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JOINT GLOBAL OCEAN FLUX STUDY (JGOFS)

Phytoplankton Production and Food Web Processes • Carbon Dioxide Exchange and Biogeochemical Cycles • Deep Ocean-Carbon Export (Biological Pump) • Ecosystem Variability and Climate Change • Ecosystem, Biogeochemical and Ocean Carbon Models

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JGOFS sampling in waters covered with pancake ice, Prydz Bay, Antarctica (67S 75E), during the early summer. Samples were collected from the icebreaker RSV Aurora Australis for the measurement of carbon, nutrients and phytoplankton pigments.

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Introduction to the Joint Global Ocean Flux Study (JGOFS)

Little was known about the role of the ocean in the global carbon cycle during the first half of the 20th century. Although earth scientists were aware that the ocean carbon reservoir was about 60 times that of the atmosphere, a system-level understanding of the ocean carbon cycle had not yet emerged. A few visionaries expressed concerns about the potential effect of fossil fuel emissions on atmospheric temperature. But it was not until the late 1950s and the International Geophysical Year that scientists made a concerted effort to assess the influence of human activities on atmospheric carbon dioxide (CO₂) levels and thus on global temperature. Atmospheric time-series measurements, begun in 1958 at the summit of Mauna Loa in Hawaii, began to show thought-provoking seasonal cycles and increasing concentrations of CO₂ in the atmosphere.

During the 1950s, scientists began to measure primary production in the ocean using carbon-14 isotopes and to make new global estimates based on the results. Their numbers (20–50 Pg C yr^{-1}) were much lower than earlier ones based on bottle measurements of dissolved oxygen in the ocean (50–130 Pg C yr^{-1}). The global primary productivity maps that followed in the 1960s and 1970s conveyed the message that the temperate and subtropical ocean basins had much smaller phytoplankton populations and experienced much less seasonal and interannual variability than either the continental margins or the polar regions. Temporal and spatial variability in these vast ocean regions first became known from ocean time-series work in the 1960s and from the observations made by the satellite-borne Coastal Zone Color Scanner in the late 1970s and early 1980s.

With the steady annual increase in atmospheric CO_2 established by the time-series measurements at Mauna Loa, scientists determined that roughly half of the fossil fuel emissions were remaining in the atmosphere. Other studies indicated that the ocean was absorbing a good part of the remaining anthropogenic CO_2 . About the same time, palaeontologists and geochemists measuring the inorganic carbon chemistry of deep glacial ice cores discovered that atmospheric CO_2 levels varied in phase with warm and cold eras in the earth's history. This discovery led to speculation as to which biogeochemical and physical processes in the ocean and on land contributed to the dramatic changes in CO_2 levels in the atmosphere.

Two later discoveries shattered the long-standing view that seasonal changes did not affect the deep ocean. One was that deepsea organisms exhibited seasonal growth patterns, and the other was that particle export into the deep ocean, captured in sediment traps, followed the seasonal cycles of primary productivity in surface waters. These observations linked the rapid biological processes that govern fixation of carbon in the upper ocean with the slow physical circulation that ventilates the deep waters and the chemical transformations that occur there. The simultaneous publication of several papers describing the role of ocean biological and physical processes in the regulation of atmospheric CO_2 set the stage for the two large, synthetic ocean studies of the late 1980s and 1990s, the World Ocean Circulation Experiment (WOCE) and the Joint Global Ocean Flux Study (JGOFS). Climatologists, geochemists, oceanographers and ecologists agreed that a concerted effort to study earth systems was needed to address the growing concern about global warming. By the mid-1980s, several mesoscale ocean programs had been successfully completed, new satellite technology was emerging, and scientists were addressing questions about ocean biogeochemical cycles, increases in anthropogenic CO_2 in the atmosphere, global warming and environmental change. With the establishment of the International Geosphere-Biosphere Programme (IGBP), planners developed a framework for envisioning interdisciplinary research in the context of earth systems science. It took a combination of concern about environmental change, technological advances, and political will, expressed in new funding commitments, to reach this point.

An international and multidisciplinary program with participants from more than 30 nations, JGOFS was launched in 1987 at a planning meeting in Paris under the auspices of the Scientific Committee of Oceanic Research (SCOR), a committee of the International Council of Scientific Unions (ICSU). The SCOR report that followed provided the scientific justification, goals and objectives, organizational structure and recommended research activities for an ocean biogeochemical observing program (JGOFS Report No. 5, *Science Plan*, August 1990).

Two years later, JGOFS became one of the first core projects of the International Geosphere-Biosphere Programme (IGBP). Long-term time-series projects were begun at sites near Bermuda and Hawaii in the fall of 1988. With leadership from scientific committees in Canada, France, Germany, The Netherlands, the United Kingdom and the United States, the North Atlantic Bloom Experiment (NABE), a multinational pilot study for future process-study projects in other ocean basins, got underway the following spring. The launching of JGOFS research with NABE reflected the impetus provided by data from satellite-mounted instruments and deep sediment traps, both of which identified high-latitude blooms as conspicuous features of the ocean biosphere.

The following pages outline the progress of JGOFS from its preliminary pilot study to comprehensive observations and modelling studies worldwide. JGOFS achievements point the way toward an integrated understanding of the role of ocean ecology, circulation and carbon cycling in the whole earth system.

Roger B. Hanson Executive Director JGOFS International Project Office Bergen, Norway January 2001

A New Vision of Ocean Biogeochemistry After a Decade of the Joint Global Ocean Flux Study (JGOFS)

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The Joint Global Ocean Flux Study (JGOFS) has completed a decade of intensive process and time-series studies on the regional and temporal dynamics of biogeochemical processes in five diverse ocean basins. Its field program also included a global survey of dissolved inorganic carbon (DIC) in the ocean, including estimates of the exchange of carbon dioxide (CO_2) between the ocean and the atmosphere, in cooperation with the World Ocean Circulation Experiment (WOCE).

This report describes the principal achievements of JGOFS in ocean observations, technology development and modelling. The study has produced a comprehensive and high-quality database of measurements of ocean biogeochemical properties. Data on temporal and spatial changes in primary production and CO_2 exchange, the dynamics of of marine food webs, and the availability of micronutrients have yielded new insights into what governs ocean productivity, carbon cycling and export into the deep ocean, the set of processes collectively known as the "biological pump."

With large-scale, high-quality data sets for the partial pressure of CO_2 in surface waters as well for other DIC parameters in the ocean and trace gases in the atmosphere, reliable estimates, maps and simulations of air-sea gas flux, anthropogenic carbon and inorganic carbon export are now available. JGOFS scientists have also obtained new insights into the export flux of particulate and dissolved organic carbon (POC and DOC), the variations that occur in the ratio of elements in organic matter, and the utilization and remineralization of organic matter as it falls through the ocean interior to the sediments.

JGOFS scientists have amassed long-term data on temporal variability in the exchange of CO_2 between the ocean and atmosphere, ecosystem dynamics, and carbon export in the oligotrophic subtropical gyres. They have documented strong links between these variables and large-scale climate patterns such as the El Niño-Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO). An increase in the abundance of organisms that fix free nitrogen (N₂) and a shift in nutrient limitation from nitrogen to phosphorus in the subtropical North Pacific provide evidence of the effects of a decade of strong El Niños on ecosystem structure and nutrient dynamics.

High-quality data sets, including ocean-color observations from satellites, have helped modellers make great strides in their ability to simulate the biogeochemical and physical constraints on the ocean carbon cycle and to extend their results from the local to the regional and global scales. Ocean carbon-cycle models, when coupled to atmospheric and terrestrial models, will make it possible in the future to predict ways in which land and ocean ecosystems might respond to changes in climate.

INTRODUCTION

During the 12 years since its first field studies were launched, the Joint Global Ocean Flux Study (JGOFS) has amassed a data set of unprecedented scope and detail that is yielding new insights into old questions about the role of the ocean in the global cycling of carbon. The JGOFS decade has coincided with and contributed to the blossoming of ocean biogeochemistry as a discipline with a focus on the linkages among physical, biological and chemical factors in the production, transport and transformations of carbon and other biogenic elements in the ocean.

A comprehensive and quantitative understanding of the way the ocean carbon cycle functions is essential to our ability to predict the consequences of rising levels of carbon dioxide (CO₂) and other "greenhouse" gases in the atmosphere. The importance of the ocean in the natural regulation of atmospheric CO₂ levels was recognized more than 60 years ago. However, lack of data from many regions and the difficulty of making precise and accurate measurements have, until recently, hampered calculations of the distribution and amounts of carbon in various forms in the ocean and the exchange of CO₂ with the atmosphere. Con-

Table 1. The Scientific Goals of JGOFS.

To determine and understand on a global scale the processes controlling the time-varying fluxes of carbon and associated biogenic elements in the ocean, and to evaluate the related exchanges with the atmosphere, sea floor, and continental boundaries.

To develop a capability to predict on a global scale the response of oceanic biogeochemical processes to anthropogenic perturbations, in particular those related to climate change.

ceptual advances that fostered a better understanding of ocean ecosystems and biogeochemical cycles were needed as well.

The JGOFS Science Plan, published in 1990, sets forth two primary goals (Table 1). The strategy for addressing these goals has included a series of process studies in regions of the ocean that are thought to contribute the most to the flux of carbon between the ocean and the atmosphere, a global survey of dissolved inorganic carbon (DIC) parameters in ocean waters, and several long-term measurement programs at sites in key ocean basins (Fig. 1). JGOFS is also committed to the development of models that can assimilate results from field studies, produce accurate large-scale descriptions of ocean biogeochemical phenomena and predict oceanic responses to environmental changes. The final component of the JGOFS strategy is a comprehensive and accessible database of results.

