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⓭ Temporal studies of biogeochemical dynamics in oligotrophic oceans

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Introduction

The Joint Global Ocean Flux Study (JGOFS) includes three major field components: time-series studies, process studies and a global survey. In the United States, the time-series component is represented by two open-ocean stations, one near Bermuda (Bermuda Atlantic Time-series Study; BATS) and one near Hawaii (Hawaii Ocean Time-series; HOT). The goal of the research at both sites is to achieve an improved understanding of the time-varying fluxes of carbon and other biogenic elements within the ocean and the exchanges with the atmosphere, usually divided into three specific science questions and one technology-related objective:

- to understand the seasonal and interannual variations in ocean physics, chemistry and biology;
- to understand the relationships between the external physical forcings and the biological rate processes;
- to understand the processes that determine sea-surface p_{CO_2}, including thermodynamics, particle export and gas exchange; and
- to provide a test bed for the introduction and validation of new oceanographic instruments and technologies.

These goals are supplemented by more specific research objectives that are related to regional biogeochemical dynamics at each site and, to some extent, the interests and backgrounds of the scientists who are involved. These more specific goals include the need to understand the cycling of nitrogen as a control on the carbon cycle, the role of dissolved organic materials in both the elemental cycles and the net exports from the surface waters, and the role of community structure in affecting the cycling of elements. More recently, nitrogen fixation has been under increased study at both sites as this process appears to be crucial

to understanding the seasonal and inter-annual patterns in the cycling of carbon, nitrogen and phosphorus in the sea.

Organisation of the HOT and BATS programmes

The HOT and BATS programmes were initiated in October 1988 (Michaels & Knap, 1996; Karl & Lukas, 1996). The stations are funded primarily through research grants from the US National Science Foundation. Although time-series research is closely related to monitoring and the JGOFS stations have some monitoring role, the explicit goal of the US JGOFS time-series research is to obtain an understanding of basic ocean processes. The monitoring function is related to the documentation of change over the time scale of the programmes, partly in the hope that putative climate changes or the incremental changes in biogeochemistry associated with ocean feedbacks will become apparent.

Many of the initial results of the research from these two programs have already been published. In this chapter, we summarise only a few of the observations and trends from both stations in the context of a comparison between the two sites. Although both stations are nominally located in low-biomass, low-nutrient oceanic gyres, they differ in latitude and seasonality and consequently in the rates and mechanisms of biogeochemical cycling. For the details of each specific study, we cite the appropriate literature and concentrate on the comparison between sites.

The HOT programme includes two separate components, the JGOFS programme with a focus on biogeochemistry and a World Ocean Circulation Experiment (WOCE) component that concentrates on the physical oceanography of the region. At BATS, all of the measurements were initially included in the JGOFS programme. Both sites also received 'seed' funding from the US National Ocean and Atmosphere Administration (NOAA) to initiate measurements of dissolved inorganic carbon (DIC) species at a very high level of precision and accuracy. The US National Aeronautics and Space Administration (NASA) has funded bio-optics and satellite oceanography programmes at Bermuda. Both programmes have also benefited from institutional support. For example, the Hawaii programme received significant matching funds from the state of Hawaii, and the Bermuda Biological Station for Research funded the purchase of a dedicated research vessel and other improvements to the physical infrastructure that were required to allow the BATS programme to be successful.

The combination of funding and focused research goals is a necessary but not sufficient condition for the operation of a time-series station. These stations also

Table 13.1. *Common measurements made at the BATS and HOT sites (each site also makes many additional measurements that are not performed at the other)*

Parameter	Depth range (m)	Technique/instrument
Continuous electronic measurements		
Temperature	0–4200	Thermistor on SeaBird SBE-911 plus CTD
Salinity	0–4200	Conductivity sensor on SeaBird SBE-9/11 plus CTD
Depth	0–4200	Digiquartz pressure sensor on SeaBird SBE-9/11 plus CTD
Dissolved oxygen	0–4200	SeaBird polarographic oxygen electrode
Fluorescence	0–500	SeaTech fluorimeter
Meteorological data	sfc	Mooring, ship and land stations
Surface p_{CO_2}, T, S, fluorometry	sfc	Underway system on some research vessels
Discrete measurements from Niskin bottles or nets		
Salinity	0–4200	Conductivity on guideline Autosal 8400A
Oxygen	0–4200	Winkler Titration, automated endpoint detection
Total CO_2	0–250	Automated colorimetric analysis
Alkalinity	0–250	High precision titration
p_{CO_2}	sfc, 0–250	Underway p_{CO_2} analysis, extraction
Nitrate	0–4200	CFA colorimetric
Nitrite	0–4200	CFA colorimetric
Phosphate	0–4200	CFA colorimetric
Silicate	0–4200	CFA colorimetric
Dissolved organic carbon	0–4200	High-temperature, catalytic oxidation
Dissolved organic nitrogen	0–4200	UV oxidation
Dissolved organic phosphorus	0–4200	UV and chemical oxidation
Particulate carbon	0–4200	High-temperature combustion, CHN analyser
Particulate nitrogen	0–4200	High-temperature combustion, CHN analyser
Particulate phosphorus	0–300	Chemical oxidation
Fluorimetric chlorophyll *a*	0–250	Acetone extraction, Turner fluorimeter
Phytoplankton pigments	0–250	HPLC, resolves 19 pigments
Bacteria	0–3000	Fluoroescence microscopy or flow cytometry
Zooplankton biomass	0–200	Day and night tows with 200 μm mesh net
Rate measurements		
Primary production	0–140	Trace-metal clean, *in situ* incubation, ^{14}C uptake
Bacterial activity	0–140	Thymidine and/or leucine incorporation
Particle fluxes	150,200,300	Free-drifting cylindrical traps (MultiPITs)
Mass		Gravimetric analysis
Particulate carbon flux		Manual swimmer removal, acidification, CHN
Particulate nitrogen flux		Manual swimmer removal, CHN analysis
Particulate phosphorus flux		Manual swimmer removal, chemical oxidation

require a staff of dedicated and well-trained scientists and other support personnel. Both stations have been extremely fortunate in attracting exceptional technical staffs who have been able to maintain a high level of data quality in the face of occasionally trying circumstances and the inevitable doldrums that come from repeated sampling of the same system. As these stations have matured, it has become apparent to the principal investigators that the human infrastructure is one of the most challenging components of running and sustaining a time-series station of this complexity. We are most grateful for the dedication of our technical staffs and both we and the entire scientific community who will also use these data owe them a debt of gratitude for their collective efforts.

The sampling at these stations is nominally monthly. The more striking seasonality at the Bermuda station dictated that the sampling frequency at this site be increased to bi-weekly in the spring. The Bermuda station is located approximately 80 km southeast of Bermuda near the site of a long-term (since 1976) sediment trap mooring started by Werner Deuser (WHOI) and now operated by Maureen Conte (WHOI). The BATS site is approximately twice as far offshore as the Hydrostation S station, the site of one of the longest continuous ocean time-series studies. The bi-weekly sampling at Hydrostation S began in 1954 and continues to this day. The Hawaii station is approximately 100 km north of Oahu. The Hawaii sampling also includes regular sampling at a near-shore station at the beginning of each cruise. Both stations measure a sub-set of the core JGOFS parameters (Table 13.1) and have spent considerable effort to ensure that the data quality is high and comparable, both to each other and to the standards of the broader oceanographic community. Details of the analytical and quality control procedures are available in the published papers (Michaels *et al.*, 1994*b*, 1996; Karl & Lukas, 1996).

Seasonal and inter-annual ecosystem patterns

The basic seasonal and inter-annual patterns at each of the sites have been well described elsewhere (Karl & Michaels, 1996). For the purposes of this chapter, we concentrate on a direct comparison of the general patterns in the basic biogeochemistry between the two oceanic time-series stations. The BATS site is approximately 8 degrees of latitude further north (*c.* 500 miles) than the HOT site and this difference is quite apparent in the strength of the seasonality in the thermal structure. The Bermuda site is characterised by a nearly 10 °C seasonal variation in surface temperature and fluctuations in mixed-layer depth between a few metres in the summer and over 250 m in some winters (Fig. 13.1). The seasonal variation in SST is much smaller at the HOT programme station

