

**Ecological Determinants of Oceanic Carbon Cycling
(EDOCC):**

A Framework for Research

Final Report from the EDOCC Workshop

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I. EXECUTIVE SUMMARY

For 420,000 years prior to the Industrial Revolution, the atmospheric concentration of CO₂ was tightly bounded between 190 and 280 ppm. Such highly constrained boundaries require strong stabilizing feedbacks in the global carbon cycle. The emergent pattern of increasing atmospheric CO₂ in this cycle reflects the balance of fluxes among the oceanic, atmospheric and terrestrial carbon pools and a mix of geological and biological processes. However, our comprehension of the processes that control atmospheric CO₂, carbon fluxes, and the feedbacks that constrain them, are inadequate. Within the past 200 years, anthropogenic activities have led to a secular increase in atmospheric CO₂ with levels climbing above 365 ppm. Whether this increase will have any significant climatological effect is at the center of the major international policy debate. In order to model and predict the consequences of this change in the global carbon cycle it is critical to understand the role of the ocean carbon cycle in modulating future changes in atmospheric CO₂ and climate.

Biology plays a significant role in maintaining the gradient of CO₂ between the surface and deep ocean. There is ample evidence in the long term (> 0.5 mya) geological record that global scale changes in the transfer of carbon to the ocean interior by biological processes have played a role in past changes in atmospheric CO₂ concentrations and climate. Some of these biological processes have also been responsible for the sequestration of carbon to the ocean's interior on various time-scales in the past. These processes, collectively termed the **biological pump** (Fig. 1), consist of complex networks of organisms, which -as **a system**- export organic carbon to the deep ocean and drive most of the oxidation-reduction processes at depth. Upon the resulting remineralization of the organic carbon, much of this C is maintained in inorganic form at high concentrations while a smaller fraction is deposited to the sediments. This naturally occurring, biologically mediated net flux can isolate CO₂ from the atmosphere for millennia. If the biological pump did not exist - if there were no life in the oceans - models predict that atmospheric CO₂ concentrations would rise to levels of 680 ppm; i.e. 400 ppm higher than pre-industrial records.

The **structure** of oceanic food webs influences the quality and amount of carbon export from particular ecosystems, as well as the elemental ratios of its biota and the inorganic nutrient pools in the water. Food web structures vary in space and in time over seasonal, annual, decadal, and geologic scales. Elemental stoichiometries, the ratios of one element to another in either the particulate or dissolved phase, are often key elements of geochemical models. They are emergent properties of marine ecosystems, dictated by the differential partitioning of elements as they flow through the food web. We do not fully understand what constrains these ratios, but do know that results of geochemical models can be very sensitive to assumptions about these stoichiometries.

To delineate the role of biological processes in the oceanic carbon cycle and the Earth's climate system (past, present and future) we must understand the basic mechanisms of the biological pump. We need to determine the physical forcing and chemical factors that define and constrain food web structures. We must understand the biological response of these systems to external perturbation. Perhaps most importantly, we must understand how the interactions among organisms or functional groups (see Sidebar below) leads to emergent patterns in

biogeochemistry as well the modulating or exacerbating the feedbacks in the biological system which lead to system stability or destabilization.

During the past decade, the combined effort of the Joint Global Ocean Flux Study (JGOFS) and the World Ocean Circulation Experiment (WOCE) has provided an unprecedented understanding of oceanic carbon distribution and major biogeochemical cycles. The results of these programs underline the importance of ecosystem dynamics and foodweb structure in controlling the rates of carbon fixation and fate of organic carbon in the marine environment.

We therefore propose a program of focused studies that integrate physical, biogeochemical and biological observation, experimentation and modeling over relevant spatial and temporal scales to 1) determine the probable responses of marine ecosystems to climate shifts, 2) identify feedbacks from these systems to climate and 3) elucidate the factors that contribute most significantly to ecosystem resilience and stability and thereby determine the efficiency of the biological pump and its current and probable future behavior.

Four major sub-themes for research were identified: 1) Physical forcing controlling food web dynamics, carbon fluxes and biogeochemistry; 2) Biological interactions controlling food web dynamics, carbon fluxes and biogeochemistry; 3) Chemical-biological interactions controlling food web dynamics, carbon fluxes and biogeochemistry; 4) Ecosystem changes and carbon cycle feedbacks

Several specific examples of research questions were also articulated. They included issues relating to foodwebs such as: How can we better conceptualize marine food webs? What are the food web structure characteristics of major ocean biomes, and what controls these configurations? How are these controls modulated in space and time to produce observed distributions? What controls massive episodic blooms of various species of organisms? Important Biogeochemical questions posed included: What are the controls on vertical and horizontal structure of organic matter, its remineralization and its relationship to the ventilation of the sea? What is the role of the continental margin in the production, cycling and transfer of carbon? What controls the carbon:carbonate rain ratio and how does it control surface pCO₂? What controls the balance of N₂ fixation and denitrification in the world's oceans? What are the possibilities for and dynamics of feedbacks between ocean biogeochemistry as mediated by changes in atmospheric CO₂.

The ultimate goal of this effort will be to improve our mechanistic understanding of the role of the ocean biota in ocean carbon cycling, the probable responses of the marine biota and ecosystems to anthropogenic changes in global cycles and climate, and the feedbacks of the ocean ecosystem on climate. It will also help us understand some of the risks involved in mitigating anthropogenic CO₂ by attempts to change the biological pump through ocean fertilization. Such an effort will be best performed and understood in the context of an integrated and comprehensive program involving all the allied disciplines of oceanography, as well as parallel related efforts in the atmospheric and terrestrial realms.

II. PROGRAM RATIONALE

Our current conceptual model for the cycling of carbon in much of the ocean assumes that nutrient availability, mostly as fixed inorganic nitrogen, limits net plant growth and that the cycling of carbon can be linked to other cycles of biologically active elements (bio-elements) by Redfield stoichiometry (i.e. the apparent closely constrained ratios of oceanic planktonic biomass and inorganic nutrients at depth of about 106:16:1 for the atomic ratio of C:N:P). This is expressed in current models by a simplified version of the new production hypothesis (Dugdale & Goering, 1967) that concentrates on the dynamics of nitrate and ammonium as a reflection of new (i.e. added principally by physical mechanisms from depth) and local regenerative processes, respectively. The carbon cycle is then derived by simple multiplication of the nitrogen fluxes by 6.6 (moles/mole). This is computationally tractable and, in many cases, seems to represent the dynamics of the CO₂ drawdown of a spring bloom or upwelling in highly productive areas.

The attractive simplicity of this approach, and its successful application in limited regions of the ocean, has led to (1) representation of biological functions as a “black box” (Fig. 1) and (2) extrapolation of the “black box” approach to the global ocean. However, this method has unintended consequences for our understanding of the dynamics of oceanic processes and how we represent them in models. The implicit tight biological coupling between carbon and nitrate plus

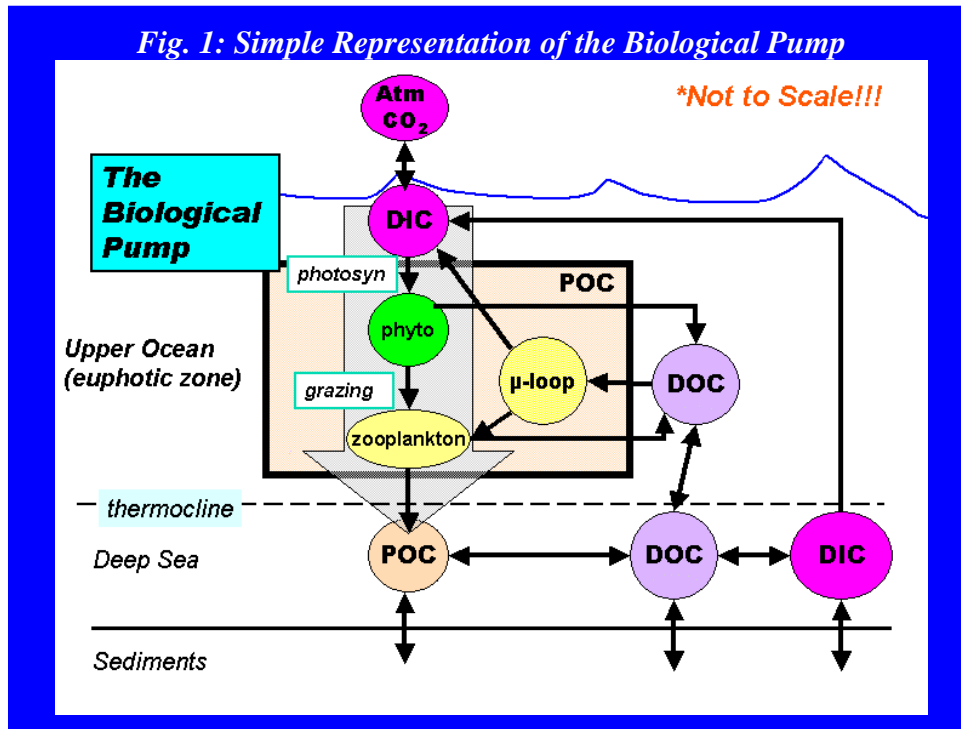
Definitions and Concepts: Functional Groups

In all ecosystems, organisms provide biogeochemical, as well as ecological, “services”; that is they *function* to link metabolic sequences and properties to form a continuous, self-perpetuating network of elemental fluxes. The biologically mediated fluxes of elements between the upper ocean and the ocean interior are critically dependent upon key groups of organisms. Similarly, organisms that catalyze phase state transitions from either gas to solute/solid or from solute to solid/gas phases mediate fluxes between the atmosphere and ocean as well as between the ocean and the lithosphere. For example, autotrophic carbon fixation¹ converts gaseous CO₂ to a wide variety of organic carbon molecules, virtually all of which are solid or dissolved solids at physiological temperatures. Respiration accomplishes the reverse. Nitrogen fixation converts gaseous N₂ to ammonium and thence to organic molecules, while denitrification accomplishes the reverse. Calcification converts dissolved inorganic carbon and Ca to solid phase calcite and aragonite whereas silicification converts soluble silicic acid to solid hydrated amorphous opal. Each of these biologically catalyzed processes is dependent upon specific metabolic sequences (i.e., gene families encoding a suite of enzymes) that evolved over hundreds of millions of years of Earth’s history, and have, over corresponding periods, led to the massive accumulation of calcite, opal, and organic matter in the lithosphere. Presumably because of parallel evolution as well as lateral gene transfer, these metabolic sequences have frequently co-evolved in several groups of organisms that, more often than not, are not closely related from a phylogenetic standpoint (Falkowski and Raven 1997). Based on their biogeochemical metabolism, these homologously similar sets of organisms can be clustered into “functional groups” or “biogeochemical guilds”; i.e., organisms that are related through common biogeochemical processes rather than phylogenetic affiliation.

¹ “Fixation” is a term that means to make non-volatile, as in conversion of a gas to another phase state.

ammonium fluxes restricts strongly the potential effect of marine ecosystems in the sequestration of atmospheric CO₂.

