we have aggregated all autotrophic plankton into a single PFT. This is a clearly an oversimplification since different taxonomic groups often have distinct roles in food web processes and biogeochemical carbon fluxes. Indeed, most models consider several phytoplankton functional types, i.e., at least small and large phytoplankton (the threshold between the two types being generally 1, 2, or 5 μm) and sometimes more; for example, *Le Quéré et al.* [2005] identify the following six phytoplankton PFTs as important to quantify biogeochemical cycles in the ocean: picophytoplankton (0.2–2 μm, e.g., picoeucaryotes, and non N_2-fixing photosynthetic bacteria such as *Synechococcus* and *Prochlorococcus*), phytoplankton N_2 fixers (e.g., *Trichodesmium*, and N_2-fixing unicellular cyanobacteria), phytoplankton calcifiers (e.g., coccolithophorids), phytoplankton DMS producers (e.g., *Phaeocystis*), nanophytoplankton (e.g., autotrophic dinoflagellates, and Chrysophyceae) and phytoplankton silicifiers (e.g., diatoms).

2.1.2. Aggregate PFT2: Heterotrophic Bacteria (HB)

[16] The smallest independent living cells in the sea belong to procaryotes. This group contains *Eubacteria* (i.e., bacteria and cyanobacteria) and *Archaea*. Free-living heterotrophic bacteria range in size from ~0.2 μm to 1.2 μm. Archaea are ubiquitous, but are generally thought to have a higher relative abundance (to bacteria) in extreme (deep or cold) environments [*Fuhrman et al.*, 1992; *Karner et al.*, 2001; *Church et al.*, 2003], which include most of the mesopelagic layer. Since *Archaea* have not been cultured, nothing is known about their physiological characteristics, hence, HB here refers only to *Eubacteria* (excluding cyanobacteria which are functionally part of phytoplankton). Water column bacteria can use directly (i.e., without hydrolysis) molecules as small as ammonia and urea (0.5 nm) and as large as glucose (0.7 nm). Heterotrophic bacteria solubilize larger organic molecules by exoenzymes before their uptake. This mechanism allows heterotrophic bacteria to solubilize all DOM or POM in the sea, including the largest organic "particles," i.e., dead baleen whales 30 m long. Heterotrophic bacteria thus both transform and remineralize the OM. Their main contribution to the biogeochemical cycling of carbon is the remineralization (i.e., respiration) of organic carbon back to CO_2, being responsible for most community respiration in the euphotic zone of oceans [*Sherr and Sherr*, 1996; *Rivkin and Legendre*, 2001].

2.1.3. Aggregate PFT 3: Microzooplankton (μZ)

[17] Protozoa, such as flagellates and ciliates, are the two main groups of organisms that make up the nanozooplankton (2–20 μm) and microzooplankton (20–200 μm). These two size groups are collectively called here "microzooplankton." Microzooplankton generally feed on a narrow size range of particles that are commensurate with their own small sizes. Heterotrophic (and mixotrophic, see below) microflagellates (μ-flagellates) are the main predators of bacteria and picophytoplankton. Their sizes range is between 1.5 and 15 μm, and those of their prey are between 0.2 and 1 μm. Heterotrophic dinoflagellates (15–100 μm) actively ingest phytoplankton, especially single cells and short chains of diatoms smaller (5–25 μm) than themselves [*Lessard and Swift*, 1985; *Jeong and Latz*, 1994; *Sherr and Sherr*, 1994; *Neuer and Cowles*, 1994]. Ciliates (7–700 μm) ingest flagellates, phytoplankton and, in some cases for the smaller ciliates, bacteria [*Sherr and Sherr*, 1987; *Gonzalez et al.*, 1990]. Hence their food particles mostly range in size from 0.6 to 25 μm. Other protozoa include the foraminifers, which have siliceous or calcareous tests. Microzooplankton also include young stages of several planktonic and benthic organisms. These young stages often develop on their yolk reserves, and those that feed ingest particles 0.2–15 μm. Microzooplankton both transform and remineralize the OM. They contribute to several biogeochemical carbon fluxes, i.e., calcification (foraminifers), heterotrophic respiration (all taxa) and the deep transport of organic compounds (mostly sinking calcareous tests of foraminifers, which often dominate the deep sea sediments in warm oceans).

2.1.4. Aggregate PFT 4: Large Zooplankton (LZ)

[18] The large zooplankton include mesozooplankton (200 μm to 20 mm), fish larvae or ichthyoplankton (1–50 mm long) and macroplankton (20–200 mm). Mesozooplankton, which consume phytoplankton and microzooplankton [*Ohman and Runge*, 1994; *Broglio et al.*, 2004], are generally dominated by small pelagic crustaceans, particularly copepods. Mesozooplankton can efficiently feed on particles ranging from 5 to 500 μm (the upper bound approximately corresponds to the size of long phytoplankton

chains). Fish larvae make up a special group of temporary planktonic organisms. The size of larval fish food is 50 μm to 4 mm. Macroplankton include large pelagic crustaceans (e.g., euphausiids) and various groups of gelatinous plankton (e.g., jellyfish, Portuguese man-of-war, ctenophores). Many of these organisms are active predators, which can capture relatively large prey (>200 μm). Large zooplankton both transform and remineralize the OM. They contribute to heterotrophic respiration (all taxa) and the deep transport of organic compounds (mostly vertical migrations, and also sinking fecal pellets).

2.1.5. Aggregate PFT 5: Microphagous Macrozooplankton (MM)

[19] In addition to large zooplankton, the other major consumers of phyto- and microzooplankton are the large planktonic microphages (10–150 mm). These organisms are characterized by their ability to efficiently collect particles more than 5000 times smaller than themselves. They include mucous net feeders (salps, doliolids and pteropods), appendicularians, and a few pelagic crustaceans among which the Antarctic krill (large euphausiid crustaceans; because of their strong swimming ability, these can also be included in the nekton). The range of their food particles includes that of large zooplankton, but it may extend down to 1 μm, hence the resulting range of 1–500 μm [*Fortier et al.*, 1994; *Vargas and González*, 2004]. Microphagous macrozooplankton both transform and remineralize OM. They contribute to several biogeochemical carbon fluxes, i.e., calcification (pteropods), heterotrophic respiration (all taxa) and the deep transport of organic compounds (fast-sinking fecal pellets, and sinking calcareous shells of pteropods).

2.1.6. Other Potentially Important Plankton Functional Type: Mixotrophs

[20] Planktonic organisms that use both photosynthesis and heterotrophic feeding are called mixotrophs. They include cells with chloroplasts that take up organic particles (phagocytosis), such as phytoflagellates, and taxa without chloroplasts that acquire and exploit either whole algal cells (symbiosis) or isolated chloroplasts (pseudosymbiosis). Mixotrophic taxa are found among foraminifers, flagellates and ciliates. For simplicity, we do not consider mixotrophic organisms here as a separate PFT.

2.1.7. Large Pelagic Organisms

[21] The large pelagic organisms include the megaplankton (i.e., gelatinous organisms 0.2–2 m) and the nekton. The latter include the fish, which range in size from a few centimeters (e.g., 2- to 3-cm-long anglemouths) to the 15 m long basking shark and the large nekton (3 to 30 m long), i.e., large fish, most marine mammals (the largest being baleen whales, up to 30 m long) and some large invertebrates (e.g., giant squid, up to 16 m long). These large organisms are not considered here, because their adult stages do not contribute significantly, at the scale of the World Ocean, to the food web processes that affect OM and the biogeochemical fluxes of carbon in the upper ocean.

[22] Figure 2 illustrates the feeding relationships among the five PFTs. Phytoplankton and all heterotrophs produce DOM, which is used by heterotrophic bacteria. Phytoplankton cells are grazed by micro-, large and microphagous zooplankton. Heterotrophic bacteria are preyed upon by microzooplankton (and some microphagous zooplankton; not illustrated).

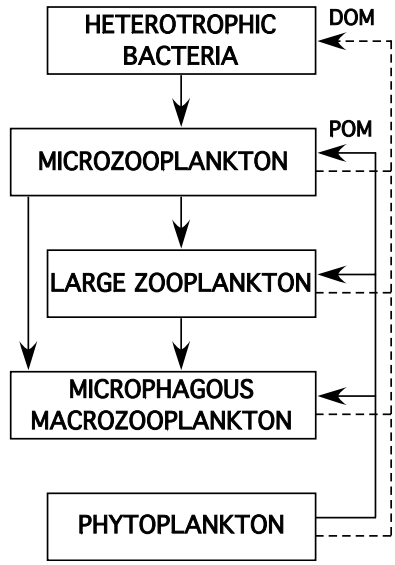

Figure 2. Feeding relationships among the five aggregate PFTs described in the text and tables.