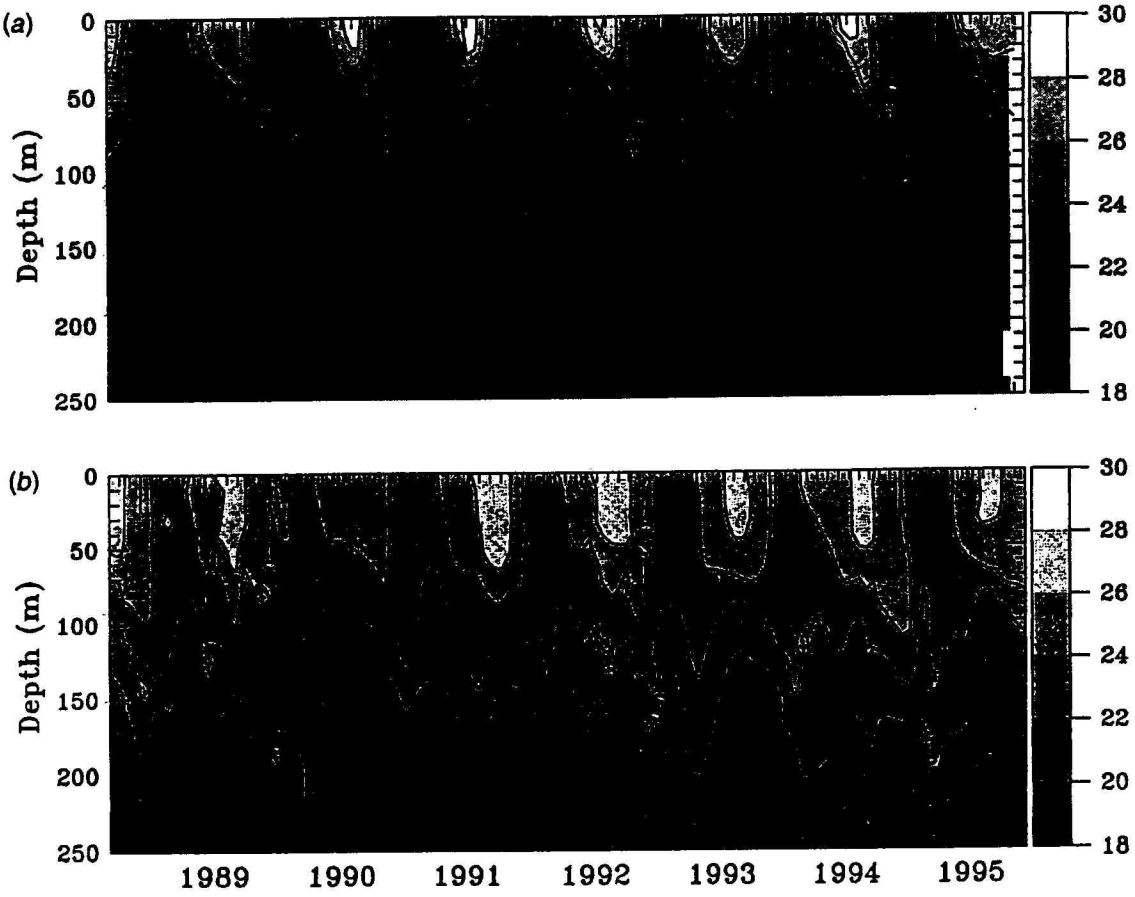


Figure 13.1 *Contour plot of temperature (°C) at BATS (a) and HOT (b), October 1988 – January 1996.*

ALOHA and the mixed layer rarely extends deeper than 100 m (Fig. 13.1). Bermuda is also characterised by a layer of near-isothermal waters between 300 and 600 m, the so-called 18° water that is formed to the north each winter and subducts below the Sargasso Sea. At Hawaii, the stratification is strong and fairly continuous throughout the upper 1000 m.

This sharp difference in the mixing and stratification seasonality is subsequently reflected in both the nutrient dynamics and biological productivity. The deep mixing near Bermuda intrudes into the nitricline and brings nitrate to the surface during most winters (Fig. 13.2). This nitrate injection lasts from a few days to a few months and it is rapidly consumed as the upper ocean is re-stratified in early spring. The integrated stock of nitrate that is introduced into the euphotic zone and subsequently consumed is up to 0.1–0.2 mol N m^{-2} in the BATS time series (1988–1995) and is inferred to reach 0.5–0.6 mol N m^{-2} (Michaels *et al.*, 1994*b*) in some of the years with the deepest mixed layers in the Hydrostation S time series (1954–1995).

Before the HOT programme, few data were available to document temporal or spatial variability in the inorganic nutrient concentrations in surface waters of

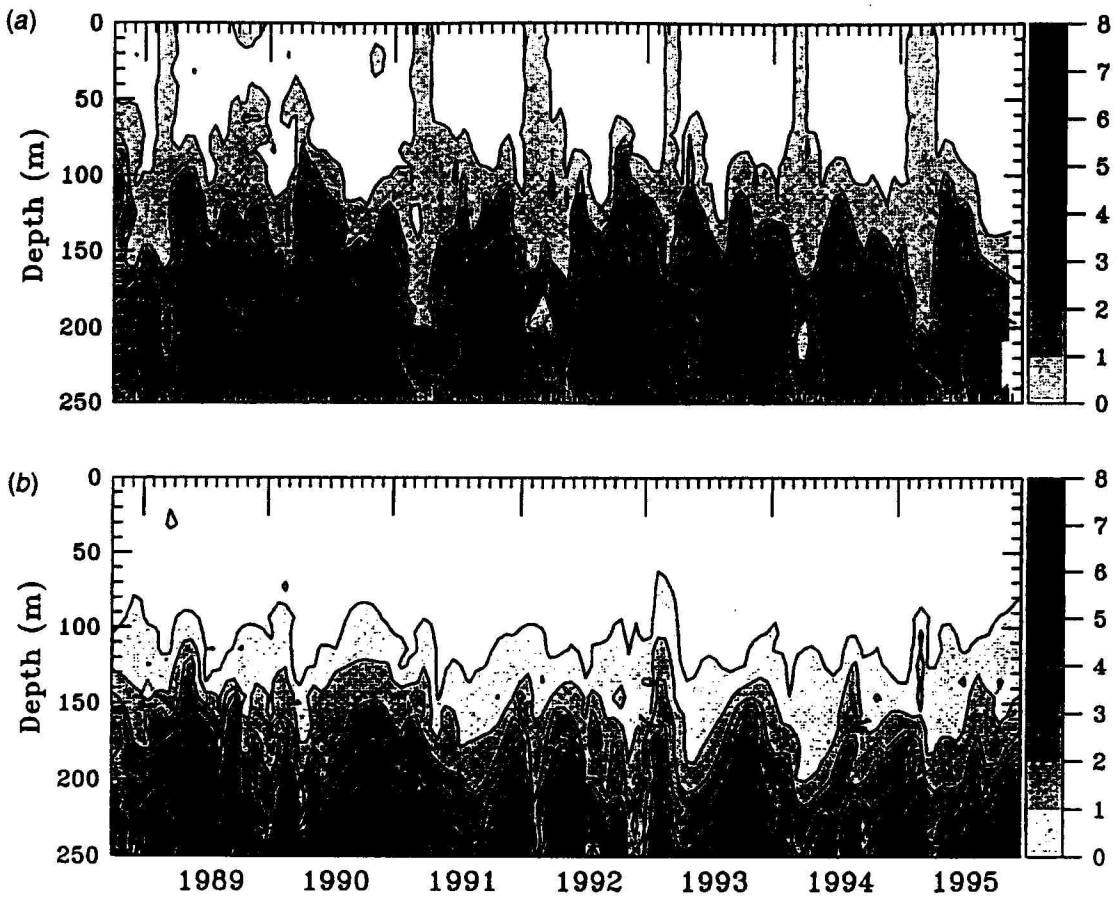


Figure 13.2 *Contour plot of nitrate (μmol kg^{-1}) at BATS (a) and HOT (b), October 1988 – January 1996.*

the North Pacific gyre. The majority of published surface water NO_3^- concentrations were below the detection limit for the standard automated nutrient analyses ($\leq$ 50 nmol kg^{-1}; see, for example, Hayward, 1987). A more detailed analysis based on high-precision, high-sensitivity nutrient measurements at Station ALOHA is now beginning to document a dynamic nutrient field in the oligotrophic North Pacific. The time-series data set can be summarised as follows: (1) NO_3^- is always detectable in surface waters (0–50 m) but the concentration rarely exceeds 10 nmol kg^{-1}; (2) NO_3^- concentrations exhibit a temporally variable increase with depth between 50 and 100 m with typical vertical NO_3^- gradients of 20–40 μmol N m^{-4}; and (3) the top of the nitricline ranges from 75 to 175 m. Furthermore, at least six events have been encountered during the approximately 300 days of at-sea observations (Fig. 13.3). These nutrient intrusions probably supply the majority of the NO_3^- used for new production at Station ALOHA. Even if one excludes these large mixing events from consideration, the month-to-month variability in total 0–100 m depth-integrated NO_3^- exceeds an order of magnitude (e.g. < 0.05–0.96 mmol N m^{-2}, excluding the six events in excess of 1 mmol N m^{-2}). This substantial