The interactions of producers and consumers have profound consequences for the biogeochemistry of the ocean (Longhurst, 1991; Legendre & Rasoulzadegan, 1996). Partitioning of carbon amongst the various reservoirs (dissolved inorganic carbon [DIC], dissolved organic carbon [DOC], particulate organic carbon [POC], and particulate inorganic carbon [PIC]) is strongly dependent upon biological transformations that vary greatly with community composition and food web structure.



particulate organic carbon [POC], and particulate inorganic carbon [PIC]) is strongly dependent upon biological transformations that vary greatly with community composition and food web structure. This partitioning in turn impacts the nature of the transport pathways by which carbon is cycled throughout the ocean (Wassmann, 1998).

For example, in current day systems dominated by very small (< 0.2 μm) primary producers that are heavily grazed by the herbivores of the microbial loop, carbon export through POC sinking is generally low. In contrast, episodic blooms of large-celled phytoplankton seem to temporarily escape grazing control and result in large POC export events. Although the real ocean is very much more complicated, this simplistic example illuminates a central issue: ***food web structure is a key ecological determinant of ocean carbon cycling and may be far more important in determining the quality and quantity of the export of organic matter than previously thought. Improving our understanding between structure and function will be valuable to modeling global processes.***

Although the inventories of organic carbon in the ocean are relatively small compared with inorganic carbon, biological processes contribute to the generation and maintenance of a CO₂ concentration gradient with depth and to the sequestration of atmospheric CO₂ in the ocean interior. The biological pump is driven in effect by a spatial separation between photosynthesis and respiration. Phytoplankton photosynthesis lowers the partial pressure of CO₂ in the upper ocean and promotes the invasion of CO₂ from the atmosphere or reduces the evasion in areas of very high pCO₂. Upon sinking of part of the newly formed organic matter into the dark ocean interior, the oxidation of the material by heterotrophic respiration raises the concentration of

dissolved inorganic carbon and ultimately, the $p\text{CO}_2$ of that water when it returns to the surface. The export of organic carbon from the surface into the thermocline presently accounts for ca. 11-16 Gt C per annum; approximately 25% of the total primary production in the world oceans (Falkowski *et al.*, 1998; Laws *et al.*, 2000). The maintenance or modification of this surface-deep sea gradient in dissolved inorganic carbon is one of the dominant mechanisms through which ocean biology influences atmospheric CO_2 .

Oceanic productivity and the biological pump are not directly limited by inorganic carbon. The efficiency of the biological pump can be altered by: (a) enhanced utilization of residual nutrients in the upper ocean; (b) the addition of one or more nutrients limiting primary production; (c) a change in the elemental ratios of the organic matter in the ocean; (d) a change in the remineralization length-scale and/or (e) an increase in the ratio of the organic/inorganic (i.e., calcium carbonate) carbon in the sinking flux (Sarmiento, 1992). As analyses of gases trapped in ice cores suggest that atmospheric CO_2 has not varied by more than ca. 10 ppm over the past 5000 years, it is often assumed that these five processes were close to steady-state before the beginning of the Industrial Revolution. If this assumption holds, then the biological pump in the ocean has not and will not contribute significantly to the absorption of anthropogenic CO_2 (Sarmiento, 1992) and it can safely be ignored in planning society's response to climate change. However, increasing evidence suggests that these assumptions do not hold, and must be examined more critically. In other words, biological processes relevant to the air-sea carbon fluxes are those that entail deviations from the simple Redfield coupling of bio-elemental fluxes in seawater or the simple assumptions of perpetual steady state behavior in a changing world. Many of these assumptions have been described, but are not usually the focus of research.

Simple assumptions of a fixed bio-elemental stoichiometry and a nitrate-based new production system imply that all of the DIC that is required to fuel phytoplankton growth is introduced from below to the surface when nutrients are upwelled or mixed into the euphotic zone. The DIC arises by the same remineralization processes that produced the nutrient. Since the simple N cycle (i.e. one that does not include N_2 fixation and denitrification) has no gas exchange component, a simple carbon system that is linearly linked to nitrogen will have no net gas exchange either. For the biological pump to sequester *anthropogenic* CO_2 , or to influence the net atmospheric CO_2 balance during a period of anthropogenically-induced change, the pump must deviate from a steady-state over relatively short time scales in a monotonic fashion. The uptake of CO_2 from the atmosphere is nominally balanced by outgassing when the high- $p\text{CO}_2$ waters next ventilate, concurrently returning inorganic nutrients to the surface. In steady state, these two fluxes will be equal and there will be no change in the net sequestration of carbon in the ocean. However, imbalances between uptake and outgassing leading to deviations from steady state can have a profound effect on atmospheric CO_2 by influencing the total stock of DIC in the ocean, 38,000 Gt C, over its millennial residence time.

However, if the fixed stoichiometry assumption is relaxed in a non-steady state world, the carbon flux in any given ecosystem will no longer be a simple function of the availability of the limiting nutrient. An increased C:N ratio of export compared to uptake has been described in many studies and seen at both US-JGOFS time-series stations, BATS and HOT (Lohrenz *et al.*, 1992; Christian *et al.*, 1997; Bissett *et al.*, 1999). Dissolved organic carbon and nutrient pools

may have elemental ratios removed from Redfield stoichiometry. If these pools are also considered in the link between nutrients and the resultant carbon dynamics, there can be a net transfer of carbon from the atmosphere to the deep sea on the time-scales of the ventilation of those deeper water masses. A similar transfer can also occur if the time/length scale at the depth for remineralization of carbon is larger than that of nitrogen. On millennial time-scales, this enriched deep carbon will ultimately ventilate back to the surface. Reductions in the relative remineralization length scales for C, or of the C:N ratio of export would accordingly lead to increases in atmospheric CO₂ over these same time-scales. ***Consequently, on interannual, decadal and centennial scales a change in the rate and nature of biological activity (and export in particular) can have a net effect on the atmospheric carbon concentration.***

Another deviation from these simple assumptions is the inclusion of a gas phase or air-sea exchange to the nitrogen cycle, nitrogen deposition from the atmosphere and biological nitrogen fixation. These sources of nitrogen promote an additional drawdown of CO₂ that requires a gas exchange for carbon at some appropriate stoichiometry. On a global scale, N deposition may play a modest, but increasing role (Galloway *et al.*, 1995). We are just coming to realize, however, that nitrogen fixation from the dissolved gas phase, which is ultimately equilibrated with the atmosphere, may be very important in the carbon dynamics on the interannual scales of climate variability and on the centennial to millennial scales of global change (Hood *et al.*, 2000a; Falkowski, 1997). Episodic deposition of aeolian iron, an essential micro-nutrient thought to be limiting phytoplankton production in large regions of the ocean, and pulsed land-sea exchanges can also modify carbon dynamics, relative to the simple nitrate-based model.

The key point is that the examination of the rate processes and simple elemental dynamics in the upper ocean that come from the basic paradigm (new production or export) may be less critical than understanding how the deviations from this paradigm affect the links between key elements and the oceanic biota. One of the strongest lessons from the two JGOFS time-series stations (HOT & BATS) is the recognition of the importance of processes that are at odds with the assumptions of the simplest versions of our basic archetypes. When we include these processes and changed assumptions, we discern air-sea carbon dynamics that differ from the patterns in our simple models. For example, Hood *et al.* (2000b) estimated nitrogen fixation rates in a North Atlantic ecosystem model yielded significantly different results between fluxes derived by using summer inorganic carbon draw down within the euphotic zone and those derived from sediment trap estimates of particulate nitrogen export.

The goals of EDOCC, then, are to define the factors controlling the components, processes, stabilizing feedbacks and efficiency of the biological pump, to improve our ability to predict the responses of the systems composing the pump to natural or anthropogenically-induced external forcing and to assess the implications of changes on the oceanic ecosystem at large. In EDOCC, we envision and wish to encourage development of a program with a specific focus on food web dynamics including the biogeochemical outcomes of food web perturbations and shifts which 1) comprehensively considers the physical structuring and forcing of these systems, 2) explicitly considers ocean ecosystems as complex adaptive systems, 3) takes both an observational and experimental approach, and 4) takes full advantage of the modern molecular, satellite, modeling and computational resources available to assess the interactions of the oceanic biota with the physical and chemical environment over the relevant spatial and temporal scales.

III. MAJOR RESEARCH THEMES

The extent and efficiency of carbon processing in the oceans can be related to the structure of marine food webs that are, in turn, governed by interactions among an hierarchy of physical, chemical and biological factors. These factors, which may influence food web structures in a bottom-up (i.e. from the level of primary producers) or top-down (i.e. from the consumer, grazers and predators) manner, are themselves linked to global climate and can be expected to change during upcoming decades. For example, the composition of the planktonic community is strongly controlled by temperature, light, and the availability of macro- and micronutrients. Climate processes influence each of these factors. Similarly, climatic factors such as temperature can affect top predators and fisheries, which may cascade down the food chain. Multiple stressors at both ends of the spectrum may influence food webs and carbon flux in the oceans in ways that we cannot presently model and/ or predict.

To better understand the interactions among oceanic carbon fluxes, food web dynamics and environmental controls, four key (and interdependent) areas are identified for augmented and targeted research. These areas are:

- 1. Physical forcing controlling food web dynamics, carbon fluxes and biogeochemistry**
- 2. Biological interactions controlling food web dynamics, carbon fluxes and biogeochemistry**
- 3. Chemical-biological interactions controlling food web dynamics, carbon fluxes and biogeochemistry**
- 4. Ecosystem changes and carbon cycle feedbacks**

III. 1 Physical/Biological Interactions

In 1948, Hutchinson helped define biogeochemistry as the study of fluxes of biologically essential elements between the biotic and abiotic components of a system. The biological assimilation, biochemical transformation, physical transport, and geological sequestration and mobilization of many elements are self-perpetuating and self-regenerating, leading to a “cycling” of the elements. Although the *biogeochemical cycle* for each element is unique, general reaction pathways can be discerned depending upon the chemistry of the element, its role in metabolism, and its distribution on Earth. Like life itself, biogeochemical cycles are far from thermodynamic equilibrium, have evolved over hundreds of millions of years, and are interdependent, forming biogeochemical *systems* replete with feedback controls (Schlessinger 1997). Biogeochemical cycles depend upon, and co-evolved with, specific metabolic pathways. Hence, biogeochemical cycles depend on, and are a selective force in metabolic (i.e. biological) diversity. Over geological time, biogeochemical cycles are responsible for altering the chemistry of the ocean, atmosphere and terrestrial ecosystems, such that rate-limiting reactions within key cycles modify the tempo and mode of evolution.

At the foundation of biogeochemical research is the effort to understand how temporal and spatial patterns of elemental distributions and fluxes develop from the microscopic to global scale. These distributions can tell us about past processes and are crucial because they affect the future development of ecosystems. From an ecological perspective, the quantitative description and interpretation of spatial and temporal gradients and discontinuities (e.g. patchiness) provide an understanding of the forces controlling the balance between gains and losses. The underlying biological processes driving this balance are complex, spanning physiological (within individuals) to evolutionary time scales.