Microzooplankton are eaten by large zooplankton and microphagous macrozooplankton. Some large zooplankton are eaten by microphagous macrozooplankton. All planktonic heterotrophs regenerate inorganic nutrients, which are used by phytoplankton and heterotrophic bacteria.

[23] Among the challenges in defining the minimum number of PFTs to be used in models is that, in some groups of organisms (e.g., zooplankton and fish), the young and adult stages differ in body size by several order of magnitudes. Thus their functions in OM cycling and associated biogeochemical carbon fluxes differ depending on their life cycle stages. One solution to the problem is the "rhomboid approach" of *de Young et al.* [2004], in which biological resolution in the model is concentrated at the level of the target taxon (e.g., representation structured in developmental stages) and decreases with distance up and down the trophic scale. Another general approach is the "trophic continuum model" of *Cousins* [1980, 1985], which combines trophic categories and the sizes of organisms. This approach was implemented by *Moloney and Field* [1991] and *Moloney et al.* [1991] in their model of planktonic marine food webs.

2.2. Food Web Processes That Affect Organic Matter (OM)

[24] The structure and interconnectivity of the pelagic food web influence the cycling and transformation of OM in the upper ocean. Pelagic marine organisms synthesize, remineralize (i.e., change the chemical state from organic to inorganic) and transform OM. When transforming OM, organisms modify the size of OM, and change its bioavailability without changing its chemical state, i.e., the carbon-hydrogen bonds found in essentially all organic material are retained. Changes in size affect the fate of OM, such as in situ recycling *versus* transport to depth. Changes in bioavailability affect both the fate of OM and its recycling (remineralization versus food web transfer). Hence we propose that upper ocean models include at least the three classes of food web processes defined below, and summa-

Table 2. Three Classes of Food Web Processes That Affect OM, Detailed for the Five Aggregate PFTs Defined in Table 1[a]

OM	PH	HB	μZ	LZ	MM
Synthesis	photosynthesis N_2 fixation				
Transformation: size decrease		solubilization of POM	DOM excretion, POM fragmentation	DOM excretion, POM fragmentation	DOM excretion
Transformation: size increase		body mass	body mass, small fecal pellets	body mass, large fecal pellets	body mass, large fecal pellets, clogged houses
Transformation: bioavailability		DOM more refractory			
Remineralization	low	DOM: very high	POM: high	POM: high	POM: low

[a]See text (section 2.2) for details.

rized in Table 2 for each of the five aggregate PFTs types defined in Table 1.

2.2.1. Food Web Process 1: OM Synthesis

[25] The synthesis of OM by phytoplankton (i.e., primary production) is the first step in OM cycling in the upper ocean. Autotrophic phytoplankton use the free energy of sunlight to create chemical reducing potential and fix carbon and other chemical elements (e.g., N, P, Si, Fe) into organic matter. In the upper ocean, OM is synthesized by phytoplankton (net primary production is restricted to the euphotic zone). Primary production in the ocean is generally limited by the supply of bioavailable inorganic elements, and depending on the region and season, primary production can be limited by Fe, Si, N or P. In areas where phytoplankton can reduce N_2 gas to NH_4, they would not be N limited.

2.2.2. Food Web Process 2: OM Transformations by Organisms (Three Types)

[26] The second class of food web processes that affect OM is biotic transformations. This includes changes in both OM size (decrease or increase) and bioavailability. Changes in size may be due to the processing of organic substrate or food by the four aggregate heterotrophic PFTs described in section 2.1 (i.e., phytoplankton synthesize OM, but do not transform it). Two types of processes can cause decreases in OM size: the excretion of DOM by planktonic animals, and the fragmentation of food into smaller particles (e.g., sloppy feeding by planktonic crustaceans). In heterotrophic bacteria, the equivalent process to fragmentation would be the solubilization of POM by the action of exoenzymes. The processes that cause increase in OM size are: incorporation of dissolved or particulate OM into the body masses of heterotrophic organisms, the production of fecal pellets by all planktonic grazers that feed on small organic particles and the shedding of clogged houses by appendicularians (microphagous macrozooplankton). The colonization of transparent exopolymer particles (TEP) and organic aggregates by heterotrophic bacteria initially causes an increase in OM size, but as the aggregates sink, their progressive solubilization due to the action of bacterial exoenzymes leads to a decrease in OM size. Values in Table 3 are examples of the efficiencies of processes involved in OM size transformation, for the aggregate heterotrophic PFTs.

[27] Food web–mediated changes in the bioavailability of OM can occur in two general ways. First, as POM is progressively broken down by the mechanical activities of grazers and the actions of bacterial exoenzymes or digestive enzymes of grazers, the OM material become more labile or bioavailable. Secondly, DOM becomes increasingly refractory because the more labile components are preferentially assimilated by heterotrophic bacteria. As the DOM ages with the sinking or downward advection of water masses, the ratio of labile to refractory DOM decreases with depth. Since the growth efficiency (GE) of bacteria is lower when organic substrates are more refractory (i.e., higher C:N ratio or fulvic and humic acid content [*Kroer*, 1993; *Jørgensen et al.*, 1994; *del Giorgio and Cole*, 1998]), the fraction of the substrate that is remineralized to CO_2 vs. assimilated increases with depth.

2.2.3. Food Web Process 3: OM Remineralization

[28] The third food web process that affects OM is remineralization of OM back to CO_2 (i.e., respiration) and inorganic nutrients. All living organisms, both autotrophic and heterotrophic, generate metabolic energy from catabolic metabolism, and for most aerobic organisms, reducing energy is produced during respiration. This leads to the remineralization of organic carbon back to CO_2, and in the case of organic nitrogen (i.e., proteins and amino acids), the release of NH_4 and urea. The latter are nutrients assimilated by phytoplankton and sometimes bacteria [*Kirchman*, 2000]. Table 4 summarizes available information for the respiration process. Here we define remineralization efficiency as $1 - GE$. In oceans, GE is influenced by a number of factors, which include temperature and substrate quality; generally GE is an inverse function of temperature. Phytoplankton respiration is generally of the order of 10–20% of gross primary production [e.g., *Cloern et al.*, 1995]. The organic substrate used by heterotrophic bacteria is DOM, and at temperatures ranging from 5° to 25°C, bacteria release

Table 3. Efficiency of the Four Food Web Processes That Transform OM[a]

Transformation Processes	HB	μZ	LZ	MM
DOM excretion	0	0.40	0.05	0.05
Fragmentation	0.75	0.10	0.20	0
Body mass	0.25	0.30	0.35	0.40
Fecal pellets and houses	0	0.20	0.40	0.55
Increase (total)	0.25	0.50	0.75	0.95

[a]These processes are mediated by the aggregate PFTs defined in Table 1. Phytoplankton are omitted from this consideration because they synthesize OM but do not transform it. Because the four processes are collectively responsible for all changes in OM size, the sum of transformation efficiencies in each column is 1.0. It is assumed here that the substrate or food processed by each PFT are excreted as dissolved organic matter (DOM), decomposed or fragmented (for heterotrophic bacteria, this corresponds to solubilization of particles), incorporated into body masses, or egested as fecal pellets (the latter includes here the shedding of clogged houses by appendicularians). DOM excretion and OM fragmentation cause OM size decrease. The incorporation into body mass and fecal pellet formation causes size increase. The last row in the table is the transformation efficiency of the two processes causing OM size increase, i.e., the sum of the two rows immediately above. Values in the table are examples of possible values.

Table 4. Carbon Remineralization Efficiency of the Aggregate Five PFTs Defined in Table 1, Estimated at Three Temperatures[a]

Temperature, °C	PH	HB	μZ	LZ	MM
5	0.05	0.68	0.41	0.61	0.71
15	0.10	0.78	0.55	0.64	0.75
25	0.15	0.89	0.69	0.68	0.77

[a]Remineralization efficiencies for phytoplankton were based on respiration = 0.1 gross primary production (see text). Growth efficiency was computed from the temperature versus growth efficiency relationships for heterotrophic bacteria and microzooplankton as reported by *Rivkin and Legendre* [2001] and for large zooplankton (here copepods) as reported by *Ikeda et al.* [2001] (recalculated from their Table 1 and Figure 4). Growth efficiencies for microphagous macrozooplankton (here appendicularians) are a personal communication from F. Lombard, A. Sciandra, and G. Gorsky (Laboratoire d'Océanographie de Villefranche, unpublished model results).

between 70 and 90% of the ingested carbon as CO_2, respectively. Although some microzooplankton can directly assimilate small amounts of DOM [*Tranvik et al.*, 1993], most of their nutrition is from POM. At temperatures ranging from 5° to 25°C, microzooplankton release between 40 and 70% of the ingested carbon as CO_2, respectively. Comparable values are 60 and 70% for copepods (large zooplankton) and 70 and 75% for appendicularians (microphagous macrozooplankton).