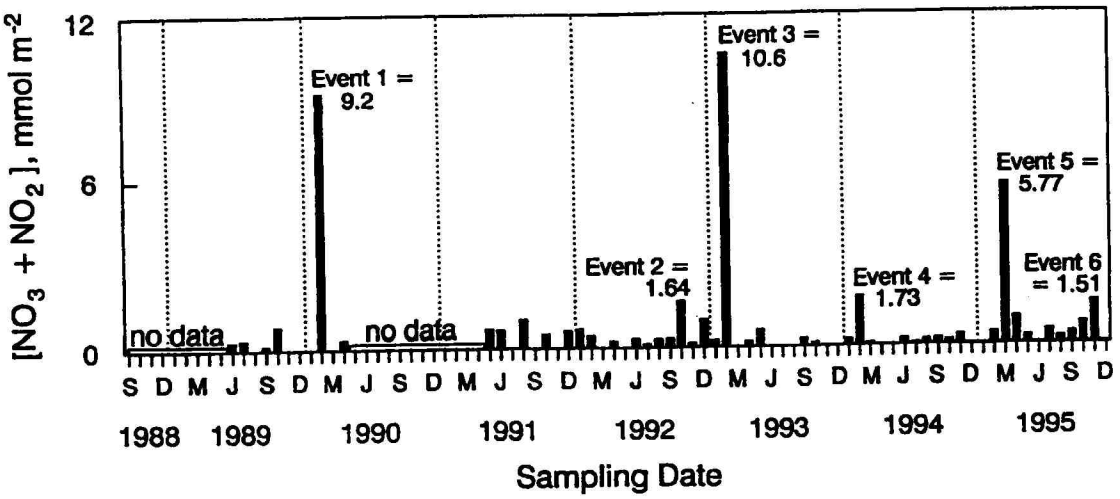


Figure 13.3 *Temporal variability in the depth-integrated inventories of nitrate plus nitrite concentrations (mmol m^{-2}) measured at Station ALOHA. The four 'events' shown are believed to be manifestations of mixing and/or stirring processes. With the exclusion of these perturbation events, the background mean and standard deviation values for the upper water column (0–100 m) inventories are 0.474(± 0.48) mmol m^{-2}, respectively (n = 41).*

variation is still two orders of magnitude smaller than the spring nutrient intrusions at BATS. The role of eddies and other mesoscale features in the temporal variability of NO_3^- at HOT is currently unknown, but is suspected to be substantial.

The deep mixing at Bermuda does not result in surface soluble reactive phosphorus (SRP) concentrations that exceed the detection limits of the analysis (0.05 μmol kg^{-1}) (Fig. 13.4). Nitrate: SRP ratios in the upper 1000 m at Bermuda occur at ratios that are significantly above the nominal Redfield ratio of 16 mol: 1 mol (Michaels *et al.*, 1994*b*), in part because SRP is depleted relative to nitrate to a depth of approximately 150 m. This SRP depletion is in a depth range (100–150 m) usually thought of as a zone of high net re-mineralisation. In addition, the deep mixing in spring probably introduces less SRP than would be required to support Redfield ratio growth. Yet the nitrate still disappears within a few weeks of stratification. This nutrient-ratio anomaly is not understood, but it may reflect either the variability in nutrient stoichiometries and processes that are possible in nature or the yet unmeasured role of dissolved organic nutrients.

Soluble reactive phosphorus (SRP) is also low but temporally variable in the surface waters near Station ALOHA throughout the year (Karl & Tien, 1997). During the first 6-year period of observation, upper water column (0–100 m) SRP concentrations varied from more than 150 nmol kg^{-1} to less than 10 nmol kg^{-1}, and generally conformed to one of two distinct concentration–depth patterns: 'Type I' profiles were characterised by uniform SRP

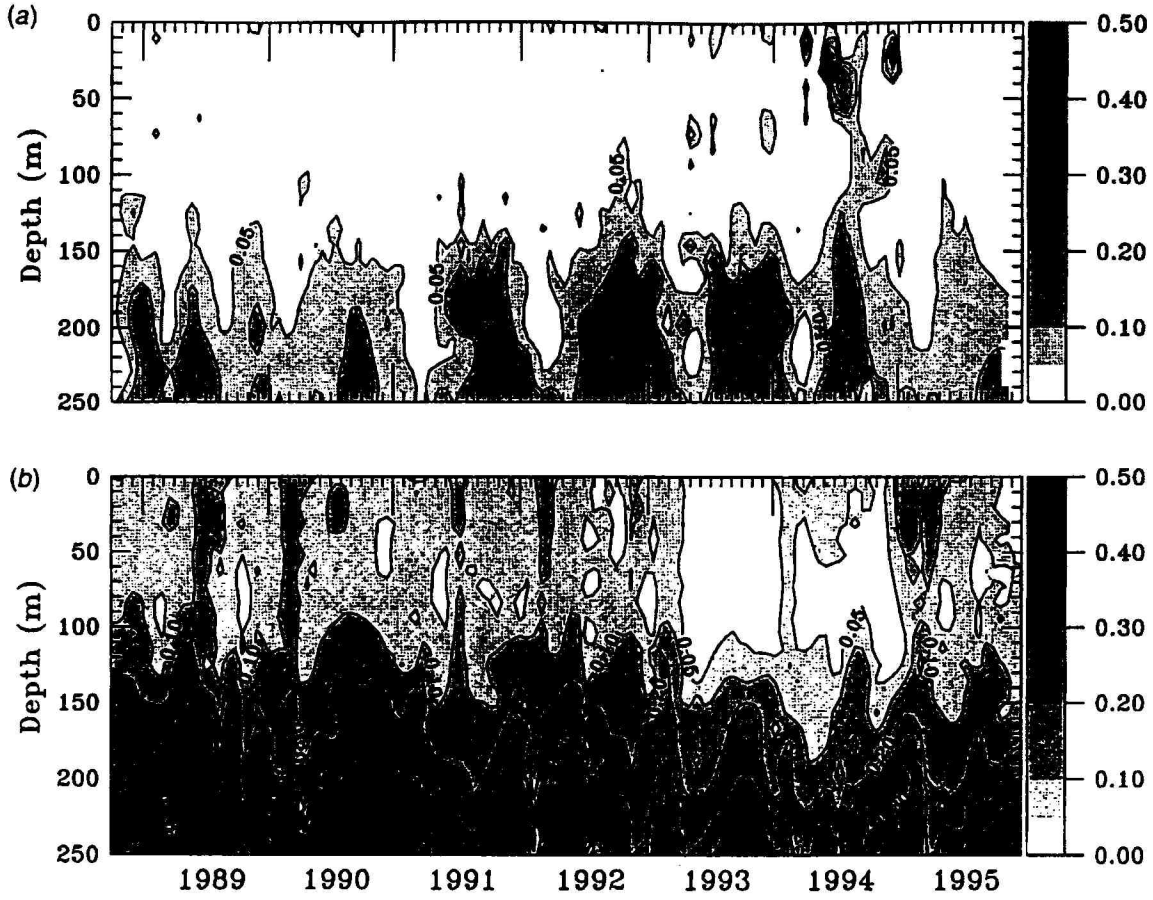


Figure 13.4 *Contour plot of soluble reactive phosphorus (SRP) (μmol kg^{-1}) at BATS (a) and HOT (b), October 1988 – January 1996.*

concentrations with depth (concentration gradients less than 0.05 μmol m^{-4} SRP) and 'Type II' profiles were characterised by distinct near-surface (0–30 m) SRP concentration maxima. The Type I profiles were further divided into low (Type I-L) or high (Type I-H) categories based on whether the average SRP concentration was less than 60 or greater than 60 nmol kg^{-1}, respectively (Fig. 13.5). Three independent, but not mutually exclusive, models are presented to explain these time-varying SRP concentrations: (1) convective mixing; (2) atmospheric deposition; and (3) upward P flux. The upward P flux model, including both passive (upward particle flux) and active (biological transport) processes, is the most consistent model for the available data set (Karl & Tien, 1997).

We have also observed a systematic decrease in the SRP pool inventory (0–100 m) from an initial value of 10 mmol P m^{-2} to 5 mmol P m^{-2} during the 6-year observation period (Fig. 13.6). This loss of bioavailable P from the surface waters is consistent with the hypothesised role of N_2 fixation as a major source of new N for the oligotrophic North Pacific gyre during the period 1988–1994 (see subsequent section).

