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Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry

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Abstract

The Bermuda Atlantic Time-series Study (BATS) commenced monthly sampling in October 1988 as part of the US Joint Global Ocean Flux Study (JGOFS) program. The goals of the US JGOFS time-series research are to better understand the basic processes that control ocean biogeochemistry on seasonal to decadal time-scales, determine the role of the oceans in the global carbon budget, and ultimately improve our ability to predict the effects of climate change on ecosystems. The BATS program samples the ocean on a biweekly to monthly basis, a strategy that resolves major seasonal patterns and interannual variability. The core cruises last 4–5 d during which hydrography, nutrients, particle flux, pigments and primary production, bacterioplankton abundance and production, and often complementary ancillary measurements are made. This overview focuses on patterns in ocean biology and biogeochemistry over a decade at the BATS site, concentrating on seasonal and interannual changes in community structure, and the physical forcing and other factors controlling the temporal dynamics. Significant seasonal and interannual variability in phytoplankton and bacterioplankton production, biomass, and community structure exists at BATS. No strong relationship exists between primary production and particle flux during the 10 yr record, with the relationship slightly improved by applying an artificial lag of 1 week between production and flux. The prokaryotic picoplankton regularly dominate the phytoplankton community; diatom blooms are rare but occur periodically in the BATS time series. The increase in Chl *a* concentrations during bloom periods is due to increases by most of the taxa present, rather than by any single group, and there is seasonal succession of phytoplankton. The bacterioplankton often dominate the living biomass, indicating the potential to consume large amounts of carbon and play a major ecological role within the microbial food web. Bacterial biomass, production, and specific growth rates are highest during summer. Size structure and composition of the

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plankton community may be an important factor controlling the quality of dissolved organic matter produced and could affect production of bacterioplankton biomass. Larger heterotrophic plankton play an integral role in the flux of material out of the euphotic zone at BATS. Protozoans are abundant and can constitute a sizable component of sinking flux. Zooplankton contribute significantly to flux via production of rapidly sinking fecal pellets, and vertically migrating zooplankton can actively transport a significant amount of dissolved organic and inorganic carbon and nitrogen to deep water. An important question that remains to be further addressed at BATS is how larger climatological events drive some of the interannual variability in the biogeochemistry. © 2001 Published by Elsevier Science Ltd.

1. Introduction

To improve our ability to predict the effects of climate change on ecosystems requires a comprehensive understanding of global biogeochemical cycles and how they relate to climate processes. The oceans play a central role in shaping climate by absorbing and exchanging carbon dioxide with the atmosphere, and by exchanging and sequestering heat. The ocean is one of the largest of the carbon reservoirs, and on decadal or longer time scales it is the ocean's ability to absorb carbon dioxide that controls the atmospheric CO₂ concentration (IPCC, 1990). The ocean is thus an important reservoir for anthropogenic CO₂ and can potentially modify hypothesized human-induced changes to the climate system (Sarmiento et al., 1995). Any detailed study of climate therefore must include a thorough understanding of ocean biogeochemical processes together with an understanding of the coupling between the ocean and atmosphere.

Long-term time series are a powerful tool for investigating ocean biogeochemistry and its effects on the carbon cycle. The seasonal dynamics of carbon and nutrient cycles in the upper ocean determine the productivity of ecosystems, the net exchange of carbon dioxide between the atmosphere and the ocean, and the distribution of many elements in the sea. Understanding the overall elemental cycle requires that we understand each of its component processes.

The Bermuda Atlantic Time-series Study (BATS) commenced monthly sampling in October 1988 in the western North Atlantic subtropical gyre as part of the US Joint Global Ocean Flux Study (JGOFS) program, along with a companion time-series station off Hawaii, the Hawaii Ocean Time-series (HOT). The goal of the US JGOFS time-series research is to better understand the basic processes that control ocean biogeochemistry on seasonal to decadal timescales (SCOR, 1987). More specifically, the focus of BATS and HOT is to understand the time-varying flux of carbon and associated elements in the ocean. To reach this understanding requires that all of the major sources, sinks, and transformations of these elements be measured accurately and the causes of those changes explicated. The time-series studies also play a crucial role in recent JGOFS synthesis and modeling efforts as they provide a consistent, ongoing program for testing and validation of the time-dependent models that will be used for prediction (e.g., Sarmiento et al., 1993; Bisset et al., 1994; Hurtt and Armstrong, 1996; Doney et al., 1996).

Bermuda was chosen for a US JGOFS time series in part to build on the rich history of existing open-ocean and atmospheric time-series programs. Hydrostation S, located 22 km southeast of Bermuda, was started by Henry Stommel and colleagues in 1954 (Schroeder and Stommel, 1969; Joyce and Robbins, 1996) and is the longest continuous open-ocean time series in the world. In

addition to Hydrostation S, a 20 + yr time series of deep-ocean sediment trap collections began in 1978 (Deuser and Ross, 1980; Deuser, 1986; Conte et al., 2001), and atmospheric chemistry and deposition measurements began in 1980 (e.g., Jickells et al., 1984; Galloway et al., 1992; Prospero, 1997). The Hydrostation S program attracted other time-series investigations near Bermuda that began before the inception of BATS. These are detailed in Michaels and Knap (1996), with references included on the CD-ROM accompanying this issue. Other time-series programs have been initiated since the inception of BATS in 1988. Ocean optics and remote-sensing programs at BATS provide an important link between ocean biogeochemistry and satellite oceanography (Siegel et al., 1995; Siegel and Michaels, 1996; Nelson et al., 2001; Siegel et al., 2001). A testbed mooring program has been initiated near the BATS site to develop and test new instrumentation, ground-truth satellite ocean color data, and provide high-temporal-resolution physical, bio-optical, and biogeochemical data in support of BATS (Dickey et al., 1998, 2001).

At time of writing, BATS is celebrating its 10th anniversary of continuous ocean hydrography and biogeochemical measurements. This overview focuses on patterns in ocean biology and biogeochemistry over a decade at the BATS site, and aims to provide a background for other papers in this issue as well as to discuss emerging science issues. A previous BATS overview (Michaels and Knap, 1996) provided organizational details that we will not repeat here. However, we update details regarding cruises and ancillary research programs on the accompanying CD ROM. We will concentrate on seasonal and interannual changes in community structure at BATS and the physical forcing and other factors controlling the temporal dynamics. The structure of planktonic communities profoundly affects chemical cycling of nutrients as well as particle export and sequestration of organic material (Michaels and Silver, 1988; Peinert et al., 1989; Legendre and Le Fevre, 1995; Wassman, 1998). Herein we examine variation in temporal and vertical structure in the planktonic community at BATS, including phytoplankton community structure and production, bacterial biomass and production, and particle structure and flux. The potential impact of episodic events, nutrient inputs, the role of the protozoa and zooplankton, and the role of dissolved organic matter are discussed as potential sources of variability and modulators of patterns, many of which will be discussed further in other papers in this volume. This will enable us to ascertain the stability of the ecosystem in this part of Atlantic, and explore the factors that might give rise to longer-term change.

1.1. Physical setting

The BATS site is situated in the western North Atlantic subtropical gyre or Sargasso Sea. The Sargasso Sea is bounded on the west and northwest by the Gulf Stream and to the south by the North Atlantic equatorial current (Fig. 1). The BATS region is characterized by weak geostrophic recirculation, with net flow towards the southwest (Siegel and Deuser, 1997) that drives net Ekman downwelling rates of $\sim 4 \text{ cm d}^{-1}$ (McClain and Firestone, 1993), and by high eddy energetics. These mesoscale eddy phenomena include cold core rings (Richardson et al., 1978; The Ring Group, 1981) and smaller cyclonic and anticyclonic eddies (e.g. McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998; Siegel et al., 1999). Between 25°N and 32°N subtropical frontogenesis between westerlies and easterlies enhances the slope of the meridional seasonal thermocline and helps generate the baroclinic eddies (Halliwell et al., 1994).

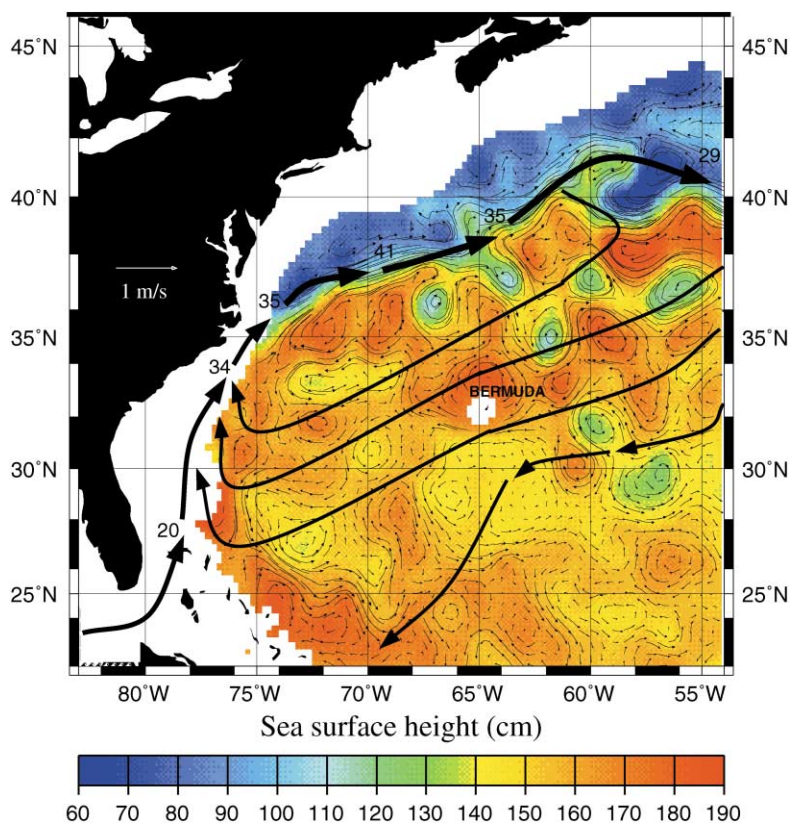


Fig. 1. Satellite image of Sargasso Sea showing surface height (SSH) and geostrophic velocity, illustrating typical mesoscale variability. The mean direction of the currents, and the location of Bermuda are also shown. The long-term mean circulation of the warm waters (temperature $> 17^{\circ}\text{C}$) of the subtropical gyre is shown as thick black arrows where the numbers indicate the transport in Sv. SSH and geostrophic flows are computed from near real-time altimeter data courtesy of University of Colorado (<http://www-ccar.colorado.edu/~realtime>) and referenced to the 1500 bar. The mean circulation is adapted from Worthington (1976).

Between 25°N and 32°N there is a transition region between: (1) relatively eutrophic waters to the north wherein form the subtropical mode water (STMW or 18°C mode water), subject to deep winter mixing and associated nutrient enrichment of the surface layer (Worthington, 1976; Talley and Raymer, 1982; Woods and Barkman, 1986) and (2) a relatively oligotrophic subtropical convergence zone to the south where nutrient-rich mode water underlies the permanently stratified euphotic zone for most of the year (Siegel et al., 1990a; Halliwell et al., 1991; Malone et al., 1993). Formation of STMW occurs each winter as the passage of cold fronts across the Sargasso Sea erodes the seasonal thermocline and causes convective mixing, resulting in mixed layers of 150–300 m depth. STMW sinks and spreads southward separating the seasonal and permanent thermoclines (Worthington, 1976; Halliwell et al., 1994), recognizable by a minimum in the profile of potential vorticity (Talley and Raymer, 1982). In summer, the region is dominated by a high-pressure system that bars further frontal passage. Conditions are then ripe for the formation of

a shallow, fresh, warm mixed layer, which typically shoals to less than 20 m. Rain forms low-salinity layers in the surface 10 m that could stimulate bloom formation (Michaels et al., 1993). Summer and early fall tropical storm activity brings increased wind, changing the thermal and physical structure and hence ecosystem dynamics (Nelson, 1998; Bates et al., 1998a; Dickey et al., 1998). In intermediate waters of the Sargasso Sea, significant climatic events driving convection in the Labrador Sea (such as North Atlantic Oscillation shifts) can be clearly observed with a 6-yr lag (Curry et al., 1998). This may allow prediction of intermediate water changes in the BATS region.

2. Methods

Here we briefly summarize the methods used at BATS, describing in slightly more detail methods pertaining to plankton community structure. Further details of the BATS sampling scheme, analytical methods, data quality control and intercalibration procedures, and history of sampling procedures appear in a previous overview (Michaels and Knap, 1996), the BATS methods manuals (Knap et al., 1993a, 1997b), and BATS data reports (Knap et al., 1991, 1992, 1993b, 1994, 1995, 1997a). Table 1 (updated from Michaels and Knap, 1996) lists the core measurements made at the BATS site.

2.1. Site and sampling scheme

The BATS station lies 82 km southeast of the island of Bermuda (31°40' N, 64°10' W), approximately 8 km south of the Ocean Flux program (OFP) long-term deep sediment trap mooring (Conte et al., 2001) (Fig. 2). Bottom depth at the BATS deployment area is ~ 4680 m. The BATS core cruises consist of a single 4–5 d cruise at monthly intervals. Between January and April an extra “bloom cruise” is added to increase sampling frequency to bimonthly during the spring-bloom period. Additional “validation cruises” ($2\text{--}4\text{ yr}^{-1}$) resolve spatial variability of biogeochemical parameters near BATS.