JGOFS has completed a decade of field studies in key regions of the global ocean. These studies have brought together data on chemical fluxes, biological processes and the physical forces that constrain them. They have substantially increased our understanding of the pathways by which carbon moves through the ocean in various forms, organic or inorganic, in particles or dissolved in the water. They have also improved our knowledge





Global Survey of Carbon Dioxide in the Ocean JGOFS investigators carried out measurements of inorganic carbon system parameters on World Ocean Circulation Experiment (WOCE) hydrographic sections, indicated here with red lines, between 1990 and 1998.

Remote Sensing Measurements of Ocean Color

Data from ocean-color measurements aboard satellites are used to estimate phytoplankton pigments in the euphotic zone of the ocean. Results shown are annual averages from data collected by the SeaWiFS sensor, launched into orbit in August 1997.



Intensive Studies

Figure 2. The Biological Pump.



Biologically mediated

transformations of carbon in the ocean take place *via* the small plankton, which primarily recycle CO_2 within the euphotic zone, and the larger plankton, which generate most of the flux of organic carbon in particulate and dissolved form to the deep ocean. Some of the carbon that reaches the deep ocean is remineralized into dissolved inorganic form, some is consumed at the benthic surface, and a small portion is buried in the sediments of the sea floor.

of the ways in which biogeochemical systems vary over time as well as from one region of the ocean to another; we know far more about the effects of mesoscale processes and episodic events than we did 12 years ago. Finally, the availability of remote-sensing data from instruments on satellites is making it possible to extend the inferences made from the JGOFS field studies to regional and global scales.

This Special Report describes the case for studying the ocean carbon cycle, some of the most significant findings from the JGOFS field program, some of the results emerging from the synthesis and modelling efforts currently underway, a summary of major JGOFS achievements thus far, and a summary of the work that remains to be done.

THE ROLE OF THE OCEAN IN THE GLOBAL CARBON CYCLE

With 50 times more carbon dioxide (CO₂) than the atmosphere, the ocean contains the largest reservoir of carbon actively circulating in the biosphere. Over the long term, the ocean carbon cycle plays the dominant part in the natural regulation of CO₂ levels in the atmosphere and their contribution to global temperature. We have known since the 1970s that the ocean as a whole is a "sink" for CO₂ from the atmosphere. But we also want to know how large this sink is, what processes govern its size and distribution, and how it might change during future decades.

Before we can determine the distribution and fate of anthropogenic CO_2 , carbon that is released into the atmosphere through human activities such as the burning of fossil fuels or conversion of forested lands into pasture or croplands, we must first understand the natural cycle of carbon in the ocean. Depending on whether the partial pressure of carbon dioxide (pCO₂) in the ocean is greater or less than that of the atmosphere, the gas is taken up or given off by the surface waters. Also referred to as dissolved inorganic carbon or DIC, total CO_2 is cycled within the ocean in two ways, one physical and the other biological.

A number of processes govern the transport of carbon in the ocean from the surface to deep waters and sediments of the ocean floor as well as its cycling among various organic and inorganic forms. CO_2 is more soluble in the cold surface waters of the North Atlantic, North Pacific and Southern Ocean than it is in warmer regions of the ocean; these colder and denser waters take up the gas from the atmosphere and sink to form deep waters that circulate slowly through the ocean. Although some of the CO_2 absorbed in the polar regions is released elsewhere through upwelling, this "physical (or solubility) pump" helps to keep the surface waters lower in CO_2 than the deep water, thus promoting an overall flux of the gas from the atmosphere into the ocean.

Planktonic algae in the well-illuminated surface ocean or euphotic zone take up nutrients and CO_2 through the process of photosynthesis; the rate at which this process occurs is called the primary productivity. Some of the organic matter thus created is cycled through the food web in the upper ocean, and some sinks to the bottom in particulate form, circulates through the water column as dissolved organic carbon (DOC), or is remineralized into DIC in the deeper waters. This "biological pump," illustrated in Figure 2, contributes to the gradient in CO_2 concentration between the surface and the deep waters as well as exporting carbon to the sea floor and sediments.

These natural cycles have been disrupted in recent times by the addition of roughly 5.5 petagrams of carbon per year (Pg C yr⁻¹) released into the atmosphere as a result of human activities. About 35% of this anthropogenic CO₂ is absorbed by the ocean, most of it into the deep waters (Fig. 3). The traditional assumption has been that the physical pump rather than the biological pump has been responsible for the increased uptake. Because phytoplankton growth is not, in general, limited by the availability of CO₂, increases in the DIC concentration in the surface waters do not increase primary productivity directly.

The biological pump could, however, be affected by changes in atmospheric CO_2 levels and temperature in a variety of subtler ways. If climate changes were to alter patterns of ocean circulation, for example, changes would occur in the upwelling of nutrients, such as nitrate or silicate, that are essential for the growth of the phytoplankton in the euphotic zone. The distribution of trace metals such as iron that are required for algal metabolism, could be affected as well. Researchers have discov-

Figure 3. The Global Carbon Cycle.



Average annual fluxes between global carbon pools are given in petagrams of carbon per year (Pg C yr⁻¹). Figures in blue in each box denote the global inventory in Pg C, while figures in red show the average annual increases in the inventory associated with anthropogenic input. The fluxes associated with the shelf and slope waters are still uncertain. Figure based on the 1995 Intergovernmental Panel on Climate Change (IPCC) analysis with additions from JGOFS results.

ered in the last few years that low iron concentrations in many areas of the ocean have a significant effect on the rate at which the algae grow. Most of the iron in the ocean is deposited by winds blowing off the land. The amount thus supplied might change if the heating of the atmosphere were to strengthen winds or alter their patterns.

The Ocean Uptake of CO₂

The carbon flux numbers shown in Figure 3 represent a simple summary of a complex reality. Some regions of the ocean release more CO_2 into the atmosphere than they absorb; others take up more than they give off. Gas fluxes vary by season as well as region; we now know that they are affected on longer time

Figure 4. The Flux of Carbon Between Ocean and Atmosphere.

Global map shows average annual exchange of CO_2 across the sea surface. Blue and purple colors denote regions in which the ocean takes up large amounts of CO_2 ; red and yellow colors denote regions in which large amounts of CO_2 are emitted into the atmosphere. Reprinted from (2).



scales as well by large-scale oceanic and atmospheric shifts, such as occur in the El Niño-Southern Oscillation (ENSO) cycle.

One of the most important achievements of the JGOFS global CO₂ survey and other field programs is that we now have a picture of how the ocean breathes in different parts of the globe (1, 2). Figure 4 shows the average annual exchange of CO₂ across the sea surface for all regions of the ocean. Blue and purple colors mark the regions in which large amounts of CO₂ are taken up from the atmosphere, while yellows and reds mark regions that give off the most CO₂ into the atmosphere. As this picture was assembled, our knowledge about the processes that regulate this exchange has matured.

Our observations suggest that the CO_2 "bulge" in the equatorial Pacific releases 0.8–1 Pg C into the atmosphere during a normal year; it is the largest continuous natural source of CO_2 in the ocean. The primary cause is the vigorous upwelling that occurs along the equator, driven by the divergence of surface currents. The cold upwelling water comes from relatively shallow depths, a few hundred meters at most. As it warms on its journey to the surface, it holds less CO_2 . The gas trapped in the water escapes into the air.

Another important cause of the outgassing of CO_2 in the equatorial Pacific is the relatively low level of biological activity. Although the upwelling water brings abundant nutrients to the surface, the phytoplankton lack sufficient iron to make full use of them. Dense "blooms" of large, fast-sinking phytoplankton

seldom occur, and the export of carbon from surface waters to the depths is generally low relative to higher latitude waters.

We can also see from Figure 4 that the North Atlantic is the most intense region for CO_2 uptake in the global ocean. As the Gulf Stream and the North Atlantic Drift transport warm water northwards, it cools and releases heat into the atmosphere. The cooler water is more able to absorb CO_2 . The North Atlantic is also one of the most productive ocean regions because of an abundant supply of nutrients, including iron. Thus, in contrast to the equatorial Pacific, biological and physical factors combine to create a substantial, though seasonal, net flux of CO_2 from the atmosphere into the North Atlantic. Other important uptake regions are also those in which the surface ocean is cooled and biological activity is high.

The overall features of the global ocean-atmosphere CO_2 flux map owe their distribution to natural heat transport and biological activity, processes that have been going on for thousands of millennia. Where, then, is the ocean sink for the CO_2 produced by human activities? In response to rising atmospheric concentrations, the natural ocean sources seem to have become slightly weaker while the natural sinks seem to have become slightly stronger, leading to a net ocean uptake of 2 Pg C yr⁻¹ as CO_2 .

While readily observed in the atmosphere, the anthropogenic CO_2 signal constitutes a small-scale perturbation of a huge natural flux in the ocean. Oceanographers have long tried to estimate this fraction in order to improve our knowledge of the global

Figure 5. Anthropogenic Tracers in the North Atlantic.



budget of fossil fuel CO_2 . JGOFS investigators are now using a new direct-determination technique based on differences between pre-industrial and contemporary values of the DIC content of the ocean, together with the data amassed during the global survey of oceanic CO_2 , to make regional and global estimates of the distribution of anthropogenic carbon.