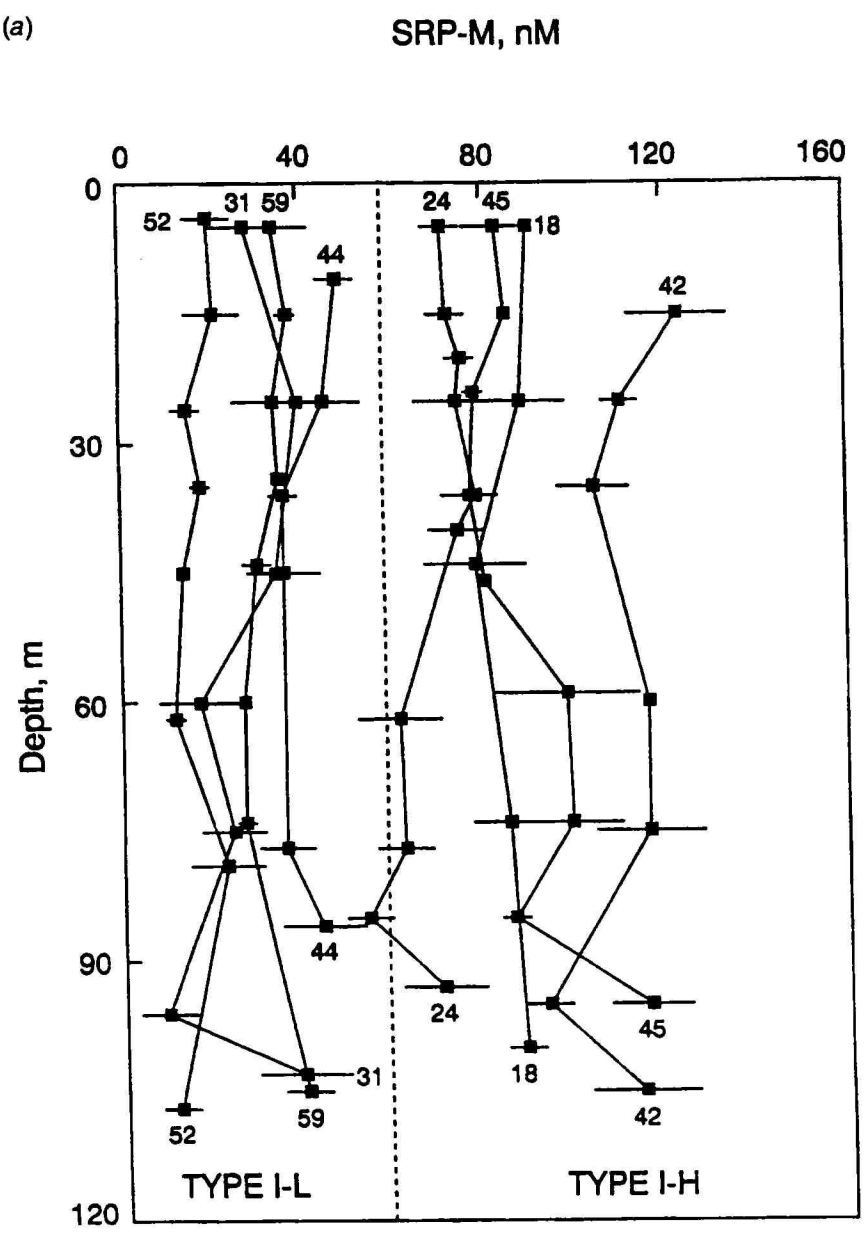
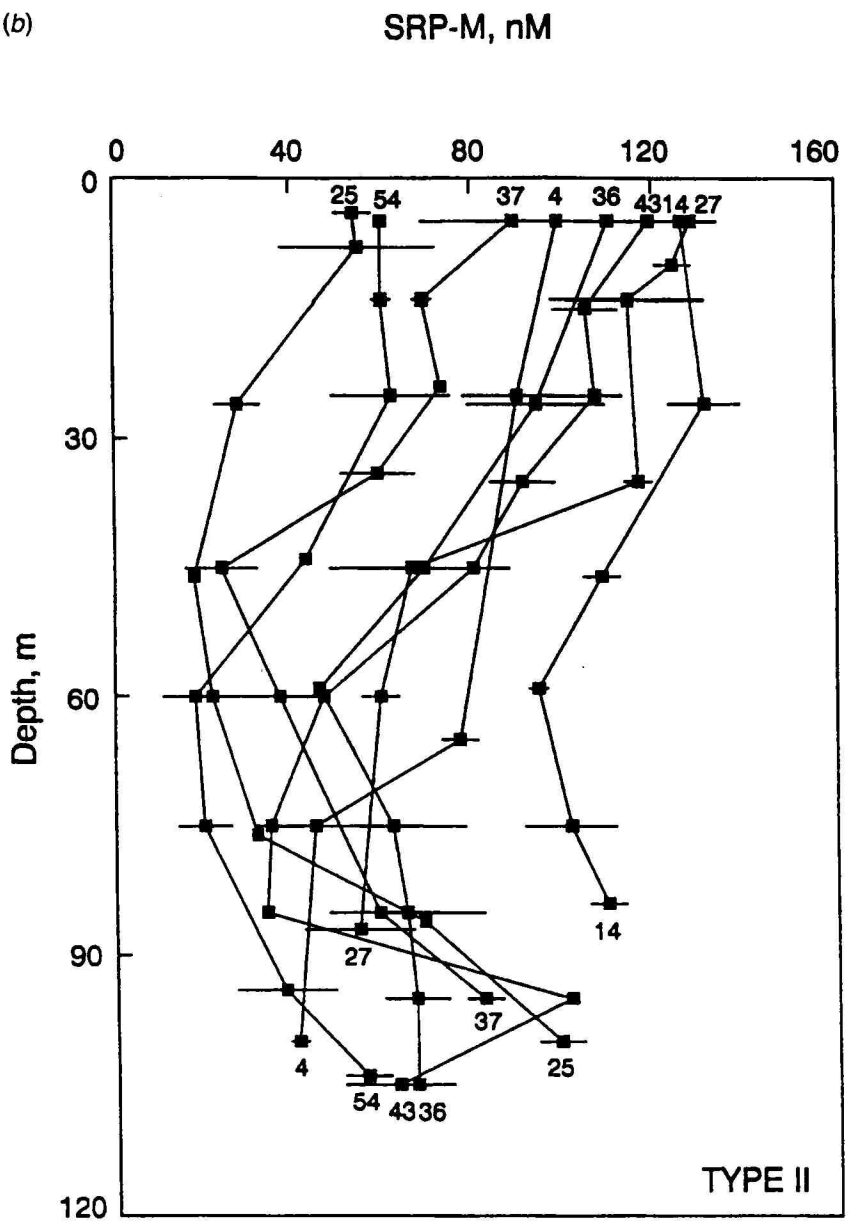


Figure 13.5 *Selected SRP-M (SRP by MAGIC procedure) concentrations with depth at Station ALOHA, showing two different profile patterns: (a) Type-I profiles displaying a relatively constant SRP concentration with depth; and (b) Type-II profiles displaying near-surface enrichments of SRP relative to mid-euphotic zone concentrations. The number above and below each profile indicates the HOT cruise on which each data set was collected. The data shown are mean values, ± 1 standard deviation (n = 3).*

The seasonality of deep mixing at Bermuda induces seasonal fluctuations in phytoplankton biomass and productivity that are tightly phased with the timing of nutrient addition, whereas in Hawaii the seasonality is less pronounced (Figs. 13.7, 13.8). Some of the correlation between nutrient addition and plankton blooms may also be due to the aliasing of the bi-weekly to monthly cruises sampling eddies with different histories and bloom development. However,



there is a reasonable relationship between the depth of the winter mixed layers and the peak values of spring production at BATS, with the exception of a single deep mixed layer in spring 1994 (Fig. 13.9). This anomalous mixed layer was warm and nutrient-free for its depth and was obviously due to the sampling of a large warm eddy.

Carbon dynamics and secular p_{CO_2} increases

Both stations show a seasonality in the total DIC at the surface, with the BATS station having a range of 60 μmol kg^{-1} and a range at HOT of 20 μmol kg^{-1}. This