[29] Figure 3 illustrates the relationship between two of the above food web processes that affect OM, i.e., size increase and remineralization by the four aggregate heterotrophic PFTs. The *x* axis is the transformation efficiency of food resources leading to an increase in OM size; it is the sum of the efficiencies of processes causing increase in OM size. The corresponding values are in the last row of Table 3. The *y* axis is remineralization efficiency (i.e., 1 − GE). The corresponding values, at three temperatures, are in Table 4. This figure shows that the transformation efficiency of food (or substrate for bacteria) leading to increased OM size rank orders the four heterotrophic PFTs in the same way as in Figure 2, whereas remineralization orders them differently. The functional relationship between food web functioning (i.e., feeding relationships among PFTs (Figure 2)) and the food web processes that affect OM (Figure 3) is therefore complex. Figure 3 will be further developed in section 2.4.

2.3. Biogeochemical Carbon Fluxes

[30] There are several reactive compounds that are exchanged between the ocean and the atmosphere that are of significance to climate (e.g., CO_2 of atmospheric and marine origins, volatile organic halides, DMS produced by pelagic marine organisms). However because the scope of this paper is the upper ocean and the cycling of these compounds except carbon takes place in the euphotic zone, the present discussion of biogeochemical fluxes will only consider carbon.

[31] Pelagic marine organisms produce carbon compounds that are both organic (POC and DOC) and inorganic (mostly $CaCO_3$), respire part of the organic compounds within the upper ocean and contribute to the deep transfer of the organic and inorganic materials. We propose that upper ocean models include at least the four biogeochemical carbon fluxes summarized in Table 5, for the five aggregate PFTs defined in Table 1.

2.3.1. Biogeochemical Carbon Flux 1: Net Photosynthesis

[32] Phytoplankton net photosynthesis transforms dissolved inorganic carbon (DIC) into organic carbon (POC + DOC). Because of technical constraints, the field estimates of phytoplankton production are generally net of respiration. Hence the corresponding biogeochemical carbon flux is net photosynthesis. Seawater contains more DIC in the forms of HCO_3^- and CO_3^{2-} than CO_2, which is the inorganic carbon species used in the photosynthetic process. Some plants can transport HCO_3^- ions into the cell, where it is transformed into CO_2 and used in the Calvin cycle to form organic carbon, but most phytoplankton cannot. Hence even if phytoplankton photosynthesis is not generally limited by the availability of DIC, it has been proposed that during dense blooms, phytoplankton may at times become limited by the availability of CO_2 [e.g., *Riebesell et al.*, 1993]. According to environmental conditions and the physiological state of phytoplankton, the amount of DOC exuded by phytoplankton ranges from <10 to >50% of net primary production [*Falkowski and Raven*, 1997].

2.3.2. Biogeochemical Carbon Flux 2: Calcification

[33] During calcification, the precipitation of $CaCO_3$ is accompanied by the release of CO_2. It is sometimes assumed that the ratio of CO_2 evasion to $CaCO_3$ precipitation (Ψ) equals 1, but in the highly buffered seawater, Ψ cannot exceed 0.6 [e.g., *Frankignoulle et al.*, 1994]. Because calcification is often accompanied by the photosynthetic uptake of CO_2 and other biological processes, generally $\Psi <$ 0.6 [e.g., *Copin-Montégut and Copin-Montégut*, 1999]. In any case, because $\Psi > 0$, there is net evasion of CO_2 from the ocean to the atmosphere. The main planktonic marine calcifiers are coccolithophorids (phytoplankton), foramini-

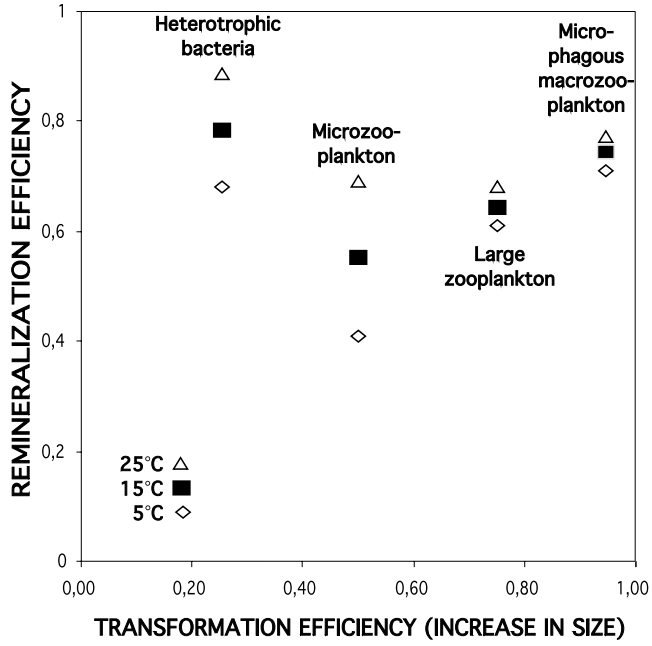

Figure 3. Positions of the four aggregate heterotrophic PFTs in a diagram summarizing two food web processes that affect organic matter, i.e., transformation due to the processing by organisms and remineralization, at three temperatures.

Table 5. Four Biogeochemical Carbon Fluxes, Detailed for the Aggregate Five PFTs Defined in Table 1

C Fluxes	PH	HB	μZ	LZ	MM
Photosynthesis	DIC → OC				
Calcification	coccolithophorids		foraminifers		pteropods
Heterotrophic respiration	net photosynthesis	DOC: very high	POC: quite high	POC: high	POC: low
Deep transfer: OC	phytodetritus			seasonal migrations	fecal pellets
Deep transfer: $CaCO_3$	coccoliths		foraminifer tests		pteropod shells

fers (microzooplankton; protists) and pteropods (microphagous macrozooplankton; mollusks).

2.3.3. Biogeochemical Carbon Flux 3: Heterotrophic Respiration

[34] Respiration is the catabolic counterpart of photosynthesis, by which living organisms produce metabolic energy from the progressive oxidation of organic carbon. Thus reduced organic carbon is oxidized to CO_2. Although all living organisms respire, because the field estimates of phytoplankton production are net of respiration, the biogeochemical carbon flux considered here is heterotrophic respiration. Table 6 presents estimates of the fraction of net primary production that is respired by the four aggregate heterotrophic PFTs in the upper ocean, at three representative temperatures. This table shows the dominant role of heterotrophic bacteria in the respiration of phytoplankton production over the upper ocean, irrespective of temperature.

2.3.4. Biogeochemical Carbon Flux 4: Deep Transfer of Organic Carbon and $CaCO_3$

[35] Mechanisms involved in the transfer of organic compounds below the permanent pycnocline include the downward transport of DOC, sinking of phytodetritus, vertical migrations of large zooplankton, and sinking of fecal pellets. DOC is transported downward by vertical mixing [*Copin-Montégut and Avril*, 1993; *Carlson et al.*, 1994; *Williams*, 1995; *Emerson et al.*, 1997; *Alldredge*, 2000], or laterally (isopycnal transport) from higher to lower latitudes [*Hansell and Carlson*, 1998]. Because these transport mechanisms are not biologically controlled, they are not discussed here. Sinking phytodetritus often include nutrient limited and/or aggregated phytoplankton. Because diel vertical migrations mostly occur within the upper ocean, they do not generally contribute significantly to the sequestration of organic carbon. However, in areas where the permanent pycnocline is shallow (e.g., some tropical waters), zooplankton may migrate daily below the upper ocean (e.g., see *Andersen et al.* [1997] for macroplankton and micronekton in the tropical Atlantic), so that the vertical flux of their respiratory carbon may contribute to sequestration [e.g., *Longhurst et al.*, 1990]. In contrast, deep (i.e., ontogenetic) seasonal migrations transfer organic carbon below the upper ocean, where there it may degraded and respired by microbes. The remineralization of plankton carcasses leads to the sequestration of CO_2 in deep waters [*Legendre and Rivkin*, 2002, and references therein]. The fecal pellets of many large zooplankton (e.g., copepods) sink, but because of their relatively low settling velocities ($\sim$100 m d^{-1}), they are usually largely ingested (coprophagy) or fragmented (coprohexy) by zooplankton, or degraded by bacteria in the upper few hundred meters. This results in the release of most of the fecal carbon as DOC, or its remineralization to CO_2 above the permanent pycnocline [*Fortier et al.*, 1994, and references therein]. In contrast, the fecal pellets of some microphagous macrozooplankton and euphausiids sink very rapidly (up to 2700 m d^{-1}), so that they escape the upper ocean relatively intact, i.e., before the POC is converted to DOC and released to the surrounding seawater [see *Fortier et al.*, 1994; *Legendre and Rivkin*, 2002].