Results from the sub-polar North Atlantic (Fig. 5) show that the whole water column is already contaminated with fossil fuel CO_2 . This deep penetration is the result of the active deepwater formation in this region. A comparison with chlorofluorocarbon (CFC-11) data shows similar distributions. This may appear surprising because CFC-11, an entirely man-made substance, has only been introduced since the end of World War II, while anthropogenic carbon has been entering the ocean for more than two centuries. The answer lies in the rapid renewal of deep North Atlantic waters, within which vigorous mixing between old and newly formed deep-water parcels erodes the effects of differing atmospheric histories. Within the North Atlantic, the northward transport of DIC by the meridional overturning circulation represents an important source of the anthropogenic CO_2 currently being stored in this region.

Similar results are emerging from studies of other ocean basins. The international and multidisciplinary effort now underway to put together a global ocean CO_2 data set and to calculate the distribution of anthropogenic carbon will, for the first time, enable us to make comparisons between estimates derived from observations and those generated by modeling simulations.

Ocean Food Webs

JGOFS investigators have carried out multinational, multi-ship process studies in a number of ocean basins to study the details of the complex food webs that make up the biological pump (Fig. 2). One of the many advances achieved has been the realization that the largest portion of the primary production is consumed by the smallest zooplankton, such as protozoa or the larvae of larger zooplankton. These microzooplankton also graze on the bacteria that consume the large quantities of DOC in seawater produced by the phytoplankton and the feeding activities of zooplankton.

Bacteria recover carbon released in dissolved organic form by other plankton and transfer it into the food web in what is called the microbial loop. Very little carbon is exported by this route to the deep ocean and sediments. The links in the classical marine food web, on the other hand, begin with the primary production of larger algae such as diatoms and dinoflagellates, followed by grazing by large zooplankton such as copepods and euphausiids, and ultimately by the higher trophic levels. Although only a small percentage of the primary production passes along this pathway, the production of large, fast-sinking faecal pellets and aggregations of diatoms and other algae provide the major part of the export of carbon to the deep ocean. The discovery of massive fluxes of diatomaceous material into the deep sea in the North Atlantic, illustrated in Figure 6, provided an early inspiration for JGOFS and a key to understanding the connection between plankton community structure and biogeochemical flux.

It is becoming clear that different plankton communities are characterized by different mixtures of bacteria, phytoplankton and zooplankton, and that they vary considerably in their contribution to the export of carbon into the deep ocean. Many ecosystems seem to maintain a balance between production and consumption for most of the year. In these systems, large export events represent departures from this balance, usually caused by physical phenomena such as mixing associated with storms, the onset of monsoons, or the development of a seasonal thermocline in spring.

In the North Atlantic, the warming of well-mixed surface waters in the spring gives rise to a strong bloom in which producFigure 6. The Flux of Biogenic Material to the Sea Floor.



Photographs illustrate the arrival of large quantities of diatomaceous "fluff" at a depth of 4000 meters in the North Atlantic in July. This material was derived from a spring bloom at the surface several weeks before. The newly-arrived "fluff" blankets the sediment surface, giving it a smoother appearance. (Photographs courtesy of Richard Lampitt and Michael Conquer, Southampton Oceanography Centre).

tion exceeds consumption. Organic particles accumulate and eventually sink. When nutrients are exhausted and the bloom collapses, massive depositions like the one shown in Figure 6 can be seen within a few days to weeks on the sea floor 3000 to 4000 meters below the surface. Marginal ice-zone ecosystems in the Weddell and Ross seas along the coast of Antarctica also experience large blooms, followed by massive fluxes of particles to the deeper waters and the sea floor. Both these regions have been explored in detail during JGOFS process studies.

In oligotrophic waters, such as occur in the subtropical gyres near Bermuda and Hawaii, and in iron-limited ecosystems, plankton communities are dominated by organisms smaller than 20 microns in size, and the algae are consumed almost completely by microzooplankton. Export of particulate organic matter from the surface waters is minimal. JGOFS process studies in the equatorial Pacific and in parts of the Arabian Sea, as well as the ongoing investigations at the Bermuda Atlantic Time-Series (BATS) and Hawaii Ocean Time-series (HOT) sites, have provided new information on these minimal-flux systems (4).

To achieve a predictive understanding of ocean biogeochemistry, we need more detailed knowledge about different ecosys-





During the IronEx II experiment in the eastern equatorial Pacific, investigators fertilized an area of 64 km² with iron. Phytoplankton photochemical quantum efficiency (the fraction of absorbed photons used in photosynthesis) increased in the area enriched with iron from less than 0.3 (blue) to greater than 0.55 (red) in surface waters down to 30 meters depth. Reproduced from (8).

tem states and the transitions between them. We need to know more about the biology of key species that characterize their dynamics and dominate fluxes. For example, the balanced, minimum-flux systems can produce small blooms of diatoms when they receive periodic inputs of iron during storms. JGOFS has provided the first global-scale view of these processes and their connection to biogeochemical flux patterns.

The Role of Iron

In most areas of the ocean, the strength of the biological pump is controlled by the availability of macronutrients such as nitrate, phosphate and silicate in the euphotic zone. This is not the case, however, in the subarctic Pacific, the equatorial Pacific and the Southern Ocean. These regions, often characterized as "high nutrient-low chlorophyll" (HNLC) waters, comprise about 30% of the global ocean. An alteration in the magnitude of the biological pump in HNLC regions could significantly affect the ocean's capacity to take up CO₂. Therefore, researchers in the late 1980s put considerable effort into investigating the factors that affect algal biomass in HNLC regions, among them iron availability, light levels and grazing control by zooplankton.

Because algae require iron for the synthesis of enzymes involved in photosynthesis, respiration and nitrogen fixation, an insufficient supply of this element may result in slow cell growth. Paleoclimatological records obtained from the Vostok ice core in Antarctica provide tantalising evidence of an inverse relationship between iron supply to the ocean and atmospheric CO_2 levels (5, 6). Does iron supply control the magnitude of algal biomass in HNLC regions? Major improvements over the last decade in the precision and accuracy of methods of measuring very small amounts of iron and the availability of sulfur hexafluoride (SF₆), an inert chemical tracer detectable at low levels, has made it possible to carry out *in situ* iron fertilization experiments in the open ocean. Two such experiments were conducted in the eastern equatorial Pacific in recent years, IronEx I in the fall of 1993 and IronEx II in the spring of 1995 (7). During IronEx II, investigators mapped parameters inside and outside an iron-enriched patch covering 64 square kilometers. They observed increases in the photosynthetic efficiency, growth rate, biomass and production of phytoplankton (Fig. 7), despite increased grazing by zooplankton within the patch. They also recorded decreases in macronutrient levels and in the partial pressure of CO_2 in the surface waters. An observed shift from small phytoplankton to large, fast-sinking diatoms confirmed that iron supply controls stocks of large algal cells in this region.

In January 1999, an international JGOFS team conducted an *in situ* test of the iron limitation hypothesis in the Southern Ocean 2500 kilometers southwest of New Zealand and south of the Antarctic Polar Front. Although the response of the biota was much slower in the frigid antarctic waters than in the equatorial region, participants in the Southern Ocean Iron Release Experiment (SOIREE) obtained results similar to those observed during IronEx II (9). Because the vertical exchange between deep and surface waters is more rapid in the Southern Ocean than in the equatorial Pacific, however, we can hypothesize that vertical export processes are more sensitive to increased iron supply in the former region than the latter.

The Export of Carbon from the Euphotic Zone

One of the main goals of JGOFS is to determine rates and amounts of organic carbon exported from the euphotic zone into the ocean interior. Before JGOFS, the conventional wisdom dictated that, at steady state, the export of particulate organic material should equal the new production, which is the portion of total primary production that is driven by new nutrients (primarily nitrate) entering the euphotic zone.

Among the methodological advances made during JGOFS has



been the development of techniques for using thorium 234 (234 Th), a relatively short-lived decay product of uranium 238 that sticks to particles, as a means of tracing the export flux of particulate organic carbon (POC) in the ocean (10). Data from JGOFS studies that used 234 Th to trace the export of carbon from the upper ocean show that low export of POC relative to primary production is characteristic of much of the ocean. The overall ratio of export to production is less than 5–10% (Fig. 8). Exceptions to this pattern generally occur during episodic events, such as spring blooms at mid- and high latitudes, and export pulses, such as those associated with the end of the southwest monsoon in the Arabian Sea in late summer. Ecosystems in which high export occurs are often characterized by the presence of large phytoplankton, especially diatoms.

A new aspect of this story was revealed during JGOFS when investigators discovered that a significant fraction of the export flux was in the form of dissolved organic carbon (DOC). Process studies in the equatorial Pacific showed that the export flux of POC was less than new production at most stations; the difference between the two was used to estimate the role of DOC as a sink for new production. Carbon budgets constructed for the US JGOFS time-series sites near Hawaii and Bermuda show that DOC export is an important component of total export in the subtropical oligotrophic gyres as well. Although quantitative estimates of these fluxes are difficult to make, recent calculations suggest that DOC contributes up to 20% of total carbon exported from the surface ocean to the depths. The ratio of DOC to POC varies, however, over time and from one region to another.