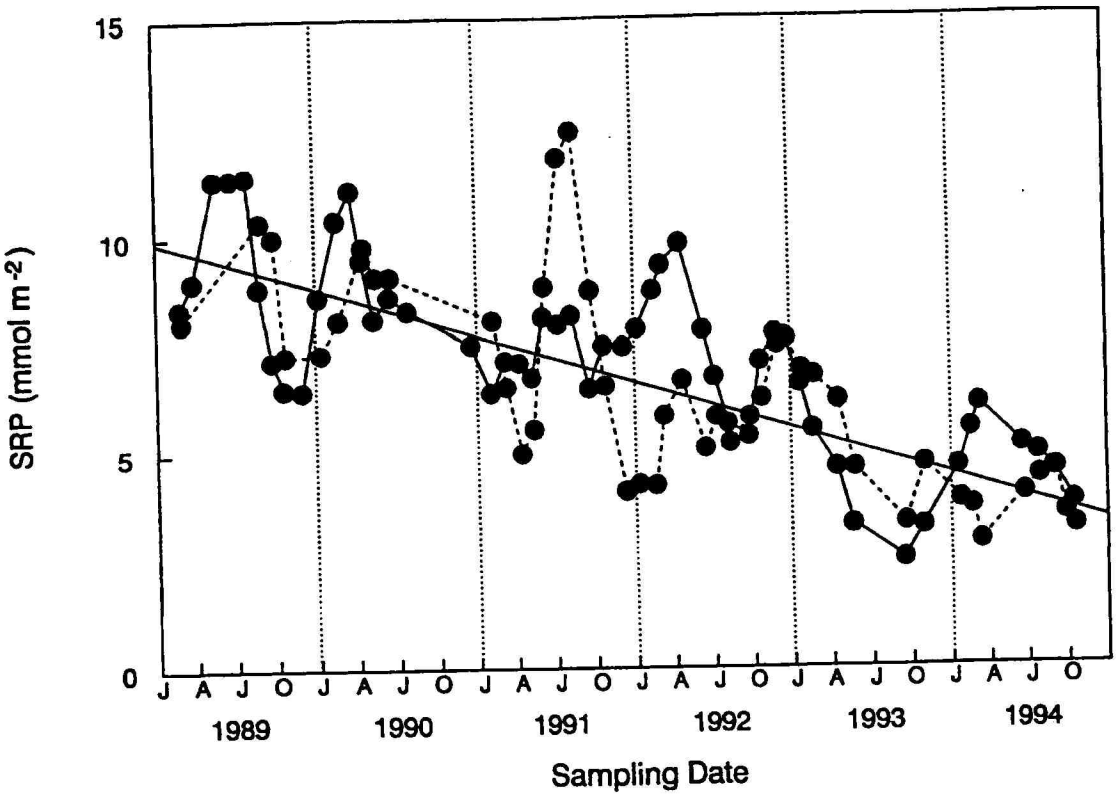


Figure 13.6 *Time series of depth-integrated (0–100 m) SRP inventories at Station ALOHA for the period 1989–94. The data points are the 3-point running mean values for either SRP-AA (SRP measured by autoanalyser, solid line) or SRP-M (SRP measured by MAGIC, dashed line). The model I linear regression fit for the SRP-M data set is: SRP (mmol m^{-2}) = 9.95 − [0.003 × (days since 1 Jan 1989)].*

seasonality is due to a combination of mixing, gas exchange and export. The deep mixing in winter at BATS brings DIC-rich waters to the surface. A small amount of this DIC is removed during the spring bloom as the 0.2–1.0 μmol kg^{-1} of nitrate removal results in 1–7 μmol kg^{-1} of DIC removal, assuming Redfield C: N stoichiometry.

The seasonal fluctuations in DIC and temperature result in a seasonal pattern of p_{CO_2} at the surface (Bates *et al.*, 1996) and thus of gas exchange. Despite the higher DIC in the winter, both stations are sinks for CO_2 at this time because the cooler waters lower p_{CO_2} (Bates *et al.*, 1996; Winn *et al.*, 1994). In the summertime, p_{CO_2} is elevated by the warmer temperatures causing an outgassing. On an annual basis, both sites are weak sinks of the order of 0.5–1.0 mol m^{-2} yr^{-1} (Bates *et al.*, 1996; Winn *et al.*, 1994). At HOT, the seasonal fluctuations in gas exchange are comparable to the net changes in DIC in the upper ocean, whereas at BATS the seasonal gas exchange is not large enough to explain the seasonal fluctuations in DIC in the upper 150 m (Michaels *et al.*, 1994*a*). If fact, BATS has an anomalous summertime

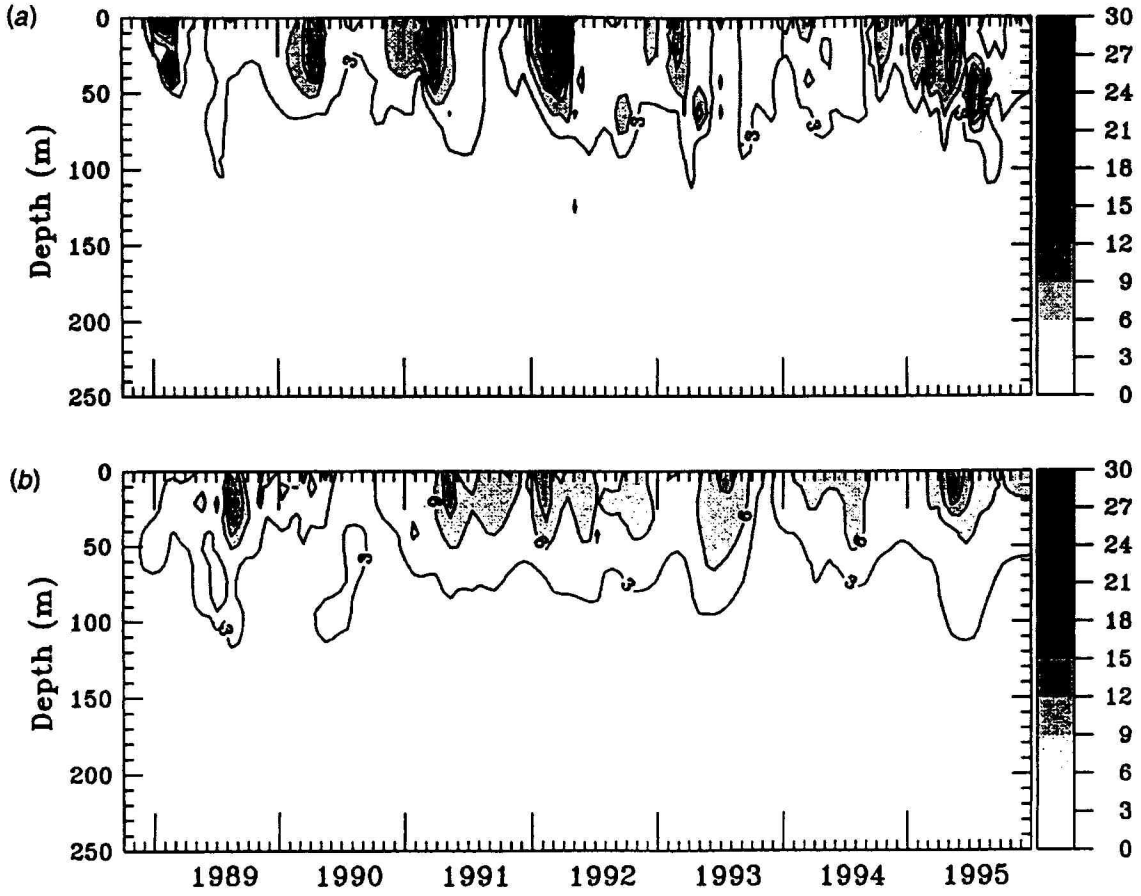


Figure 13.7 *Contour plot of primary productivity (mg C m^{-3} d^{-1}) at BATS (a) and HOT (b), October 1988 – January 1996.*

drawdown of DIC of the order of 3 mol m^{-2} that cannot be explained by the balance of fluxes as currently measured (Michaels *et al.*, 1994*a*).

Inter-annual variability in primary production and particle export

Both HOT and BATS stations show inter-annual fluctuations in production and flux that might be related to the large-scale climate system. At HOT, there is a measurable increase in productivity, a decrease in particle flux and an apparent alternation from nitrogen limitation to phosphate limitation in the transition from the La Niña conditions of 1989–1991 to the El Niño condition of 1991–93 (Karl *et al.*, 1995). At BATS, mixed layers were deeper during the 1991–93 El Niño period and this pattern also seems to occur in the 42 year record at Hydrostation S (Michaels *et al.*, 1996). As these deep winter-mixed layers are correlated with the intensity of the spring blooms (Fig. 13.9), there is a pattern comparable to HOT with an increased production during ENSO; however, at BATS, this is limited to the spring. Both stations share the decrease