[36] The deep transfer of $CaCO_3$ includes calcareous parts from calcifying organisms (section 2.2). The coccoliths on the surface of coccolithophorid cells are too small to sink on their own; they are mainly transported to depth by sinking aggregates and fecal pellets of large grazers. The calcareous tests of foraminifers and shells of pteropods sink to depth upon death of these organisms. Temperature, hydrostatic pressure and salinity influence the dissolution of $CaCO_3$. The combination of high pressure and low temperature causes $CaCO_3$ to dissolve in deep waters; the depth at which $CaCO_3$ starts to dissolve is known as the lysocline, and it is generally located below the upper ocean.

[37] Figure 4 illustrates how the five aggregate PFTs control the four carbon fluxes and the other crucial biogeochemical fluxes mentioned at the beginning of this section. It must be noted that the flux of aeolian nutrients is into the ocean, that of DMS is out of the ocean and the net flux of CO_2 can be into or out of the ocean.

Table 6. Fraction of Net Primary Production Remineralized (%PPR) Above 1000 m by Each of the Four Aggregate Heterotrophic PFTs Defined in Table 1[a]

Temperature, °C	HB	μZ	LZ	MM
5	0.88	0.04	0.07	0.01
15	0.90	0.04	0.05	<0.01
25	0.93	0.04	0.03	<0.01

[a]Carbon remineralization (i.e., respiration (R)) can be estimated from production (P) and growth efficiency (GE) [see *del Giorgio and Cole*, 1998; *Rivkin and Legendre*, 2001], i.e., $R = (P/\mathrm{GE}) - P$. Since we are computing here %PPR by each heterotrophic PFT at various temperatures, not the absolute remineralization rates, we need to know temperature-dependent GE and relative P for each PFT. We estimated temperature-dependent GE as described in Table 4. Although P can be readily estimated for HB, there is little quantitative information on P for μZ, LZ, and MM. In order to compute %PPR, we made several simplifying assumptions. (1) Since P and biomass (B) in planktonic organisms are usually linearly related, we substituted B for P. (2) *Tanaka and Rassoulzadegan* [2002, Table 3] determined the biomasses of HB and μZ (flagellates and ciliates) in the 110–1000 m depth stratum of the Ligurian Sea (western Mediterranean), monthly over an annual cycle; the mean (± standard deviation) ratio HB:μZ = 7.4 ± 1.7. (3) *Scotto di Carlo et al.* [1984] estimated the biomasses (wet weights (WW)) of LZ (copepods) and MM (appendicularians and doliolids) in the upper 1000 m of the Tyrrhenian Sea (western Mediterranean) from February to October; we converted WW into carbon: C = WW × F, where F = 0.095 for LZ and 0.2 for MM; the resulting biomasses are 380 and 39 mg C m^{-2} for LZ and MM, respectively. In *Tanaka and Rassoulzadegan* [2002, Table 3], the μZ biomass 5–1000 m is 520 mg C m^{-2}. Combining the values from the two western Mediterranean sites provided two additional biomass ratios μZ:LZ = $\sim$1.4 and LZ:MM = $\sim$10. (4) We computed carbon remineralization as $R = (B/\mathrm{GE}) - B$, taking B ratios MM:LZ:μZ:HB = 1:10:14:100. (5) Assuming that these ratios are representative of the world ocean, we used them and GE from Table 4 to estimate the fractional contribution of each heterotrophic PFT to respiration. A sensitivity analysis, where μZ, LZ, and MM were sequentially doubled or halved, did not change the general trend; in all cases, HB accounted for >80% of the upper ocean PPR.

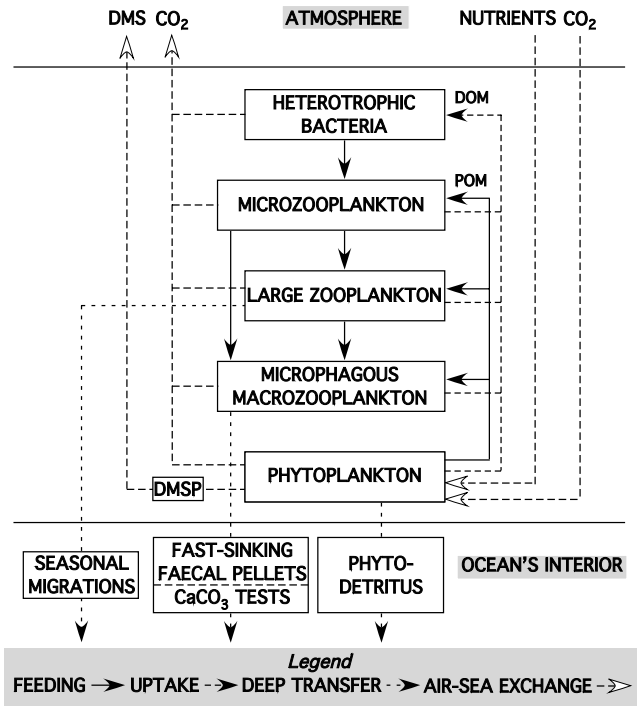

Figure 4. Roles of the five aggregate PFTs in controlling the four carbon fluxes discussed in the text, and the fluxes of reactive compounds between the atmosphere and the ocean (aeolian nutrients, DMS, and CO_2).

2.4. Combining PFTs, Food Web Processes, and Biogeochemical Fluxes

[38] Figure 5 combines the aggregate PFTs, the two food web processes quantified in Tables 3 and 4 and illustrated in Figure 3 (i.e., size increase transformation due to the processing by organisms, and remineralization) and the biogeochemical carbon fluxe quantified in Table 6 (i.e., upper ocean respiration), at three temperatures. The purpose of Figure 5 is to show that, subject to further research and modeling efforts, functional relationships could be derived among PFTs, food web processes and biogeochemical fluxes, within the context of our proposed framework. Such relationships could be used to explore the effects of the changing climate and other types of anthropogenic forcing on the ocean.

[39] In Figure 5, the fraction of net primary production that is remineralized above 1000 m by each of the four heterotrophic PFTs varies coherently with the efficiencies of PFTs at remineralizing OM and transforming its size distribution. This preliminary result, which needs to be confirmed by numerical models, supports our idea that the class of models we propose here should take into account the interactions among functional biodiversity, ecosystem functioning, and the fluxes of elements and associated feedbacks (section 2).

3. Climate-Driven Changes in the Characteristics of the Upper Ocean: Possible Effects on Pelagic Ecosystems

[40] Since the beginning of the Industrial Revolution (~1750), about 340 Pg of carbon (1 Pg = 10^{15} g) have been released into the atmosphere in the form of CO_2 [*Houghton and Hackler*, 1995]. Most of this carbon comes from the combustion of fossil fuels, but a significant fraction is associated with changes in land use, such as deforestation. Atmospheric CO_2 concentrations increased from ~280 ± 10 ppmv, the level it had been for several thousand years, to 367 ppmv in 2000 [*Houghton et al.*, 2001]. The present atmospheric CO_2 concentrations are higher than in the past ~500,000 years, and the rate of increase is greater than in the past 20,000 years. Projections are that the atmospheric CO_2 will increase to 500–900 ppmv by 2100 [*Houghton et al.*, 2001].