On each core cruise a 400-m surface-tethered sediment trap array is deployed 9 km south of BATS (to avoid entanglement with the Bermuda Testbed Mooring). The array is allowed to drift for 3 d, and its location is monitored via an ARGOS/GPS transponder and ship relocation. Once the array is deployed, the ship proceeds to the BATS station to commence sampling. On each core cruise, CTD profiles and water collections are made at 36–48 depths during a series of 4–7 casts from the surface to 4200 m. A dusk–dawn in situ primary production array is also deployed. Since June 1994, continuous surface seawater measurements of temperature, salinity, fluorescence, and $p\text{CO}_2$ have been made from a flow-through seawater system (Bates et al., 1998b).

2.2. Hydrography

A Sea-Bird CTD instrument package is mounted on a 24-position General Oceanics Model SBE 32 rosette containing 12-l Teflon-coated Niskin bottles. The instrument package includes sensors for continuous measurement of pressure, temperature, conductivity, dissolved oxygen, and fluorescence. The continuous CTD data are calibrated by water collected in discrete Niskin bottle samples on the rosette.

Table 1
Core measurements made at the BATS site

Parameter	Depth range (m)	Technique/instrument
<i>Continuous electronic measurements</i>		
Temperature	0–4200	Thermistor on SeaBird SBE-911plus CTD
Salinity	0–4200	Conductivity sensor on SeaBird SBE-911plus CTD
Depth	0–4200	Digiquartz pressure sensor on SeaBird SBE-911plus CTD
Dissolved oxygen	0–4200	SeaBird Polarographic Oxygen Electrode
Beam attenuation ^a	0–200	SeaTech, 25 cm Transmissometer
Fluorescence	0–500	Chelsea Instruments Fluorometer
PAR ^a	0–200	Biospherical Scalar Irradiance Sensor, 400–700 nm
<i>Discrete measurements from Niskin bottles on CTD</i>		
Salinity	0–4200	Conductivity on Guildline Autosol 8400A
Oxygen	0–4200	Winkler Titration, automated UV endpoint detection
Total CO ₂	0–500	Automated coulometric analysis
Alkalinity	0–500	High precision titration
Nitrate	0–4200	CFA colorometric with Technicon AA
Nitrite	0–4200	CFA colorometric with Technicon AA
Phosphate	0–4200	CFA colorometric with Technicon AA
Silicate	0–4200	CFA colorometric with Technicon AA
Dissolved organic carbon	0–4200	High-temperature combustion
Dissolved organic nitrogen	0–4200	UV oxidation
Particulate organic carbon	0–4200	High-temperature combustion, CHN analyzer
Particulate organic nitrogen	0–4200	High-temperature combustion, CHN analyzer
Particulate silica	0–4200	Chemical digestion, colorometric analysis
Fluorometric chlorophyll <i>a</i>	0–250	Acetone extraction, Turner fluorometer
Phytoplankton pigments	0–250	HPLC, resolves 19 pigments
Bacteria	0–3000	DAPI stained, fluorescence microscopy
<i>Rate measurements</i>		
Primary production	0–140	Trace-metal clean, in situ incubation, ¹⁴ C uptake
Bacterial activity	0–1000	[³ H-methyl] thymidine incorporation
Particle fluxes	150, 200, 300	Free-drifting cylindrical trap (MultiPITs)
Mass flux		Gravimetric analysis
Total carbon flux		Manual swimmer removal, CHN analysis
Organic carbon flux		Manual swimmer removal, acidification, CHN analysis
Organic nitrogen flux		Manual swimmer removal, CHN analysis

^aCurrently measured on BATS cruises as part of Bermuda bio-optical program.

Dissolved oxygen is sampled and processed before all other measurements to avoid compromising the samples by atmospheric gas exchange. Oxygen samples are drawn into individual 115-ml BOD flasks and analyzed using the Winkler titration method. The auto-titrator used by BATS originally followed the design of Williams and Jenkinson (1982), but was replaced in 1993 with a UV endpoint detector system developed by Robert Williams (Scripps Institute of Oceanography). This substantially increased system precision, so now only 25% of oxygen samples are replicated. Samples for dissolved inorganic carbon (DIC) and alkalinity are drawn after the oxygen samples or

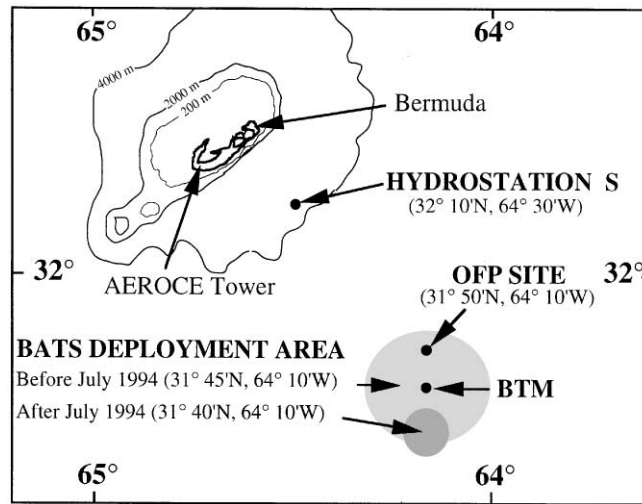


Fig. 2. Map of the ocean southeast of Bermuda showing the sampling locations for the various time-series studies: AEROCE, Air-Ocean Chemistry Experiment; OFP, Ocean Flux Program; BTM, Bermuda Testbed Mooring (adapted from Michaels and Knapp, 1996).

sampled first on a subsequent cast. DIC samples are fixed with saturated mercuric chloride solution, the bottles sealed, and the samples analyzed with an SOMMA-coulometer system (Bates et al., 1996).

Samples for dissolved organic carbon and nitrogen are drawn after the gas samples and analyzed via high-temperature combustion and UV oxidation, respectively (Hansell and Carlson, 2001). Salinity samples are taken next, and analyzed within one week of collection on a Guideline model 8400A Autosol Salinometer (standardized against IAPSO standard seawater to an analytical precision of ± 0.001).

Samples for nitrate + nitrite, soluble reactive phosphate (SRP), and silicic acid are filtered through 0.8 μm Nuclepore filters using in-line polycarbonate filter holders attached to the Niskin spigots, then frozen until analysis. Prior to March 1996, silicic acid samples were refrigerated at 4°C, and analyzed within a few days. Tests of frozen versus refrigerated samples indicated no significant difference between storage methods (Dore et al., 1996). All nutrient samples are analyzed within 2 weeks on a technicon AutoAnalyzer II with an analytical precision of approximately 0.03–0.05 $\mu\text{mol kg}^{-1}$.

2.3. Suspended particles and particle flux

Particulate organic carbon (POC) and nitrogen (PON) samples are filtered onto precombusted Whatman GF/F glass fiber filters (nominal pore size 0.7 μm). Samples are frozen until analysis, then thawed, dried, fumed with concentrated HCl, and redried. They are then analyzed with a Control Equipment Corporation (CEC) 240-XA Elemental Analyzer, which is standardized using acetanilide as a reference. Empty filters are run as blanks. Particles may sink below the spigot of Niskin bottles (“dregs”) and hence are not accounted for in total POC measurements (Gardner, 1977).

Experiments at BATS demonstrate that this can underestimate total POC/N by an average of 26% (Gundersen et al., 2001).

The configuration of the sediment trap array is described in Lohrenz et al. (1992) and follows the basic MultiPIT design (Knauer et al., 1979). The sediment trap tubes (cross-sectional collection area = 0.0039 m²) are mounted on a stainless-steel frame (before 1994 polyvinylchloride crosses were used). The frame is attached to the array line at 150, 200, and 300 m depths (and 400 m before September 1990) and an Aanderaa RCM-7 current meter is deployed at 160 m depth. The flotation system includes both subsurface and surface floats with an intervening 5 m section of bungee cord to reduce the transfer of surface wave motions to the subsurface line. The traps are deployed, recovered, and processed with traditional VERTEX methods (Knauer et al., 1979; Lohrenz et al., 1992). Zooplankton swimmers are removed manually with fine forceps as the filters are examined at 250–500× magnification. Total mass flux is determined gravimetrically and the carbon and nitrogen content of a subsample is determined with a CHN analyzer.

2.4. *Pigments and primary production*

Chlorophyll samples are filtered onto Whatman GF/F glass fiber filters, frozen in liquid nitrogen, and analyzed by both fluorometric and high-performance liquid chromatography (HPLC) techniques. Fluorometric analysis requires a smaller volume of water (0.5–1.0 l) than HPLC analysis (4 l). We describe the HPLC technique in further detail as it pertains to phytoplankton community structure data presented in this overview.

Phytoplankton community structure is determined by HPLC analysis of phytoplankton pigments. The HPLC method used at BATS is a modified version (Bidigare, 1991) of Wright et al. (1991) and can be found in the BATS methods manual (Knap et al., 1997b). Samples for fluorometric analysis are collected from GO-Flo bottles used to collect primary production samples, while HPLC samples are collected from mid-day CTD casts when spectral data are being collected. HPLC samples are filtered onto Whatman GF/F filters and stored in liquid nitrogen until analysis. Pigments are analyzed with a Spectra-Physics model SP8800 liquid chromatograph calibrated with pigment standards. The Chl *a* and *b* concentrations reported here may include contributions of the pigments divinyl chlorophyll *a* and *b*, respectively, which are exclusive to marine prochlorophytes and cannot be completely separated by existing HPLC methods (Chisholm et al., 1988; Ondrusek et al., 1991). In addition, the method does not separate lutein from zeaxanthin. However, the use of “on-line” diode array spectroscopy (400–700 nm) revealed that the lutein + zeaxanthin peak is dominated by the prokaryotic pigment marker zeaxanthin.

The pigment algorithms of Letelier et al. (1993) were used to partition Chl *a* biomass among the different phytoplankton groups. These algorithms were used to determine the taxon-specific contribution to the deep chlorophyll maximum layer (DCML). We restricted the analysis to the DCML, as the algorithms were developed for shade-adapted cultures (Letelier et al., 1993). Although the pigment algorithm coefficients were developed for the HOT site, the algorithm results compare favorably with electron microscope studies performed at HOT and BATS (Andersen et al., 1996). The sum of the taxon-specific Chl *a* concentrations determined with the algorithms correlated extremely well with the total HPLC Chl *a* at the depth of the DCML at BATS (see results). Recent studies of variations of pigment ratios under nutrient- and light-limited growth indicate Chl *a*:carotenoid ratios are a conservative approach for calculating contribution of

different phytoplankton taxa (Goericke and Montoya, 1998). This suggests that these algorithms are appropriate for both these open-ocean sites.

Primary production is measured by the uptake of ^{14}C in dawn to dusk in situ incubations. All the sampling and sample processing employs trace-metal-clean procedures (Fitzwater et al., 1982) with water collected from GO-Flo bottles deployed on a Kevlar line. Recent tests of the trace-metal-clean procedures for primary production indicate that they are satisfactory; with a few exceptions, GO-Flo samples were uncontaminated with iron or at most only a few tenths of a nmol kg^{-1} above the background as measured with an automated trace-element sampler (E. Boyle, pers. comm.). Incubations are conducted in situ at eight standard depths (1, 20, 40, 60, 80, 100, 120, and 140 m). Details of the primary production methods are found in the BATS methods manual (Knap et al., 1993a, 1997b) and in Lohrenz et al. (1992).

2.5. *Bacteria abundance and production*

Bacterioplankton enumeration via epifluorescent direct counts began at the inception of BATS in October 1988. Prior to October 1990, however, samples were sent away for preparation and counting. Due to shipping delays, sample preparation often took place weeks after collection. Subsequent studies have demonstrated that storage artifacts can result in underestimating cell abundance if samples are not prepared within a few days of collection (Turley and Hughes, 1992; Gundersen et al., 1996). For the purposes of this overview we will present only the data collected when sample preparation and analysis were performed at BBSR.

Samples for bacterioplankton enumeration are preserved with particle-free glutaraldehyde (final concentration of 1.0%) and stored at 4°C until slide preparation. Samples are filtered onto blackened $0.2\ \mu\text{m}$ polycarbonate filters, stained with DAPI (4,6-diaminino-2-phenylidole; Porter and Feig, 1980), and mounted immediately on microscope slides. Slides are counted with a Zeiss epifluorescent Axioskop microscope and UV filter set (365-nm excitation with a 420-nm barrier filter).

Bacterial production (added to BATS core regime in January 1991) is estimated using a modified version of the { ^3H -methyl}-thymidine (^3H -TdR) technique (Fuhrman and Azam, 1980; Ducklow et al., 1992; Knap et al., 1993a, 1997b). Whole seawater collected via GO-Flo bottles is incubated in triplicate with ^3H -TdR (specific activity $> 80\ \text{Ci mmol}^{-1}$) in the dark at in situ temperatures for 2–4 hs. In 1998 we adopted the microcentrifuge method (Smith and Azam, 1992) for processing ^3H -TdR samples (6 months of overlap between both methods indicated good agreement). The microcentrifuge method uses significantly less isotope and reagents, produces less radioactive waste, and generates a very low blank, allowing greater sensitivity for low rates. As of February 1998, ^3H -TdR incorporation measurements have been extended to 1000 m.

Because bacterial carbon biomass and bacterial carbon production are measured indirectly (i.e., by cell counts and radioisotope incorporation), one of the most difficult problems in the analysis of bacterial data sets is accurately estimating biomass and biomass production. No universally accepted conversion factor exists for converting either abundance to biomass or ^3H -TdR incorporation to biomass production (Ducklow and Carlson, 1992; Caron et al., 1995a). For this overview, we chose a conservative open-ocean carbon conversion factor of $10\ \text{fg C cell}^{-1}$ (Ducklow and Carlson, 1992; Caron et al., 1995a) and a thymidine conversion factor of $1.63 \times 10^{18}\ \text{cells mol}^{-1}$ thymidine that was empirically derived from waters in the vicinity of BATS (Carlson et al., 1996).

