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Refining Our Understanding of Oceanic Biogeochemistry and Ecosystem Functioning

On societally relevant time scales (e.g., decades to centuries), oceanic biological processes sequester large quantities of atmospheric carbon, thereby modulating CO_2 concentrations in the lower atmosphere [*IPCC*, 2001]. The complex physical and biogeochemical interactions that regulate carbon fluxes between the atmosphere and the surface ocean—apparently random physical events, fluctuations in community structure and function, natural climate cycles, and long-term changes in anthropogenic forcing—are best studied within the framework of ocean time-series observations. Such thinking led in 1988 to the initiation of the U.S. JGOFS (Joint Global Ocean Flux Study) time-series programs in the subtropical North Atlantic (BATS = Bermuda Atlantic Time-series Study) and North Pacific (HOT = Hawaii Ocean Time-series), and motivates continuing observations into the foreseeable future. After 14 years of intensive physical, biological, and biogeochemical sampling in these regions, the paradigms that initially guided our understanding and research of ocean ecosystems have been found wanting, and new perspectives have emerged to provide a stimulating foundation for continued investigations.

The Surface Ocean Carbon Cycle and Pre-JGOFS Paradigms

In 1988, our understanding of the controls on the ocean carbon cycle was based on several long-standing paradigms (see *Karl et al.*, 2001b for more detailed discussion). First, surface ocean plankton were believed to assimilate dissolved nutrients in fixed stoichiometric ratios that matched the availabilities of carbon (C), nitrogen (N), and phosphorus (P) in deep water. Second, from the belief that the oceans were predominantly N-limited, primary production was partitioned into two categories, based on assimilation of "new" versus "regenerated" N substrates, and termed new and regenerated production. Third, new production was believed to scale to levels of primary production in a given region and equal the particulate C (POC) export from the surface ocean. Lastly, it was widely believed that plankton communities in the subtropical oceans existed in a "climax state" in which biomass and compositional structure displayed no seasonal or long-term trends. Each of these paradigms has been altered significantly by time-series observations over the past decade. This article presents an overview of the new perspectives that have emerged from JGOFS, as well as related plans for future time-series activities.

Primary Production, Particle Export, and the Biological Carbon Pump

Prior to JGOFS, the gravitational POC flux from the euphotic zone was thought to dominate biological carbon sequestration (i.e., the Biological C Pump). In contrast to expectations, however, no useful relationships have been found between primary production and POC flux at either the BATS or HOT sites [e.g., *Karl et al.*, 2001b]. Instead, export pathways that were poorly quantified a decade ago—"active carbon transport" by diel migrant zooplankton and food web influences on the partitioning of primary production between POC and dissolved organic carbon (DOC)—have emerged as significant terms in the Biological C Pump. While exhibiting similar levels of annual primary production [*Karl et al.*, 2001b], total carbon export at BATS is ~45% higher than at HOT (Table 1), due entirely to the greater seasonal convective mixing export of DOC [e.g., *Carlson et al.*, 1994]. Annual gravitational POC and active zooplankton flux estimates at BATS and HOT are quite comparable. Thus, while POC export remains the largest single component of annual C export, we now recognize that between 24% and 43% of the annual carbon export is accounted for in alternate pathways. Even though these alternate pathways of carbon export are now quantified, the physical and biological processes that modulate the balance between them remain elusive. The question originally posed by the time-series sites—what controls carbon export flux—is therefore still an open and active area of research.

Decadal Variability in Nutrient Limitation: Role of N_2-Fixers

Historically, biologists and geochemists have been at odds about whether N or P limits marine primary production [e.g., *Codispoti*, 1989]. Leaving aside the recognized importance of iron, *Michaels et al.* [2001] hypothesized that feedback-dependent oscillations between N- and P-limited states could be mediated by N_2 fixation. The dominant oceanic N_2-fixing species were believed to be *Trichodesmium spp.* and the symbiont *Richelia*. New molecular biological techniques employed at HOT and in the tropical Atlantic, however, have found a broad phylogenetic diversity of single-celled prokaryotes that possess and express the genes for N_2-fixation [*Zehr et al.*, 2001], enhancing the important role of N_2-fixers in the global N cycle. For example, over the past decade at HOT there has been a systematic decrease in the value of $\delta^{15}N$ of the gravitational POC flux at the base of the euphotic zone from a mean value close to isotopically "heavy" nitrate ($\delta^{15}N = 6.5‰$) to a mean value close to isotopically "light" N_2 ($\delta^{15}N = 0‰$) [*Dore et al.*, 2002]. These data suggest that over decadal time scales, fluctuations in N_2-fixing primary producers and the preferential drawdown of P (relative to nitrate) may drive oscillations between N- and P-limitation. The cycling of systems between these alternate states appears to impact the biological structure and function of communities in the present ocean and will affect our ability to predict the ocean's response to global environmental change.