[41] The ocean is a major sink for anthropogenic CO_2, absorbing 25 to 35% of the fossil fuel CO_2 emissions [*Prentice et al.*, 2001]. This "anthropogenic" flux is superimposed on a geographically and temporally varying pattern of large natural exchanges. The atmosphere-ocean exchanges are determined by a variety of processes, including heating and cooling of surface waters, biological uptake and export of organic carbon from the surface layer to deep waters, marine calcification, and the upwelling of carbon-rich deep waters. In the preindustrial ocean, regions where the net flux of carbon was from the ocean to the atmosphere (source regions) were interconnected to sink regions by oceanic circulation and the transformation of sinking particles. The increasing partial pressure of CO_2 (pCO_2) of the

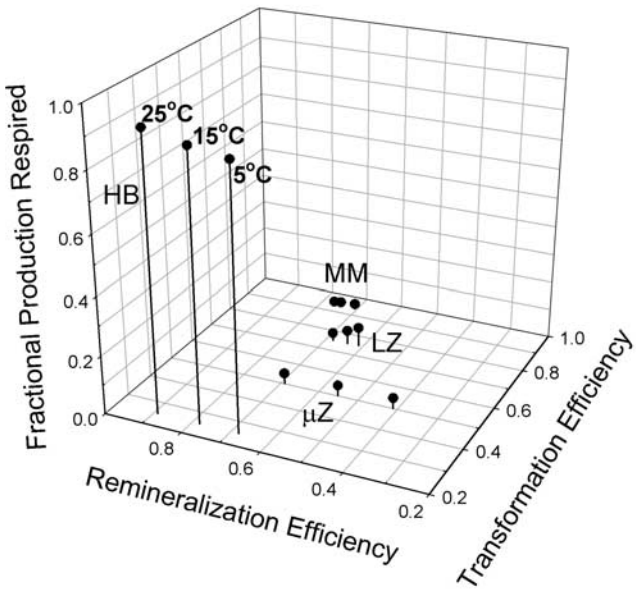

Figure 5. Three-dimensional plot showing relationships among food web and biogeochemical characteristics of the five aggregate PFTs examined in Tables 3, 4, and 6. The *z* axis represents the fraction of net primary production that is remineralized above 1000 m (Table 6); the *y* axis represents the remineralization efficiency (Table 4); the *x* axis represents the transformation efficiency at increasing the size of organic matter (Table 3). Remineralization above 1000 m and remineralization efficiency were computed at 5°, 15°, and 25°C. Abbreviations are as follows: PH, phytoplankton; HB, heterotrophic bacteria; μZ, microzooplankton; LZ, large zooplankton; MM, microphagous macrozooplankton.

atmosphere since ~1750 has tended to increase the air to sea flux in CO_2 sink regions, and decrease the sea to air flux in the source regions, leading to increased carbon storage within the ocean.

[42] Potential changes in the air-sea carbon flux are difficult to predict with our current level of understanding of ocean processes, or from comparisons with the past. Factors that drive changes in the partitioning of carbon between the ocean and the atmosphere can be subdivided into two interactive categories, i.e., physicochemical and biologically mediated.

3.1. Physicochemical Factors

[43] The physicochemical factors that influence the partitioning of carbon are relatively well understood. We briefly describe here those that may have effects on upper ocean ecosystems.

3.1.1. Warming

[44] The increase in emissions of greenhouse gases and accumulation of CO_2 in the atmosphere has increased the Earth's temperature by ~1°C in the last 50 years [*Houghton et al.*, 2001]. Most of this increase has occurred in two periods, i.e., from about 1910 to 1945 and since 1976, and the largest recent warming took place in the extratropical Northern Hemisphere during winter. The warming rate since 1976 (0.17°C per decade) has been slightly higher than the rate of warming during the 1910 to 1945 period (0.14°C per decade), although the total increase in temperature is larger for the 1910 to 1945 period. The most recent warming period also has a faster rate of warming over land compared with the oceans, with a projected 1.5 to 5.8°C increase in the next 100 years. The increased air temperatures have warmed the upper 3000 m of the World Ocean, with the upper 300 m showing an average >0.3°C warming between ~1948 and 1998 [*Levitus et al.*, 2001].

[45] The solubility of gases in water decreases with increasing temperature. Hence global warming will increase surface water temperatures and progressively reduce the effectiveness of the ocean sink for CO_2. Temperature changes can also drive biologically mediated effects (see section 3.2).

3.1.2. Change in pCO_2

[46] The increasing CO_2 concentrations in seawater will cause decreases in both pH and the $CaCO_3$ saturation state of seawater (Ω). A lower pH can adversely influence the metabolism of animals [*Pörtner et al.*, 2005], whereas lower Ω reduces the calcifying ability of organisms. Overall, doubling of preindustrial atmospheric CO_2 concentration could cause a reduction up to 50% in marine $CaCO_3$ production [*Feely et al.*, 2004, Table S1]. This would cause a proportional reduction in global $CaCO_3$ precipitation (of which 90% is caused by planktonic organisms, i.e., coccolithophorids, foraminifers and pteropods); reduced calcification reduces the vertical transport of calcium carbonate (and hence alkalinity) to the deep sea, which increases the CO_2 storage capacity of the surface ocean [*Riebesell*, 2004]. In addition, the ability of surface waters to dissolve anthropogenic CO_2 tends to decrease as more CO_2 is taken up. Future decreases in ocean buffering, associated with higher CO_2 concentrations, will significantly decrease the effectiveness of the ocean sink [*Sarmiento et al.*, 1995].

3.1.3. Sea Ice Extent

[47] Changes in sea ice extent in the Southern Ocean are hypothesized to have caused large changes in atmospheric pCO_2 over glacial-interglacial timescales, through controls on the rate of air-sea CO_2 exchange [*Stephens and Keeling*, 2000]. A rectification of the biologically driven air-sea carbon flux has been proposed for seasonally ice covered regions associated with the timing of biological production, gas exchange and sea ice cover [*Yager et al.*, 1995]. In the Arctic, the average extent of sea ice cover in summer has declined by 15–20% over the past 30 years; this decline is expected to accelerate, with the near total loss of sea ice in summer being projected to occur before 2100 [*Arctic Climate Impact Assessment*, 2004].

3.1.4. Freshwater Input

[48] Global climate models predict that the global water cycle will change considerably in geographic extent and intensity. There is an expected increase in meltwater flux and river runoff from continental and oceanic ice-covered areas. These projected changes will have significant effects on ocean circulation, ecosystems and surface water chemistry.

3.1.5. Wind, Storms, and Mixing

[49] In the open ocean, storms events are important in driving exchanges across the air-sea interface [e.g., *Bates et al.*, 2002] and for deepening the near-surface mixed layer, which in turn entrains dissolved inorganic nutrients and carbon into surface waters. The resulting transient phytoplankton blooms often rapidly sink to depth [*Legendre*, 1990, and references therein]. Wind patterns also determine the strength of Ekman pumping and coastal upwelling, therefore controlling the upward flux of nutrients and CO_2 between depth and the surface mixed layer. Climate models predict changes in storminess, but agreement among the models is poor with suggestions that there may be fewer small extratropical storms, but more larger and stronger storms. Such changes in the frequency and intensity of storm events will have consequences for upper ocean ecosystem dynamics, carbon cycling and biogeochemical fluxes, as well as for aeolian delivery of potentially limiting nutrients (e.g., Fe and N) to the ocean surface.

3.2. Biologically Mediated Factors

[50] The biologically mediated factors that influence the partitioning of carbon are less well understood than the physicochemical ones. Although biological systems have generally been viewed as playing little direct role in the uptake of anthropogenic CO_2, they can be profoundly influenced by the physiochemical factors described in section 3.1.

[51] There are at least three categories of biologically mediated factors that could alter the future air-sea and water column vertical fluxes of carbon, nutrients and climate active properties [*Falkowski et al.*, 1998; *Boyd and Doney*, 2003]: changes of nutrient inventories within the ocean, changes in the utilization efficiency of major nutrients at the ocean surface, and changes in the elemental composition of biogenic material sinking from the surface ocean (including the organic carbon to calcium carbonate "rain ratio" of the material exported from the surface layer). The two main types of processes that could lead to changes in these factors are alterations in the external supply of biologically limiting nutrients (e.g., Fe and N), and/or changes in pelagic marine ecosystems.

3.2.1. External Supply of Biologically Limiting Nutrients

[52] Phytoplankton growth is limited by light and the bioavailability of various elements that include N, P and Fe. It is now clear that Fe from terrestrial sources can play an important role in biological activity in all pelagic regions of the world ocean. In high-nutrient low-chlorophyll (HNLC) regions, such as the subarctic Pacific Ocean, the equatorial Pacific Ocean and the Southern Ocean, iron supply can be the major limiting factor of primary productivity [*Boyd*, 2002]. Macronutrients, such as nitrogenous compounds, are also delivered from the atmosphere and may influence primary productivity in some regions.