Deep-sea Fluxes

The dead organic matter that makes up the POC export settles into the deep ocean and is mostly remineralized there, producing CO_2 that is removed from exchange with the atmosphere until the deep water returns to the surface over centuries or millennia. Some of this carbon eventually reaches the ocean floor, where it is buried in the sediments and sequestered from the atmosphere for millions of years. Changes in these processes can produce changes in the atmospheric balance of greenhouse gases. The remains of organisms and inorganic particles deposited in the sediments also yield insights into past oceanic processes, including changes in ocean productivity associated with the waxing and waning of the ice ages.

Deep moored sediment traps deployed in many parts of the global ocean have provided insights into the regional and temporal distribution of fluxes into the deep sea. In general, the proportion of primary production reaching the deep sea does not vary much with latitude. On the global scale, about 1% of the total net primary production, equivalent to about 0.34 Pg C yr^{-1} , reaches the deep sea below 2000 meters. The Southern Ocean is the region that exports the highest proportion of its primary production (3%) while the equatorial Pacific exports the lowest (1%). Some of the regional export fluxes, as measured at 100 and 1000 meter depths, are shown in Table 2.



Data from deep moored sediment traps and benthic samplers can be used to validate our conceptual and mathematical models of the flux of POC from surface ocean to sea floor. Although models must reflect our understanding of upper ocean food webs and the transformations that organic carbon undergoes as it sinks through the water column, they are ultimately constrained by the numbers derived from deep-ocean measurements of carbon flux.

The ratio of silica to calcium in the particle rain provides evidence about the type of phytoplankton that is predominant in the primary production in a given region or season of the year, information that is relevant to the uptake of CO_2 from the atmosphere. Regions that are rich in silica support the growth of diatoms, which use this element to form their hard shells. Regions that lack silica favor the growth of coccolithophorids, which form shells of calcium carbonate.

The ocean biological pump operates in two somewhat different modes depending on the availability of silica in surface waters, which varies from season to season in some locations as well as from region to region. Because the formation of calcium carbonate shells, unlike silica shells, releases CO_2 into the water, less CO_2 is taken up in the surface ocean when the biological pump is operating in what we might call "carbonate mode." More organic than inorganic carbon is delivered to the depths when the pump is operating in "silica mode"; the ratio is reversed when it is not.

Since direct measurements of deep ocean respiration are still rare, global estimates of its magnitude have been extrapolated from empirical relationships. Such estimates indicate that the respiration of the organisms below 1000 meters totals 1.2×10^{14} moles of oxygen per year, and that 45% of all respiration in the deep sea occurs at the sea floor (Fig. 9). This result implies a global organic carbon flux to the deep sea floor of approximately

 0.2 Pg C yr^{-1} , a figure that agrees well with estimates based on sediment trap samples and primary production measurements.

BUILDING THE GLOBAL VIEW: THE EXTENSIVE STUDIES

The JGOFS research strategy was built on the premise that our capacity to describe ocean biogeochemical cycles and to predict their response to anthropogenic perturbations depends upon linking local and regional measurements of biogeochemical processes to large-scale observations of critical properties. The research programme, accordingly, included extensive surveys of such oceanic properties as dissolved inorganic carbon (DIC) concentrations, the partial pressure of carbon dioxide (pCO₂) in air and sea, phytoplankton pigments, nutrients, temperature and salinity in addition to the intensive process and time-series studies conducted in selected regions of the ocean (Fig. 1). The goal of the extensive studies has been to build global data sets that could improve descriptions of biogeochemical variability and inventories of critical elements, elucidate links between physical, geochemical and biological processes and phenomena, and provide the means of evaluating global-scale modeling results.

Calculating the Productivity of the Ocean

Regional differences in the ocean have distinctive effects on the processes that govern the way the biological pump functions. JGOFS investigators have pursued two different strategies to assess the spatial and temporal variability of primary production at regional to global scales. In one approach, the global ocean is divided into "provinces," within which biogeochemical cycles are considered to be structurally homogeneous. Despite this spatial homogeneity, however, biogeochemical cycles everywhere



Figure 9. Carbon Fluxes into the Deep Ocean.

in the ocean are strongly affected by seasonal changes and episodic events, such as storms, monsoons, windborne iron deposition, upwelling or eddies, that have an impact on the major pathways of the carbon cycle.

These regional differences make it a challenge to measure the primary production of the great ocean basins. The problem is one of phytoplankton physiology. If we know the biomass of the algae, the level of irradiance at the sea surface and the photosynthetic response per unit of algal biomass and irradiance, we can then estimate the primary production in a given area of the sea surface. The first difficulty, however, is that the biomass of phytoplankton, as measured by its chlorophyll concentration, has a dynamic range in the ocean of more than 4 orders of magnitude. Therefore, this method will not yield useful large-scale results unless we can measure phytoplankton on synoptic scales.

Remote-sensing measurements of phytoplankton pigment levels in the surface ocean can provide the information we need. The Coastal Zone Color Scanner (CZCS) radiometer, the first satellite-mounted ocean color instrument, measured pigments in every part of the global ocean from 1978 until 1986. JGOFS investigators made use of the archived data from CZCS measurements to produce the first global maps of annual primary production. Given knowledge of average conditions over regions and seasons for levels of chlorophyll and surface irradiance determined from the CZCS data, they used the photosynthetic response of the algae arranged by region and season to calculate primary production.

In another approach, investigators relate variations in photosynthetic parameters to one or more independent variables, such as temperature, mixed-layer depth or light. Global seasonal-toannual estimates of primary production are now being derived from data on phytoplankton pigments measured by the Sea-viewing Wide Field-of-view Senor (SeaWiFS), which was launched into space in 1997 (Figs. 10a and b).

These two approaches yield similar global estimates of primary production. The latter method, however, does not make reference to the physical location of a chlorophyll sample but rather assumes that common variables operate throughout the ocean. Another oceanographic satellite sensor, the Advanced Very High Resolution Radiometer (AVHRR), detects variations in ocean temperature fields on the same time and space scales as the variations in chlorophyll detected by SeaWiFS. These data make it





possible to set the dynamics of marine ecosystems in their physical context.

Mapping the Exchange of CO_2 between Ocean and Atmosphere

Sound scientific knowledge about the fate of anthropogenic carbon emitted into atmosphere is essential as governments debate plans for emissions control and carbon storage. Among the goals of JGOFS is to improve our understanding of the role of the ocean as a sink for anthropogenic CO_2 . Achieving this goal requires the construction of global ocean inventories of both total inorganic carbon and the anthropogenic fraction and the development of better estimates of the distribution, intensity and seasonality of the exchange of CO_2 between the ocean and the atmosphere.

One of the fundamental components of the overall JGOFS strategy has been a global survey of dissolved inorganic carbon (DIC) in the ocean. Precise and accurate measurements of DIC are critical to assessing the uptake of carbon in the oceans and to understanding the physical and biogeochemical processes that are responsible for regulating the flux of CO_2 across the air-sea boundary.

The global survey of CO_2 in the oceans was carried out in cooperation with the World Ocean Circulation Experiment (WOCE), which measured hydrographic features, nutrients, oxygen and man-made tracers such as chlorofluorocarbons on a series of transects between 1990 and 1998. JGOFS scientists measured basic parameters of the ocean carbonate system on more than 40 WOCE Hydrographic Programme transects, covering nearly every major region of the global ocean.

The survey began in the South Atlantic in early 1990 and ended in the North Atlantic in 1998. More than 100 000 samples were collected and analyzed for total DIC, the partial pressures of CO_2 in the water and atmosphere, total alkalinity and pH, an order-of-magnitude increase over the quantity of data collected by the last global carbon survey in the 1970s.

Building a global picture of the exchange of CO_2 between ocean and atmosphere requires accurate and comparable results. One of the accomplishments of the JGOFS survey has been an extraordinary advance in the accuracy and precision of measurements. It was achieved through the development and use of standard methods and certified reference materials for calibrating instruments and the development of automated seagoing analyzers, which were used on the majority of survey cruises.

The global survey of CO_2 has yielded data on the magnitude of the exchange between ocean and atmosphere and the distribution of regions that take up or release CO_2 (Fig. 4). JGOFS investigators are using these data to produce estimates of the global annual ocean uptake of CO_2 as well as estimates of the global annual ocean uptake of CO_2 as well as estimates of the amounts, distribution and transport of the anthropogenic CO_2 that has penetrated the ocean since the industrial revolution (Fig. 5). New information is emerging on seasonal cycles in the flux of CO_2 between the ocean and the atmosphere. Finally, inventories and flux estimates derived from CO_2 survey data will provide powerful constraints on efforts to model global carbon fluxes.

REGIONAL DIFFERENCES: THE INTENSIVE STUDIES

The following sections present highlights of JGOFS studies in major ocean basins over the past decade, focusing on the effects of regional differences on the global carbon cycle.

The Equatorial Pacific

As the largest natural oceanic source of carbon dioxide (CO_2) released into the atmosphere, the equatorial Pacific plays a critical role in the global carbon cycle (13–15). Upwelling along the equator brings water rich in nutrients and dissolved inorganic

carbon (DIC) to the surface in a region that extends, during normal years, from the coastal waters of South America as far west as 160°E. Physical processes and biological productivity control the magnitude of this source of CO_2 from year to year.

The western limit of the upwelling region is well defined by a front with marked changes in temperature, salinity, nitrate and chlorophyll levels and the partial pressure of CO_2 (Fig. 11a). The position of this front, which affects the east-west extension of the equatorial upwelling and thus the overall amount of CO_2 exported to the atmosphere, depends on a set of oceanic and atmospheric conditions associated with El Niño-Southern Oscillation (ENSO) cycles in the Southern Hemisphere.