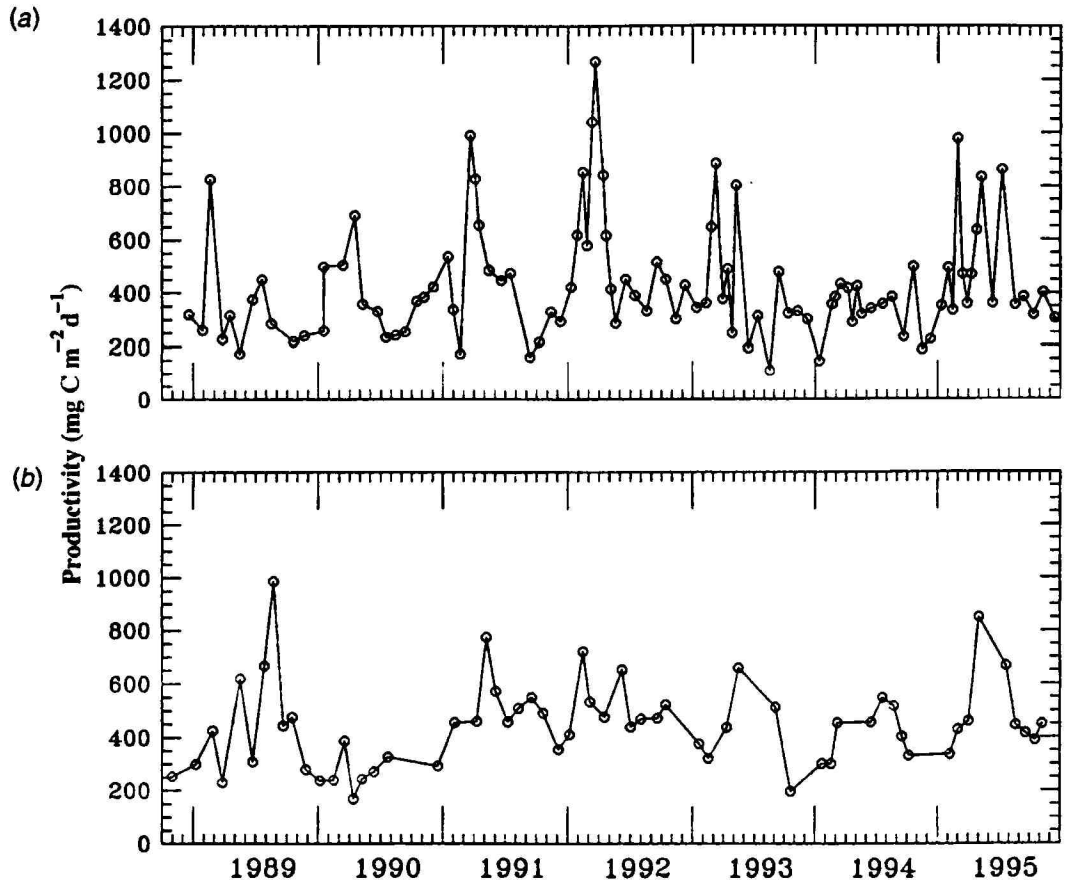


Figure 13.8 *Time series of integrated primary productivity at BATS (0–140 m integral) (a) and HOT (0–200 m integral) (b), October 1988 – January 1996.*

in the annual particle flux during 1991–93. Although there are a variety of speculations about the reasons for these ENSO-correlated patterns in the biogeochemistry, we still do not have full explanations. However, it is precisely in the identification of links between climate and biogeochemistry that we should look for the feedback mechanisms that may allow ocean biogeochemistry to have an effect on climate.

Nitrogen fixation

Nitrogen fixation has emerged at both stations as an important process for understanding the coupled nitrogen and carbon cycles. There are distinct differences in how each station has approached this problem. At HOT, nitrogen fixation is inferred from an examination of the biology and nutrient dynamics of the euphotic zone (Karl *et al.*, 1997). At Bermuda, the evidence comes from an investigation of the nutrient dynamics of the mesopelagic and a study of the anomalous nitrate: phosphate ratios at these depths. In both cases, this process seems quantitatively important and may explain some of the seasonal and

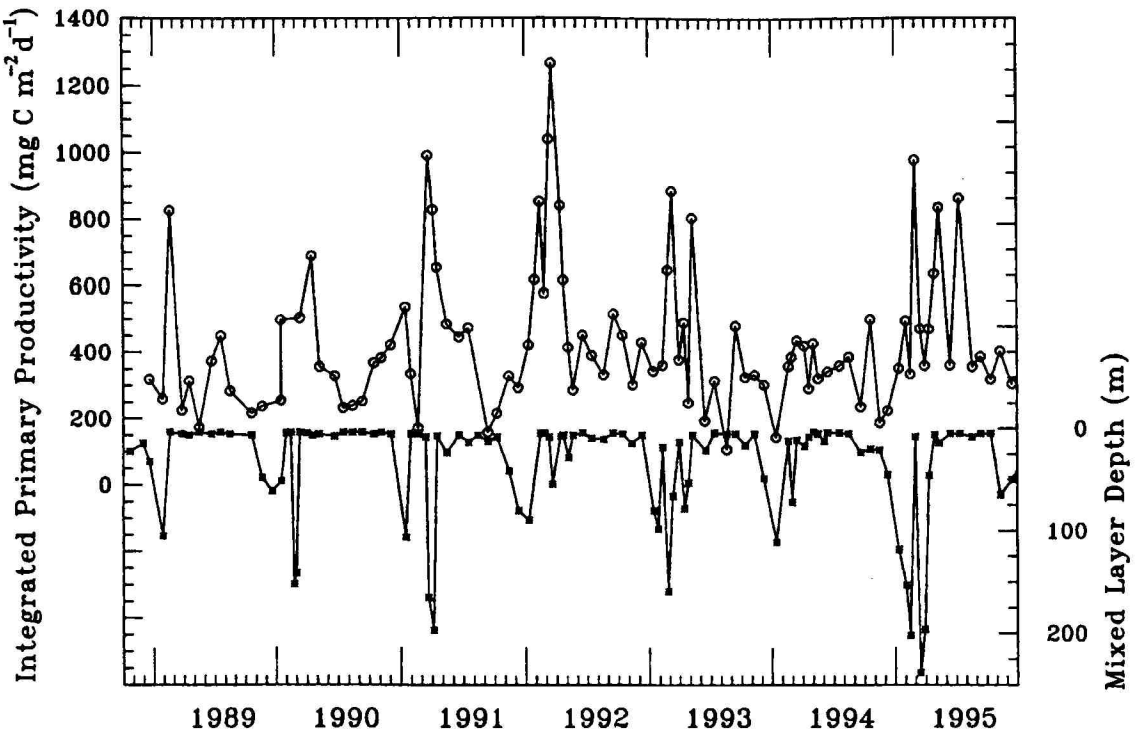


Figure 13.9 *Time series of integrated primary productivity at BATS (upper line) and the mixed layer depth on each cruise (lower line).*

interannual patterns in nutrient dynamics, primary production and particle export. However, nitrogen fixation is rarely included in models of the upper ocean and the data from HOT and BATS indicate that this may be an important oversight that needs to be reconciled.

Nitrogen fixation at HOT

Several independent lines of evidence from Station ALOHA suggest that nitrogen fixation is an important source of new nitrogen for the pelagic ecosystem of the subtropical North Pacific Ocean. The evidence is derived from independent measurements and data syntheses, including: (1) *Trichodesmium* population abundances and estimates of their potential rates of biological nitrogen fixation; (2) measurements of *Trichodesmium* nitrogenase activity (acetylene reduction assay) and extrapolations to nitrogen fixation rates; (3) assessment of the molar N: P stoichiometries of near-surface dissolved and particulate matter pools; (4) application of a one-dimensional N and P mass balance model; (5) observations of a secular decrease of 50% in the soluble reactive phosphorus (SRP) pool in the upper water column (0–100 m) and corresponding increase in the soluble non-reactive P (SNP) pool; and (6) seasonal variations in the natural ^{15}N isotopic abundances of particulate matter exported to the deep sea (Karl *et al.*, 1995, 1997). Considered separately, none of these data sets provides conclusive evidence for the quantitative role of nitrogen

fixation. However, when viewed together and in the full context of the other HOT programme time-series observations, a conclusion regarding the significance of nitrogen fixation in the subtropical North Pacific Ocean is inescapable.

Excess nitrate and nitrogen fixation at BATS

In the Sargasso Sea, the ratio of nitrate to phosphate in the upper 1000 m exceeds the nominal Redfield ratio of 16. The waters above 1000 m are ventilated on time scales of decades or less (Sarmiento, 1983; Jenkins, 1988; Sarmiento *et al.*, 1990) and in the areas where these isopycnal surfaces outcrop, the concentrations of both nitrate and phosphate are often near zero. At steady state, the anomalous nutrient ratios on these isopycnal surfaces in the regions away from the ventilation areas must be sustained by a continual production of nutrients at these higher ratios to sustain the gradients. The rate of production of this excess nitrate has been estimated by using the well-studied resident times of these layers and the observed isopycnal gradients of the nutrient ratios (Michaels *et al.*, 1996).

If the organisms that compose the bulk of the organic biomass in sinking material have N: P elemental concentrations near the Redfield ratio of 16: 1, the re-mineralisation of this biomass will lead to the production of 16 mol of nitrate for every 1 mol of phosphate produced. If organisms such as nitrogen-fixing cyanobacteria create biomass that is richer in nitrogen (more correctly, phosphate-poor) this will yield the re-mineralisation of more than 16 mol of nitrate for every 1 mol of phosphate. Conversely, denitrification would remove nitrate with respect to phosphate and decrease the measured *in situ* ratio. We define a parameter called 'Excess Nitrate' as the concentration of nitrate in excess (or deficit) of that expected from the re-mineralisation of phosphate at Redfield stoichiometries:

$$N^* = \text{Excess nitrate} = [NO_3^-] - 16 \times [PO_4^{3-}],$$

where $[NO_3^-]$ and $[PO_4^{3-}]$ are the concentrations of nitrate and phosphate, respectively. In a mean profile of Excess Nitrate at the BATS site, or in GEOSECS and TTO data for the central Sargasso Sea, N^* is elevated throughout the upper 800 m. If we compare the excess nitrate at BATS or the TTO stations with that from the regions where each density surface outcrops during the winter ventilation, we can determine an excess nitrate gradient (Fig. 13.10). This gradient can be compared to the ventilation time scale of each isopycnal surface to calculate the rate of supply of excess nitrate that would be required to maintain the gradient (using techniques described by Sarmiento, 1983). This calculation is similar to the approach commonly used to estimate oxygen utilisation rates (OUR) in the same region (Sarmiento *et al.*, 1990).