[53] The potential for short-term biological control of pCO_2 has been shown during iron-enrichment experiments [*Boyd et al.*, 2004; *Coale et al.*, 2004, and references therein]. However, changes in the supply rate of N nutrients, from internal sources (i.e., mixing from below) or aeolian delivery, and resulting from in situ N fixation or denitrification, can also alter nutrient inventories, carbon export and surface water pCO_2. A relationship between N fixation and external inputs of Fe has been proposed [*Falkowski*, 1997; *Berman-Frank et al.*, 2001; see also *Sanudo-Wilhelmy et al.*, 2001]. Recent evidence has suggested that N fixation in both the subtropical Atlantic and Pacific Oceans has increased in the past two decades. In the North Pacific Ocean, large-scale, low-frequency physical changes in the mixed layer have been proposed as the causal mechanism [*Karl*, 1999], while in ocean regions downwind of major dust-generating areas, increased Fe deposition by dust is thought to increase N fixation rates, e.g., dust from Africa in the tropical Atlantic Ocean and Caribbean Sea [*Falkowski et al.*, 1998].

[54] Estimation of dust deposition in the ocean is highly problematic. The total input of Fe to the ocean from the atmosphere has been estimated (with large uncertainties and interannual variability) to be between 15 and 100 Tg yr^{-1}. The patterns of Fe inputs are uneven, with the lowest oceanic deposition rates in regions that are far from terrestrial sources (e.g., HNLC areas). Moreover, since only 0.8–2.1% of the amount of total deposited iron is soluble in seawater [*Jickells and Spokes*, 2001], a small fraction of the deposited Fe is bioavailable.

[55] Significant quantities of N nutrients (from anthropogenic sources, primarily the combustion of fuels and the utilization of fertilizers) are delivered from the land to the ocean via the atmosphere [*Cornell et al.*, 1995, 2003; *Jickells*, 2002]. Delivery of atmospheric N nutrients to coastal regions in Europe and North America is estimated to have increased by 50–200% during the past 50 years [*Paerl*, 1995]. Similarly, the riverine inputs of inorganic N and P to the ocean for the 1990s [*Smith et al.*, 2003] are about three times higher than the estimates for the 1970s [*Meybeck*, 1982]; some of the difference between the two periods could reflect the more extensive data set for the 1990s and different methods of extrapolating from specific sites to the global coastal zone, but much of the difference is probably real. Because of changes in land use practices, storm frequency and hydrology in coming decades, the amounts and geographical distributions of atmospheric and riverine inputs may change, depending on population and industrial growth in various regions.

[56] There is delivery of anthropogenic N nutrients to offshore regions where N is the limiting nutrient, such as the subtropical gyres of the North and South Pacific Oceans. While estimates suggest that, at present, atmospheric N nutrients inputs are small relative to the annual delivery from below to surface waters in these regions, the atmospheric input to the ocean is highly episodic, often coming in large pulses limited to a few days [*Spokes et al.*, 2000]. Such pulsed deposition has the potential to differentially impact primary production and phytoplankton ecology more than uniform inputs of similar magnitude. Overall, the deposition of N nutrients from the atmosphere may increase phytoplankton production in the open ocean and coastal waters, leading to changes in CO_2 exchange and the emission of other climatically important trace gases.

3.2.2. Changes in Pelagic Marine Ecosystems

[57] Changes in the relative and absolute distributions of calcareous and siliceous planktonic organisms have been correlated with significant changes in surface water alkalinity, pCO_2, air-sea fluxes and rain ratios in the past ocean [*Archer and Maier-Reimer*, 1994]. The structure of marine ecosystems is affected by climate-related factors that include temperature, cloudiness, nutrient availability, mixed layer physics and sea ice extent. The increases in temperature and CO_2 concentration are two direct forcings on pelagic marine ecosystems that could affect the upper ocean biogeochemical processes over the next 100 years; these two forcings are briefly discussed in the following two paragraphs.

[58] Current Intergovernmental Panel on Climate Change scenarios and coupled atmosphere-ocean climate models predict increased air and surface seawater temperatures over the next 100 years. In contrast to the terrestrial biosphere, where the effects of warming on plant growth and soil respiration have been extensively studied, there has been remarkably little analysis to date of the potential consequences of systematic warming on upper ocean processes. *Laws et al.* [2000] found that the ratio of carbon export from the euphotic zone to total primary production in the ocean surface layer varies inversely with ambient temperature. This implies that the "export efficiency" will decrease in response to the expected warming of surface waters. This is consistent with the finding that bacterial growth efficiency decreases and bacterial respiration increases with increasing temperature [*Rivkin and Legendre*, 2001], i.e., since bacterial respiration represents a large fraction of community respiration, warming of surface waters should result in more rapid near-surface respiration of organic material, consistent with a lowering of export efficiency.

[59] *Riebesell* [2004] reported that increased CO_2 concentrations could affect pelagic marine ecosystems through differences in inorganic carbon acquisition among major phytoplankton groups. Because of these differences, increasing CO_2 is expected to increase the competitive advantage of phytoplankton taxa with a lower affinity for CO_2, e.g., diatoms over coccolithophorids. Hence a future ocean with higher CO_2 concentrations may lead to a shift in the abundances of phytoplankton functional groups and their relative contributions to global ocean productivity. He also reported that high CO_2 has caused enhanced OC production during the course of phytoplankton blooms, and increased C:N and C:P of OC in mesocosm experiments.

Table 7. Predicted Changes in Marine Pelagic Ecosystems in a High-CO_2 World (Section 3.3) and Corresponding Effects on Ecosystem Structure, Food Web Processes That Affect OM, and Biogeochemical Carbon Fluxes in the Upper Ocean, Without (Section 3.4) and With (Section 3.5) Fe Fertilization

Predicted Changes and Corresponding Effects	High-CO_2 World	Fe Fertilization of High-CO_2 Ocean
Predictions for the euphotic zone	lower primary production; smaller phytoplankton; lower zooplankton biomass; lower export	initially: enhanced growth of diatoms and possibly export
Ecosystem structure in the upper ocean (PFTs, Table 1)	decreased relative abundance of large zooplankton; increased relative abundances of microzooplankton and perhaps microphagous macrozooplankton	shift toward larger PFTs
Food web processes that affect OM in the upper ocean (Table 2)	higher remineralization of POM and DOM; reduced particle size	shift toward larger particles
Biogeochemical carbon fluxes in the upper ocean (Table 5)	enhanced evasion of CO_2 from ocean to atmosphere; lower carbon sequestration	areas of deep subduction: enhanced sequestration; other areas: remineralization in upper ocean; ventilation back to atmosphere

Hence CO_2 fertilization has the potential to increase carbon sequestration in the ocean. A reversed effect, not discussed by *Riebesell* [2004], could be a decrease in sequestration caused by reduced $CaCO_3$ ballasting of sinking particles, due to a decrease in calcification by pelagic organisms.

[60] There are additional classes of carbon transformations that may indirectly respond to climate forcings. For example, the conversion of DOC to POC can be mediated by aggregation on bubbles. On a global scale, this conversion rate has been estimated to be of the order of 2 Pg C yr^{-1} [*Monahan and Dam*, 2001]. This physicochemical process, which may in turn affect the lifetime of DOC in the surface ocean and the overall rate of microbial respiration, is potentially sensitive to the frequency of storms and the process of wave breaking and bubble formation. The overall significance of such a process on large-scale carbon cycling, although presently unclear, may well be important in changing the size and bioavailability of OM and the trophic pathways for OC transformation.

[61] The integrated effects of such mechanisms on the net air-sea CO_2 flux and ocean carbon sequestration is a very complex scientific issue, which involves many research areas. The latter include deep ocean circulation, subsurface remineralization, top-down controls on ecosystem structure and trophic interactions, biogeochemical dynamics in coastal zones and modeling the global ocean carbon cycle.