3. Results and discussion

3.1. Hydrographic and biogeochemical variability at BATS

The basic seasonal pattern of hydrography and biogeochemistry in the upper Sargasso Sea has been well documented (e.g., Menzel and Ryther, 1960, 1961a; Lohrenz et al., 1992; Michaels et al., 1994b; Michaels and Knap, 1996). The area is characterized by deep winter mixing (range ~ 200 m) and strong summer thermal stratification. Interannual differences in the seasonal cycle of the Sargasso Sea relate to variability of winter mixing depth and 18°C mode water formation (Talley and Raymer, 1982). In the intermediate and deep waters of the Sargasso Sea, studies have focused on interannual variability of the thermocline structure (Joyce and Robbins, 1996; Curry et al., 1998) and particle export to the deep ocean (see Conte et al., 2001). As a context for papers within this special volume, we review the temporal variability of hydrography and biogeochemistry during the last decade at BATS. The upper ocean at BATS is highly variable on timescales ranging from diurnal to seasonal, annual, and interannual.

The annual cycle of hydrography in the upper ocean at BATS is primarily driven by seasonal changes in surface heat flux and wind stress. Strong thermal stratification is present from April to October, largely due to higher heat fluxes and lower wind stresses. In the summer, mixed-layer temperatures range from 27 to 29°C (Fig. 3), and there is a fresher mixed layer, a subsurface salinity maximum, and strong density gradients in the upper 100 m (Fig. 4). Warming and cooling of the surface layer (~ 1 – 2 m), associated with the diurnal thermal cycle, ranges from ~ 0.2 to 2.5°C depending on day-to-day changes in net daytime surface heat fluxes (controlled by amount of cloudiness and wind stress) and mixed-layer depth (Bates et al., 1998b). In winter, the mixed layer is more saline and temperatures range from ~ 19 to 21°C , while mixed-layer depths vary from 150 to 300 m (Figs. 3 and 4). Total carbon dioxide concentrations within the mixed layer are highest in winter due to vertical entrainment of TCO_2 -rich subsurface water (Fig. 5a; Bates et al., 1996), while oxygen is typically oversaturated in the surface layer (Fig. 5b).

The annual cycle of biogeochemistry is intricately linked to the physical forcing, since vertical mixing brings nutrients into the euphotic zone during winter (Fig. 6). Typically, this annual upward nutrient flux supports a short spring-bloom period (January–March) of higher primary production rates (Fig. 7a), enhanced concentrations of chlorophyll biomass (Fig. 7b), and higher concentrations of suspended particulate organic carbon and nitrogen (Fig. 8). During thermal stratification in summer, measurable nutrients are absent within the euphotic zone (Fig. 6; see Lipschultz, 2001), primary production rates are lower (Fig. 7a), a subsurface chlorophyll maximum is present (Fig. 7b), and TCO_2 concentrations reach their minima (Fig. 5a).

From 1988 to 1998, there was significant interannual variability in the seasonal cycle of hydrography and biogeochemistry. Year-to-year differences in wintertime nutrient fluxes, rates of primary production, and chlorophyll biomass were largely tied to variability of wintertime mixing. The deepest wintertime mixing (> 200 m) occurred in 1989, 1991–1992, and 1995–1996 (Fig. 3); typically these years had the highest rates of primary production and biomass accumulation during the spring. In 1994, a deep-mixed layer of 300 m was observed on a single cruise (Fig. 3); this feature has been attributed to an anomalously warm mesoscale eddy advected into the region (Michaels and Knap, 1996). With the exception of this deep-mixed layer, winter mixed layers in 1994 were shallow. In those years with shallow winter mixed layers (1994 and 1997), nitrate was low or not

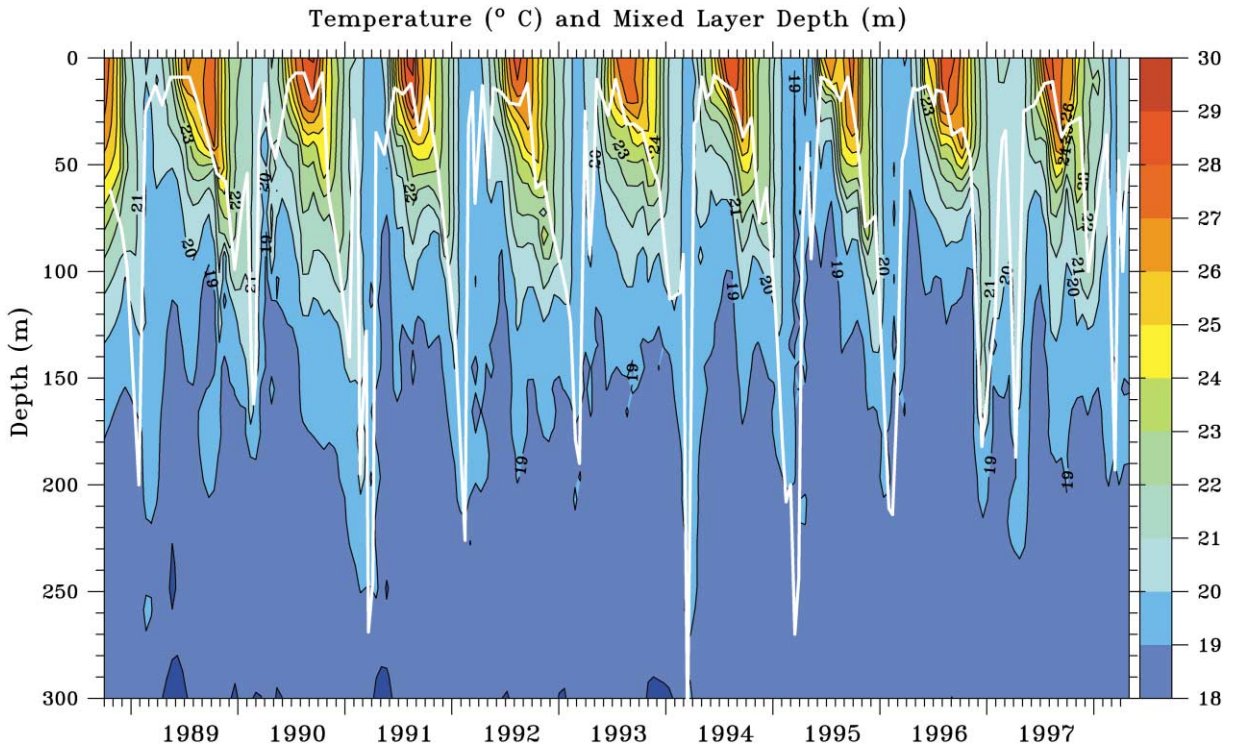


Fig. 3. Time-series contour plot of temperature with a 1°C contour interval. Mixed-layer depth is overlaid as a solid white line. Mixed-layer depth defined by using a variable sigma theta criteria (Sprintall and Tomczak, 1992) and assuming a 0.3°C diurnal temperature change.

detected in the euphotic zone (Fig. 6) and rates of primary production were low during the spring compared to other years (Fig. 7a). Significant year-to-year changes in the seasonal cycle of salinity also were observed. In 1997, anomalously high-salinity (> 36.8) water was present in the upper ocean from January to August (Fig. 4a), which appears to be locally driven by excess evaporation over precipitation.

Interannual variability in the biogeochemistry at BATS also may be partially due to the degree of surface stratification (Fig. 9). We developed a summer “stratification index” to examine the relationship between summer biogeochemistry and intensity of summer stratification. The stratification index is the density difference between 40 m (to avoid the surface fresh rain layer) and 160 m (to extend beyond the seasonal thermocline), averaged over the four months of July–October for each of 9 yr of the time series. The larger the stratification index, the more intense the summer stratification that year. This index plotted against measurements of nitrate and nitrite, Chl *a*, and primary production integrated over the surface 140 m, and over the same summer period for each year, indicates a weak, but positive relationship (Fig. 9). Thus, at least a portion of the interannual variability in summer biogeochemical measurements can be attributed to the degree of stratification.

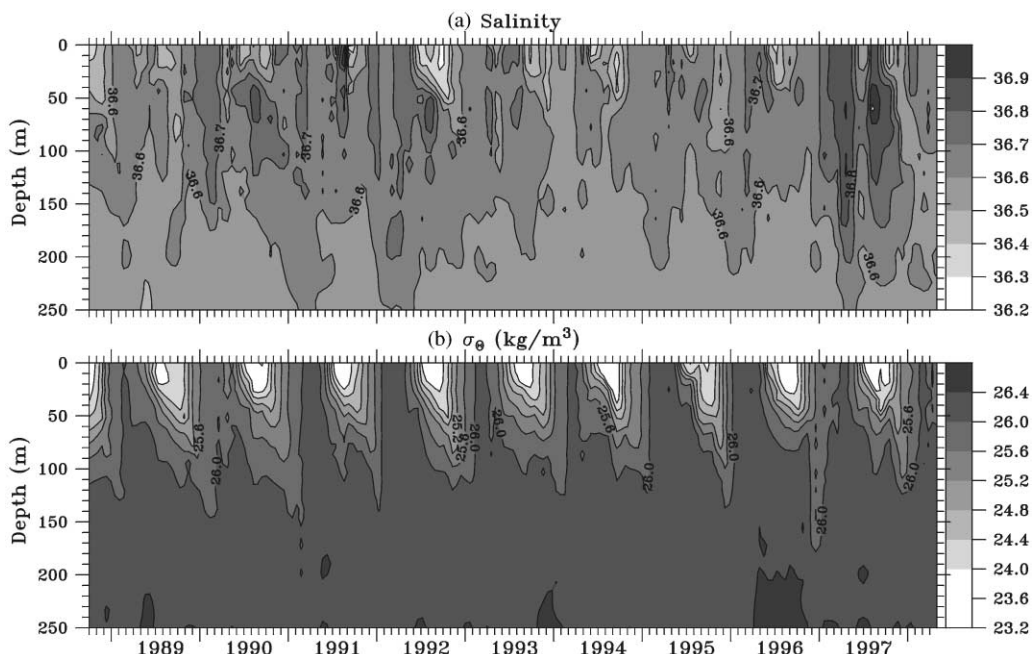


Fig. 4. Time-series contour plots of (a) salinity with a contour interval of 0.1 on the practical salinity scale, and (b) density with a contour interval of 0.4 kg m^{-3} .

Despite the intensive measurements of upper-ocean biogeochemistry at BATS during the last decade, open questions remain about the overall system dynamics. Previous results from BATS indicate that the site displays a variety of unresolved paradoxes. First, short-term measurements of nitrogen uptake, export, and cycling indicate a high degree of recycling and a low rate of export. However, nitrogen cycling estimates by geochemical tracers that average over years to decades indicate 3–5 times higher new production in the Sargasso Sea than the shorter term, discrete measurements indicate (Jenkins and Goldman, 1985). This dichotomy is still not completely resolved but has been attributed to analytical questions, time and space scales of sampling (Jenkins and Goldman, 1985), and unresolved processes that may partially explain the discrepancy, such as vertical flux of dissolved organic carbon (Carlson et al., 1994) and nutrient injection by mesoscale eddies (McGillicuddy and Robinson, 1997).

The second is a carbon-system imbalance at BATS. A detailed examination of all forms of carbon during the stratified summer period indicates that the spring–fall decrease in the 0–150 m carbon stock is three times larger than the sum of the biotic and abiotic vertical fluxes of carbon (Michaels et al., 1994a). Michaels et al. (1994a) suggest that either the sediment traps at BATS are inaccurate, or that the seasonal cycle is affected by horizontal advection. More recent results exacerbate this imbalance, or partially resolve it. Model estimates of nutrient supply from mesoscale eddies increase annual net new production on the order of $0.5 \text{ mol N m}^{-2} \text{ yr}^{-1}$ (McGillicuddy and Robinson, 1997). This eddy-induced nutrient upwelling would bring upwelling of DIC in Redfield proportion, making the carbon imbalance greater (McGillicuddy et al., 1998). New

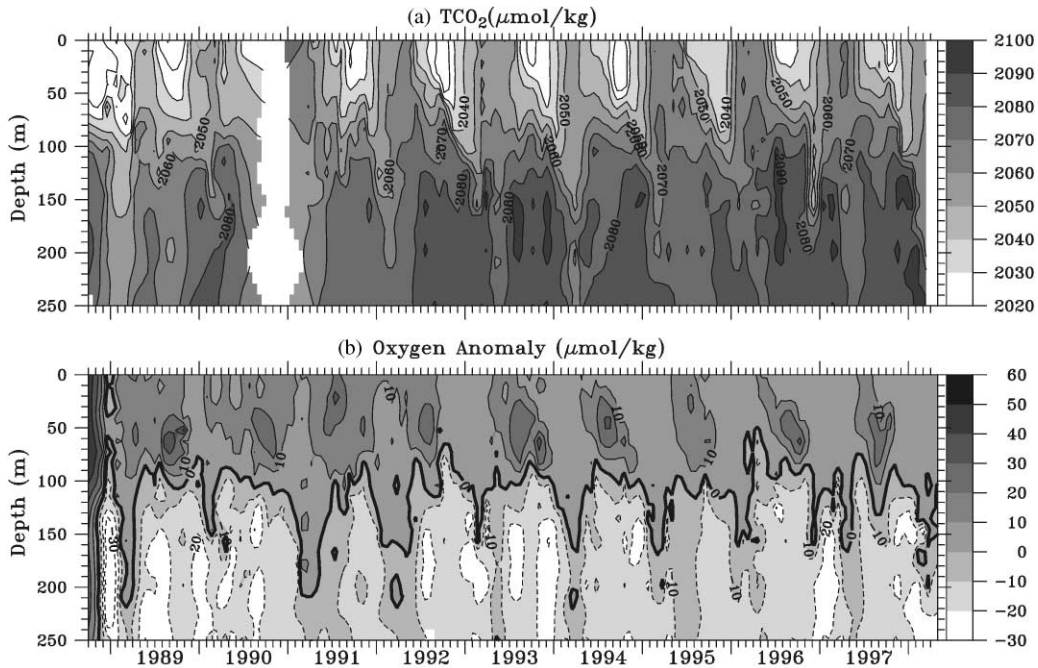


Fig. 5. Time-series contour plots of (a) dissolved inorganic carbon with a contour interval of $10 \mu\text{mol kg}^{-1}$, and (b) oxygen anomaly (the difference between the measured and saturation oxygen concentrations) with a contour interval of $10 \mu\text{mol kg}^{-1}$ (negative anomalies are dashed).

estimates of zooplankton vertical fluxes of dissolved organic and inorganic carbon slightly close the discrepancy (Steinberg et al., 2000), as would higher rates of CO_2 loss through gas exchange at the sea surface due to episodic events such as hurricanes (Bates et al., 1998a).