One of the hypotheses of JGOFS research in the equatorial Pacific has been that variations in the air-sea exchange of CO_2 related to ENSO cycles have a major effect on the extent to which this region serves as a source of CO_2 to the atmosphere. During El Niño events, easterly trade winds in the equatorial

Figure 11. Climate, Physics and the Air-Sea Flux of $C0_2$ in the Equatorial Pacific.

a: The western limit of the upwelling region that releases CO_2 into the atmosphere in the equatorial Pacific is marked by clear changes in biogeochemical features. (Courtesy of Robert Le Borgne, Centre Oceanologique de Marseille).



Pacific weaken and reverse, and the warm pool of the western Pacific moves east. Kelvin waves propagate from west to east, depressing the thermocline in the east, while Rossby waves generated by the weakened trade winds cause the thermocline in the west to shoal.

Data from JGOFS studies in the region show that these processes reduce pCO_2 in the surface water at the height of El Niño events and thus reduce the flux of CO_2 from the ocean into the atmosphere. About 0.2 to 0.4 PgC yr⁻¹ are released to the atmosphere from the equatorial Pacific during strong El Niño events, such as occurred in 1997–1998, less than half of the 0.8–1.0 PgC yr⁻¹ released during non-El-Niño periods (Fig. 11b). This difference is enough to account for approximately one-third of the atmospheric anomaly during an El Niño period.

During decades dominated by strong El Niños, such as the 1990s, the ocean retains several petagrams more carbon in the form of CO_2 than it does during normal periods. We can con-

clude that ENSO cycles are a major controlling factor in the interannual variability of the exchange of CO_2 between the ocean and the atmosphere.

JGOFS studies in the equatorial Pacific have substantially improved our knowledge of biological as well as physical controls on regional carbon fluxes. We have found that the rates of biological processes are much more variable and the export of particulate organic carbon much lower than expected. Additional carbon is exported in dissolved organic form from the equatorial region. In this high-nutrient, low-chlorophyll (HNLC) region, the availability of iron limits rates of primary and new production, and nutrients are recycled efficiently in the euphotic zone.

Because they control upwelling and the depth of the nutricline and thus the vertical transport of iron into the euphotic zone, Kelvin waves and tropical instability waves appear to control variability in carbon fluxes on scales of days to months. Kelvin waves depress the nutricline in the central and eastern Pacific,



lowering productivity in surface waters. Tropical instability waves occur at the boundary between the South Equatorial Current and the North Equatorial Countercurrent. Strong mixing associated with such waves transports iron into the euphotic zone, enhancing primary and new production.

During a JGOFS cruise in August 1992, the convergence of waters associated with one of these tropical instability waves was so intense that it produced a front with breaking waves visible from the deck and on the ship's radar. This front, known as "the line in the sea", was also seen by the crew of a space shuttle that passed over the region (Fig. 11c). The strong physical convergence caused an aggregation of phytoplankton cells into a thick patch in the top few centimeters of the water, which exhibited high rates of photosynthesis. The concentration of large phytoplankton such as diatoms by frontal motions such as this one may contribute to episodic pulses of carbon export in the equatorial Pacific.

The North Atlantic

Physical and biological processes act together in the North Atlantic to make it the region with the most intense uptake of CO_2 in the global ocean (17, 18). Because of its ample supply of nutrients, including wind-borne iron from the Sahara Desert, this basin is among the most biologically productive oceanic regions in the world.

The spring bloom in the North Atlantic is a conspicuous event; images from satellite-mounted ocean color sensors show the sudden explosion of chlorophyll that fills the basin north of 40°N in April and May each year. During the North Atlantic Bloom Experiment (NABE) in 1989, observations at 47°N, 20°W showed that the bloom consisted of two phases. The first phase primarily comprised large diatoms, which require silicate to grow, while the second consisted of small flagellates (Fig. 12a). The relative timing of these two phases has a large effect on nutrient utilization and export of carbon to the deep ocean.

NABE observations also revealed links between mesoscale circulation and the biological dynamics of the spring phytoplankton bloom. Small-scale temporal and spatial variability in surface pCO_2 at temperate latitudes appeared to be tied to the dynamics of the bloom, which were, in turn, related to the mesoscale eddies. NABE also produced evidence of intense nutrient regeneration during the bloom, supported by large stocks of microzooplankton and high rates of respiration.

The Bermuda Atlantic Time-Series (BATS) study, which includes process studies as well as long-term monitoring, has provided unique insights into the functioning of the North Atlantic subtropical gyre ecosystem. The intensity of the spring bloom is linked to the strong interannual and decadal variability of physical processes, especially the depth of winter convective mixing, that affect nutrient supply to the euphotic zone. Nitrogen fixation by prokaryotic microorganisms, supported by windborne iron deposition, provides a source of new nitrogen for the system in addition to nitrate introduced during seasonal mixing.

Dissolved organic carbon (DOC) accumulates in early spring as a result of the seasonal increase in primary production (Fig. 12b). The DOC that accumulates over spring and summer (resident-DOC) is exported from the surface ocean during turbulent mixing the next winter. DOC freshly produced during the mixing (fresh-DOC) is exported along with the resident-DOC. The amount of fresh-DOC exported, defined as the difference between total and resident-DOC export, depends on the maximum depth of mixing during the winter overturn (Fig. 12c); the greater the mixing to depths below the nutricline at 200 meters, the greater the export of fresh- and resident-DOC. During years of deep mixing and high export, DOC represents as much as 40% of the annual carbon export from the surface into deeper waters as measured by oxygen utilization rates. During years of shallow mixing, the contribution of the DOC is as little as 15%. Further measurements of DOC and dissolved organic nitrogen (DON) are essential for a better understanding of the North Atlantic carbon cycle.

The Arabian Sea

Although tropical, the Arabian Sea experiences intense seasonal changes associated with alternating monsoon winds. It also exhibits the greatest range of variability found in any ocean region. The more vigorous southwest monsoon blows from June to September, while the weaker northeast monsoon blows from December to February. As a result, surface circulation patterns reverse themselves semi-annually. During the inter-monsoon periods, the winds wane in strength and slowly reverse their direction. Whereas surface and deep waters are well oxygenated, waters between depths of 100 and 1200 meters are almost devoid of oxygen. The Arabian Sea thus offers an opportunity to study biogeochemical processes over a wide range of climate and oceanographic conditions (21–24).

The southwest monsoon causes vigorous upwelling along the

Figure 12. Spring Blooms and the Flux of DOC in the North Atlantic.

a: The spring bloom at 47°N, 20°W, sampled during NABE, showed a succession of dominant phytoplankton species. Large diatoms bloomed first, using up almost all of the available silicate and about half of the nitrate. A subsequent bloom of small flagellates used up the remaining stock of nitrate. (Courtesy of Michael Fasham, Southampton Oceanography Centre).



Somali and Omani coasts, which stimulates massive and longlasting phytoplankton blooms over a wide region. Data from the Indian Ocean Expedition in the 1960s suggested that the magnitude of the bloom and primary production during the northeast monsoon was significantly lower than during the southwest monsoon. JGOFS process studies, conducted over a larger area, have shown that primary production in general is higher than previously thought and that the difference between the two monsoon periods is much less (Fig. 13a).

The pattern of carbon cycling in the Arabian Sea differs from those of most other regions in that a higher fraction of the production is exported out of the surface waters. Unlike the situation in the temperate Atlantic where protozoans dominate grazing, larger zooplankton such as copepods act as the gatekeepers to the export process in the Arabian Sea, where their reproduction coincides with the phytoplankton bloom. The large zooplankton produce faecal pellets with high sinking rates, and they migrate vertically, providing a mechanism for the active export of organic carbon into the deep sea. This export, coupled with

the absence of a high-latitude source of oxygenated water, produces a midwater zone that is depleted in oxygen.

Instruments mounted on an air-sea interaction buoy moored in the Arabian Sea between 1994 and 1996 were used to measure the coupling between atmospheric forcing and ocean properties. Deep sediment traps deployed throughout the region at depths down to 3500 meters sampled the flux of particulate material that falls through the water column. The sea-surface temperature plot in Figure 13b shows the cooling that occurs during both monsoons. The winds of the northeast monsoon, together with heat loss from the ocean, lead to a deepening of the mixed layer. The deepening of the mixed layer during the southwest monsoon, on the other hand, depends on wind-driven mixing. Although the export flux in the Arabian Sea lags behind the rise and fall in surface productivity by a month or two, deep sediment trap samples show that it tracks the pattern of the surface blooms that occur during periods when the mixed layer is shoaling and nutrient concentrations are high. Silica to calcium ratios are higher during mass flux peaks, which suggests that dia-

b: Vertical profiles of DOC measurements at the BATS site (31°50'N, 64°10'W) over one year (1992). The red bars indicate the average range of DOC values (micromolar) during deep mixing in the winter. Redrawn from (19).



Redrawn from (20).

Figure 13. Effects of the Monsoons on Physical Environment and Biogeochemical Processes in the Arabian Sea.



toms play a large role in the blooms and subsequent export (Fig. 13b).