3.3. Possible Effects on Marine Pelagic Ecosystems

[62] At large spatial and temporal scales, marine pelagic ecosystems have evolved in such a way that there is a close coupling between autotrophic production of organic matter and consumption by heterotrophic organisms. At the local spatial and short temporal scales, autotrophic and heterotrophic processes may be uncoupled, such imbalances leading to the net accumulation, or apparent net deficit (i.e., respiration > net production) of organic carbon or other bioreactive elements. For example some regions of the World Ocean are net autotrophic (primary production > heterotrophic respiration) whereas others are net heterotrophic (primary production < heterotrophic respiration) [e.g., *del Giorgio et al.*, 1997; *Duarte and Agusti*, 1998; *Duarte et al.*, 2001; *Alvarez-Salgado et al.*, 2001]. Net heterotrophy requires the transport of dissolved and/or particulate organic matter from regions of net autotrophy to those with net heterotrophy. Similarly, there are seasons and years with excess primary production and others with excess heterotrophic consumption and remineralization. Overall, the two processes are almost equal in the upper ocean, so that only <1% of global primary production of 55 Pg C yr^{-1} is transported below the depth of the permanent pycnocline (i.e., the global average downward flux at 2000 m is 0.34 Pg C yr^{-1} [*Lampitt and Antia*, 1997]). Hence sequestration results from a very small imbalance between two large processes. This small imbalance is maintained by the biological carbon pump.

[63] The main food web components responsible for the above imbalance can be assessed by considering the organisms that remineralize the slowly sinking OM, and those that produce the rapidly sinking OM that escapes degradation and remineralization in the upper ocean. Heterotrophic bacteria account for most of the upper ocean remineralization [*Sherr and Sherr*, 1996; *del Giorgio and Cole*, 1998, 2000; *Rivkin and Legendre*, 2001, and references therein]. As shown in Table 6, bacteria account for 88–93% of the remineralization of net primary production in the upper ocean. The processes that lead to the deep transfer and sequestration of biogenic carbon are mediated primarily by a few groups of organisms. These processes are: the aggregation of some dense blooms of diatoms, the sinking of foraminifers, the seasonal ontogenetic migrations of large zooplankton, and the production of fast sinking fecal pellets by euphausiids and salps, appendicularian houses and pteropod shells (Table 5 and section 2.3). Some organic compounds can reside in the body masses of large organisms for long periods before being remineralized, but the ultimate fate of that OM is remineralization, normally in the ocean but sometimes on continents (e.g., commercially harvested marine resources, which are consumed on land).

[64] Climate driven changes in the physiochemical and biological factors discussed in sections 3.1 and 3.2 could affect the abundances and activities of heterotrophic bacteria and of the organisms involved in the deep transfer of biogenic carbon. This would modify the marine food web–mediated interactions between the ocean and the remainder of the Earth system, as discussed in sections 3.4 and 3.5 and summarized in Table 7.

3.4. Predictions for the Upper Ocean in a High-CO_2 World

[65] Changes in ocean biology and biogeochemistry in response to climate forcings have been examined in various studies using coupled general circulation and biogeochem-

ical models. For example, *Bopp et al.* [2001] and *Bopp* [2002] forced the future ocean with an increase in atmospheric concentrations of CO_2, from $1 \times CO_2$ to $2 \times CO_2$ at a rate of 1% per year. The food web component of the biogeochemical model included two phytoplankton compartments: diatoms, which required high concentrations of both Si and Fe, and nanophytoplankton, which did not require Si and could grow at low Fe concentrations. The model also had two zooplankton sizes classes: microzooplankton and mesozooplankton. This ecosystem representation enabled a ''large cells'' loop, which exported carbon efficiently, and a ''small cells'' loop, within which there was mostly regeneration and remineralization.

[66] The model simulations predicted increases in sea surface temperature and stratification, a decrease in nutrient supply to the surface and increased available light. This resulted in latitude-dependent changes in phytoplankton biomass and production, and in carbon export from the euphotic zone, i.e., increases in high latitudes and decreases in low latitudes. The net effect was a global decline in chlorophyll (8.5%), primary production (8.9%) and POC export (6%). Changes in food web structure were also predicted, with a 6.3% decrease in phytoplankton cell numbers, and a shift in phytoplankton taxa where diatoms decreased by ~10% relative to smaller phytoplankton cells.

[67] The predicted lower primary production, shift toward smaller phytoplankton and lower zooplankton biomass in the euphotic zone, and lower export from that zone have consequences on the three components of models discussed in sections 2.1–2.3, i.e., ecosystem structure (PFTs), food web processes that affect OM and biogeochemical carbon fluxes in the upper ocean in a high-CO_2 world. These are briefly discussed in the following paragraphs.

3.4.1. Ecosystem Structure (PFTs, Table 1)

[68] The shift toward lower primary production would lead to a decrease in the heterotrophic biomass that could be sustained in the upper ocean. This would favor such organisms as salps (microphagous macrozooplankton) that can out compete large zooplankton at low food concentration [*Le Fèvre et al.*, 1998], e.g., the replacement of krill by salps in the Southern Ocean as a consequence of decreasing phytoplankton and ice algae since the 1970s [*Atkinson et al.*, 2004]. The shift toward smaller phytoplankton could select against large herbivorous zooplankton (and perhaps some of the large herbivorous microzooplankton, e.g., heterotrophic dinoflagellates), which is consistent with the predicted lower zooplankton biomass; it could also select for microzooplankton. The overall result would be a decrease in the relative abundance of large zooplankton, and increase in the relative abundances of microzooplankton and perhaps microphagous macrozooplankton. The direct effect on heterotrophic bacteria cannot be predicted at this time.

3.4.2. Food Web Processes That Affect OM (Table 2)

[69] The generally higher water temperature would enhance remineralization of POM and DOM. The lower abundances of large zooplankton should reduce the fragmentation of food into smaller particles, the transfer of OM into the body masses of large organisms and the production of relatively large fecal pellets. The net effect of these processes could contribute to reduce particle size in the upper ocean.

3.4.3. Biogeochemical Carbon Fluxes (Table 5)

[70] The generally higher water temperature would reduce CO_2 solubility in seawater and increase remineralization, which would enhance the evasion of CO_2 from the ocean to the atmosphere. This, combined with lower primary production and export from the euphotic zone and the general shift toward smaller particles in the upper ocean, would lower carbon sequestration.

[71] The general response of the upper ocean under the predicted higher atmospheric concentrations of CO_2 would therefore be (Table 7): lower primary production; shift toward smaller phytoplankton; decrease in the relative abundance of large zooplankton and increase in the relative abundances of microzooplankton and possibly microphagous macrozooplankton; general decrease in particle size; higher remineralization of POM and DOM, including higher respiration; and lower carbon sequestration.

3.5. Predictions for the Effect of Fe Fertilization of the Upper Ocean in a High-CO_2 World

[72] What would be the effect of fertilizing with iron the high-CO_2 ocean described in section 3.4? Overall, Fe fertilization would tend to shift the pelagic ecosystem toward an increase in the relative abundances of larger phytoplankton and zooplankton. Iron fertilization has been shown to produce rapid growth of diatoms [e.g., *Boyd*, 2002; *Tsuda et al.*, 2003]. From a comparison of eight mesoscale Fe fertilization experiments in HNLC areas, *de Baar et al.* [2005] concluded that the primary factor limiting phytoplankton growth in these waters is the light climate, as determined by the depth of the wind mixed layer, and the second is the supply of iron. According to these authors, dominance of light climate implies that simple stoichiometry arguments of Fe for C, N, P or Si being assimilated at fixed ratios by phytoplankton generally do not hold. This is even more the case because the added [Fe(II)] is rapidly lost via the formation of colloids. In some regions, the magnitude of the response may be determined by the rate of supply of silicic acid to the euphotic zone [*Boyd et al.*, 2004; *Coale et al.*, 2004]. The latter may be determined, in part, by the vertical distribution of bacterial-dependent Si recycling [*Bidle et al.*, 2002] and the physical mechanisms of silicic acid upward transport. Hence the Fe-enhanced growth of diatoms would rapidly decline or stop depending on the supply rate of silicic acid, and be followed by the growth of nonsiliceous phytoplankton. Blooms dominated by diatoms efficiently export carbon downward from the euphotic zone, whereas communities dominated by other types of plankton tend to recycle and retain carbon in the upper ocean. The net result of the initial Fe fertilization would therefore be a shift toward larger PFTs and more generally larger particles in the upper ocean, and storage there of some atmospheric carbon in organic and inorganic compounds.