From a physical perspective, the marine environment experiences forcing across a spectrum of spatial and temporal scales. These forces directly affect biogeochemical processes. However, because biological processes have intrinsic time-scales (e.g., genetically constrained generation times), physical perturbations with similar temporal scales will be most effective in altering a particular biological process. And yet, because individuals and populations to which they belong may operate over different spatial and temporal scales, the scales of disturbance perceived by an organism are not necessarily the same as those perceived by the population. In the physical realm, energy generally cascades down the size spectrum, whereas in the ecological realm the principal flux of information and material appears to travel up the hierarchical structure and process scales (Platt and Sathyendranath, 1995). In essence, there is considerable complexity in the scales over which physical and ecological processes operate.

As a result of this non-linearity between environmental forcing and biological responses, it is not presently possible to extrapolate biological responses across scales. However, in order to achieve a better capacity to predict ecosystem evolution as a result of climate change and its potential effect on the alteration of biogeochemical cycles, it is necessary to understand how perturbations at a given scale propagate across the time-space spectrum. These points have already been raised in theoretical ecology (Pimm, 1991; Levin, 1992). They are of particular relevance in oceanography given the limited range of scale at which our observations are made, and the large ecosystem-biosphere scale at which our results need to be extrapolated in order to understand and predict the response and role of biology in the global carbon cycle.

Understanding the structure and regulation of marine food webs is a complex, four-dimensional (space and time), coupled physical-chemical-biological problem. While the dissolved components of oceanic carbon are passively transported with the flow, the particulate fraction (i.e. organisms) can have directed motion through the water (arising from either swimming or buoyancy effects). Convolution of the intrinsic biological and chemical transformations of marine food webs with these transport processes can make for exceedingly complex dynamics. Because marine food webs are so inextricably embedded within ocean circulation and mixing processes, research on biological and chemical aspects must go hand-in-hand with an integrated physical oceanographic component.

It is important to realize that, in order to assess the response of marine biota to climate change and its effect on carbon sequestration, time scales encompassing a range of natural, as well as human induced perturbations will have to be addressed. In this context, the use of ice and

sediment paleo-environmental records is a powerful tool to assess long-term fluctuations of the cycling of major biogeochemical elements, their feedbacks and linkages. Also, the study of interannual to decadal changes in ecosystem dynamics in response to regime shifts and potential changes in ocean circulation will strongly benefit from past and present research efforts such as JGOFS, LTER, WOCE, and TOGA as well as the proposed OCTET and SOLAS initiatives.

III. 2 Biological Interactions and Carbon Fluxes

A major challenge in carbon cycle research is to understand mechanistically the key biological processes that control the amount of primary production that reaches the deeper layers of the ocean. Biological processes and interactions play significant roles in the flow of carbon to the deep ocean. For example, the CO₂ sea-air exchange at any place and time is a function of wind speed and the difference between the partial pressures of CO₂ in the water and air. Interestingly, wherever the seasonality of plankton production is pronounced, the sign of the exchange changes with seasons independent of water temperature and contrary to the direct effect of sea surface temperature on CO₂ solubility (e.g. Cooper, 1933). In many open ocean regions, biological processes seem to have a stronger effect on pCO₂ than sea surface temperature (T. Takahashi, http://Alpha1.msrc.sunysb.edu/octet/Workshop_Report.html). *Thus, for predicting changes in pCO₂ and carbon export in the upper layers, a mechanistic understanding of the roles of biology, from community composition to community production are required.*

The composition of planktonic marine communities has direct implications for the magnitude of vertical fluxes. Some primary producers (e.g. diatoms) have high sinking rates, resulting in rapid flux and removal of carbon from the euphotic zone. This rapid, episodic settling circumvents the upper water column food web (e.g. Fowler & Knauer, 1986) and may even bypass some of the midwater recycling, thus increasing remineralization length scales. Other groups of primary producers (e.g. picoplankton) foster recycling of organic matter and nutrients within the surface layer, and low export rates. The composition of the primary producer community has implications for the structure and function of the secondary producers as well, as the consumer community can directly affect the efficiency of export. In turn, grazing effects can control the structure of the primary producer community. These examples illustrate that structure of the food web and the resultant primary producer community are intimately linked, and have complex interactions that ultimately control the directions and magnitudes of flows of carbon, nutrients and energy.

The DOC pool is very large, and the magnitude of the DOC fluxes are significant relative to primary production (e.g. Carlson *et al.* 1994). This makes DOC potentially important in understanding the ultimate fate of carbon and the recycling of carbon from the deep ocean to the atmosphere on millennial time scales (see below). Uptake and turnover of DOC, the first step in the microbial loop, is a critical pathway in the marine carbon cycle. Release of DOC by phytoplankton, grazers, and viral lysis can account for high microbial loop activity (50% of ¹⁴C primary production) without evoking unusual DOC sources or production mechanisms (Nagata, 2000). Much of the microbial loop activity leads to the loss of fixed carbon from those parts of oceanic food webs, which consist of higher trophic levels and organisms that produce sinking

particles. Consequently, determining the relative importance of microbial food webs versus food webs directly producing sinking particles is critical in understanding the role of the oceans in carbon cycling.

III. 3 Chemical-Biological Interactions – *Nutrient Limitation*

The concentration and chemical form of elements, including trace metals and nutrients, are some of the most fundamental determinants of the ecological characteristics of biological communities. Complex biogeochemical cycles provide for fluxes and transformations among different realms of the oceans (surface waters, the deep ocean, coastal and deep ocean sediments) that can sequester or make available elements important for life. Superimposed on the global distribution and flux of the natural biogeochemical cycles, are the anthropogenic disturbances that have wide ranging effects on many cycles including those of carbon, nitrogen, sulfur, and iron.

Chemical compounds can have both positive and negative effects on the distribution, species composition and productivity of marine organisms. Nitrogen, phosphorus, silicate and iron are the foci of current studies at sea and in the laboratory on how the availability of nutrients can control growth and productivity, but some elements such as free copper can also affect the distribution of organisms in more complex ways, as limiting nutrients at some concentrations, toxic at higher free-ion concentrations. The distribution of phytoplankton species can reflect the distribution of metals, with substantial differences in distribution of strains in coastal and oceanic waters. For example, iron, zinc and manganese requirements for coastal phytoplankton species are substantially greater than for oceanic species. These requirements are consistent with the differences in availability of these trace metals in coastal and oceanic regimes. Such controls may be important in determining the roles of different species and functional groups in productivity, but also play roles in anthropogenic feedbacks on the marine carbon cycle.

Over the past decade, it has become increasingly recognized that excess surface macronutrients (phosphate and nitrate) are found in at least three major oceanographic regimes, namely the eastern Equatorial Pacific, the Subarctic Pacific, and the Southern Ocean. The late John Martin and co-workers proposed that the so-called, high-nutrient, low chlorophyll (HNLC) conditions characterizing these three areas are a consequence of iron limitation (Martin 1991). Three purposeful iron enrichment experiments, two conducted in the eastern Equatorial Pacific and one in the Southern Ocean, supported the iron-limitation hypothesis, and provided concurrent evidence that Fe facilitated utilization of macronutrients leads to a drawdown of $p\text{CO}_2$ in surface waters (Boyd 2000; Coale, et al. 1996). Direct experimental verification in the Subarctic Pacific remains to be seen. However, should iron fertilization experiments in the three HNLC regions continue to support the fundamental concept, the potential exists that large, natural sink for CO_2 could have been activated in the geological past.

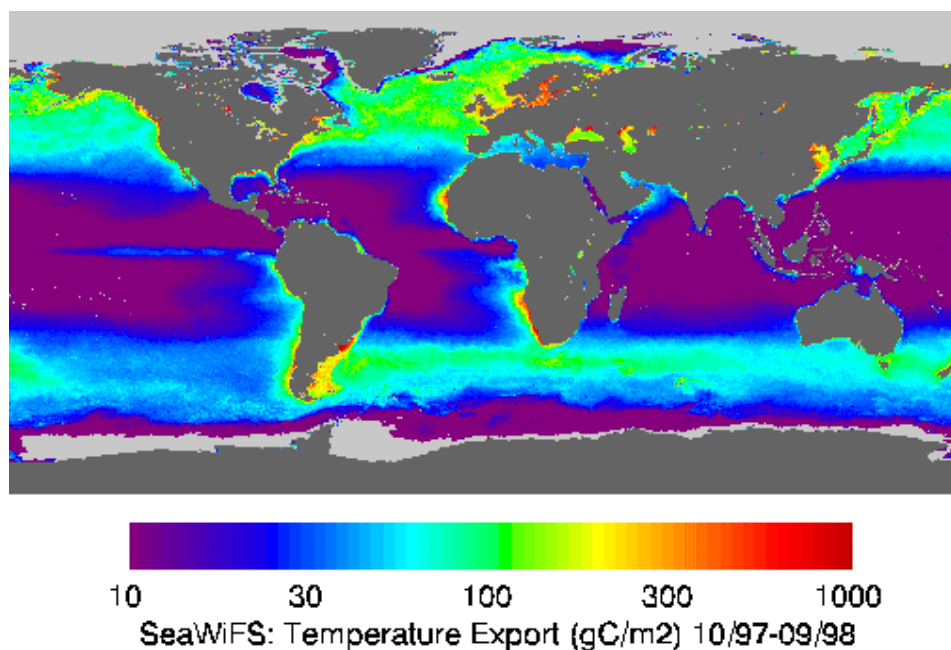
In HNLC regions, the efficiency of export production is related to the production of diatoms (Dugdale & Wilkerson 1998). Simply put, the sinking flux of silicate is thought to be proportional to the export of organic carbon (Falkowski *et al.* 1998), while the overall sinking

flux relative to primary production (i.e., the export flux ratio), appears to be dependent upon upper ocean temperature (Laws *et al.* 2000; Fig. 2). In the Southern Ocean, where export flux is potentially extremely high, micronutrient limitation appears to limit primary production. However, even if nitrate and phosphate were to be consumed, the Si/C ratio in diatoms is approximately 4 fold higher than the average for cosmopolitan diatoms communities under nutrient replete conditions. The difference has been suggested to be a consequence of chronic iron limitation that physiologically constrains the production of organic matter while having less impact on the precipitation of biogenic opal in diatom frustules (Hutchins & Bruland 1998). Thus, if the silicate/organic carbon ratios in Southern Ocean diatom communities conformed with those from other oceanic regions, approximately four times as much organic carbon could be fixed for the same orthosilicic acid inventory.