Decadal-scale Climate Forcing and Phytoplankton Community Structure

As one of the oldest and largest biome on Earth, and without dramatic seasonal variations in physical forcing, the North Pacific Subtropical Gyre had long been thought to contain a stable climax community. Based upon observations at HOT, however, it appears that changes in the phase of low-frequency climate patterns—for example, the Pacific Decadal Oscillation—have led to a "regime shift" in phytoplankton community structure and biomass, from larger eukaryotes to smaller prokaryotes [*Karl et al.*, 2001]. Research at BATS and in the sub-arctic Pacific also suggests that low-frequency climate patterns are important determinants of interannual variability. At BATS, an inverse correlation has been found between the NAO index and the relative abundance of haptophytes (e.g., coccolithophores), while at the sub-arctic Pacific time-series station PAPA, deep particulate inorganic C flux (dominated by haptophytes) and the Southern Oscillation Index (SOI) are positively correlated [*Wong and Crawford*, 2002]. A complete explanation of these different responses in different ocean basins remains obscure, but it is now clear that even the relatively "stable" ocean gyres are responsive to shifts in low-frequency climate forcing.

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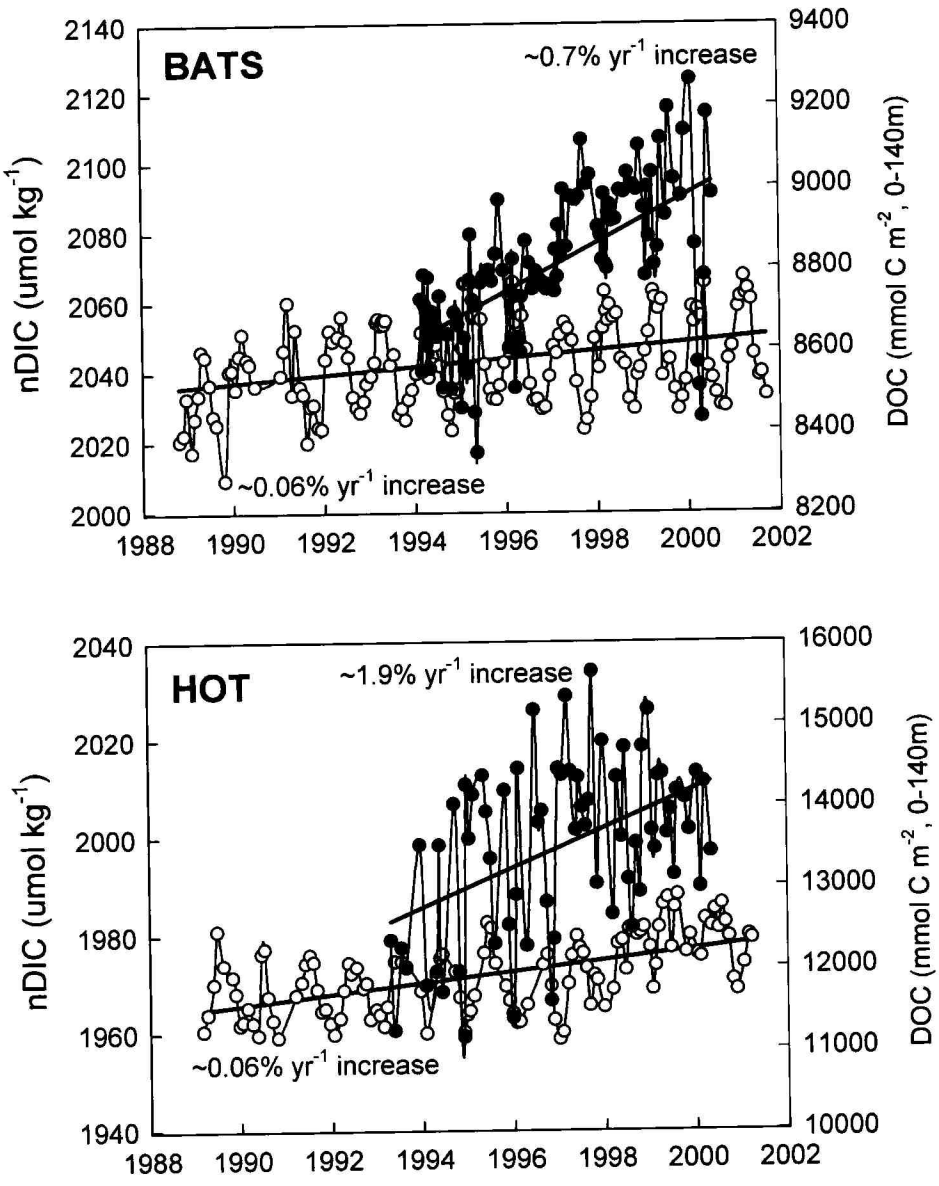