The Southern Ocean

The Southern Ocean, which circles the globe south of 50°S, links the Pacific, Atlantic and Indian oceans with major sites of deep-

Figure 14. The Biological Pump in the Southern Ocean.

water formation in the Weddell Sea and Ross Sea along the coast of Antarctica (Fig. 14 center panel). This highly heterogeneous region contains a number of distinct biogeographical provinces, including frontal systems, the permanently open ocean zone, the seasonal sea-ice zone and the coastal and continental shelf zone (26–28).



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The Southern Ocean encompasses regions that exhibit a net release of CO_2 into the atmosphere as well as ones that exhibit a net uptake. Warm water is transported toward the pole by thermohaline circulation and cools, increasing its capacity to absorb gas from the atmosphere. On the other hand, deep water enriched in CO_2 from the remineralization of biogenic detritus is brought back to the surface through upwelling south of the Antarctic Polar Front, releasing the gas into the atmosphere. On an annual basis, the region experiences a net CO_2 flux into the ocean of 0.2–0.9 Pg C yr⁻¹.

Key factors controlling the annual air-sea fluxes of CO_2 and primary production in the Southern Ocean include the effects of annual fluctuations in sea ice, oceanic boundaries, such as frontal zones, as well as iron and silica limitation of phytoplankton growth. The nutrient-rich waters of the Antarctic Polar Frontal Zone in the Atlantic sector favor the growth of spiny diatoms during the summer (Fig. 14a). The mass sedimentation of these diatoms, with their thick siliceous frustules, transports carbon and silica into the deep sea and the ooze on the sea floor.

The complex polar frontal zone sheds mesoscale eddies, favoring local upwelling and downwelling. The upwelling transports iron into the upper mixed layer, which favors phytoplankton production. On the other hand, downwelling transports CO_2 into intermediate layers of water that transport dissolved gases north. The net result is that the polar front is a location of enhanced CO_2 fixation with strong biological and physical pumps.

The effect of iron as a control on surface ocean productivity has been observed in a fertilization experiment southwest of New Zealand as well as in naturally fertilized HNLC regions, such as that to the southeast of Kerguelen Island in the Indian Ocean sector (Fig. 14b). Results lend strength to the hypothesis that iron controls surface concentrations of CO_2 in the Southern Ocean as it does in the equatorial Pacific.

Surface waters in antarctic coastal regions such as the Ross Sea are largely undersaturated with respect to atmospheric CO₂ during the austral summer when they are free of ice, primarily because of the photosynthetic drawdown of CO₂ (Fig. 14c). In the Ross Sea, variations in pCO₂ levels in surface waters as large as 100 micro-atmospheres occur over spatial scales as small as a few kilometers. These variations are closely linked to the drawdown of CO_2 by marine biota and appear to depend on the types of organisms present. For example, the growth of diatoms, evidenced by the drawdown of silica in surface waters, is responsible for CO₂ uptake in the area of the Ross Sea east of about 174°E. On the other hand, the phytoplankton Phaeocystis *antarctica*, which utilizes CO_2 but not silica, is responsible for the drawdown of CO₂ in the area west of 174°E (Fig. 14c). Understanding the causes of local dominance of different species as well as the factors that control export of carbon to the ocean interior remains a critical but unresolved problem.

Large zooplankton play a major role in carbon cycling in the Southern Ocean. Recent studies off the island of South Georgia show shifts in community domination between krill (Fig. 14d) and copepods. These shifts between grazers result in dramatic differences in the carbon flux with the larger krill producing larger, faster-sinking faecal pellets and therefore a higher export flux. Similar observations have been made elsewhere with regard to shifts between krill and gelatinous salps, which in turn are related to sea-ice conditions. Krill are favored by extensive sea ice in winter, whereas salps prefer open water. The impact on the carbon cycle of a possible shift to a salp-dominated system caused by overfishing of krill needs to be evaluated.

The North Pacific

The North Pacific can be viewed as a large estuary in which a strong halocline at 100–120 meters depth separates the surface from deeper waters. Nutrient concentrations in deep waters are

the highest in the global ocean because it is the terminal region for the abyssal circulation. High primary productivity and strong air-sea interactions characterize the region's carbon cycle.

Time-series stations have operated for many years in the eastern subarctic (29) and subtropical North Pacific (4), and JGOFS is currently completing its final process study in the Pacific. The newly established Kyodo North Pacific Ocean Time-series (KNOT) station is in operation in the western subarctic gyre off Kuril Islands (44°N, 155°E). The study focuses on the western subarctic Pacific in order to highlight the differences in the carbon cycle between this region and the eastern subarctic Pacific. For example, it is well known that phytoplankton blooms only occur in the western subarctic Pacific, although both regions are HNLC areas. Higher levels of windborne iron from Asia in the west may account for this difference.

In the eastern subarctic Pacific, the winter supply of nitrate to the surface has decreased since 1991 as a result of the increased stratification associated with El Niño events (Fig. 15a). In addition, time-series data from Station PAPA show that nitrate and silicate utilization rates have increased during El Niño years. Sediment traps show a concurrent increase of 10% to 15% in the flux of biogenic elements. These changes have caused the late summer depletion of nutrients to extend further offshore from the west coast of Canada (Fig. 15a). Episodic inputs of windborne iron from Asia may also be affecting biological productivity and thus the uptake of nutrients.

It will be important in the future to distinguish the biogeochemical consequences of these two sources of interannual variability. Our ability to do so would be greatly improved if it were possible to measure nitrate distributions over large time and space scales with instruments mounted on satellites. The greatest impediment to making such measurements has been the lack of a remotely measurable signal for nitrate. As a result, most attempts at estimating nitrate from space have been based upon measurements of proxies such as sea-surface temperature, which has a negative correlation with nitrate.

Until recently the use of temperature as a proxy for nitrate has been limited because of the variable nature of temperature-nitrate algorithms. A recent study has shown that this limitation can be overcome if biologically mediated changes in the relationship between temperature and nitrate are taken into account. Adding chlorophyll as a factor to nitrate algorithms has yielded significant improvements in estimates of nitrate concentrations from sensors on satellites (31) (Fig. 15b). This capability provides a solution to the problem of under sampling in regions and seasons where shipboard observations are difficult to conduct.

The Continental Margins

Areas of the ocean adjacent to continents receive, transform and transport a large amount of terrigenous and anthropogenic material to the open ocean. They include continental shelves such as the Mid-Atlantic Bight and the East China Sea, marginal seas such as the Bay of Biscay (33), North Sea and the Red Sea, coastal zones with strong boundary currents such as the Peruvian and Benguela current systems, polar margins such as the Bering Sea and Ross Sea, and tropical coasts such as the Great Barrier Reef.

The role of continental margins in the global carbon cycle has not been fully assessed yet, in part because of the inherent difficulties in quantifying the biological and chemical activities in these heterogeneous and variable environments (Fig. 16a). Whether margins are a net sink or source of CO_2 is still an open question. JGOFS and Land-Ocean Interactions in the Coastal Zone (LOICZ), another core project of the International Geosphere-Biosphere Programme (IGBP), have joined forces to promote research in these areas (32).

Conventional wisdom suggests that continental margins should be a net source of CO_2 , whether from coastal upwelling or from oxidation of terrigenous organic matter. However, surveys in the North Sea and the East China Sea showed significant under-saturation of pCO₂ in surface waters associated with high levels of primary productivity in both areas (Fig. 16b). These results suggest that both regions are net sinks for CO₂. If similar results are found in other regions, the total uptake of CO₂ in the continental margins could be as much as 0.2-1 Pg C yr⁻¹, a significant component in the global carbon cycle. Winter data are sparse, however, and prevent accurate calculation of annual fluxes. Both the processes controlling CO₂ uptake in the coastal

waters and the seasonal fluctuations must be better understood before a reliable estimate can be reached.

Carbon dioxide taken up at the continental margins will be released back to the atmosphere unless the carbon is buried in sediments or transported into the deep ocean. Studies in the Mid-Atlantic Bight indicate that little organic matter survives bacterial attack in the shelf sediments, and at most a small percentage of the carbon fixed during primary production is transported across the shelf to the deep ocean. More recent measurements over continental slopes off northeastern Taiwan in the Pacific

Figure 15. Nitrate in the North Pacific.



and off Cape Hatteras in the Atlantic hint at offshore export facilitated by currents that veer off the shelf at a few specific sites, sweeping organic sediments offshore. At high-latitude margins, some of the absorbed CO_2 may be carried offshore when cold shelf waters sink into the intermediate layer of the open ocean. This is what happens in the Bering Sea and the Sea of Okhotsk, regions in which CO_2 is transported into the North Pacific.

ASSESSING CHANGES OVER TIME

One of the enduring legacies of JGOFS will be the long-term time-series stations and sampling programs established during the study. Some time-series programs were built upon previous



projects with several decades of data on ocean properties and processes at a given location. Some will continue operations in the new millennium. These programs provide an insight into changes in ocean carbon and nutrient cycles on seasonal, interannual and decadal time-scales. Knowledge of natural temporal variability will provide insight into relationships between ocean biogeochemical cycles and climate, and the resulting data will provide boundary constraints on modeling simulations.

The Hawaii Ocean Time-series (HOT) and Bermuda Atlantic Time-Series (BATS) stations are both located in oligotrophic subtropical gyres that are weak net sinks for carbon dioxide (CO_2) (4). The sampling record at each station shows that the concentration of dissolved inorganic carbon (DIC) is increasing



as a result of the increase in atmospheric CO_2 (Fig. 17) (34, 35). Temporal variability in the uptake of carbon, whether it is the result of biological factors or changes in solubility, which are linked in turn to variations in mixing processes, provides a number of clues to the interaction between ocean biogeochemistry and global climate.