Evidence for Fe limitation of the 'biological pump' in extensive areas of the paleo- and modern ocean has accumulated from examination of geochemical records and recent micro- and mesoscale bioassay experiments. The ~400 kyr record demonstrating the inverse relationship between dust load (hence, Fe) and CO₂ trapped in air bubbles in the Vostok ice core, Antarctica (Petit *et al.* 1999) supports, but does not prove, the idea that periods of low atmospheric CO₂ and presumably high rates of marine

C sequestration are related to enhanced Fe availability in ocean surface waters. On longer time scales (mya), sediment cores underlying the equatorial Pacific HNLC region demonstrate that periods of high opal accumulation rates that accompany diatom driven carbon export likely correspond to periods of enhanced upwelled Fe fluxes (Wells 1999). Thus, on geological time scales, natural variations in aeolian iron appear to be correlated with ca. 100 ppmv changes in atmospheric CO₂. Is this relationship causal or coincidental?

Figure 2. Calculated export fluxes of organic carbon for the world ocean based on the model of Laws *et al.* (2000). Note the relatively low export in the Southern Ocean. The low values in this region are a consequence of relatively low primary productivity due to the inefficient utilization of nutrients.



Utilization of nutrients in HNLC regions is not the only mechanism by which the ocean absorbs atmospheric CO₂, however. Quantitative analysis of nitrate/phosphate ratios in all three major ocean basins reveals depletion in inorganic nitrogen. This depletion has been hypothesized to be a consequence of a slight imbalance between N₂ fixation and denitrification during interglacial periods (e.g., the contemporary ocean. See below.). As N₂ fixation requires a large flux of iron, it has been suggested that the enhanced aeolian fluxes of iron characterizing glacial periods stimulated N₂ fixation, which, in turn increased the fertility of the low-nutrient, low-chlorophyll (LNLC) subtropical gyres. The latter regions occupy 74% of the ocean surface.

Because the ratio of the sinking flux of particulate organic N and particulate P exceeds the N:P ratio of the dissolved pool of inorganic nutrients in the ocean interior, on average the upward flux of inorganic nutrients must be slightly enriched in P relative to N in relation to the elemental requirements of the photoautotrophs (Redfield 1958). Hence, although there are some exceptions (Gruber & Sarmiento 1997), at the present time, dissolved, inorganic fixed nitrogen generally limits primary production throughout most of the world oceans (Barber 1992; Dugdale 1967; Falkowski 1997; Ryther 1969). Second, the N:P ratio of the dissolved pool of inorganic nutrients in the ocean interior was established by biological processes, not *vice versa* (Redfield 1958). The average Redfield N:P ratio of 16:1 for particulate organic matter (Copin-Montegut & Copin-Montegut 1983; Redfield 1958) is an upper bound for the two elements in the dissolved inorganic phase in the ocean interior. In the contemporary ocean, the average N:P ratio of dissolved inorganic nutrients in the ocean interior is approximately 14.7 by atoms (Fanning 1992; Gruber & Sarmiento 1997), or less (Anderson and Sarmiento 1994). The deficit in dissolved inorganic fixed nitrogen relative to soluble phosphate in the contemporary ocean interior implies a slight imbalance between nitrogen fixation and denitrification (Codispoti 1995). Finally, if the net biologically mediated exchange of CO₂ between the atmosphere and ocean requires a change in either the concentration of limiting nutrients, or efficiency of their utilization (Broecker 1982), and dissolved inorganic nitrogen rather than phosphate limits productivity in the oceans, then it follows that the ratio of nitrogen fixation to denitrification plays a critical role in determining the net biologically-mediated exchange of CO₂ between the atmosphere and ocean (Codispoti 1995; Falkowski 1997). It has been suggested that this ratio changes on time scales of 10³ years, as a consequence of aeolian iron delivery to the LNLC regions of the oceans, thereby stimulating N₂ fixation (Falkowski 1997). Further, this process has been hypothesized to have played a substantial role in the drawdown of atmospheric CO₂ during glacial periods (Broecker & Henderson 1998; Falkowski 1997). At present we have no direct experimental evidence to support this hypothesis.

In many open ocean regions, iron is principally provided by atmospheric fallout (Duce & Tyndall 1991); winds and precipitation in the source region are likely to be altered under a climate change scenario with implications for responses in both current HNLC and LNLC regions.

Ecological Stoichiometry

Ultimately, the cycling of elements in ecosystems is controlled by coupling between the abiotic properties and distributions of elements and the metabolic requirements of organisms. The extent to which the flux of individual elements matches population and community requirements, can determine the productivity of the ecosystem, as well as the rates of movement and pathways of the elements themselves.

All organisms have requirements for specific elements in particular relatively narrow proportions according to their physiological condition and overall life history strategy (Falkowski, 2000; Kirchman, 2000). Thus, through their activities, organisms release and transform elements into different chemical forms with differing physical and chemical properties (e.g. solubility and stability). These requirements on the part of organisms can lead to transient or long-term sequestration of elements which can in turn influence biogeochemical cycles. For example, iron release in surface waters results in precipitation of insoluble iron compounds at ambient pH unless complexed in an organic form (Hutchins *et al.*, 1999). Particulate matter reaching the deep ocean is remineralized, providing inorganic nutrients to be upwelled in ratios reflecting the composition of organisms contributing to the downward particulate flux as well as dissimilative (e.g. denitrification) and differential regeneration processes. These ratios have long been assumed to reflect innate, fixed, properties of biological materials. However, the idea that the coupling of major elements (C, N, P) in organisms occurs in fixed proportions (e.g. the Redfield ratio of 106:16:1) is increasingly at odds with direct measurements and is coming into greater question as biologists gain insight into the nutritional physiology of diverse biota.

With respect to the carbon cycle, the role(s) that the marine biota play in controlling the flux of carbon between the atmosphere and deep water is *inter alia* governed by the relationship between biological requirements for elements in relation to their short-term supply, and the potential for longer term ecological shifts in requirements as communities adapt to changes in availability or other environmental factors by a shift in species. From laboratory studies we know that the ratios of elements in phytoplankton are highly plastic, and elemental ratios can vary as a function of growth rate due to shifts in biochemical allocation (Goldman *et al.*, 1979). Higher in the food web, consumer taxa homeostatically regulate their elemental composition but ratios differ among species according to major life history characteristics (for example fast growing organisms have a larger proportion of ribosomes with P-rich ribonucleotides, whereas slow growing organisms have a larger proportion of N-rich proteins; Elser *et al.*, 1996). We also know from studies in lakes that the effects of differences in the C:N:P stoichiometry of key food web components can be manifested at the ecosystem scale and alter biogeochemical cycling in major ways (Elser & Urabe, 1999).

The single largest biochemical constituent of most unicellular algae is protein (Parsons *et al.* 1961). To quote Jack Myers, the essential features of unicellular algae are: "organisms small in size with a minimum of skeletal crud, rich in protein as cellular machinery and with potential for an intrinsically high metabolic rate" (Myers 1980). As proteins require a significant investment in reduced nitrogen, the relatively low C/N ratios of unicellular algae reflect the relative abundance of protein. The single largest investment of phosphorus is nucleic acids,

specifically ribosomal RNA. Is there a biologically constrained ratio of nucleic acids to proteins in unicellular organisms (Elser *et al.* 1996)? Is there some canonical ratio of (e.g.) ribosomes to protein within eucaryotic cells that is highly constrained? For example, when cells are growing at an optimal rate, does the ratio of ribosomal RNA to protein conform to a common value for all procaryotes and eucaryotes? Many investigators have noted a strong correlation between bulk RNA and growth rate (i.e. the rate of protein synthesis) (Dortch *et al.* 1983; Kemp 1995; Sutcliff Jr. 1965). In procaryotes, there is strong experimental evidence that this relationship is causal. It is linked to the synthesis and abundance of guanosine 5'-diphosphate, 3'-diphosphate (ppGpp), a molecule that influences the initiation of rRNA synthesis and protein elongation (Glass *et al.* 1986; Rojas *et al.* 1984; Ryals *et al.* 1982). The pool of ppGpp is negatively correlated with growth and under conditions of nutrient limitation, ppGpp increases as rRNA synthesis decreases and growth rates decline. In eucaryotes, other signal molecules regulate the feedbacks between rRNA and protein syntheses. What are the factors that control these biochemical stoichiometries in marine organisms?

In ocean ecology we are just beginning to understand the real biological constraints on the flexibility of elemental ratios due to such shifts in simple biochemical composition. We know even less about how organisms could adapt or evolve to change their elemental requirements in response to a changing environment. Thus, stoichiometric relationships of multiple elements throughout marine food webs likely have important but unappreciated implications for understanding carbon cycling in the oceans, and for predicting the long-term effects of global perturbations on oceanic food webs. New laboratory and field technologies, combined with the rapid progress in the development of biological and ecosystem models appear to provide a unique opportunity to integrate our understanding of the cellular biology of organism growth with our increasing knowledge of global biogeochemical cycling.

III. 4 Ecosystem Changes and Carbon Cycle Feedbacks

Ecosystems are complex systems. At their core, they are composed of a large number of interacting, adaptable populations and communities. Through these interactions emerges the structure and function of the ecosystem. The interactions are non-linear and the outcomes can be surprising and non-intuitive. Small changes in the system or models of the system can have very divergent results. Yet, out of all of the potential of a complex system for many unpredictable outcomes, consistent patterns often repeatedly emerge. The understanding and prediction of ecosystem patterns in space and time is at the heart of ecology and at the root of any real ability to relate ecosystem structure to biogeochemistry.

Process reversibility and the concept of stable states

The concept of succession (Clements, 1916), as the process used to describe the evolution of communities, is generally accepted in the analysis of ecosystem dynamics. However, the succession model implies that all possible ecosystem states can be arranged in a time continuum moving toward a stable or climax state. If the climax community is perturbed, its state is moved

away from climax, but should return to it through a predictable sequence in time. In other words, this Clementian view of ecosystem evolution and climax allows for stochastic disturbances, but is deterministic in regard to the response of the community to perturbations. Under this linear model, it is possible to predict the evolution of an ecosystem based on its response to previous disturbances.

However, in non-linear systems, a stable state may be local, rather than global (May, 1974). For example, punctuated equilibria in evolution models suggest that mutation events in single species occur rapidly during discrete periods (instability), followed by periods of reduced or no activity (the system has reached a stable state; Bak *et al.*, 1993; see also Kellog, 1975). When dealing with non-linear systems in which multiple stable states can exist under similar physical settings, understanding the characteristics of the ecosystem in terms of its stability (or hysteresis i.e. the lag in the response of a body to an external change in forces) at any distinct composition becomes critical to the development of predictive models. However, the concept of ecosystem stability has no single definition (Connell & Sousa, 1983) and depends strongly on the scale of observation (Levin, 1992). Hysteresis is tightly coupled to the concepts of resistance and resilience, where resistance is the tendency for a system to remain in equilibrium while subjected to perturbation (Connell & Sousa, 1983) and resilience is the capacity to return to the pre-disturbance stable state following a disturbance (Pimm, 1984). Resistance and resilience are strongly influenced by food web structure, and can be used to understand those mechanisms responsible for oscillatory and chaotic behavior of particular systems (Edelstein Keshet, 1988)

Although most studies in ecosystem stability have been done in terrestrial and freshwater ecosystems, the first-order principles driving these systems must also apply to marine ecosystems. Some examples of hysteresis and oscillatory behavior found in the marine literature include the recovery of fisheries from, e.g., overfishing, and the recovery of coastal systems from eutrophication (Richards & Rago, 1999; Livingston *et al.*; 1999), as well as the shift between coral and algal dominance in tropical reefs (Hughes, 1994), and between oxic and anoxic periods in the Baltic Sea (Janson & Velner, 1995).