Third, the cycling of C, N, and P at BATS is apparently not at the traditional Redfield ratios (Michaels and Knap, 1996; Cotner et al., 1997). The Redfield ratio (Redfield et al., 1963) is a fundamental assumption used to model ocean uptake of CO_2 on a global scale. The summer drawdown of DIC by primary production in the surface waters, mentioned above, occurs in the absence of measurable nutrients (Bates et al., 1996) and is an extreme example of non-Redfield ratio DIC depletions in the North Atlantic (Sambrotto et al., 1993). At BATS, nitrate:phosphate ratios in the upper thermocline consistently exceed the Redfield ratio of 16 (Michaels et al., 1994b). This pattern differs from that found in much of the world's oceans where N:P ratios in surface waters are below the Redfield ratio (Fanning, 1992), presumably because phosphate is labile and regenerated more quickly from organic matter than nitrate (Ryther and Dunstan, 1971). This raises questions about what mechanisms cause the observed ratios. Michaels et al. (1994a) speculate that the pattern may be due to one of many possible causes: an advected feature; heterotrophic uptake of phosphate below the euphotic zone; storage of phosphate by live algae such as diatoms as they sink through the thermocline; and vertical migration of nitrogen-fixing cyanobacterial colonies such as *Trichodesmium* sp., descending to depth to incorporate phosphate, and then ascending to fix carbon and nitrogen (Karl et al., 1992). Recent analyses of this anomaly indicate that nitrogen

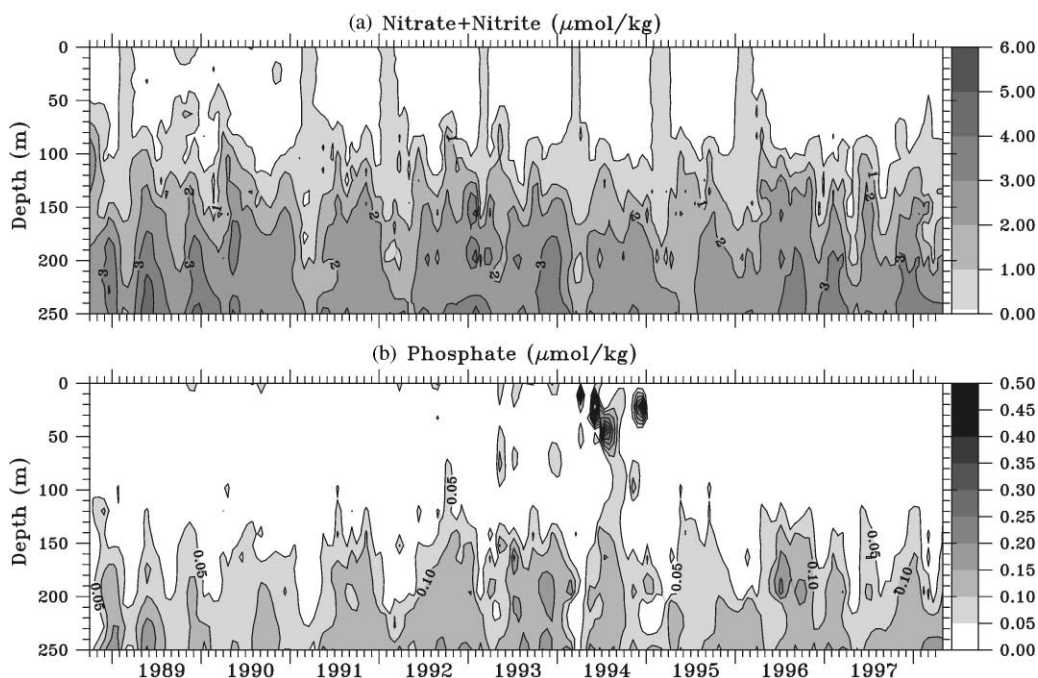


Fig. 6. Time-series contour plots of (a) nitrate + nitrite with a contour interval of $1 \mu\text{mol kg}^{-1}$ (with exception of first interval of $0.1 \mu\text{mol kg}^{-1}$), and (b) soluble reactive phosphate with a contour interval of $0.05 \mu\text{mol kg}^{-1}$.

fixation may indeed be a likely source of new nitrogen to the Sargasso Sea (Michaels et al., 1996; Gruber and Sarmiento, 1997). Another potential source of new nitrogen to the Sargasso Sea may be upward transport by vertically migrating *Rhizosolenia* mats, which appear to be an important source of new nitrogen to the surface waters of the North Pacific gyre (Villareal et al., 1999). These unresolved paradoxes, common to most of the Sargasso Sea, are major conceptual uncertainties in our understanding of the oceanic carbon cycle and must be adequately explained to fully model the role of the oceans in the global carbon budget.

3.2. Particle flux

Spring is frequently the season for higher particle fluxes at BATS, although subsequent peaks occur throughout the year. Although production peaks coincide with particle fluxes in the first several years of the time series (Fig. 10) (Asper et al., 1992; Michaels and Knap, 1996), the correlation between production and particle flux at BATS during the entire 10 yr record is weak (regression equation: $y = 0.03x + 13.6$, $r^2 = 0.16$, where y is trap POC flux at 150 m and x is 0–140 integrated primary production in $\text{mg C m}^{-2} \text{d}^{-1}$). Given the integration time scales for these two different measurements, and the time required for particles to sink from the surface waters, it is perhaps not too surprising they are not fully in sync. We determined if a temporal lag would improve the relationship between production and flux. Assuming average particle sinking rates of $50\text{--}100 \text{ m d}^{-1}$ (e.g., Andersen and Nival, 1988), the deeper traps may be expected to have a lag of

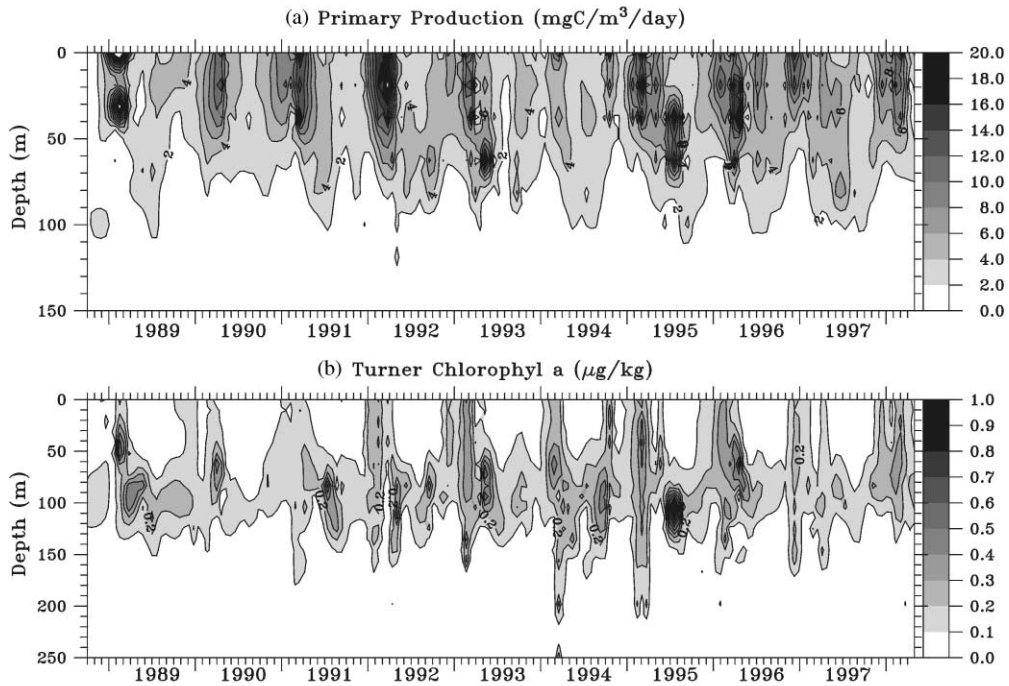


Fig. 7. Time-series contour plots of (a) primary production with a contour interval of $2 \text{ mgC m}^{-3} \text{ d}^{-1}$, and (b) chlorophyll *a* with a contour interval of $0.1 \text{ } \mu\text{g kg}^{-1}$.

about 1 week. Production and trap data were thus linearly interpolated on a regular 1-week time scale and cross-correlation analysis was performed on this data set. Results indicate that POC flux at all depths is best correlated with primary production at the 1-week time period (Fig. 11). (Note: the zero time-lag correlation is representative of the interpolated time-series, not cruise-by-cruise comparison as reported in the regression above.) However, the improvement is slight, and we conclude that the relationship between primary production and flux is reasonably synoptic as measured by our current sampling strategy. Particle fluxes in the 150-m sediment traps at BATS are only a fraction of the integrated primary production (mean \pm 1 standard deviation = $6.9 \pm 3.6\%$, range 2.1–21.6%, $n = 107$, for entire time series). Annual, time-integrated primary production and sediment trap POC flux for each year of the time series are given in Table 2, also indicating a low mean export ratio of 0.06. As noted above and elsewhere (e.g., Lohrenz et al., 1992) these particle fluxes represent only a fraction of the geochemical estimates of total organic matter export in the Sargasso Sea (Jenkins and Goldman, 1985).

Although elevated sediment trap fluxes do not always correlate with production peaks, they do appear to correspond well with the depth of mixing. For example, peaks in 150-m trap POC flux consistently occurred when mixing was below 150 m (Fig. 10; see asterisks). This was true whether integrated production was high or low. In addition, productivity peaks that occurred when mixing was shallower than 150 m, never had corresponding high flux at 150 m (e.g., spring 1990, summer 1995). The deeper 200 and 300 m traps exhibit the same pattern; many of the elevated trap fluxes

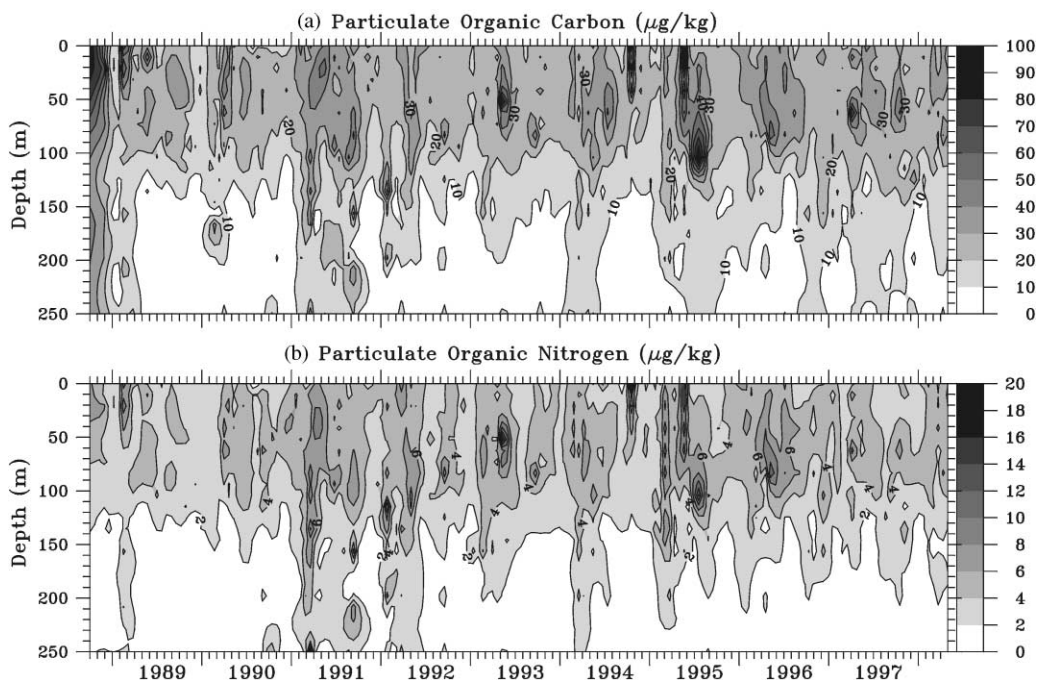


Fig. 8. Time-series contour plots of (a) particulate organic carbon with a contour interval of $10 \mu\text{g kg}^{-1}$, and (b) particulate organic nitrogen with a contour interval of $2 \mu\text{g kg}^{-1}$.

correspond to mixing events that are deeper than the depth of the traps. For example, four of the highest 200-m trap fluxes in the time series correspond to mixing events deeper than 200 m, and the only time when mixing exceeded 300 m was in February of 1994 (attributed to an advected eddy; Michaels and Knap, 1996), which has a corresponding flux peak. The strong correlation between depth of physical mixing and trap flux, and the weak correlation between primary production and trap flux suggest that part of the BATS surface trap record may be biased by sampling artifact due to physical dynamics during deep-mixing events. Physical mixing of the water column may affect trapping efficiency and hydrodynamics within traps. Studies with new trap designs (e.g., Buesseler et al., 2000; Valdez and Price, 2000) currently underway at BATS will help address these issues.