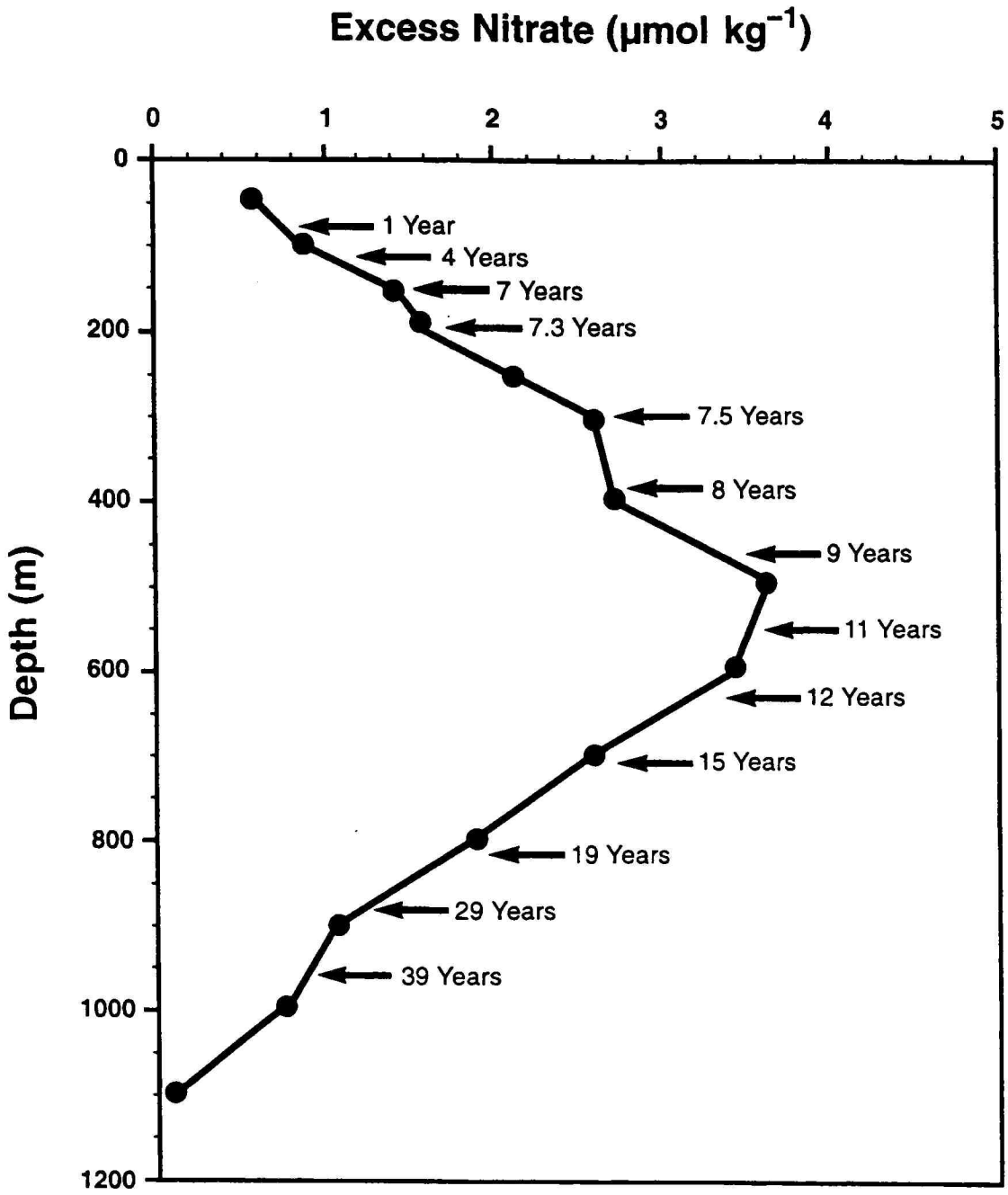


Figure 13.10 *Excess nitrate gradient at BATS. Excess nitrate is calculated as described in the text. The gradient is calculated by subtracting the value at the outcrop of the isopycnal surface from the value at BATS (see text). Ages indicate the ventilation residence time of that isopycnal surface.*

From these calculations, Michaels *et al.* (1996) estimated that 3.7–6.4 × 10^{12} mol of 'excess' nitrate are created in the Sargasso Sea each year. The range in the estimates is largely a function of the different residence time estimates for each density surface and less a function of the uncertainty in the magnitude of the horizontal N^* gradient. In a different and more detailed analysis of N^* conducted by Gruber & Sarmiento (1996), they find a lower rate

of excess nitrogen creation (2×10^{12} mol yr^{-1}). There are two possible sources of the nitrate excess in the main thermocline: nitrogen fixation and/or differential fluxes or lability in dissolved organic nitrogen compared with dissolved organic phosphorus. Unfortunately, neither process is well constrained by direct measurement. However, in a discussion of the available data, it appears that nitrogen fixation and the creation and export of high N:P organic biomass is the more likely explanation for this pattern.

Nitrogen fixation as a source of the excess nitrate may resolve some of the unanswered questions about the anomalous carbon drawdown in the Sargasso Sea (see above). Each year, between April and December, approximately 3 mol m^{-2} of carbon disappear from the surface waters at BATS (Michaels *et al.*, 1994*b*) in the absence of significant nitrate. If nitrate was mixed up from below, carbon would also be imported, as the deeper water has elevated DIC. Nitrogen fixation would cause the uptake of dissolved CO_2 as the new reduced nitrogen is converted into biomass. This may occur at the typical Redfield ratio of 6.6 mol C: 1 mol N, or probably at a much higher ratio as the most conspicuous diazotroph, *Trichodesmium* sp., uses a carbohydrate ballasting process to regulate buoyancy. Using C:N ratios of both 6.6 and 15, we estimate the total carbon uptake in the surface waters overlying the Sargasso Sea as 24–96 $\times 10^{12}$ mol C yr^{-1} (0.3–1.2 $\times 10^{15}$ 15 g C yr^{-1}). In the seasonal environment of BATS, this would probably be confined to the summer–autumn period where oligotrophy is conducive to nitrogen fixation, but could occur year-round to the south. Approximately 50–80% of this carbon would be sequestered for multi-year time scales, but little for time scales of longer than a decade. The area over which this nitrogen fixation probably occurs is approximately 20×10^{12} m^2, which gives an annual carbon fixation rate of 1.2–4.8 mol C m^{-2} yr^{-1}. This rate is very similar to the observed summertime carbon drawdown at the BATS site (Michaels *et al.*, 1994*a*,*b*).

Trichodesmium sp. and most other marine diazotrophs require elevated cell quotas of iron, approximately 100–1000-fold higher than those required by organisms that utilise nitrate (Hutchins, 1989; Rueter *et al.*, 1992; Elardo, 1994). The iron supply to the Sargasso Sea is primarily through the deposition of Saharan dust (Prospero *et al.*, 1996). Model estimates of total dust deposition to the Sargasso Sea between 10 and 40°N latitude (excluding the areas near the African coast) are approximately 44×10^{12} g dry mass yr^{-1} (Prospero *et al.*, 1996). Assuming 3.5% iron by mass, dust would supply 2.8×10^{10} mol Fe yr^{-1}. *Trichodesmium* sp. typically has an N:Fe ratio of the order of 1000 mol N: 1 mol Fe (range = 200–3000; Hutchins, 1989; Rueter *et al.*, 1992; Elardo, 1994). The export of particulate biomass produced by nitrogen fixing organisms would probably transport the intra-cellular iron to depth as well. Thus, the total iron

deposition could support an annual excess nitrate production rate from nitrogen fixation of as much as 28×10^{12} mol N yr^{-1}. Much of the atmospheric iron is insoluble and thus unavailable to nitrogen-fixing phytoplankton. The iron supply would support the estimated excess nitrate production if *Trichodesmium* sp. were able to utilise about 13–23% of the iron supply. Interestingly, the relatively close match between the estimated nitrogen fixation rate and the rate that is potentially supported by the iron deposition may indicate that Fe supply limits the total amount of nitrogen fixation that can occur. Fe inputs are concentrated in the summer, a good temporal match to the timing of the DIC drawdown. There is a large decadal variation in dust deposition as a result of the large expansion of the Sahara in the early 1970s. If dust supply controls this process, we may thus expect annual and decadal fluctuations in nitrogen fixation that could drive 0.3–1.2 Gt C yr^{-1} fluctuations in the northern hemisphere atmospheric CO_2 stocks. However, the main thermocline ventilates on time scales of 7–30 years. Thus, nitrogen fixation in the Sargasso Sea cannot result in the sequestration of large amounts of CO_2 on the longer time scales associated with the anthropogenic signal in the atmosphere.