Over the past two decades, the effect of natural climate oscillations and climate change in pelagic ecosystems thought to be strongly resilient has become evident (Karl *et al.*, 1995, 2000; Roemmich & McGowan, 1995; McGowan *et al.*, 1998). Although we do not fully understand the mechanisms driving these changes, long-term alterations of the food-web structure and carrying capacity of the marine ecosystems are important issues to science and society. Climate change will affect and probably intensify naturally occurring oscillations such as El Niño (Fedorov & Philander, 2000; see also for the observed multi-decadal cyclic shifts of biota in entire ocean basins that suggest switching two stable states induced by small physical changes, section IV.3). How and to what degree marine ecosystems may respond to these physical changes through negative or positive feedback mechanisms are difficult questions that need to be addressed in order to develop predictive models of marine and, hence, biosphere elemental fluxes.

Carbon Cycle feedbacks

Of particular relevance to our societal concerns are the possible changes in carbon flux between the atmosphere, the terrestrial realm and marine ecosystems, and the potential feedback mechanisms that regulated the rate of change of atmospheric CO₂ (Sarmiento & Wofsy, 1999). At a global scale, some feedback mechanisms may be driven by biochemical processes and involve ecosystem responses that enhance or decrease carbon sequestration through, for example, changes in the net balance between photosynthesis and respiration rates (Sherr & Sherr, 1996). While the response of environmental systems to climate perturbations is purely reactive, human responses can have both, reactive and proactive elements. Hence, feedback mechanisms probably will affect as well as involve changes in policies of industrialized societies regarding greenhouse gas emissions and the management of natural resources.

To a large extent, modeled scenarios of past, present, and future atmospheric CO₂ concentration are expected to help dictate proactive societal responses to atmospheric CO₂ buildup and global warming. However, these modeled scenarios assume no significant alterations in marine ecosystem structures and their geographical distribution. This static representation of marine ecosystems limits the extent to which feedback mechanisms can be built into predictive models, and is due, in part, to our rudimentary ability to predict the response of these ecosystems to climate change. Nevertheless, there is ample evidence that oceanic ecosystems respond significantly to inter-decadal and long-term climate change, and that these responses may have significant effects in marine biogeochemical cycles and the anthropogenic carbon sequestration capacity of the ocean (Karl *et al.*, 1995, 2000). ***Hence, we must recognize that our inability to predict ecosystem changes represents a major limitation in our capability to model future atmospheric CO₂ concentrations and global warming.***

IV. High Priority Science Questions

The following are several specific examples of questions that are encompassed by our major themes. These examples are not exhaustive and are not prioritized.

Food Web Issues

1. How can we better conceptualize marine food webs? The Functional Groups Concept

A major difficulty in developing a predictive understanding of marine ecosystems involves the degree to which biodiversity and interactive complexity are represented in ecosystem models. Current models tend to be overly simplistic, and yet incorporating this diversity and complexity (much of which we are learning about) in heuristic models may not be feasible. Hence, a middle ground that incorporates the essential functional components represented by particular guild of organism needs to be established.

Biogeochemical cycles are driven by specific "functional groups" of organisms that specialize in specific metabolic sequences. For example, photoautotrophs and chemoautotrophs reduce oxidized carbon to form organic matter. Heterotrophs oxidize reduced carbon to produce carbon dioxide and release inorganic nutrients. Operationally, functional groups are defined here according to biogeochemical role rather than phylogenetic affiliation. Over the course of evolutionary time, many phylogenetic divisions of photoautotrophs have emerged in the oceans, yet each has the same basic biochemical machinery required to produce oxygen and reduce inorganic carbon. Within this diverse group however, some sets of organisms play more important roles than others in specific biogeochemical fluxes. For example, the appearance of diatoms in the Cenozoic (ca. 120 million years ago), led to the emergence of an especially efficient conduit for carbon export from the upper ocean to the interior. In the contemporary ocean, diatom blooms are often highly correlated with export production.

Calcifying organisms, such as coccolithophores, form a second functional group within the oceanic photoautotrophs. In contrast to diatoms, coccolithophorid production is thought to contribute to the evasion of CO₂ from the ocean to the atmosphere on ecological time scale. On geological time scales however, marine calcification, including that in coral reefs, is the largest sink for CO₂.

The fixation of N₂ is a strictly prokaryotic metabolic process that requires a localized anaerobic environment. Except for diazotrophic (organisms which use nitrogen gas) photoautotrophs, combined nitrogen is required to sustain photoautotrophic growth. At first glance, there is a paucity of diazotrophs in the contemporary ocean, suggesting some constraint on the tempo of evolution of the responsible organisms. In the oceans N₂ fixation appears to be largely mediated by phytoplanktonic cyanobacteria, of which the genus *Trichodesmium* is particularly important in the upper layers of the oligotrophic tropics and sub-tropics (Capone *et al.* 1997). A role for picoplanktonic cyanobacteria, photosynthetic, heterotrophic or photoheterotrophic bacteria in nitrogen fixation, while suspected, remains unknown. Furthermore, apart from coastal environments, nitrogen fixation on the seabed remains poorly studied (Capone 1988).

Currently, with respect to carbon and energy source, microbes are placed into one of two large functional groups: heterotrophs or autotrophs, with the autotrophs divided into several subdivisions based on cell size and secondary functionality such as carbonate or silicate production, or N₂ fixation (see above). Heterotrophic bacteria, on the other hand, are often considered as a single functional group relative to carbon and energy dynamics. A major revelation in recent years has been the discovery of the great diversity of prokaryotes (bacteria and archaea) in marine ecosystems. These prokaryotes, the most numerous organism in the ocean and on the planet (Whitman *et al.*, 1998), include archaea, once thought to be restricted to extreme environments, and many groups of heterotrophic bacteria as well as the dominant phototrophic organisms in the open ocean, *Prochlorococcus* and *Synechococcus*. Unfortunately, the metabolic capacities of most of these microbes are largely unknown since most have resisted isolation and subsequent growth and in laboratory pure cultures.

While the diversity of heterotrophs is recognized in the large variety and complexity of the biogeochemical cycles of major nutrients such as nitrogen and sulfur, heterotrophic bacteria should probably not be lumped together into a single functional group in the carbon cycle. For example, bacterial groups appear to differ in their use of selected components of the dissolved organic carbon (DOC) pool (Cottrell & Kirchman, 2000; although see also Ouverney and Fuhrman, 1999).

In the context of functional groups, the animals ('macro-heterotrophs') at the top of the food web are, through size-selective grazing and predation, "editors" of food webs, and distinct from the functional group definitions of autotrophs. For this reason, we need to determine to what extent community structure is dependent on the activity of high trophic levels in order to better understand factors controlling the stability and resilience of a given ecosystem state. The true variety of "editing" cannot possibly be included in models, and a major issue for a particular model will be whether to group the animals into feeding guilds (e.g., small versus large animals, and vertical migrators versus non-migrators), or to rely on the actions of a few dominant species, as it may be permissible outside the tropics and subtropics.

2. What are the food web structure characteristics of major ocean biomes, and what controls these configurations?

Although much is known about the large-scale ecological geography of the sea (e.g. Longhurst, 1998), the nature of the food web in the mesopelagic zone and in the benthos remains largely uncharacterized. If the functional group concept is to be successful, it is imperative to determine the groups and processes relevant in order to describe the dominant elemental cycles. Thus, there is a strong need to continue refining our basic descriptions of marine food webs, as well as ascertaining their signatures in terms of partitioning of carbon amongst the various reservoirs.

Fundamental to our understanding of the mechanistic controls on marine food webs are the processes that control growth, reproduction and mortality of the organisms that comprise the food web. Whereas the basic effects of resource limitation on the production of organic material are reasonably well understood, losses due to grazing, DOC production, the export of settling material and trophic cascades are relatively less well constrained. For example, microzooplankton (both protozoa and small metazoa) are the dominant consumers of phytoplankton in the ocean. What limits herbivorous microzooplankton population growth? There is some evidence that mesozooplankton can exert significant predatory control; observations at different seasons or in different regions suggest grazing of herbivorous microzooplankton by mesozooplankton is insignificant. These contrasting findings highlight the need for further examination of the cascading trophic effects of predatory micro- and mesozooplankton in both oligotrophic and eutrophic environments. In addition, the joint effect of resource limitation and predatory control remains a promising area for future research in enclosures ("mesocosms" of a few to many cubic meters content) or in open sea in "tagged" water, similar to the mentioned IRONEX study (Coale *et al.*, 1996).

With respect to grazing, understanding the structure of the consumer community is essential as it can directly determine the efficiency of export. Addressing the problem of seasonally shifting mortality for the phytoplankton, at least in regions with seasonally changing plankton production, also requires knowledge of seasonally shifting dominance of zooplankton species or functional groups/guilds (e.g., "all small omnivorous mesozooplankton species not engaging in diel vertical migration"). Small shifts in the ratio of the rate of phytoplankton cell division over the rate of mortality (e.g., from changes of resources or size-selective grazing, versus the natural seasonal shift of the zooplankton community) will alter the ratio of recycled versus new production, the net community production and the $p\text{CO}_2$. We are yet unable to predict the seasonal changes of dominant zooplankton species from environmental information, although in principle, it has been accomplished for a very few species of mesozooplankton. At present, our understanding of marine plankton community structures is insufficient to predict the impact of changes in community structure on carbon cycling and the impact of climate change on plankton community structure.

3. How are these controls modulated in space and time to produce observed distributions?

The sea provides a variety of opportunities to examine how the various mechanisms controlling food web structure are expressed. Persistent regional differences, as well as the transition zones between them, provide the basis for comparative study. Long time series observations have revealed major changes in marine food webs on interannual to decadal time scales. Karl and co-authors (Karl *et al.*, 1995, 1997; Karl, 1999) have documented some of the most striking examples of this in the open ocean, in which increases in stratification associated with El Niño and the North Pacific "regime shift" have led to an increase in the abundance of nitrogen fixing organisms, a switch from N to P limitation, and overall increase in phytoplankton biomass.