3.3. *Phytoplankton community structure*

The HPLC pigment results show significant seasonal and interannual variability in phytoplankton biomass and community structure. To describe the community structure, we discuss the HPLC pigment contours (Figs. 12–15) concurrently with the taxon-specific Chl *a* contribution to the deep chlorophyll maximum layer (DCML) as determined from the algorithms of Letelier et al. (1993) (Figs. 16 and 17). Pigment concentrations primarily depend on species composition and photoadaptive state of phytoplankton present. Thus, a high contribution to Chl *a* by a particular taxon does not mean it is also significant in numbers or biomass, as there are depth-dependant changes in accessory pigment to Chl *a* ratios due to photoadaptation (Bidigare and Ondrusek,

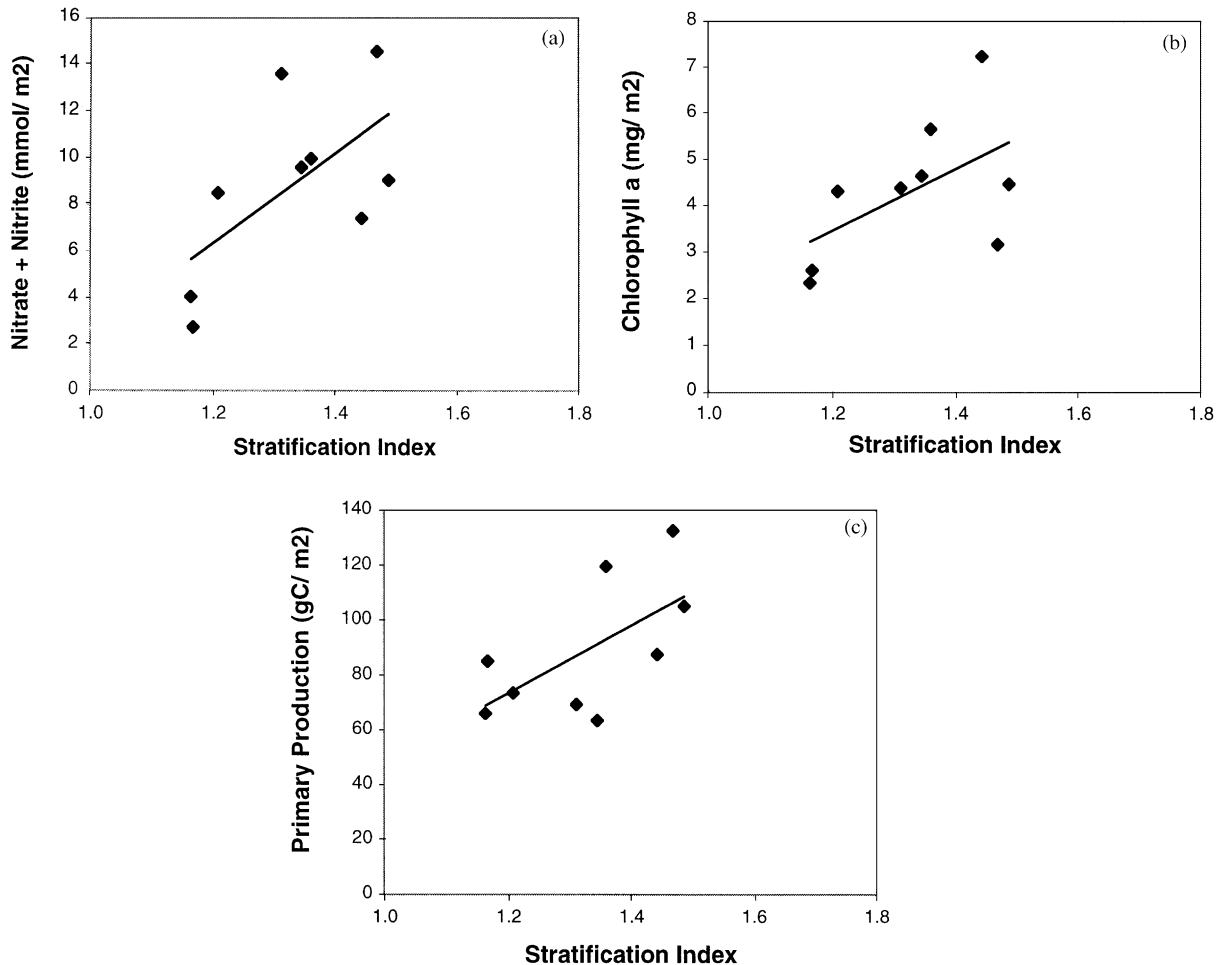


Fig. 9. Summer surface water “stratification index” versus 0–140 m, summer integrated values for (a) nitrate and nitrite, (b) chlorophyll *a*, and (c) primary production. Stratification index is the mean density difference between 40 and 160 m for each summer month (July–October) calculated for each year of the time series (1989–1997; $n = 9$). Nitrate and nitrite, chlorophyll *a*, and primary production values are 0–140 m and summer (July–October) integrated. Regression equations and statistics: (a) nitrate and nitrite: $y = 19.2x - 16.8$, $r^2 = 0.40$, $P = 0.07$; (b) chlorophyll *a*: $y = 6.8x - 4.6$, $r^2 = 0.30$, $n = 9$, $P = 0.12$; (c) primary production: $y = 123.2x - 74.7$, $r^2 = 0.39$, $P = 0.07$.

1996; Goericke, 1998; Goericke and Welschmeyer, 1998). However, the error associated with the assumption of constant pigment ratios with depth should be minimized, as we analyzed data largely from one depth stratum (the DCML is 80 m and deeper for 75% of the time series), and applied algorithms for shade-adapted cultures (Letelier et al., 1993) that should be appropriate for the DCML at BATS. Thus, any increases in Chl *a* contribution should reflect biomass increases. (Note: 0–140 m integrated pigment data also exhibited the same general seasonal and interannual trends as shown by analysis of pigments at the DCML; data not shown.)

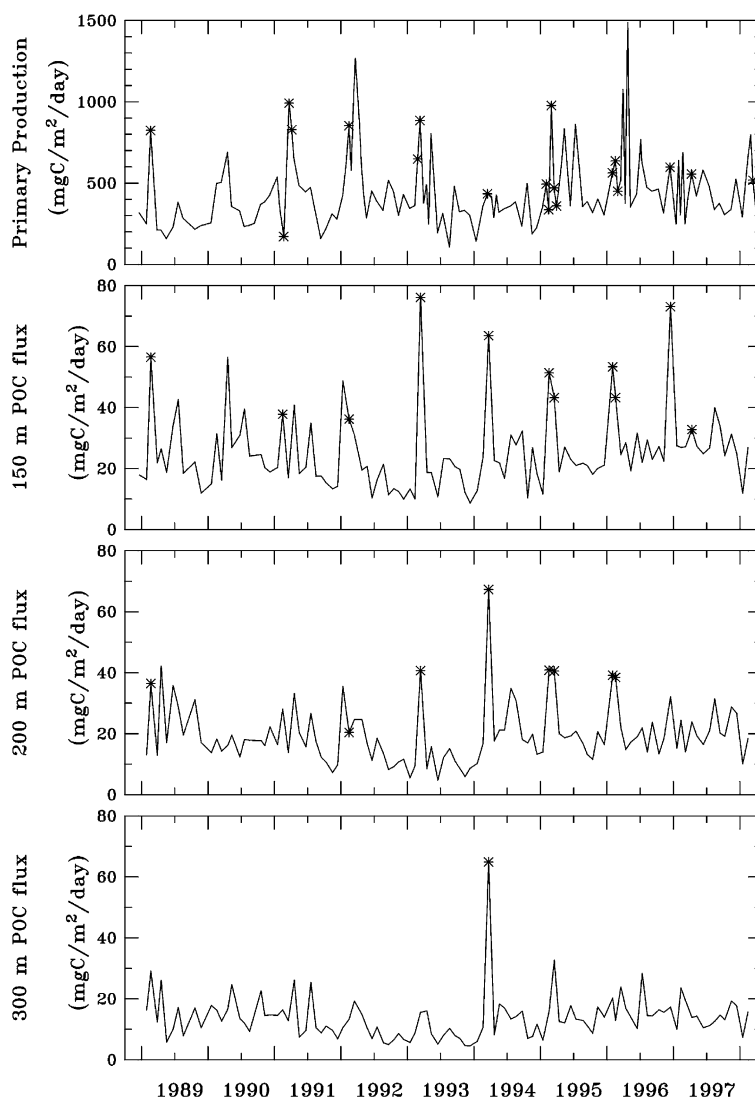


Fig. 10. Time series of integrated primary production (0–140 m) compared to the particulate organic carbon flux measured with a sediment trap at 150, 200, and 300 m. Stars indicate times of the year when physical mixing was deeper than the depth of the measurement (e.g. mixing was deeper than 150 m for integrated primary production and 150-m trap flux, and deeper than 200 m for 200-m trap flux).

Chl *a* concentration at BATS peaks between 60 and 120 m (Fig. 12a), indicating the depth range of the DCML at BATS. High surface Chl *a* concentrations in winter are associated with convective deep (> 100 m) mixed layers, but are not sustained throughout the year. Maximum Chl *b* concentrations coincide with the Chl *a* maximum for most of the time series (Fig. 12b). Chl *b* concentrations are highest below 60 m, peaking at about 100 m, which suggests the presence of prochlorophyte-like picoplankton (see below).

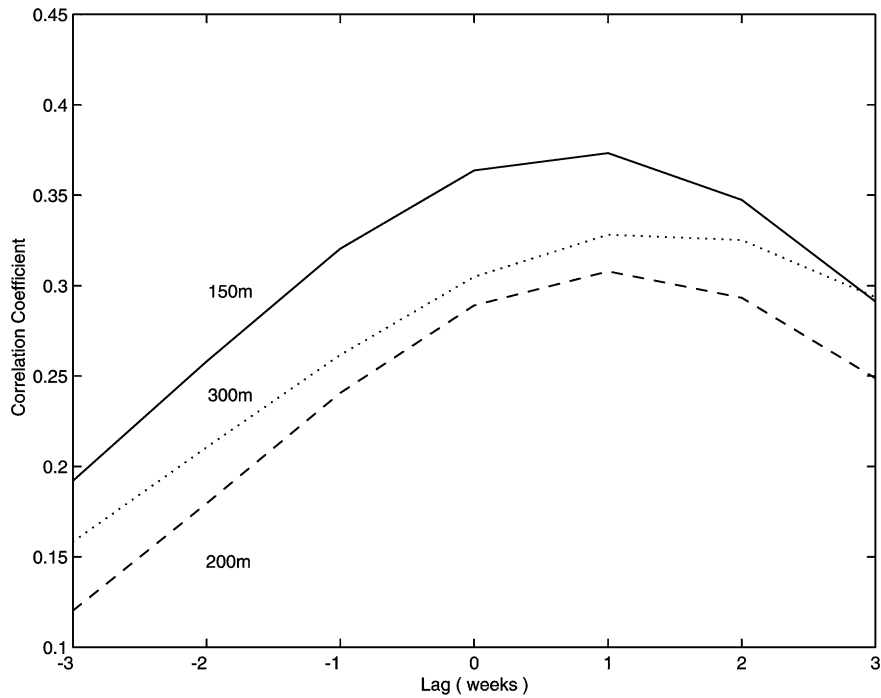


Fig. 11. Cross-correlation analysis of time-lagged integrated primary production (0–140 m) versus particulate organic carbon flux measured with sediment traps at 150, 200, and 300 m at BATS. Time-series data were linearly interpolated on a regular 1-week timescale and cross-correlation analysis was performed on this data set.