Data from BATS and HOT have provided important new information on the role of nitrogen (N_2) fixation in the ocean. The open ocean has traditionally been viewed as a nitrogen-limited habitat. However, under conditions of extreme nitrogen limitation, certain prokaryotic microorganisms, such as *Trichodesmium* colonies (Fig. 18a), grow over large areas (Fig. 18b) and utilize the nearly inexhaustible pool of dissolved N_2 gas in the sea as

Figure 18. Climate, Nitrogen Fixation and Ecosystem Change.

a: Microscopic view of radial and fusiform morphologies of *Trichodesmium* collected in the field. (Courtesy of Pernilla Lundgren and Birgitta Bergman, Stockholm University).



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Figure 17. Measuring the Anthropogenic Impact on Ocean DIC Concentrations.

Seasonal cycles of salinity-normalized dissolved inorganic carbon (NDIC) in the surface waters at the Hawaii Ocean Timeseries (HOT) and Bermuda Atlantic Time-series Study (BATS) stations. The dashed lines indicate the annually averaged increase over the period of observations. Adapted from (34 and 35).





c: Selection for Trichodesmium in the North

Pacific gyre has shifted the controlling nutrient in this ecosystem from nitrogen (N) to phosphorus (P) over the last decade. Among the biogeochemical consequences of this shift is an increase in the elemental ratio of N to P in suspended particulate matter from about 16:1 (the Redfield ratio) to values in excess of 20:1. Redrawn from (38).

(mol:mol) 30 20 Ratio å 10 0 A J O J A 1992 1 A J 1998 JOJ 1997 J O AJOJA 1993 1 Ó JO J AJ(1991 ΟJ A 10 J A 10 J А 10 J JO

b: Macroscopic

Trichodesmium

view of

bloom

d: The frequency of El Niño events in the 1990s has favored the growth of nitrogen-fixing species such as *Trichodesmium* in the North Pacific Gyre. This graph shows the upper layer water volume (solid line) in the tropical Pacific between 15°N and 15°S in 10¹⁴

 m^3 relative to its mean value of 70 x 10¹⁴ m^3 . The volume of water in the tropical upper ocean is an index of the El Niño state. Data and analysis from University of Hawaii Sea Level Center.



an alternative source of nitrogen. This metabolic switch can alter ratios of carbon to nitrogen and phosphorus and provide an efficient mechanism for a pulsed export of carbon and associated elements to the deep ocean (Fig. 18c). Under these circumstances phosphorus, iron or some other required element eventually limits productivity, but the added nitrogen has a significant effect on local and regional biogeochemical cycles.

In the subtropical Pacific, the shift from a nitrogen-limited system to a phosphorus-limited system has taken place during the decade of HOT observations (Fig. 18c and d). Estimates suggest that N_2 fixation has supported up to 50% of the export flux during this period. These observations on the role of N_2 fixation in oligotrophic open-ocean ecosystems necessitate a major reassessment of current views on ocean nutrient and carbon cycles (37, 38).

El Niño events have a marked influence on the mixing and stratification of the water column at the BATS and HOT stations. At Bermuda, the effects show up most strongly in the intensity of the spring bloom, while at Hawaii the pattern is more of a fundamental reorganization of the ecosystem. The impact of episodic events on both the normal cycling of the systems and the transport of material to the deep sea cannot be overemphasized. Short-term bursts of productivity are also associated with eddies and with rare anomalies of mixing and nutrient supply. Timeseries data from both HOT and BATS show that such events stimulate more biological activity than occurs over many months to years at background rates. Some of these events are traceable in the deep-sea records from sediment traps and may be disproportionately imporFigure 19. Interannual Variability in an HNLC Area of the Southern Ocean.

Time-depth distributions of nitrate (NO₃), silicic acid (SiO₂) and chlorophyll *a* (Chl) at the KERFIX time-series station, located at 50°40'S, 68°25'E, between January 1992 and December 1994. (Courtesy of Catherine Jeandel, Centre National d'Etudes Spatiales).



tant in the supply of food to midwater plankton and benthic organisms.

Unlike the HOT and BATS sites, the Kerfix time-series station in the Southern Ocean was located in a high-nutrient, low chlorophyll (HNLC) area. Observations between 1992 and 1994 showed that surface nitrate never fell below 23 mmol m⁻³, even in the austral summer (Fig. 19). A decline from winter levels was associated each year with a small bloom consisting primarily of diatoms with a high silica-to-nitrogen ratio, probably related to iron limitation. These blooms gave rise to depletion of silicate each summer. Up to 60% of the silicate taken up by diatoms was exported to the deep ocean. Calculations of the partial pressure of CO₂ in surface waters show that net uptake in this area has been increasing with time, especially since the 1992 El Niño event.

It will be crucial to incorporate these new insights about the

functioning of ecosystems and the sources of variability, such as El Niño events and iron deposition, into global carbon models. The data from time-series stations will then provide a crucial benchmark for validation of these models, as they become a focal point for the interaction between theory and observations.

LEGACIES OF JGOFS

The defining legacy of JGOFS will be the mathematical models of ocean ecosystems and biogeochemical processes that have been developed and validated with JGOFS observations. These models vary in complexity from simple time-dependent models of the mixed-layer ecosystem, through one-dimensional models of physical and biogeochemical processes at a given location, to three-dimensional models of the global ocean. A prerequisite for all forms of biogeochemical modeling is an ability to model



the physical processes in the ocean successfully; it is fortunate that considerable progress has been made in this field over the last 20 years.

Diagnostic and Prognostic Models

The data generated at the time-series sites have served since the beginning of JGOFS as test beds for the development of onedimensional biological-physical models. Figure 20 shows observed and modelled chlorophyll and nitrate concentrations for 1989–1993 as a function of depth and time at the BATS site in the Sargasso Sea. The simulations are driven by synoptic surface atmospheric properties derived from meteorological analyses and satellite measurements. The model shows a high degree of effectiveness in replicating the resupply of nutrients to the surface layer via deep winter convection and the subsequent winter/spring phytoplankton bloom. During the stratified summer period, surface nutrient and chlorophyll levels drop considerably. The numerical simulation and the observations both show the formation of a distinct nutricline and subsurface maximum at about 100 meters depth. The simulation also captures to some degree the interannual variability in the data, driven primarily by the strength of the late winter convection.

Larger-scale models attempt to represent whole basins. Figure 21 shows some results from a three-dimensional model of the North Atlantic designed to investigate the eddy-induced nutrient supply to the euphotic zone. It shows that areas of high nutrient supply are located in the vicinity of the Gulf Stream, the sub-polar areas where deep winter mixing occurs, and the coastal and equatorial upwelling regions. The pattern of primary production is well correlated with nutrient supply. However, the modelled primary production in the southern part of the subtropical gyre is less than 1 g C m⁻² yr⁻¹, more than an order of mag-



nitude less than that derived from observations. However, increasing the supply of alternative nitrogen sources, such as nitrogen fixation or lateral transport of dissolved organic nitrogen (DON), in the basin-scale models would not reconcile these estimates with the measured fluxes because horizontal gradients in low-latitude regions are generally too weak. Further development of large-scale models must continue with field observations to resolve discrepancies with the real world.

At the largest scale, models of the global carbon cycle are under development. These projects require the incorporation of ocean carbon cycle models into three-dimensional ocean general circulation models that can simulate the physical properties of waters as well as large-scale oceanic transport, diffusion, and convection. The earliest models only simulated inorganic carbonate chemistry in an effort to estimate oceanic changes in solubility in response to increasing levels of carbon dioxide (CO₂) in the atmosphere. More recent efforts include explicit models of the role of plankton in the carbon cycle in order to simulate biological processes, such as photosynthesis, grazing, mortality and the sedimentation of organic material, in the biological pump (Fig. 2). Evaluation of such models on the global scale requires global synthesis data sets, such as the new satellite-based estimates of surface chlorophyll or primary production (Fig. 22). Patterns captured by these models include coastal and equatorial upwelling and eutrophic areas in the North Atlantic, North Pacific and Southern Ocean, as well as in the oligotrophic gyres.

Ocean carbon cycle models require improvement in several areas. Simulated primary production is too high for the high-nutrient low-chlorophyll areas of the equatorial Pacific and the Southern Ocean, especially in the eastern austral Pacific, which suggests that the models lack some limiting factor such as windborne iron. Primary production is too low in the gyres, suggesting a lack of processes that allow biological populations to adapt to oligotrophic constraints, such as nitrogen fixation or DON advection. Continental shelf or coastal regions, such as the Indonesia and China Seas, are poorly represented because of the level of resolution in the model grids.

The frontier that lies beyond the representation of ocean bio-

geochemistry in modeling efforts is the necessity of linking ocean processes with changes in climate. This effort requires the development of coupled ocean-atmosphere models. Preliminary results from such models just becoming available show that, over the next 100 years, the ocean may become more stratified and thermohaline circulation weaker. Such changes would alter the nutrient supply to the upper ocean and have a substantial effect on the biological pump. It is thus more important than ever that we use the results from JGOFS to validate our three-dimensional ecosystem models. This is the challenge for the future.

Biogeochemical Data Sets and Data Management

Another legacy is the extensive data set collected over more than a decade of JGOFS research, which will be a resource for oceanographers and modellers for decades to come. The development

Figure 22. Third Generation of Ocean Carbon Cycle Models.