Other examples from the pelagic domain are the dramatic shifts in zooplankton biomass and salmon catches in the northeastern Pacific correlated with cyclic climatic regime shifts, on the scale of 2 - 3 decades (e.g., Francis *et al.*, 1998; Sugimoto & Tadokoro, 1998), the weather- and climate-correlated changes of zooplankton in the North Atlantic (Reid *et al.*, 1998), and the concurrent waxing and waning by orders of magnitude of the two or three dominant, but disconnected sardine species off Japan, California and Chile on the scale of approximately half-centuries (Cushing, 1995). Exactly how such transitions occur remains unknown. Do pelagic ecosystems flip-flop between states, or are different states simply superimposed on one another (see Section III.3)? What are the consequences of these flip-flops on plankton community structure and in turn on carbon cycling? In addition to the sorts of large-scale, low-frequency variations in food web structure described above, synoptic variability in the ocean (e.g. fronts, waves, eddies) provides yet another type of natural laboratory for studying controls on the spatio-temporal expression of food web structure.

Note that there are numbers of experimentally studied and mechanistically understood examples from marine rocky bottoms which support the scenario of flip-flops between semi-stable states. The vast pelagic realm, however, is likely to matter more for global carbon flux

than the scattered rocky bottoms and deserves more intense study. In the open ocean, climate change may or may not change an ecosystem from one previous state to another previous state, but conceivably might lead to new, entirely different states. Since the causal reasons even for the present flip-flops, from the physical trigger to, e.g., the changing size of fish stocks, cannot be studied experimentally in the open sea because of the large temporal and spatial scales, prediction will be very hard to achieve without sustained and dedicated effort (see also Steele, 1998, reflecting on GLOBEC).

Over geological time, the distributions of key functional groups change. For example, relative coccolithophorid abundance generally increases through the Mesozoic, and undergoes a culling at the K/T boundary, followed by numerous alterations in the Cenozoic. The changes in the coccolithophorid abundances appear to trace eustatic sea level variations, suggesting that transgressions lead to higher calcium carbonate fluxes. In contrast, diatom sedimentation increases with regressions. On much finer time scales, during the Pleistocene, it would appear that interglacial periods favor coccolithophorid abundance, while glacial periods favor diatoms. The factors that lead to glacial-interglacial variations between these two functional groups are relevant to elucidating their distributions in the contemporary ecological setting of the ocean.

“Everything is everywhere, the environment selects” goes the aphorism oft attributed to the noted microbial ecologist, Martinus Beijerinck. It is suggested that the distribution of all planktonic organisms in the oceans obeys a rule of *universal distribution and local selection*. This rule states that in any given body of water, there is a finite probability of finding any organism at any time, but that the local environment will be more conducive to the growth of some organisms than others. This rule implies that, within reason, the rules of “selection” can be largely elucidated for major functional groups. If, for example, the water column is cold and nutrient rich we may assume that nitrogen fixers will be present but not highly selected while diatoms are more likely to be abundant. Conversely, in warm, stratified, oligotrophic seas, it is unlikely that diatoms will emerge as dominant organisms, while nitrogen fixers are more likely to be abundant.

A major challenge for the next few decades will be to identify the major rules by which key functional groups are distributed in the ocean, both past and present, and to develop predictive models of their dynamics.

4. What controls massive episodic blooms ?

However, in order to achieve a mechanistic understanding of the processes governing the long term structure and evolution of pelagic and benthic communities we will have to address the causes and the ecological role of short term lived stochastic and catastrophic events. Of particular relevance to this issue is the nature of massive episodic monospecific blooms of both autotrophs and heterotrophs. Because of their monospecific nature, these blooms generate a strong uncoupling between photosynthesis and respiration in the euphotic zone, altering significantly the energy and elemental fluxes in the pelagic environment. For example, salps are holoplanktonic grazers that sometimes occur in very dense populations covering large areas

(Andersen 1998). These dense populations have major impacts on the economy of the ocean due to grazing and production of fast sinking fecal pellets (Andersen, 1998; Caron *et al.*, 1989; Perisinotto & Pakhomov, 1998). However, salp blooms appear to be highly episodic in time and space, and their prediction, as well as the assessment of their effect on pelagic elemental fluxes, constitutes a major challenge (Michaels & Silver, 1988).

The importance of blooms of autotrophs in altering biogeochemical cycles has been documented as well. For instance, the effect of blooms of the diazotrophic (nitrogen fixing) cyanobacterium *Trichosedmium* in the nitrogen and carbon cycle of pelagic oligotrophic environments has long been recognized (see Biogeochemical Issues below). However, the causes triggering these blooms, and similar blooms of diatoms in oligotrophic regions, and the fate of the organic matter generated during these events remains a matter of debate (Karl *et al.*, 2001).

Because both recurrent short-term perturbations and long-term gradual environmental changes are important forces shaping the structure of marine ecosystem, understanding what triggers short lived but intense biological events and how these events contribute to the evolution of the ecosystem will remain an important challenge in the years to come.

Biogeochemical Issues

1. What are the controls on vertical and horizontal structure of organic matter, its remineralization and its relationship to the ventilation of the sea?

By definition, in a pelagic system in which there is no net accumulation of organic matter, new production is balanced by the export of organic matter to the deep ocean. Suspended particle abundance, large particle flux, and DOM concentration all decrease below the euphotic zone, with the sharpest gradients occurring at mesopelagic depths (150-1000m). Concurrently, there are decreases in the abundance of microorganisms and changes in their species compositions, with a marked increase in the numbers of archaea. Over the past 10 years, rapid advances have been made towards understanding the controls on upper ocean primary production. However, the factors and mechanisms that control the percentage sinking loss of POC formed by the phytoplankton in the euphotic zone at a given time and area, and the vertical and horizontal structure of remineralization below, the other essential component of the carbon cycle, are not well understood. One can imagine the oceanic water column as consisting of horizons with different ventilation ages (times since/until contact with the atmosphere). The depth of organic matter remineralization will have a large impact on the air-sea exchange of carbon dioxide and oxygen and the return of nutrients to the euphotic zone over decadal to centennial time scales. ***Understanding the interplay between biology and geochemistry as drivers of organic matter remineralization will be a major challenge of the coming decade.***

A great deal has been learned about the variability and controls on particle flux in the ocean from the now global deployments of sediment traps. The carbon flux below 1000-1500m can be measured directly, or derived from a number of different approaches. However, carbon

cycling in the epi- and mesopelagic ocean (0-1000m), including along the continental margins, is complex and not understood. Hydrography, resuspension and lateral advection of particles, the hydrodynamics of sediment traps, and the presence of swimmers that enter the traps, all complicate direct measurements of particle flux. Short lived radionuclides (^{234}Th) have been used to correct particle fluxes measurements made in the euphotic zone, and similar approaches are needed to estimate carbon flux and understand carbon cycling dynamics for mesopelagic depths. The mechanisms by which particles are consumed and ultimately remineralized in the deep sea are also poorly understood. While conventional thinking had ascribed most of the utilization of sinking particles to mesopelagic animals, more recent evidence points to a significant role of particle-bound microorganisms in solubilizing the particles into DOC. Suspended free-living microorganisms then consume this DOC, mineralizing some and converting some into microbial biomass (see review by Azam 1998).

Even less is known about the controls on DOC production, utilization, and remineralization, although DOC is by far the largest reservoir of reduced carbon in seawater. Small perturbations in DOC production or consumption may potentially influence carbon sequestration and elemental ratios in seawater. DOC is a complex mixture of labile and less-labile materials, formed by many processes (often poorly characterized), and taken up or degraded by bacteria and archaea. For some time, it has been known that protists form critical links in the microbial web, and act both to mineralize organic matter and permit microbial production to be passed to higher trophic levels. The recent discovery of viruses as a significant component of marine ecosystems has pointed to a mechanism by which C flow is concentrated in the smallest, nonsinking, components, and ultimately mineralized by a trophic loop, essentially robbing production from larger organisms that are more associated with sinking (Fuhrman, 1999). Thus, variations in the viral infection of heterotrophic and autotrophic microorganisms (including phytoplankton blooms) may have a significant effect on large-scale C cycling. Also, it is now clear that seasonal entrapment and degradation of DOC below the euphotic zone is an important short term sink for carbon. There is growing evidence that a fraction of deep-sea DOC may cycle on relatively short time scales, and therefore have a more important role in the marine carbon cycle than suggested by its relative old average radiocarbon age (Hansell & Carlson, 1998). An important change in our understanding of DOC cycling has come with the recognition that a large fraction of dissolved organic matter is composed of specific biopolymers synthesized directly by phytoplankton and bacteria (Tanoue *et al.*, 1995; Aluwihare *et al.*, 1997; Aluwihare & Repeta, 1999). These biopolymers may largely define the reactive fraction of DOM that cycles on annual to decadal time scales. Mineral matrices or adsorption onto particle surfaces does not impede remineralization of dissolved biopolymers, and biopolymer accumulation in the dissolved phase must be an inherent property of their chemical structures. Using molecular biological and biochemical techniques, it may now be possible to identify and trace an important fraction of marine DOM, and understand the production, cycling and fate of specific biopolymers.

Particulate and dissolved organic matter are often treated as two distinct phases, although they fall within a continuous spectrum and there is active and rapid exchange of organic matter through all size classes. Production and remineralization of biogenic particles (including the organisms themselves) results in the formation and release of dissolved organic matter. Dissolved organic matter adsorbs onto particles, and spontaneously assembles into polymer gels

(Chin *et al.*, 1998) that may act as a "scaffolding " for microbial processes (Azam, 1998). The biological mediation of DOM- POM dynamics is a critical component of the marine carbon cycle that is only beginning to be appreciated and understood. Under some conditions, certain marine algae release dissolved organic matter that aggregates to form rapidly sinking particles. Aggregates are colonized by bacteria that both remineralized carbon and return it to the dissolved phase, thereby introducing reduced carbon at depth in the ocean. Marine bacteria that colonize macroaggregates are genetically distinct from free-living forms, and may have metabolic pathways uniquely adapted to the remineralization of complex biopolymers. The whole subject of microbial community composition and its dynamics is only now getting attention, largely with the help of new molecular techniques. Such dynamics, including the rise and fall of blooms, almost certainly affect C cycling in a major way.

2. What is the role of the continental margin in the production, cycling and transfer of carbon?

The role of the coastal ocean and continental margins in global carbon cycling remains a topic of intense debate since the inception of the JGOFS program. Several lines of evidence argue that these regions participate significantly in the oceanic carbon cycle and should be included within focused investigations of the ecological determinants of oceanic carbon cycling.

In spite of their small geographic area, coastal regions are sites of significant levels of primary and new production, organic matter metabolism (e.g. Smith and Hollibaugh 1993) and carbon burial (Berner, 1992; Jahnke, 1996). The amount and fate of this productivity is not well constrained. For example, estimates for new production in the ocean margins range from 27% to 57% of total oceanic new primary production (Wollast, 1993; Chavez & Toggweiler, 1995, respectively). Inclusion of benthic primary production in continental shelf environments (e.g. Jahnke *et al.*, 1999) and salt marshes (e.g., Pinckney & Zingmark, 1993) may increase this estimate, and perhaps tip the balance of photosynthesis vs. respiration, resulting in a "net autotrophic" coastal ocean (*sensu* Smith & Hollibaugh, 1993). Moreover, calculations of carbon respiration in the deep ocean (i.e. below the mesopelagic zone and including the sediments) suggest that deep ocean metabolism is supported significantly (by as much as 50%) by lateral transfer of carbon from continental margin environments (Jahnke *et al.*, 1990; Jahnke, 1996). Thus, there must be a strong carbon link between coastal biogeochemical processes and the deep ocean.