Table 2

Annual integrated primary production and sediment trap carbon flux at the BATS site. Primary production is 0–140 m integrated, sediment traps are at 150 m. Export ratio is calculated as flux/production. SD, standard deviation

Year	Integrated primary production ($\text{gC m}^{-2} \text{yr}^{-1}$)	Integrated sediment trap flux ($\text{gC m}^{-2} \text{yr}^{-1}$)	Export ratio
1989	114.2	9.7	0.08
1990	140.7	10.0	0.07
1991	149.2	8.4	0.06
1992	189.8	7.4	0.04
1993	139.3	7.8	0.06
1994	121.2	9.4	0.08
1995	177.4	9.5	0.05
1996	195.8	11.5	0.06
1997	159.9	11.0	0.07
Mean (± 1 SD)	154.2 (28.9)	9.4 (1.4)	0.06 (0.01)

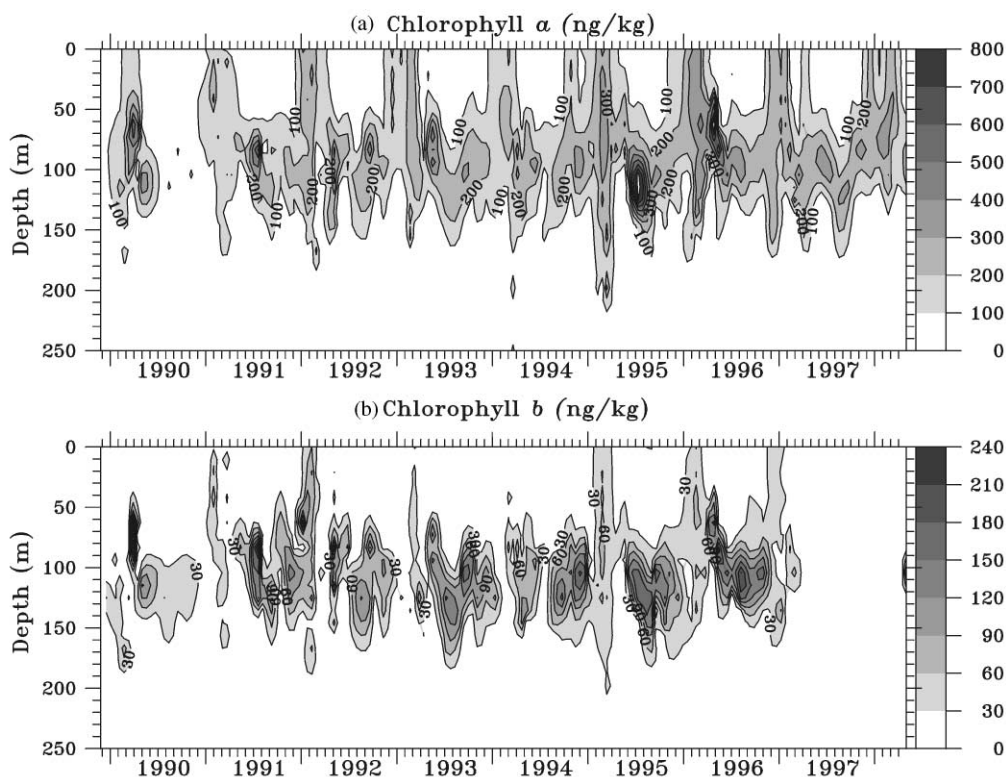


Fig. 12. Time-series contour plots of HPLC-determined pigment concentrations (ng kg^{-1}) at BATS: (a) chlorophyll *a*, (b) chlorophyll *b*.

The most abundant eukaryotic phytoplankton at BATS are the prymnesiophytes and pelagophytes. The most abundant accessory pigment at BATS is 19'-hexanoyloxyfucoxanthin (19'-hex), a signature pigment of prymnesiophytes (Fig. 13a). Highest concentrations occur during the spring blooms, and between 30 and 120 m, indicating the importance of this taxon in the formation of the DCML (Figs. 13a and 16). The highest concentration of this prymnesiophyte pigment in the entire time series occurred during the spring bloom of 1996 (Figs. 13a and 16). Other prevalent eukaryotic algae at the BATS site include the pelagophytes with the signature pigment 19'-butanoyloxyfucoxanthin (19'-but) (Fig. 13b). This pigment was formerly associated with chrysophytes, but is now recognized as the signature pigment of the class Pelagophyceae (Andersen et al., 1993, 1996). 19'-but is present in the water column for most of the year, with higher concentrations between 30 and 120 m that increase during the spring blooms. Pelagophytes are important contributors to the DCML (Fig. 16). The dominance of prymnesiophytes and pelagophytes appears to be characteristic of both Hydrostation S and HOT (station ALOHA), with the proportion of prymnesiophyte Chl *a* increasing with depth at HOT, and pelagophyte Chl *a* increasing with depth at both sites (Andersen et al., 1996). Prymnesiophytes (presumably largely coccolithophores) are consistently abundant in the time series (also see Malone et al., 1993; Goericke, 1998) and are important at other open-ocean sites as well (Letelier et al., 1993).

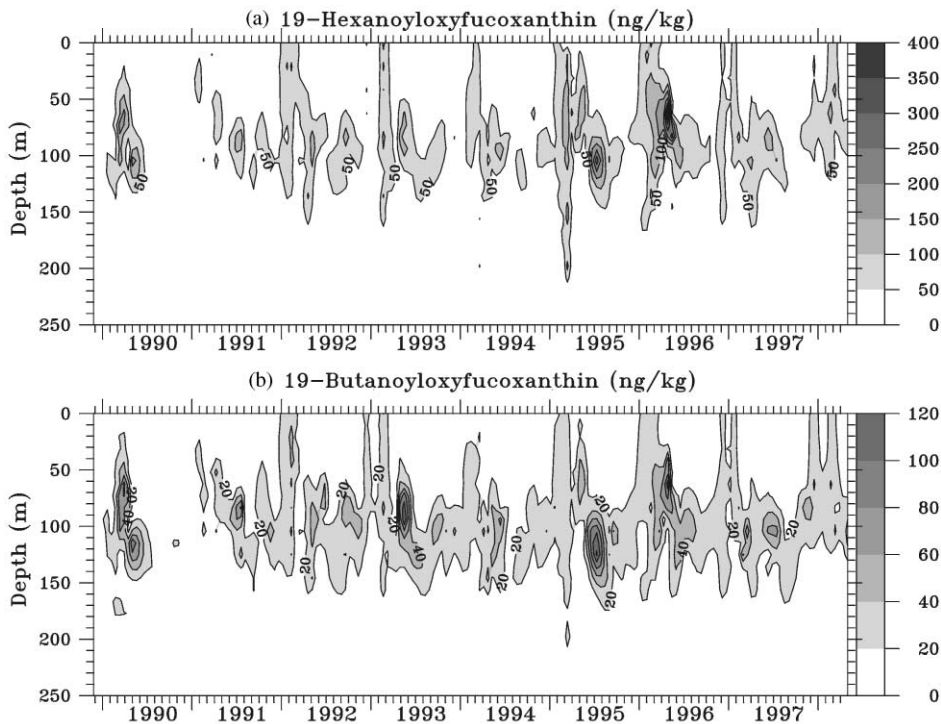


Fig. 13. Time-series contour plots of HPLC-determined pigment concentrations (ng kg^{-1}) at BATS: (a) 19'-hexanoyloxyfucoxanthin, (b) 19'-butanoyloxyfucoxanthin.

Coccolithophores are common eukaryotic phytoplankton in the Sargasso Sea (e.g., Hulbert et al., 1960; Hulbert, 1990) and exhibit pronounced seasonal, interannual, and depth changes in their species composition (Haidar and Thierstein, 2001).

Diatom blooms are rare but occur periodically in the BATS time series, and have been described previously in the Sargasso Sea (Riley, 1957; Hulbert, 1990; Siegel et al., 1990b). Fucoxanthin, which indicates the presence of diatoms, is generally present during spring blooms at all depths (Fig. 14a). Occasionally, fucoxanthin concentrations dramatically increase during late or non-spring bloom periods (e.g., April 1990, May 1993, July 1995) (Fig. 16). In July 1995, Chl *a* increased to 756 ng kg^{-1} , the second highest Chl *a* concentration at the DCML during the entire time series. The increase is evident in all accessory pigments, but most prevalently in the concentration of fucoxanthin, suggesting the presence of a diatom bloom. Analysis of an integrated phytoplankton tow to 100 m on this cruise confirmed the presence of pennate (*Nitzschia* spp.), and centric diatoms (*Chaetoceros* spp., *Rhizosolenia* spp.) These common diatom taxa have been reported in blooms at BATS by others (Malone et al., 1993; Bidigare et al., 1990).

Somewhat surprisingly, some of the most intense diatom blooms occurred in late spring or summertime, months after deep-winter-mixing events (Fig. 16), indicating that nutrient input during deep winter mixing is not a prerequisite for diatom bloom formation. Possibly nutrient inputs via N fixation in symbionts or episodic events, such as mesoscale eddy nutrient injection (e.g., McGillicuddy and Robinson, 1997), allow blooms to occur. A tight coupling between the

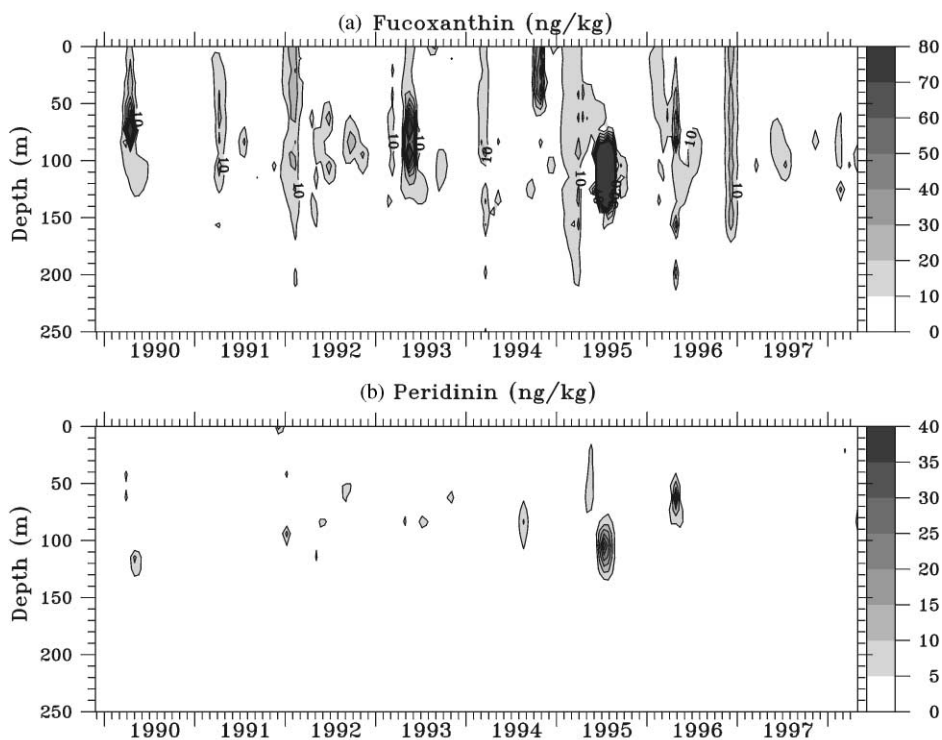


Fig. 14. Time-series contour plots of HPLC-determined pigment concentrations (ng kg^{-1}) at BATS: (a) fucoxanthin, (b) peridinin. *Note: For fucoxanthin, final contour interval is $70\text{--}600 \text{ ng kg}^{-1}$ which includes elevated pigment concentrations in April 1990 (104 ng kg^{-1}), May 1993 (143 ng kg^{-1}), and July 1995 (505 ng kg^{-1}).

accumulation of biogenic silica in the surface waters and its export from the euphotic zone (as seen previously at BATS) suggests that diatom blooms may contribute (significantly) to new production and export of organic matter at this site (Brzezinski and Nelson, 1995; Nelson and Brzezinski, 1997). Although silicic acid ($\text{Si}(\text{OH})_4$) concentrations in the surface waters at BATS are depleted year round, concentrations are never depleted to the low nanomolar levels generally observed for nitrate and phosphate in the surface waters at BATS, suggesting that some other mechanism prevents severe depletion of silica (Brzezinski and Nelson, 1995). Possibly, nitrogen and phosphorus limitation can prevent or slow further uptake of silica by diatoms, or substrate limitation of Si uptake is severe enough (i.e., diatoms are kinetically inefficient) to limit diatom growth (Brzezinski and Nelson, 1995, 1996; Nelson and Brzezinski, 1997). With the possible exception of the April 1990 bloom, these diatom blooms never showed up significantly in the BATS sediment trap carbon and nitrogen flux (contrary to evidence given above for silica), indicating that some of these events may be missed with current sampling frequency. Another possibility is that diatom carbon and nitrogen may be preferentially recycled over biogenic silica in the surface layer (the “silicate pump”; Dugdale et al., 1995) so that the traps record a significant signal in biogenic silica flux, but not in carbon and nitrogen flux.

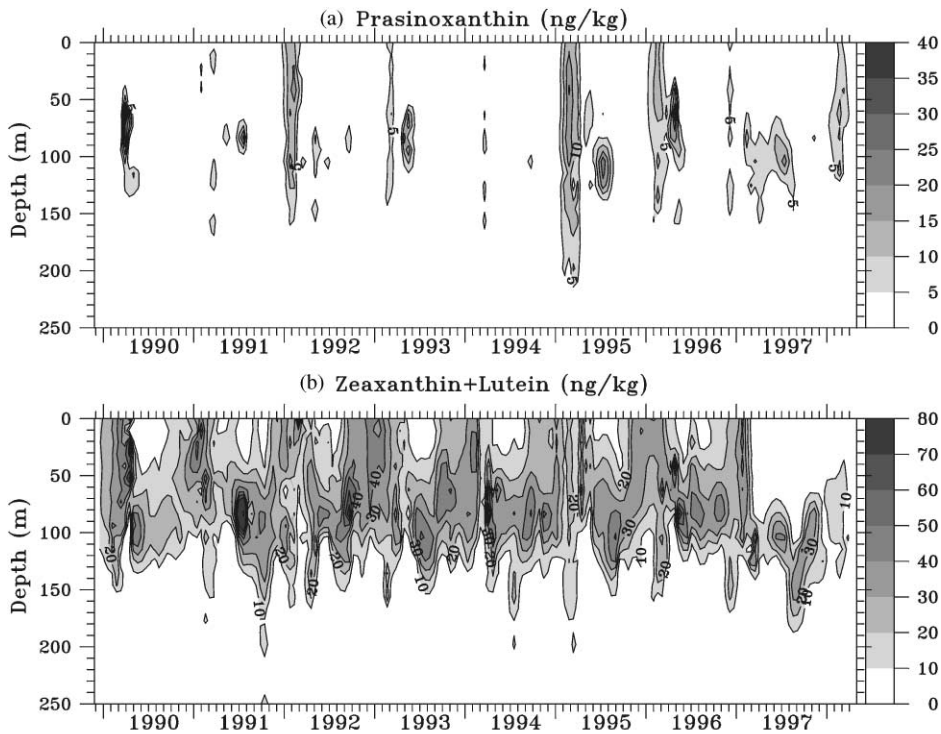


Fig. 15. Time-series contour plots of HPLC-determined pigment concentrations (ng kg^{-1}) at BATS: (a) prasincoxanthin, (b) zeaxanthin + lutein.