Surprises, assumptions and the inhererent value of long-term time series

As described above, it is apparent that both time-series studies have allowed an unparalleled look into the biogeochemistry of the two regions. These studies are neither perfect nor complete, but they do present the most intensive, time-dependent examination of our understanding of elemental cycling in the open oceans. Because open-ocean systems represent half of the surface area of the world, this understanding can be important on a global scale if it can be extrapolated to this scale. At the same time, the BATS and HOT research programmes present a mechanism to examine some of the assumptions we use as we create models to do much of the spatial and temporal extrapolation.

Our current conceptual model for the cycling of carbon in oligotrophic systems assumes that nitrogen limits plant growth and that the cycling of carbon can be linked to the nitrogen cycle by the Redfield stoichiometry. This is expressed in models by a simplified version of the new production hypothesis (Dugdale & Goering, 1967) that concentrates on the dynamics of nitrate and ammonia as a reflection of new and regenerated processes, respectively (Fig. 13.11*a*). The carbon cycle is then reflected as a simple multiplication of the nitrogen fluxes by 6.6 (mol:mol) (Fig. 13.11*b*). This is computationally tractable and, in many cases, seems to represent the dynamics of the drawdown

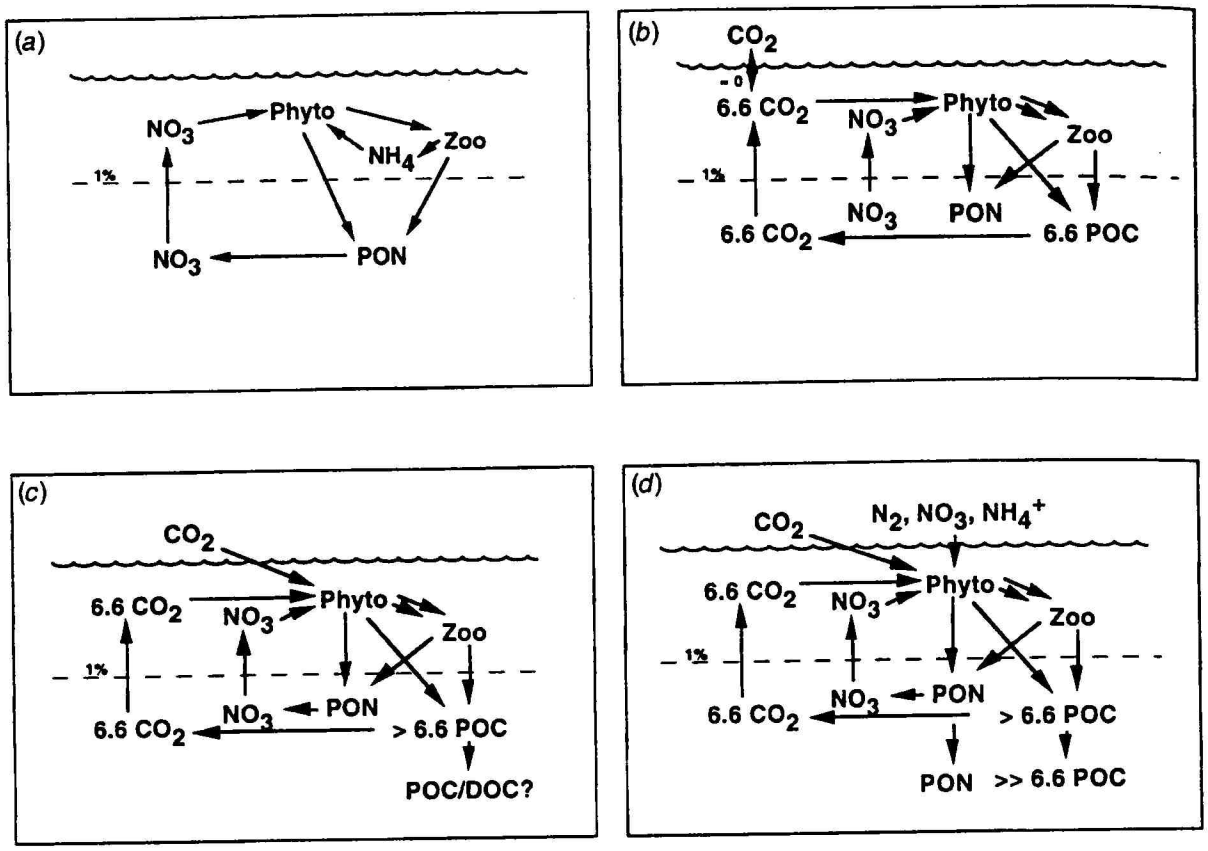


Figure 13.11 *Conceptual diagrams of the nitrogen and carbon cycle. (a) Simple nitrogen cycle as often found in numerical models. (b) Simple carbon cycle as driven by the nitrate dynamics multiplied by the Redfield C: N ratio of 6.6 (mol: mol). (c) Conceptual change in carbon fluxes if the C: N ratio of export exceeds the Redfield ratio. (d) Conceptual change in carbon fluxes if the nitrogen cycle includes an air–sea exchange component through nitrogen fixation.*

of a spring bloom or upwelling in highly productive areas. However, the assumption that this behaviour can be abstracted globally has an important and perhaps un-intended consequence.

The simple assumptions in Fig. 13.11*a,b* basically require that biological processes are irrelevant in the global carbon dynamics. In a world that operates with these simple assumptions, all of the DIC that is required to fuel phytoplankton growth is introduced when the nutrients are upwelled or mixed into the euphotic zone. Because the simple N cycle has no gas-exchange component, a simple carbon system that is linearly linked to nitrogen will have no net gas exchange either. Most of the global biogeochemical models of the ocean are represented by these dynamics. Thus, it is not surprising that they have trouble articulating the role of biological processes in the uptake of CO_2 by the ocean. Either these simple assumptions are true and ocean biology is minimally important (in which case we can probably invest our global change

effort elsewhere), or we have to study the biology of the ocean from a different perspective.

The important processes for the net role of biology in the air–sea carbon balance will be those deviations from the simple assumptions that allow for a net exchange of carbon with the atmosphere. Many of these have been described, but are not usually the focus of research. If the Redfield ratio assumption is relaxed, the carbon dynamics become more interesting (Fig. 13.11*c*, high C:N export). An increased C:N ratio of export compared with uptake has been described in many studies and is seen at both BATS and HOT. Dissolved organic carbon and nitrogen may be even more out of Redfield balance. If this dynamic is included in the link between the simple nitrogen dynamics and the resultant carbon dynamics, there is a net transfer of carbon from the atmosphere to the deep sea. This basically increases the length scale for the depth of re-mineralisation of carbon compared with nitrogen. On millennial time scales, this enriched deep carbon will ultimately ventilate back to the surface. However, on inter-annual, decadal and centennial time scales, it means that a change in the rate of biological activity (and export in particular) can have a net effect on the atmospheric carbon concentration.

The other obvious modification of these assumptions is the inclusion of a gas phase or air–sea exchange in the nitrogen cycle. This will then require a gas exchange for carbon at some appropriate stoichiometry. Nitrogen deposition and nitrogen fixation are two processes where nitrogen is introduced from the atmosphere or from a dissolved gas phase that is ultimately equilibrated with the atmosphere (Fig. 13.11*d*). On a global scale, N deposition may play a modest role (Galloway *et al.*, 1995). As described above, nitrogen fixation may be very important in the carbon dynamics on the inter-annual scales of climate variability and on the centennial scales of global change.

The key point is that the examination of the simple nitrogen dynamics and rate processes in the upper ocean that come from the basic paradigm (new production, export) may be less important than understanding how the deviations in our assumptions affect the links between elements. One of the most important lessons from the two time-series stations is that an intensive, multi-year study of each of these systems has revealed processes that are at odds with the assumptions of the simplest versions of our basic paradigms. When we include these new processes and changed assumptions, we come up with air–sea carbon dynamics that differ from the patterns in our simple models. Biology may be more important for global processes when it breaks the rules, and we have to look for these unique patterns to understand their impacts.

Conclusion

The two US JGOFS time-series stations have proved a valuable component of the overall JGOFS efforts. They have provided insights into the inter-annual variability in ocean biogeochemistry and into the processes that control this variability. As the two stations pass their tenth year of operation, longer-period patterns are also emerging. The coupling of the detailed observations at these two locations with the longer, but more limited time-series observations at the Hydrostation S (Atlantic) and Climax (Pacific) stations strongly indicate that these ecosystems vary on decadal time scales and provide potential mechanisms for feedbacks between ocean biogeochemistry and climate. JGOFS is scheduled to end within the next few years. The current plans include continuation of both US stations at least through the end of US JGOFS and hopefully for decades to come. The utility of this approach, coupled with the strong commitments to rapid and complete public release of the time-series data, make these stations a resource for the entire oceanographic community that should continue to provide insight and opportunities for a long time to come.

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