The coastal ocean also is a critical link between the terrestrial and marine biospheres. Nutrient cycling and degradation of terrestrially-derived carbon is accomplished by diverse microbial assemblages which metabolize seemingly refractory material over relatively short spatial and temporal scales (e.g. Hedges & Keil, 1995). Evidence suggests that most remineralization of this terrestrially-derived carbon occurs within the coastal ocean/continental margin. Margins also may account for a large fraction of global denitrification (Wollast, 1993; but see Marinelli *et al.*, 1998). Coastal microbial assemblages and their attendant biogeochemical functions may provide significant insight into the processes that affect the

cycling and fate of carbon in the surface and deep ocean. They also provide an excellent venue for the study of complex systems.

Given the proximity of the coastal ocean to the continents, and the high population densities along much of the world's coastlines, the coastal ocean and continental margin are vulnerable to human impacts and may provide the first indications of anthropogenic alteration of ecological state. For example, biologically diverse and highly productive coral reefs may be significantly harmed by increased organic loads, siltation, and decreased water clarity associated with eutrophication. At the same time the results of environmental perturbation associated with global change, such as sea level rise, will affect the coastal ocean and the attendant populations most immediately. Thus there is a strong economic and social incentive to invest resources in the study of coastal and continental margin processes as they relate to global carbon cycling. We grant that significant heterogeneity in coastal and continental shelf environments exists worldwide and, hence, generalizations may be even more difficult than for the water column. For example, river-dominated margins, with extensive terrestrial input to the coastal ocean (which, as a system, are perhaps heterotrophic), are likely to have different dynamics than non-depositional shelves (which may be net autotrophic), relative to the highly productive, biologically diverse coral reefs (which are currently thought to serve as a CO₂ source). These different systems merit investigation to understand the extant ecology and biogeochemistry of carbon cycling as well as the likely responses of these systems to future perturbation.

3. What controls the carbon:carbonate rain ratio and how does it control surface pCO₂?

The composition of phytoplankton assemblages affects the ratio of particulate inorganic to organic carbon in settling organic matter. This is because coccolithophores precipitate calcite, and ultimately generate the inorganic C flux, whereas other phytoplankton groups do not. The carbonate “rain ratio” is defined as the ratio of the flux of POC:PIC, and exerts an important influence on atmospheric CO₂. Production of CaCO₃ results in one mole of CO₂ and one mole of CaCO₃ for every 2 bicarbonate molecules assimilated. The pCO₂ level in coccolithophore blooms has been observed to increase (Robinson *et al.*, 1994) well above typical levels. Buitenhuis *et al.* (1996) measured a rapid dissolved CO₂ increase in a North Sea coccolithophore bloom when alkalinity decreased relative to dissolved inorganic carbon (DIC). This was followed by a long-term decrease in CO₂ due to increased sedimentation from surface waters of POC and PIC in fecal pellets. The ramifications of a changing ratio of PIC/POC formation can be crudely modeled. For example, if one increases the ratio of calcification to total production by as little as 5% (from 5% to 10%), then the ratio of CO₂ assimilated/total carbon fixed will decrease by 14%. This is because the CO₂ production during calcification partially counters the CO₂ assimilated during photosynthesis.

The other, more striking, ramification of a changing ratio of PIC production to POC production concerns carbon burial. Assuming 15% burial of surface CaCO₃, and 1% burial of organic matter (Broecker & Peng, 1982) at the deep-sea bed, changing the calcification/photosynthesis ratio from 5% to 10%, increases the burial ratio of PIC:POC by 87%. The main conclusion from these calculations is that the burial ratio of CaCO₃ C:organic C

is hypersensitive to small changes in the production of PIC and POC. This is why knowledge of calcification is so essential to understanding the role of CaCO_3 to vertical carbon fluxes in the sea.

Archer and Maier-Reimer (1994) argued that decreasing the flux of calcite from the mixed layer by 40% would decrease oceanic pCO_2 from 280 to 200ppm, equivalent to the magnitude of CO_2 changes over interglacial/glacial transitions. It is not clear whether such shifts actually occurred during glacial/interglacial transitions, and indeed there is evidence to the contrary (Sigman, 1998). Regardless of these considerations, changes in the abundance of coccolithophores in the modern ocean represent an important link between carbon cycling and ecosystem processes.

In the contemporary ocean, the export of particulate organic carbon from the euphotic zone is highly correlated with the flux of particulate silicate. Most of the silicate flux is a consequence of precipitation of dissolved orthosilicic acid by diatoms to form amorphous opal that makes up the cell walls of these organisms. The cell walls presumably help the organisms avoid predation, or if ingested, increase the likelihood of intact gut passage through some metazoans. In precipitating silicate, diatoms simultaneously fix carbon. Upon depleting the euphotic zone of nutrients, the organisms frequently sink *en mass*, and while some are grazed en route, many sink as intact cells. Ultimately, either fate leads to the gravitationally driven export flux of particulate organic carbon into the ocean interior.

Silica is supplied to the oceans from the weathering of continental rocks. Because of the precipitation of siliceous organisms however, the ocean is relatively depleted in dissolved silica. Although diatom frustules (i.e., their silicified cell walls) tend to dissolve and are relatively poorly preserved in marine sediments, enough silica is buried to keep the ocean undersaturated. As the residence time of silica in the oceans is about 10,000 years (i.e., about an order of magnitude longer than the mean deep water circulation), one can get an appreciation for the silicate demands and regeneration rates by following the concentration gradients of dissolved silica along isopycnals. While these demands are generally attributed to diatoms, radiolarians (a group of non-photosynthetic, heterotrophic protists with siliceous tests, that are totally unrelated to diatoms) are not uncommon, and radiolarian shells are abundant in the sediments of Southern Ocean. Silica is also precipitated by various sponges, and other protists. As a functional group, the silicate precipitators are identified by their geochemical signatures in the sediments and in the silica chemistry of the oceans. Diatoms can be elucidated by photosynthetic pigment analyses *in situ*, but cannot be uniquely identified from satellite imagery. Because of their importance in mediating carbon export, a significant effort was spent in JGOFS attempting to understand the factors controlling the distribution of diatoms in the world oceans. Interestingly, diatoms evolved relatively recently; the first clear evidence of their presence in the oceans is recorded in fossils from cherts dating to 120 Mybp (i.e. in the early Cretaceous). Thus, although export carbon fluxes are associated with this group of organisms in the contemporary ocean, they usurped that role from an unknown group(s) of phytoplankton that dominated earlier in the Mesozoic. What organisms mediated export of carbon in the Proterozoic (prior to the emergence of eucaryotes) and Paleozoic (prior to the dominance of the chromophyte algae) remains totally unknown.

In many oceanic and coastal regions, carbon export is dominated by diatom biomass. Recently, Dugdale and coworkers (Dugdale *et al.*, 1995) have argued that Si limitation of diatom growth constitutes a major control on C export in the equatorial Pacific. Iron also plays an important role in diatom ecology. In all three iron fertilization experiments, diatoms, not coccolithophores, have dominated the response. Yet coccolithophore blooms are a well-established phenomenon, for which we have increasingly good data due to advances in remote sensing methodologies. However, there are no clear relationships between such blooms and chemical parameters like the concentration of Fe. We know little about geochemical determinants of coccolithophore blooms, nor do we know why coccolithophores have not responded to Fe enrichments in HNLC regimes.

Culture experiments with marine diatoms have provided considerable quantitative and mechanistic understanding about the relationship between growth rates and the concentrations of Fe and Si. Predictions from culture work have generally supported observations in the field. What do culture studies with coccolithophores tell us? Coccolithophores show significant differences to diatoms in their micronutrient requirements. They have a high absolute requirement for Co and no requirement for Zn, whereas diatoms have a high Zn requirement and no Co requirement. Sunda and Huntsman (1996) argued that the relative abundance of diatoms and coccolithophores could be influenced by the relative abundance of Zn and Co. Zn: Co ratios should show significant variability under different hydrographic conditions owing to different geochemistries of each element. However, there is little information about these elements in regions where coccolithophore blooms occur.

4. What controls the balance of N₂ fixation and denitrification in the world's oceans and what are the possibilities for and the dynamics of feedbacks between ocean biogeochemistry as mediated by changes in atmospheric CO₂?

Much of the discussion of climate change involves the “effects” of global warming on ecosystems. This is certainly an important question. As seen above, many climate-related forces will have an impact on ocean ecosystems through both direct effects (e.g. nutrient fluxes, stability) or through changes in the emergent behavior of ecosystems. We have also documented that ocean biology plays a fundamental role in the ocean carbon cycle and in the sequestration of carbon in the ocean on time-scales of years to millennia. This bilateral symmetry implies the possibility of feedback loops between climate and ocean biology. These could be stabilizing feedbacks, positive feedbacks or some mix of the two. Do these feedbacks occur? Are they significant on any time-scales? What does it take to incorporate them into our climate models? Do they impact the policy process as society wrestles with the control of greenhouse gases?

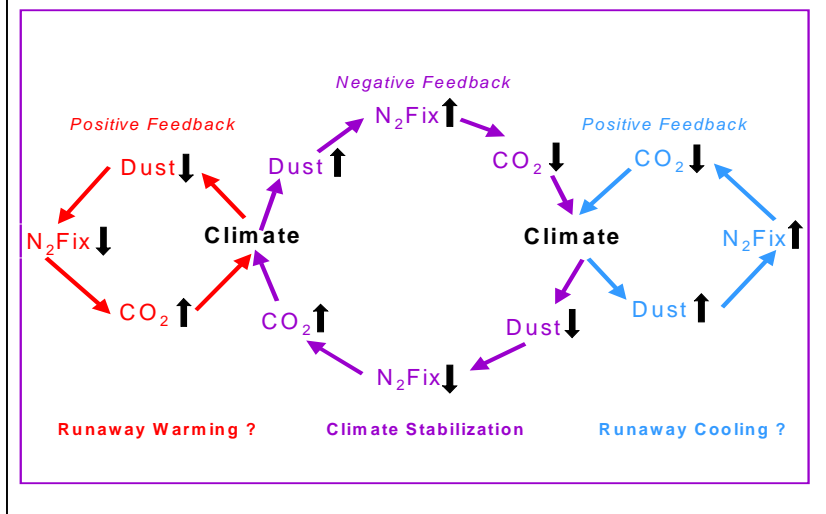
We currently have almost no real ability to address the questions of global feedbacks, even though they are likely the most important aspect of global ocean carbon biogeochemistry if they exist. There are a few, speculative suggestions of climate feedbacks that involve ocean biology. In these hypotheses, the ocean effect on climate is through its effect on greenhouse gases. The climate effect on the carbon cycle could occur through a variety of mechanisms,

usually modifications of the nutrient controls on new production. All of these feedbacks will be constrained by the relationship between the nutrient signal and the ventilation time-scale of the oceans except for processes that change the total nutrient stock in the sea.