Dinoflagellates are less important contributors to the phytoplankton community at BATS, as indicated by the low peridinin concentrations throughout the time series (Figs. 14b and 16). The prasinophyte signature pigment prasincoxanthin is also relatively low during the entire time series, although it occurs from the surface to depth during spring blooms (Fig. 15a).

The prokaryotic picoplankton regularly dominate the phytoplankton community at BATS. Although their abundance varies from year to year, the prochlorophytes consistently become abundant in late spring through early winter throughout the time series, and are usually scarce during spring blooms (Fig. 16). Cyanobacteria contribute significantly during the entire year, often peaking in late spring and summer (Fig. 16). The combined zeaxanthin (a signature pigment of cyanobacteria) plus lutein pigments exhibit high concentrations at the surface during blooms, but are more highly concentrated from 40 to 120 m (Fig. 15b). The importance of the prochlorophyte and cyanobacteria picoplankton in the western Sargasso Sea is evident from their high abundance (Chisholm et al., 1988; Olson et al., 1990a, b, Durand et al., 2001), and their higher productivity compared to the microplankton (Malone et al., 1993). The BATS time series results are similar to those of Olson et al. (1990a), who found prochlorophytes present year round near Bermuda, with lowest concentrations in winter. The prochlorophytes at BATS appear to bloom after the onset of seasonal stratification, and they bloom later and thrive deeper than the cyanobacteria (Olson et al., 1990a). *Prochlorococcus* exhibits better photoacclimative capacity than *Synechococcus* but is more

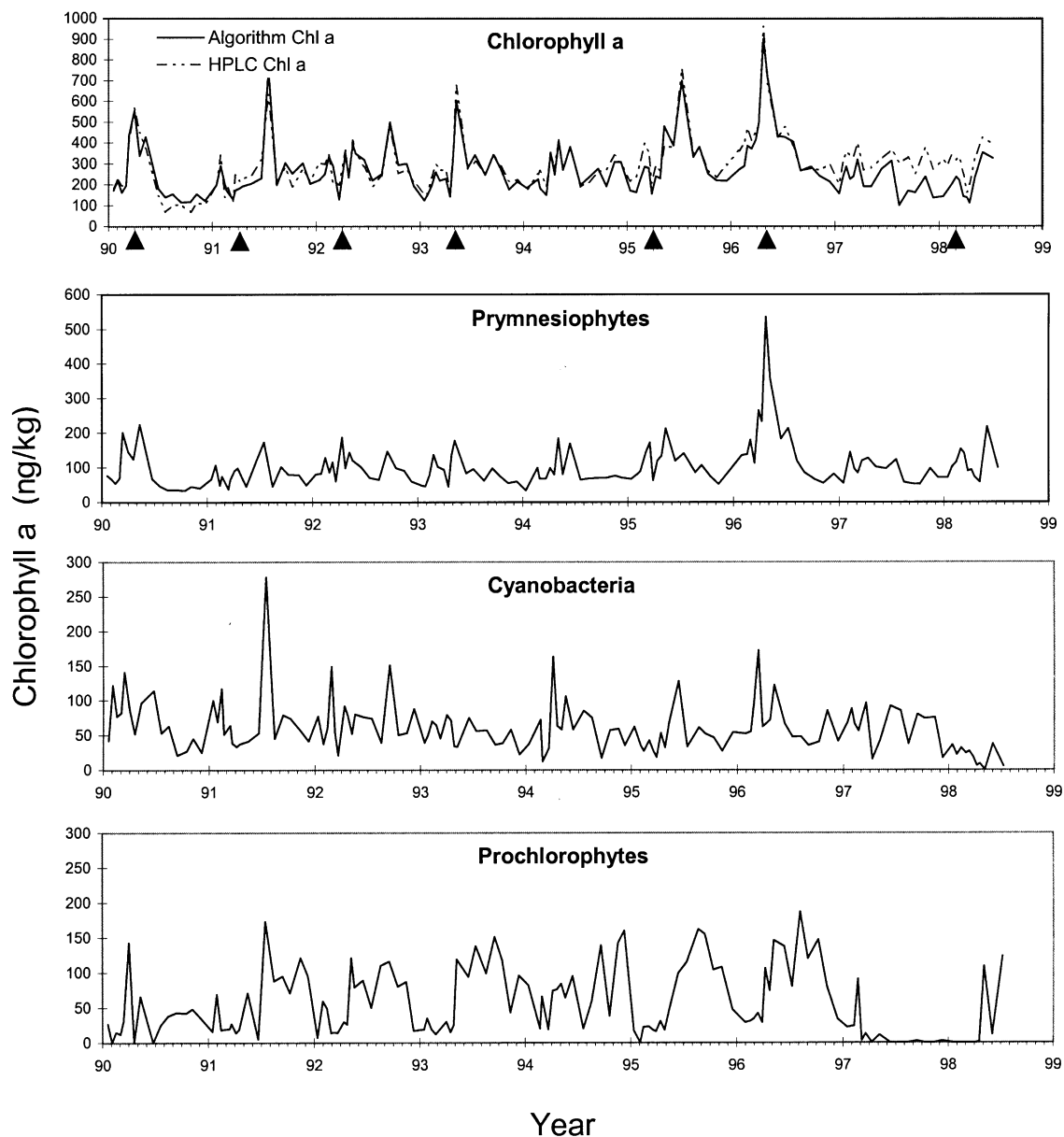


Fig. 16. Time series of Chl *a* contribution of specific phytoplankton taxa to the deep chlorophyll maximum layer as determined from the algorithms of Letelier et al. (1993). The DCML was determined for each cruise from the HPLC Chl *a* maximum. Note: Top panel compares the sum of the taxon-specific Chl *a* concentrations determined from the algorithms (solid line) with the measured total HPLC Chl *a* at the depth of the deep chlorophyll maximum layer (DCML) (dashed line). Arrows indicate spring blooms, determined from maximum integrated primary production. There was no significant spring bloom in 1994 and 1997.

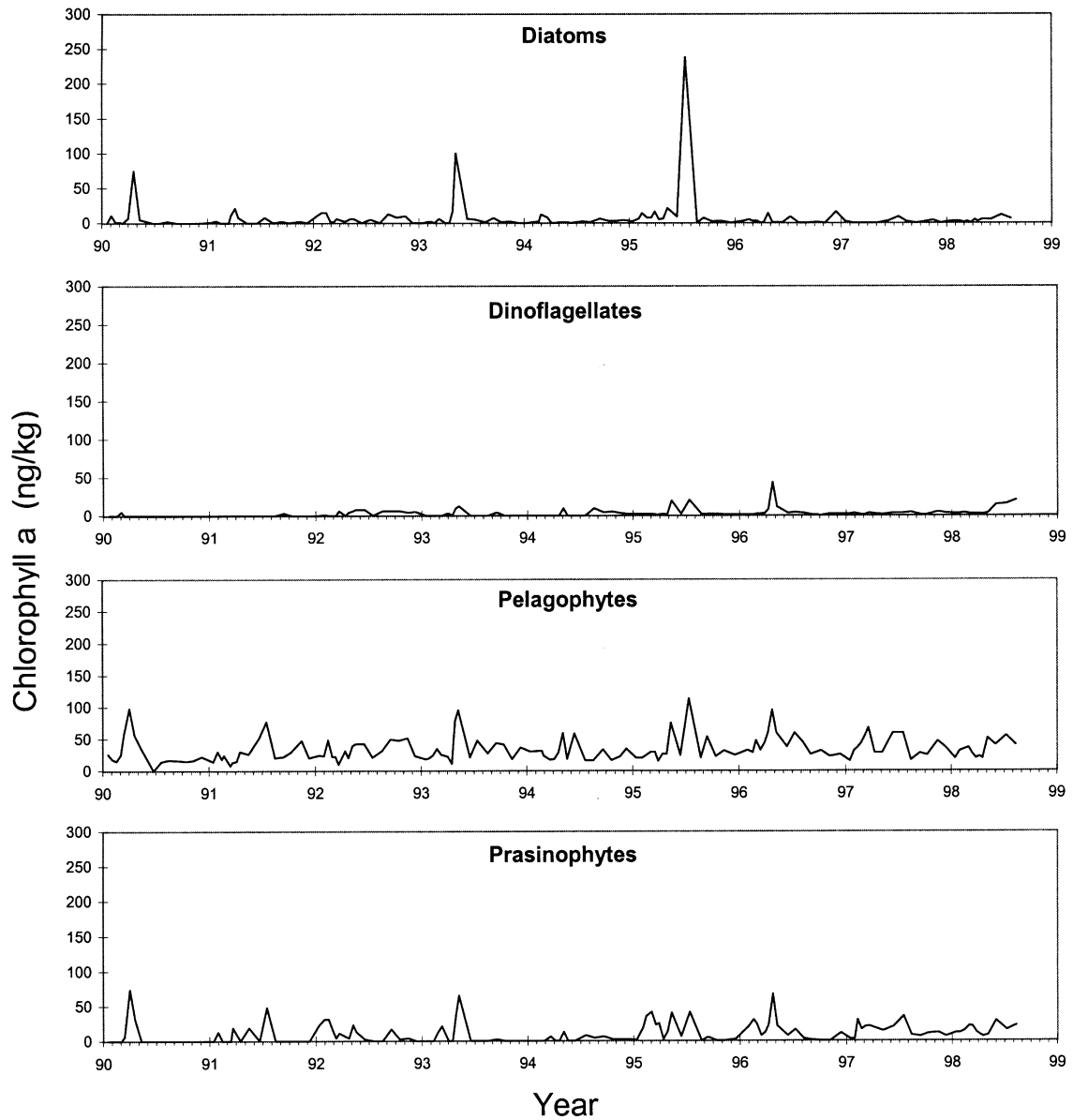


Fig. 16. (continued)

sensitive to N limitation, so is often found deeper in the euphotic zone than *Synechococcus* and closer to the nitracline (Olson et al., 1990a; Vaulot et al., 1990). Cyanobacteria have been previously reported to exhibit the opposite seasonal pattern, with higher concentrations in winter and lower in summer (Olson et al., 1990a). There is significant interannual variation in this pattern at BATS, however, as significant summertime peaks in cyanobacteria abundance often occur (Fig. 16).

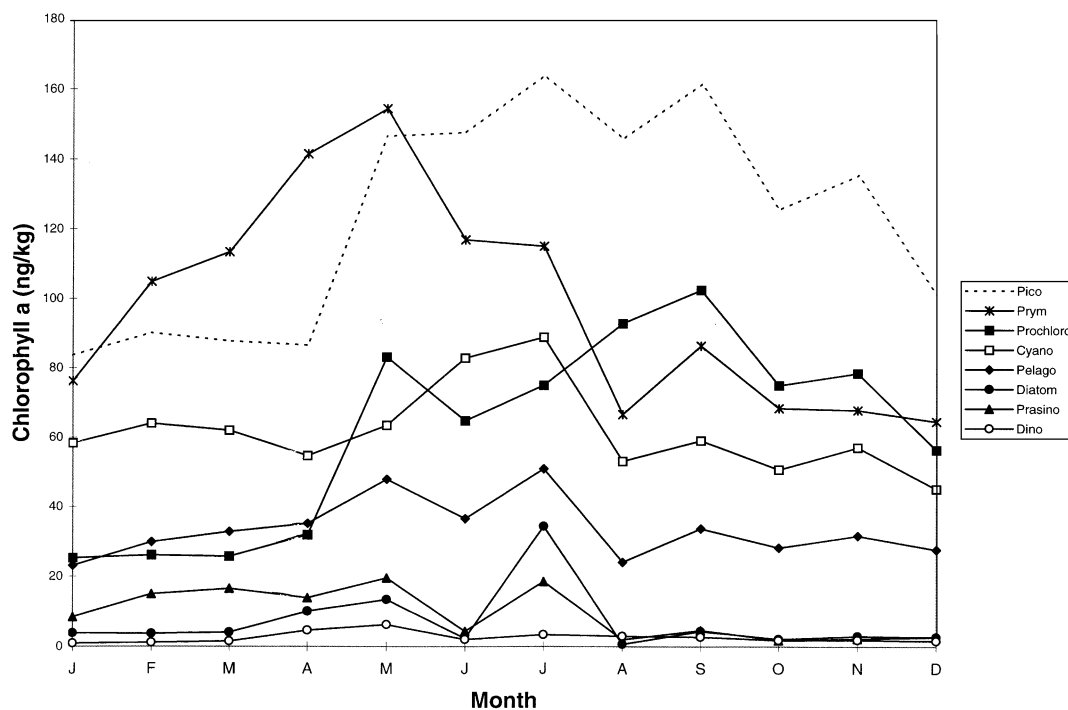


Fig. 17. Composite view of the annual cycle of phytoplankton in the deep chlorophyll maximum layer at BATS, constructed from the monthly mean of the time-series data. Chl *a* contribution of specific phytoplankton taxa to the deep chlorophyll maximum layer was determined from the algorithms of Letelier et al. (1993).