Global surface chlorophyll (in mg m⁻³) for May, estimated from ocean color measurements by the POLDER sensor on the ADEOS satellite in 1997 (top) and by SeaWiFS in 1998 (center), as well as by the Institut Pierre Simon Laplace (IPSL) Ocean Carbon Cycle Model (bottom). (POLDER image courtesy of LPCM/LOA/LSCE/CNES/NASDA. SeaWiFS image courtesy of NASA Goddard Space Flight Center. **IPSL-OCCM** model simulation courtesy of Olivier Aumont, Laboratoire des Science du Climat et de l'Environnement, and Patrick Monfray, Institut Pierre Simon Laplace).



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of high-quality, comprehensive data sets that are readily accessible to interested investigators has been among the goals of JGOFS since the program was first conceived.

Various project centers undertake data management for national JGOFS programs; some are national oceanographic data centers, and some are not. The ties that bind the national efforts together come from the JGOFS Data Management Task Team (DMTT). The JGOFS data-exchange network currently includes Australia, Canada, France, Germany, India, Japan, the United Kingdom and the United States, with links to The Netherlands and Norway.

With support from the JGOFS International Project Office, DMTT members are working to make JGOFS data readily available. Their activities include the development of World Wide Web sites that provide electronic access to JGOFS data, the creation of a JGOFS metadata catalogue that facilitates the location of particular data sets and the electronic publication of JGOFS data sets on CD-ROMs (Fig. 23).

WHAT HAVE WE ACHIEVED FROM JGOFS RESEARCH?

JGOFS has fulfilled most of the objectives set for it in 1987. Process studies have been completed in the North Atlantic, the equatorial Pacific, the North Pacific, the Arabian Sea and the Southern Ocean. The global survey of carbon dioxide (CO_2) in the ocean, conducted in cooperation with the World Ocean Circulation Experiment (WOCE), ended in 1998. The time-series stations have been providing monthly data on a continuous basis, some since 1988. Several of them will continue as part of future global ocean observing programs.

Results emerging from the JGOFS field studies are contributing to the process of reassessing old paradigms in ocean biogeochemistry and formulating new ones. Some of the main achievements to date are:

- A massive contribution to the database of sea-surface pCO₂ measurements, making it possible to produce much more reliable estimates of the global air-sea flux of CO₂.

- A worldwide survey of total dissolved inorganic carbon (DIC) in the ocean, carried out in cooperation with WOCE, which is enabling investigators to determine the global distribution, transport and inventory of anthropogenic carbon in the ocean and develop new models of the global carbon cycle.

– Improved understanding of aspects of the marine food web such as the role of iron as a limiting micronutrient, particularly for the production of larger phytoplankton, the predominance of diatoms in episodic or seasonal blooms and in subsequent sedimentation, and the dominant role of microzooplankton in the grazing of phytoplankton.

- Quantification of the seasonal changes in primary production and the subsequent flow of carbon through food webs and export to the deep ocean for many key areas of the ocean.

- Clarification of the role of dissolved organic carbon (DOC) in the ocean carbon cycle, its control by bacteria, and measurement of its contribution to export flux.

- A better understanding of variations in the elemental ratios (C:N:P:Si) of the composition of organic matter, both particulate and dissolved, and the associated ratios of the utilization and remineralization of organic matter during transport within the ocean interior. Rather than being locked in the canonical Redfield ratio, elemental ratios in marine organic matter and its transformations can vary widely with important implications for the efficiency of the biological carbon pump in different regions and under different physical and climatological conditions.

– Establishment of links between large-scale climate patterns such as the El Niño-Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO) and interannual variability in the airsea flux of CO_2 in the equatorial Pacific and the subtropical oligotrophic gyres of the North Atlantic and Pacific.

– Detection of variability in plankton species on decadal time scales by long-term observations at the time-series stations.

– Demonstration of the role played by nitrogen (N_2) fixers in the nitrogen cycle of the subtropical ocean and the contribution of N_2 fixation, in conjunction with changing physical conditions, to shifts in nutrient limitation between nitrogen and phosphorus in the oligotrophic North Pacific ecosystem.

– Development and testing of a hierarchy of new ecosystem models using time-series data and global observations from ocean color satellites.

WHAT REMAINS TO BE DONE?

Although the field studies are now complete, JGOFS still has important synthesis, integration and modelling tasks that lie ahead:

– Results from the process studies and time-series programs must be synthesized and used to validate the developing set of models. JGOFS has established a number of regional synthesis and modelling groups responsible for achieving this objective.

- The ocean time-series stations must be maintained and longterm sampling continued to allow full testing of our emerging ideas about the carbon cycle and its decadal fluctuations, especially the processes affecting subsurface particle flux, dissolved organic matter transport and remineralization in the deep ocean. - Recent observations in continental shelf systems show significant drawdown of atmospheric CO₂ and active cross-shelf export of carbon. Further study, in collaboration with the Land-Ocean Interactions in the Coastal Zone (LOICZ) project, is required to determine whether the coastal oceans as a whole represent a sink for anthropogenic carbon and to quantify the net exchange of carbon between coastal waters and the open ocean. - Three-dimensional ocean carbon models are being compared and validated against the JGOFS and WOCE large-scale data sets by the Ocean Carbon Modeling Intercomparison Project (OCMIP), co-sponsored by the Global Analysis, Integration and Modelling (GAIM) Task Force within IGBP. These models will also be used in coupled ocean-atmosphere-terrestrial models to investigate the ways in which the cycling of carbon and other biogenic elements might change under future climate-change scenarios.

– The data obtained from more than 1000 cruises must be archived and made freely available to the wider scientific community. The Data Management Task Team is responsible for delivering all national JGOFS data sets to the World Data Center-Oceanography A for future distribution and long-term stewardship.

A CHALLENGE FOR A FUTURE OCEAN BIOGEOCHEMISTRY PROGRAM

Preliminary simulations from coupled ocean-atmosphere models show an ocean over the next 100 years that is more stratified as a result of warming and freshening of the surface ocean and more sluggish as a result of slowing down of the thermohaline circulation. If these changes occur, ocean mixing would weaken the supply of nutrients to the upper ocean and the biological pump.

Until now, JGOFS investigations concentrated on the productive layer in the upper 100–200 meters and on deep ocean sediment flux near the sea floor. We recognize that most of the decomposition or diagenesis of exported organic matter in the biological pump takes place directly below the euphotic zone in the "twilight zone," which extends some 500–1000 meters in depth.

At present models of particle export and diagenesis, critical processes in the carbon cycle, are based largely on crude, empirical length-scale parameterizations. In order to achieve a prog-



nostic understanding of the carbon cycle, mechanistic formulations for particle and DOM turnover and transformation are required. These can only come from a new initiative aimed at understanding the biogeochemical and ecological processes occurring in the ocean interior.

In three years, JGOFS will end, and a new program initiative must seize the moment in ocean biogeochemistry. The research priorities of the new initiative should concentrate more effort on the dynamics of the biological pump and carbon storage, the

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structure and function of the food web and modelling in the twilight zone in particular and the ocean interior in general. These priorities are now being addressed by new national initiatives in ocean biogeochemistry and are being developed in an integrated fashion with biogeochemical experts from IGBP working in close collaboration with physical sciences colleagues in the World Climate Research Programme (WCRP) and socio-economic scientists in the International Human Dimensions Programme (IHDP).

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- in a model of the North Atlantic Ocean. Nature 394, 266–269.
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Table 3. Definition of Acronyms.

| ADEOS | Advanced Earth Observing Satellite |
|---------|--|
| AVHRR | Advanced Very High Resolution Radiometer |
| BAIS | Bermuda Atlantic Time-Series |
| | Chiorofiuorocarbons |
| CINES | Centre National d'Etudes Spatiales |
| | Deta Management Taak Taam (ICOES) |
| | Earth Decourage Satellite |
| CAIM | Clobal Analysis Interpretation and Modelling (an ICRP framework activity) |
| | High Nutrient-Low Chlorophyll |
| HOT | |
| IGRP | International Geosphere-Biosphere Programme |
| IPCC | Internovernmental Panel on Climate Change |
| | Iron Experiment |
| KNOT | Kvodo North Pacific Ocean Time Series |
| LOA | Laboratoire d'Optique Atmosphérique |
| LOICZ | Land-Ocean Interactions in the Coastal Zone (an IGBP core Project) |
| LPCM | Laboratoire de Physique et Chimie Marine |
| LSCE | Laboratoire des Science du Climat et de l'Environnement |
| NABE | North Atlantic Bloom Experiment |
| NASA | National Aeronautics and Space Administration (US) |
| NASDA | National Space Development Agency (Japan) |
| NOAA | National Oceanic and Atmospheric Administration (US) |
| OCCM | Ocean Carbon Cycle Model |
| OCMIP | Ocean Carbon Modeling Intercomparison Project (a joint JGOFS/GAIM project) |
| OCTS | Ocean Color and Temperature Scanner |
| OGCM | Ocean General Circulation Model |
| PAGES | Past Global Changes (an IGBP core project) |
| POLDER | Polarization and Directionality of the Earth's Reflectance |
| SCOR | Scientific Committee on Oceanic Research |
| SeaWiFS | Sea-viewing Wide Field-of-view Sensor |
| SSM/I | Special Scanning Microwave Imaging |
| SOIREE | Southern Ocean Iron RElease Experiment |
| TOPEX | I opography Experiment |
| WOCE | world Ocean Circulation Experiment |
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