Fig. 1. Multi-year increases in dissolved inorganic carbon (DIC; open symbols) and DOC (closed symbols) pools at BATS and HOT. Surface DIC data only are presented and are normalized to the mean surface salinity at each site (36.6 and 35.0 for BATS and HOT, respectively). DOC data are presented as the integral from 0–140m. Data are not seasonally de-trended; however, the multi-year increase for both DIC and DOC is clearly shown by the solid best-fit regression lines. All increases are significant at the $P < 0.05$ level and the percent increase given for each parameter at each site is based upon values at the beginning of each data record.

Carbon Storage in the Ocean: Accumulation of CO_2 and DOC in the Euphotic Zone

Ocean time-series records of CO_2 variability are relatively short (~14 y) compared to atmospheric pCO_2 (~47 y) or ice core records (~400,000 y), but already they reveal much about the flux of carbon between the ocean and atmosphere. Measurements show significant increases in surface concentrations of total dissolved inorganic carbon (DIC) at both BATS and HOT [Figure 1; *Karl et al.*, 2001b]. Both sites reveal complex interactions among physical forcing (e.g., wind strength, seasonal temperature changes), biological modification of oceanic CO_2 levels, and air-sea exchange of CO_2. Despite very different physical and biogeochemical regimes and annual oscillations in absolute concentrations, the rate of DIC concentration increase at both sites is similar (i.e., ~1.2 μmoles kg^{-1} y^{-1}). Primary production is approximately the same at both locations, suggesting that while biological activity is key to driving the long-term accumulation of DIC, the physical regime, especially sea-surface temperature and air-sea gas exchange, may be more important in controlling the annual oscillations in concentration. However, the importance of DOC, as a potential near-surface carbon storage term, has been a largely unforeseen product of ongoing studies at the time-series programs. Both show significant increases in DOC inventories within the euphotic zone, although the rate of increase at BATS is about one-third that observed at HOT. The most intuitive explanation for this difference is the higher seasonal export of DOC at BATS [*Carlson et al.*, 1994], but site-specific differences in DOC production and consumption pathways may also contribute. The biogeochemical dynamics of DOC cycling gain increasing importance as new prokaryotic groups are identified [*Karner et al.*, 2001; *Beja et al.*, 2002; *Rappé et al.*, 2002], shifts in phytoplankton community composition are observed (and hypothesized to occur with global warming), and changes in physical forcing modify interactions between DOM cycling and microbial biota at these ocean time-series sites.

What Does the Future Hold?

As with most scientific endeavors, more new questions have arisen as we have made progress on the old during the course of the JGOFS time-series programs. These questions run the gamut of biological, physical, and geochemical interest, but are clearly interconnected. Additional information on future time-series research topics and questions can be found at http://www.bbsr.edu/cintoo/bats/bats_questions/bats_questions.html.

Some of the questions are fairly straightforward, yet the answers obtained could profoundly affect our understanding of the marine C cycle. For example, one of the most provocative findings is the revisited importance of biological diversity, particularly among the prokaryotes. The association of diversity with a varied array of metabolic pathways should provide fresh insights into the turnover of the DOC pool and the processes that uncouple energy (i.e., light) and carbon pathways in the ocean. Based on our existing knowledge, how do we proceed to answer these new questions?

First, continuing time-series studies, at both the existing sites and additional sites in key regions, is imperative for distinguishing natural variability in biogeochemical cycles from anthropogenically-induced changes. Such long-term studies also require the careful and gradual integration of new methodologies. For instance, the "standard" set of measurements, designed to fit the ocean paradigms at the inception of the BATS and HOT programs, has expanded and become more rigorous with development of new technologies, opportunities, and paradigms. This evolution is especially important as modeling and synthesis efforts refocus observational and experimental studies in new directions.