[73] The fate of the carbon stored in the upper ocean would vary with ocean circulation. In areas of the world ocean were deep subduction could rapidly transport biogenic carbon downward to sequestration depths, some of the carbon initially stored in the upper ocean would be sequestered. In other regions, biogenic carbon would be stored in the upper ocean in the basin that was fertilized, or advected to adjacent basins. Under these conditions, even if some of

the stored carbon could be transported below the permanent pycnocline, most of it would be remineralized within the upper ocean, from where it would be ventilated back to the atmosphere within decades. Concerning the transport of carbon below the permanent pycnocline, the present results of relatively short Fe fertilizations do not provide evidence that the growth of diatoms caused by Fe addition resulted in enhanced carbon export from the euphotic zone, and consequently sequestration [*Buesseler and Boyd*, 2003; *Buesseler et al.*, 2004; *de Baar et al.*, 2005]; however, it is speculated that fertilization over longer periods may lead to export from the euphotic zone. Yet, even if the pelagic food web shifted toward the Fe-stimulated condition described above, the increased temperature of the upper ocean in a high-CO_2 world would enhance carbon remineralization, and the increased stratification could impede the replenishment of silicic acid into the euphotic zone, which in turn would limit diatom production. These two factors would constrain the efficiency of Fe fertilization at sequestering carbon, except in areas of deep subduction.

[74] Upon termination of fertilization, the upper ocean would likely revert back, within decades, to the condition described in section 3.4 for a high-CO_2 world without Fe fertilization. This would correspond, at a different spatio-temporal scale, to the observed shifts from opaline Si to $CaCO_3$ at transitions from glacial to interglacial periods, in cores taken from South Atlantic sites far north of the present Polar Front [e.g., *Falkowski et al.*, 1998]. Hence except in areas of deep subduction, Fe fertilization would have to be continued indefinitely to just retain a constant amount of carbon stored in the upper ocean, without gaining additional storage above the value resulting from the initial fertilization.

[75] In summary (Table 7), the initial Fe fertilization would store atmospheric carbon in the upper ocean. The magnitude of the storage would be determined by the depth of the wind mixed layer, the chemistry of Fe in seawater, and possibly the rate of supply of silicic acid to the euphotic zone. In order to retain the stored carbon in the upper ocean, fertilization would have to be continued indefinitely, without gaining any additional storage (except in areas of deep subduction, where biogenic carbon could be transported from the upper ocean downward). Upon termination of fertilization, the carbon that had been stored in the upper ocean would be ventilated back to the atmosphere within decades.

4. From Conceptual to Numerical Modeling

[76] There are ongoing efforts toward the development and implementation of models that integrate functional biodiversity, ecosystem functioning, and the fluxes of elements and associated feedbacks in the upper ocean. These types of models have been developed and described by, e.g., *Aumont et al.* [2003], *Bopp et al.* [2003], and *Le Quéré et al.* [2005].

[77] In developing Dynamic Green Ocean Models (DGOMs [*Le Quéré et al.*, 2005]), it was recognized that the definition of key PFTs must balance the need for sufficient complexity to address specific scientific questions against the current limitations of the observational basis for parameterizing and validating each PFT (section 2.1). The latter were based on the following criteria: that each PFT (1) had an explicit biogeochemical role, (2) could be defined by a distinct set of physiological, environmental or nutrient requirement controlling its biomass and productivity, (3) had effects on the performance of other PFTs, e.g., through selective depletion of nutrients or grazing, and (4) was of quantitative significance in at least some regions of the ocean. Ideally, each PFT should be characterized by a specific set of physiological traits (e.g., nutrient or food preference; rates of growth, respiration, mortality). However, there are difficulties deriving PFT-specific values for each of the relevant traits. When trait values are based on laboratory experiments, the latter are usually conducted on individual species, which are easy to culture but not necessarily representative of the PFT as it occurs in nature. When trait values are based on field observation, measurements may be biased by the temporal and spatial domains of the observations and thus not represent average responses. Also, some of the parameters required for the formulation of a model may not have been determined directly but derived from the measurements of proxies or related parameters. Efforts to compile the available data on a global scale are still needed. The number of PFTs that are required for a fully functional DGOM is not known. Even with a small number of PFTs, there are often poorly constrained or unknown trait values. Although the number of required traits could perhaps be minimized based on theoretical considerations, small increments in the understanding of underlying processes could lead to major improvements in the reliability of DGOMs.

[78] According to *Le Quéré et al.* [2005], the key test of a DGOM is whether it can reproduce the mean state and the variability of biogeochemical fluxes (e.g., CO_2, DMS), under present or past conditions. Many processes can be optimized to give a good representation of the mean state, but it is more difficult to optimize a model in such a way as to reproduce variability. There are also a number of less stringent tests of models that are helpful, particularly in the development phase. One is whether the model can reproduce observed patterns of PFT distributions and abundances under modern or paleoclimate conditions. Another important challenge is to reproduce the outcome of in situ experiments, e.g., mesoscale Fe fertilization (section 3.5). Data for model evaluation under present conditions include air-to-sea gas fluxes, distributions of PFT biomasses, surface-to-depth fluxes of particles or minerals and global cycles of chemical elements. Results of DGOMs so far are quite encouraging.

[79] As explained in section 2, numerical models based on the framework we propose will be depth resolved for all variables, and will explicitly represent food web processes and/or biogeochemical carbon fluxes from the surface down to the depth of sequestration, and possibly below in the ocean's interior (i.e., two-layer water column model). The actual PFTs used in models could be different according to the objectives of the models (e.g., food web functioning, or biogeochemical fluxes). One of the current challenges in defining the PFTs is accommodating the fact that, in some groups of organisms, different life stages have very different roles in OM cycling and associated biogeochemical carbon fluxes. There are at least two modeling solution to that problem, i.e., combining trophic categories and sizes of

organisms (trophic continuum model [*Cousins*, 1980, 1985]), or concentrating biological resolution at the level of the target taxa (rhomboid approach [*de Young et al.*, 2004]).

[80] Finally, studies will be conducted using coupled general circulation and biogeochemical models, in which the food web component would be as described above. Examples of such models were given in section 3.4.

5. Studies Needed to Resolve the Most Pressing Issues

[81] Given that existing information on functional biodiversity, ecosystem functioning, and the fluxes of elements and associated feedbacks in waters below the euphotic zone is quite scarce, it would be relatively easy to identify a "shopping list" of studies needed to resolve uncertainties about these. This shopping list would be quite formidable, but likely of little practical use. We prefer instead to suggest a general approach for implementing the class of models we propose for the upper ocean.

[82] The first step in approaching the upper ocean as a whole would be to assemble and synthesize the existing information on biodiversity, ecosystems processes and biogeochemical fluxes in the upper ocean, with special attention to the mesopelagic layer. From our experience, some of this information already exists, but it is presently scattered. Until recently, international programs dealing with the oceans' food webs or biogeochemistry have focused on either the euphotic zone (e.g., JGOFS and SOLAS) or the deep ocean (e.g., IMAGES, and the NEPTUNE cable network on the seabed over the Juan de Fuca tectonic plate). GLOBEC has concentrated on ecosystem dynamics in the upper 200 m of the water column, together with the appropriate linkages into deeper water. A consequence of the general focus on either the euphotic zone or the deep ocean, there have been (and still are) little human and financial resources for studying the upper ocean as a whole.

[83] Simultaneously, and as part of the first step, would be the development of models of the class we proposed here. Examples were provided in the previous section. To be successful, such efforts will require well-organized interactions between modelers and data synthesizers. Presently available data would be used to develop, parameterize and test the preliminary models. The next step would be to use available models (currently existing, under development, and/or belonging to the class proposed in this paper) to identify gaps in understanding about the upper ocean, and to use the new observations to improve these models, in a continuing interactive mode. As the models will progressively reduce uncertainties and improve our predictive capabilities, they could be used to provide more robust predictions on the effects of higher CO_2 concentrations and sequestration strategies in the upper ocean. The success of this step is crucially dependent on international programs dedicated to the study of the upper ocean as a whole. New programs such as IMBER, which are being developed within the context of the Earth System Science Partnership (which includes IGBP II) and consider processes within the whole ocean, represent the prototype for future global-scale programs.

[84] The development of models to assess the role of climate feedback on ocean ecosystems and biogeochemistry necessitates reconsidering the distinction between the euphotic zone and the underlying waters down to the permanent pycnocline. Ocean-climate models must consider the cycling of carbon within and from the upper ocean, down to the depth of sequestration, instead of only to the base of the euphotic zone. Moreover, in an Earth system integration where feedbacks and indirect effects are important, and are often the dominant drivers, models must integrate the approaches from such disciplines as functional biodiversity, ecosystem functioning, and the fluxes of elements and associated feedbacks. Programs, field studies and models must integrate these components over the whole upper ocean.

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L. Legendre, Villefranche Oceanography Laboratory, BP 28, F-06234 Villefranche-sur-Mer Cedex, France. (legendre@obs-vlfr.fr)

R. B. Rivkin, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF, Canada A1C 5S7. (rrivkin@mun.ca)