Oceanic N_2 fixation has recently been identified as a much more significant part of the oceanic nitrogen (N) cycle than previously thought. The rate of N_2 fixation in the world's oceans can have an impact on the concentration of carbon dioxide (CO_2), in the atmosphere on time-scales of decades (variability in surface biogeochemistry) to millennia (changes in the total fixed N stock from the balance of N_2 fixation and denitrification). The global rate of nitrogen fixation is now estimated to exceed 100-150 Tg N/y and global denitrification rate estimates are even higher. The balance of these two rates may directly influence the sequestration of atmospheric CO_2 in the oceans and, hence, the air-sea partitioning of carbon, by providing a new source of N to the upper water column. On longer time-scales, the balance affects the total amount of nitrate in the ocean within the permissible bounds of the variability of N:P ratios in organisms. The prokaryotic microorganisms that convert N_2 gas to reactive N are an unique subcomponent of planktonic ecosystems and exhibit a variety of complex dynamics including the formation of microbial consortia and symbioses and, at times, massive blooms. Accumulating evidence indicates that iron (Fe) availability may be a key controlling factor for these planktonic marine diazotrophs. The primary pathway of Fe delivery to the offshore upper oceans is through dust deposition (Duce and Tindale 1991). As implied earlier, an important fraction of the marine denitrification, and perhaps also nitrogen fixation, occurs on the seabed, including the intertidal zone.

To illustrate the possibilities, we present one recent proposal for a feedback between ocean biology and climate that involves our new understanding of the importance of oceanic N_2 fixation (Fig. 3). This process may directly influence the sequestration of atmospheric CO_2 in the oceans by providing a new source of N to the upper water column. Accumulating evidence indicates that iron (Fe) availability may be a key-controlling factor for these planktonic marine diazotrophs. The primary pathway of Fe delivery to the upper oceans is through dust deposition. N_2 fixers may therefore be directly involved in global feedbacks with the climate

Figure 3. Fe-N-dust feedback loops



system on many different time-scales. The hypothesized feedback mechanisms will have the following component parts: The rate of N_2 fixation in the world's oceans can have an impact on the concentration of the greenhouse gas, carbon dioxide (CO_2), in the atmosphere on time-scales of decades (variability in surface biogeochemistry) to millennia (changes in the total NO_3^- stock

from the balance of N₂ fixation and denitrification). CO₂ concentrations in the atmosphere influence the climate. The climate system, in turn, can influence the rate of N₂ fixation in the oceans by controlling the supply of Fe on dust and by influencing the stratification of the upper ocean. Humans also have a direct role in the current manifestation of this feedback cycle by their influence on dust production, through agriculture at the margins of deserts, and by our own production of CO₂ into the atmosphere.

The circular nature of these influences can lead to a feedback system, particularly on longer time-scales. On shorter time-scales it can influence the net ocean uptake of atmospheric CO₂. Other feedbacks can also be proposed and tested involving such processes as iron limitation of high-nutrient-low-chlorophyll regions and stratification influences on new production and remineralization length scales. The production of other radiatively-important gases like dimethyl sulfide (DMS) has also been implicated in hypothesized feedbacks to climate.

V. Long Lead Time and Implementation Issues

1. Relationship to and influence on other activities and agencies

Future U.S. carbon cycle research needs to be interdisciplinary involving coordinated air, sea and land components. That is the primary theme of a recent report prepared by an ad hoc committee formed at the request of the federal agencies interested in carbon cycle research (Carbon and Climate Working Group 1999). Given the complexity of the carbon cycle and the number of processes it involves, all components of a national carbon cycle research effort obviously cannot be in touch at all levels and at all times. However, EDOCC planning should proceed with consideration of other carbon cycle components.

For example, EDOCC will benefit if more is learned about basic food web structure of major ocean biomes and the controls of these configurations. Obtaining such basic knowledge for EDOCC might involve a partial or complete global survey of ocean biomes that could be part of a much more general ocean survey involving other carbon cycle components (e.g. air-sea fluxes). To make best use of research support, EDOCC investigators need to be in contact with other ocean carbon cycle programs to plan and develop joint campaigns, time series stations, and other expensive research infrastructure.

Ocean carbon cycle research needs also to be planned and interpreted in cooperation with the broader Earth Science community. For example, terrestrial ecologists are also interested in manipulating terrestrial ecosystems to study effects on carbon storage and uptake. Basic ecological principles should be common to ocean and terrestrial systems, and it makes sense to share thoughts on the results and their broader interpretation. Additionally, a process viewed from an Earth system, rather than an ocean, perspective may be interpreted somewhat differently. Those years or decades having relatively high atmospheric dust deposition in the ocean may also have higher ocean productivity (owing to mineral stimulation of photosynthesis or N₂ fixation), but does the increase in ocean productivity compensate for the loss of terrestrial production owing to desertification? The answers to these important but complex questions require at a

minimum interdisciplinary interpretation of results, if not cooperative planning of joint field and other experiments.

2. Long-lead technology and methods development

Technological developments during the upcoming decade will impact the implementation of initiatives aimed to address issues raised in EDOCC. Instrumentation and analysis techniques for satellite imagery, remote sensors, analytical procedures for chemistry and molecular biology will all provide the ability to obtain new information critical to the mission of EDOCC. The development of these techniques should be anticipated and facilitated along with the basic science programmatic objectives of EDOCC.

The National Aeronautic and Space Administration (NASA) Earth Science Enterprise initiative includes a series of sensors aimed to better understand ocean dynamics. Measurements by these sensors include ocean near-surface wind speed and direction (SeaWind), ocean color (SeaWiFS, MODIS), sea surface temperature (MODIS). Ocean surface data collected by these and other sensors mounted on international platforms will provide unprecedented spatial and temporal coverage over the next decade. Furthermore, the design and implementation of new sensors aimed to parameters such as water-column mixed-layer depth from space may help to improve the modeling of pelagic physical/biological interaction.

In situ remote instrumentation such as moored water-column profilers, benthic chambers, and autonomous underwater vehicles (AUV) are also a reality. The continuous and rapid improvement in fiber-optic and wireless telemetry, power and data storage capacity, and miniaturization of electronic components suggests the feasibility of remotely operated observatories that include a broad suite of physical, chemical, and biological methods.

Molecular biology techniques can provide high resolution information on populations, species and community structure, as well as information on physiological status. These methods, heretofore applied to visualize cells or analyze bulk water, will be applied in new technologies within the decade, undoubtedly implemented as remote instrumentation in a number of ways. The current development of DNA chips, that allow the simultaneous analysis of an entire community or alternatively, the entire genome or proteome of an organism, will be used to assay communities and the response of individual keystone organisms in applications ranging from analysis of bulk water samples (possibly sampled remotely) ultimately to deployment on moorings. Flow cytometric applications in concert with nucleic acid and immunological probes will facilitate analysis and characterization of individual cells. The molecular approaches will have important applications for analysis of microbial communities, but also for identifying small or cryptic species of macroorganisms.

Long lead times are also required to build up comprehensive models. Presently, there are many ecosystem models in 0 or 1 dimensional physical models, but coupling them to 3-d circulation models, building up appropriate data sets for initial conditions and boundary

conditions, developing appropriate diagnostic tools, etc usually requires on the order of 10 years, several people and access to high end computing.

3. Use SMP to start thinking about these issues

Modeling studies will be integral to virtually every aspect of EDOCC. For example, the question of the relative importance of external forcing and emergent behavior in controlling the time-dependent dynamics of ocean ecosystems will have to be addressed through a combination of paleo-oceanographic and modeling studies. Similarly, questions related to increased atmospheric CO₂, the carbon cycle, and possible ecosystem feedbacks to climate will also have to be addressed with models (e.g., Sarmiento *et al.* 1998). However, as discussed in (3) the development of new, and more sophisticated models, far beyond the simple NPZ-based systems which are currently employed in large-scale coupled models, will be required to answer many of the questions posed in this document.

Current efforts funded through the U.S. JGOFS Synthesis and Modeling Project (SMP) are already focusing on these kinds of modeling issues, and there is a strong interest among many of the participants in SMP in developing more flexible and sophisticated models, perhaps based upon a functional group approach. U.S. JGOFS SMP can therefore potentially provide a framework and a starting point for developing more sophisticated models that will be required in EDOCC. Moreover, leveraging current SMP funding and activities would place emphasis on the crucial role of modeling in ocean carbon cycle research at the beginning of the program, where it belongs. This, in turn, would set the stage for building a program where modeling activities are an integral part of the science from the outset.

4. Professional development courses to create model-observation connections

The next generation of studies of ocean biogeochemistry will involve both evolutionary and revolutionary approaches. The science will be ever more interdisciplinary. The links between modeling, observation and experimentation will become more seamless and every scientist will have to have a greater understanding of the contributions of each. New approaches such as those involving “complexity” mathematics, data assimilation, molecular techniques will become both critical to the science and standard parts of the scientific toolbox. This explosion of new approaches requires that many current scientists retool to incorporate these into their research and that our students be given a broader background than their advisors currently have.

It seems prudent to explicitly invest in the training of the current and future generations of scientists in the more integrative, interdisciplinary and revolutionary approaches that will be the key to tomorrow’s science. This process should start soon and be continuous into the future. For modest sums, sophisticated, intensive training courses can be created and offered. NSF already has funded excellent examples of these kinds of courses. Polar Programs offers an intensive biology course at McMurdo where students, postdocs and faculty are brought together to learn the latest in Antarctic science. Similar kinds of courses have been offered as special

summer sessions at Marine labs around the country. A careful program for offering a limited number of courses, evaluated by peer-review would help move our field forward.

5. Implementation and funding framework

For a program of this nature, we envision a diversified approach with respect to the types and scales of projects fostered. We propose an administrative structure that allows for maximum peer-review, significant flexibility and yet allows for some level of overall coordination across the entire program. There would be a scientific steering committee with the responsibility to guide the program towards its later goal and to coordinate with other related large programs. At the same time, each of the major program elements would be competed through peer-review. We envision the following kinds of program structures:

- Scientific Guidance Structure (coordination within and among program, mindful of scientific gaps)
- Large Scale Space/Time Resolution (Global coverage. Linkage with e.g. CLIVAR, repeat surveys, satellites, etc.)
- Temporal Resolution (Time-series infrastructure; hypotheses driven location; 4-16 new sites; flexible duration and design; support other/ ongoing time series projects)
- Medium Size Investigations (e.g. 2-16 PIs, Multi-year, Multi-\$\$, Annual competition, 2 awards per year, teams of teams?)
- Small Size Investigations (e.g. 1-3 PIs, traditional scale funding, 1 announcement per year, 10-20 awards per year)

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