Second, revised conceptual biogeochemical models and new mechanistic theories need to incorporate our ever-changing views of the ocean ecosystem. With the growing appreciation of the non-linearity of ocean processes, the need for large-scale hypothesis testing in the ocean has become increasingly important. Sufficient data now exist to generate explicit hypotheses that can be tested by process-oriented studies in cooperation with the time-series programs.

Table 1. Summary of the carbon export terms that are part of the biological C pump at the BATS and HOT study sites.

Year	*POC flux @ 150m (mol C m^{-2} y^{-1})*		*Zooplankton flux @ 150m (mol C m^{-2} y^{-1})*		*DOC export @ 150m (mol C m^{-2} y^{-1})*	
	BATS	HOT	BATS	HOT	BATS	HOT
1994	0.78	0.73	0.07	0.13	----	
1995	0.75	0.69	0.08	0.16	1.2	
1996	1.03	0.79	0.05	0.18	0.4	0.13 ±
1997	0.88	0.94	0.10	0.08	0.5	0.04
1998	0.94	0.91	0.12	0.15	0.4	
1999	1.00	0.94	0.12	0.20	0.4	
2000	0.71	0.84	0.09	0.17	0.7	
2001	----	----	0.14	0.16	----	----
Annual Mean	0.87	0.84	0.10	0.15	0.60	0.13
Std. Dev.	0.12	0.10	0.03	0.04	0.32	0.04
% Total Annual Export	55	75	6	13	38	12
Std. Dev.	12	3	3	3	13	1

Carbon export (mol C m^{-2} y^{-1}) from the productive surface layers is set at a 150-m reference depth, and no statements are made regarding the durations of these storage terms. POC flux is determined from the carbon content of material collected in particle interceptor traps deployed for 3-4 days each month at 150m. Zooplankton flux is the active removal of carbon (sum of respiratory CO_2 loss and DOC exudation) by vertically migrating zooplankton via normal metabolic activity (see Steinberg et al., 2000 *and* Al-Mutairi & Landry, 2001 *for details on calculations for BATS and HOT, respectively. Note: Calculations of* Al-Mutairi and Landry 2001 *also applied to BATS data give very similar results, on average within 10%, to those reported below using methods of* Steinberg et al. 2000*). For both POC and zooplankton flux estimates, time-integration was done by trapezoidal integration to minimize biases due to uneven sampling. Seasonal DOC export is based upon the seasonal increase in DOC inventories between 150 and 250m during the period of deep convective mixing. For HOT DOC inventories between 150 and 250m did not show a clear seasonal increase, but rather a monotonic increase over time due to a lack of strong seasonal convective mixing. Therefore, the annual increase in DOC inventory in that depth horizon was determined from the slope (mean ± std. dev.) of the best-fit linear regression of DOC versus time. These carbon flux estimates are gross downward fluxes and do not account for upward carbon fluxes associated, for example, with vertically migrating zooplankton or the seasonal mixing-up of CO_2 rich deep waters.*

Third, ecosystem-scale perturbation experiments, including controlled volume experiments, need to be conducted to achieve a mechanistic understanding of the biological and biogeochemical processes operating in the subtropical ocean gyres and elsewhere in the global ocean. Such controlled-volume experiments would benefit from the development of sensors for key biogeochemical variables, contemporaneous study using a variety of platforms (e.g., moorings, profiling floats, gliders, cabled bottom observatories) to connect scales, and broadening the base of sites to reflect inter-regional variability. A particular result from a meeting held in April 2002 to review the findings of the JGOFS time-series programs is support for a cabled observatory at Station ALOHA (A Long-term Oligotrophic Habitat Assessment; supported by NSF) enhanced by additional project-oriented proposals.

Fourth, characterizing the temporal and spatial scales of biological diversity is both desirable in its own right, as well as to generate a better understanding of the relationships between specific taxa and their functions. As molecular-based field applications such as genomics, proteomics, and bioinformatics become more commonplace in oceanography, sample archives from the time-series studies will be an invaluable resource for documenting long-term changes.

Lastly, additional synthesis of present data sets, as well as comparison with paleoceanographic data sets, will allow us to achieve a better understanding of key variables for constraining predictions of future climate changes and biogeochemical responses of the ocean.

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The April 2002 meeting, Shifting Paradigms: A U.S. JGOFS Ocean Time-Series Summit, supported by the U.S. JGOFS Planning Office, was held in Vancouver, British Columbia, and focused on our current and emerging knowledge of ocean biogeochemistry, scales of spatial and temporal variability, and gaps in our understanding of ocean physics, biology, and biogeochemistry that need to be addressed in future scientific research.

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