The prochlorophytes exhibit a marked decrease in 1997 compared to the rest of the time series (Fig. 16), as indicated by the virtual disappearance of the pigment chlorophyll *b* (Fig. 12b) used in the algorithm to determine prochlorophyte biomass. In spring 1998 the prochlorophytes begin to appear again. It is unclear what may have caused this decrease, and we believe we have ruled out analytical problems. It is possible that unknown physical forcing or food web shifts tied to the strong 1997 El Niño may have affected the prochlorophyte population.

The taxon-specific Chl *a* contribution at the DCML shows that for much of the 10 yr time series, the increases in Chl *a* concentrations during bloom periods are due to increases in most of the taxa present, rather than any single group (Fig. 16). The same has been found at the HOT station (Letelier et al., 1993). This contradicts the assumption commonly made for most environments and used in ecosystem models: that the addition of chlorophyll beyond certain thresholds, as in blooms, occurs mostly by increase in larger size classes such as diatoms (Raimbault et al., 1988; Chisholm, 1992; Armstrong, 1994; Hurtt and Armstrong, 1996). The mean (± 1 standard deviation) contribution of algal groups to total Chl *a* at the DCML during spring blooms (see arrows in Fig. 16) are: prymnesiophytes ($44 \pm 9\%$), cyanobacteria ($17 \pm 4\%$), prochlorophytes ($12 \pm 9\%$), pelagophytes ($11 \pm 3\%$), prasinophytes ($9 \pm 3\%$), diatoms ($6 \pm 7\%$), and dinoflagellates ($2 \pm 2\%$). The diatom blooms that apparently occurred in April 1990, May 1993, and July 1995 at BATS are the exception rather than the norm, although they are occasionally important (e.g., the July 1995

diatom bloom accounted for 34% of the total Chl *a* present in the DCML). During non-bloom seasons at BATS, the important biomass components of the DCML are prymnesiophytes, prochlorophytes, and cyanobacteria. The same is generally true when the biomass is integrated to 140 m (data not shown). Letelier et al. (1993) used accessory pigments as markers of time-dependant changes in specific groups associated with the persistent DCML at the HOT station. At HOT, the algal groups that contributed > 95% of total Chl *a* at DCML were *Prochlorococcus* (39%), cyanobacteria (24%), prymnesiophytes (22%), and chrysophytes (= pelagophytes) (13%) (Letelier et al., 1993).

Although significant interannual variability exists, results indicate a seasonal succession of phytoplankton at BATS, as shown by a composite of the monthly mean of the time-series data in the DCML (Fig. 17). At the depth of the DCML, prymnesiophytes dominate the spring and early summer seasons, while picoplankton (prochlorophytes and cyanobacteria) become dominant in late spring through winter. Cyanobacteria are present year round, becoming slightly more abundant in late summer, while prochlorophytes dominate in late summer through winter. A shift from surface *Synechococcus* to deep prochlorophyte picoplankton is characteristic of the Sargasso Sea (Olson et al., 1990a; Malone et al., 1993). Pelagophytes, prasinophytes, and dinoflagellates are present year round, with only the pelagophytes contributing significantly. Diatom blooms are rare, but occasionally occur in spring or summer.

Evidence also exists for rapid succession of phytoplankton during the spring bloom in the Sargasso Sea. Bidigare et al. (1990) showed that high fucoxanthin indicated a diatom-dominated community in the early stages of the bloom, replaced in later stages with a more diverse community of prymnesiophytes, cyanobacteria, dinoflagellates, prasinophytes, and diatoms. Changes in the assemblage occurred with depth as well, with cyanobacteria and diatoms in upper layers, prymnesiophytes at intermediate depths, and green algae (including prasinophytes) deeper still (Bidigare et al., 1990). Although seasonal succession between eukaryotic and prokaryotic picoplankton occurs in the BATS time series, it is surprising that the relative composition of the eukaryotic phytoplankton does not change more dramatically, given the changes in physical forcing in winter deep mixing and spring/summer stratification, and the many different groups of eukaryotic algae that are present, albeit in low abundance. In addition, Goericke (1998) and Goericke and Welschmeyer (1998) note no difference in growth rates of phytoplankton between summer and winter periods at the OFP station near BATS. This suggests that the phytoplankton community, and especially its eukaryotic component, is resilient to changes in physical forcing (Goericke, 1998). The result is a characteristic community shift in all phytoplankton taxa at BATS during bloom periods, albeit with an occasional diatom bloom occurring in spring or summer.

3.4. Bacterioplankton dynamics

In oligotrophic and subtropical systems such as BATS, bacterioplankton (both heterotrophic and photoautotrophic) have been shown to dominate the living biomass and play a major ecological role within the microbial food web (Cho and Azam, 1988; Dortch and Packard, 1989; Fuhrman et al., 1989; Caron et al., 1995a; Buck et al., 1996; Carlson et al., 1996). Although significant interannual variability exists in both bacterial production and biomass at BATS (Fig. 18a and b), several consistent patterns can be observed (both spatially and temporally). For example, a subsurface maximum in bacterial production occurs between 20 and 80 m (Fig. 18a),

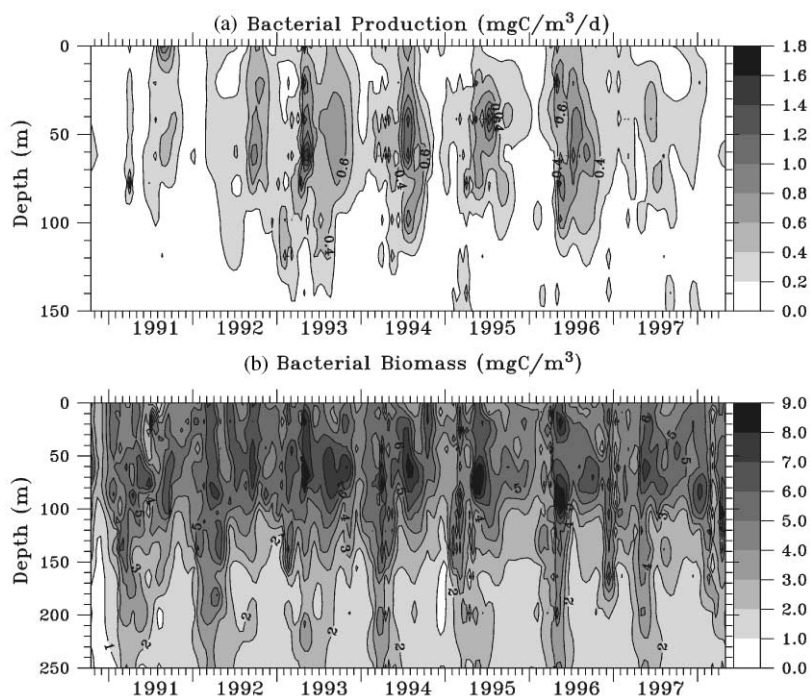


Fig. 18. Time-series contour plots of (a) bacterial production, and (b) bacterial biomass. Carbon conversion factors used are 10 fg C cell^{-1} and a thymidine conversion factor of $1.63 \times 10^{18}\text{ cells mol}^{-1}$ thymidine (Carlson et al., 1996).

which erodes in the autumn along with a decrease in integrated bacterial production (Fig. 19a). A subsurface maximum in bacterial biomass of $5\text{--}9\text{ mg C m}^{-3}$ develops between 40 and 80 m each year during the late spring, and persists throughout the summer (Fig. 18b). As the season progresses to autumn, the subsurface bacterial biomass maximum begins to erode and integrated stocks within the surface 250 m also decline (Figs. 18b and 19b). While destruction of the subsurface maximum in bacterioplankton biomass and production is largely due to deep winter mixing, the decline in integrated bacterioplankton stocks in the surface 250 m also must result from removal of bacterial biomass by grazers, viral lysis, or advection, as mixing is normally not this deep.

The contribution of inactive bacterial populations (e.g., Kirchman et al., 1982; Zweifel and Hagstrom, 1995; Choi et al., 1996) and the inclusion of photosynthetic prokaryotes such as *Prochlorococcus* and *Synechococcus* (Chisholm et al., 1988; Olson et al., 1990a; Li et al., 1992; Sieracki et al., 1995; Buck et al., 1996) are artifacts that could lead to overestimates of the contribution of viable bacterial biomass in the Sargasso Sea. The greatest overestimation of heterotrophic bacterioplankton due to the inclusion of cyanobacteria (using traditional methods of enumeration by epifluorescence microscopy) is likely to occur at the depth of the in situ chlorophyll maximum (Olson et al., 1990b, Sieracki et al., 1995). However, the summertime bacterial subsurface maximum at BATS is located above the deep chlorophyll maximum; thus the greatest overestimation of heterotrophic bacterial biomass would occur at a depth where total bacterioplankton biomass is already low. Studies using flow and image cytometry have demonstrated that heterotrophic bacterioplankton stocks dominate prokaryote abundance and contribute significantly to

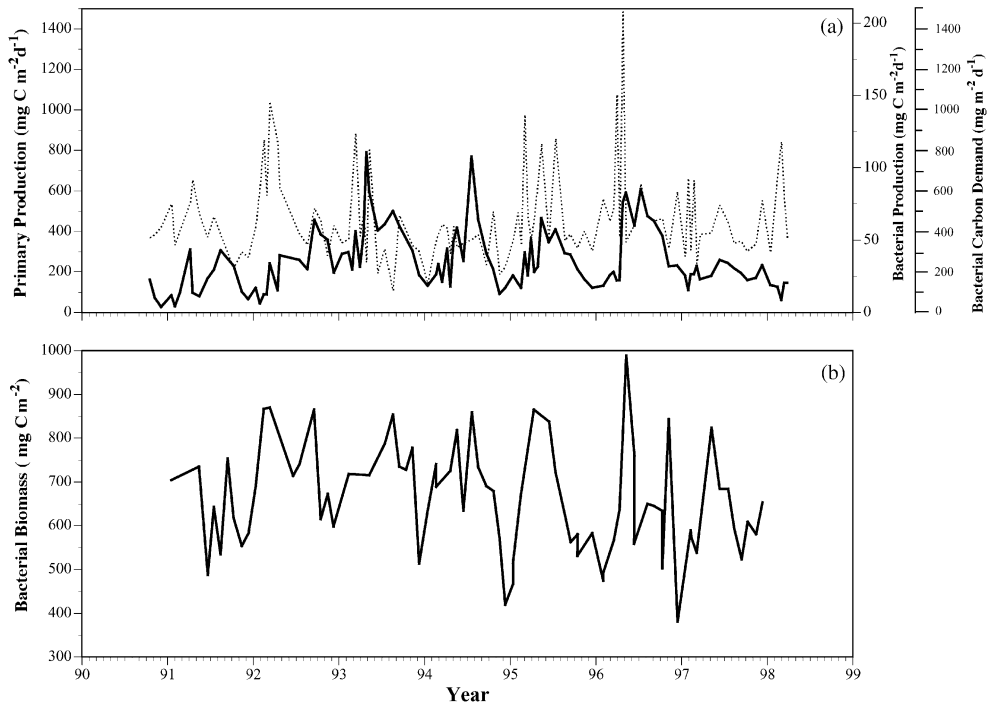


Fig. 19. (A) Integrated primary production (dashed line) compared to integrated bacterial production and bacterial carbon demand (BCD) (solid line) (0–140 m), and (B) integrated bacterial biomass (0–250 m). BCD was calculated assuming a bacterioplankton growth efficiency of 14%.

living biomass in the subtropical surface ocean (Sieracki et al., 1995; Buck et al., 1996). These studies point to the ecological importance of heterotrophic bacterioplankton and their potential to process large amounts of carbon in the open ocean.

In addition to the dynamics observed within the euphotic zone, seasonal variability also can be observed from the base of the euphotic zone (100 m) down to at least 250 m. During deep convective mixing and the spring bloom, elevated concentrations of bacterial biomass occur in the deeper 100–250 m layer (Fig. 18b). These deep-layer populations persist at elevated concentrations of 2–5 mg C m⁻³ for several months and then decrease to background concentrations of < 2 mg C m⁻³ by June or July. This increased concentration of bacterial biomass also covaries with the introduction and subsequent removal of dissolved organic carbon (DOC) within this 100–250 m layer. Oxygen stocks in the 100–250 m layer also decrease with DOC stocks (Hansell and Carlson, 2001). These data suggest that microbial degradation of DOC may partly be responsible for the decrease in oxygen concentrations. Bacterial production measurements below 140 m at BATS, initiated in 1998, will allow us to evaluate the activity of bacterioplankton within this layer.

Bacterial production and biomass accumulation covary with the development of a subsurface maximum in chromophoric (colored) dissolved organic matter (CDOM; Nelson et al., 1998). As bacterioplankton are generally considered to be dominant remineralizers of organic material,

Nelson et al. (1998) hypothesize that CDOM is produced as a by-product of bacterioplankton breakdown of DOC. They propose that the summertime subsurface maximum of CDOM results from bacterial production at depth and photobleaching at the surface. Siegel and Michaels (1996) show that CDOM absorption of UV light (photochemically active and biologically damaging) and blue light (photosynthetically active) is an important part of the photon budget. Little is known about the chemical composition of oceanic CDOM. Determann et al. (1996) used fluorescence signals to identify tryptophan and tyrosine-like compounds as components of CDOM in the eastern Atlantic. Likely components produced by bacterioplankton might include aromatic amino acids, oligopeptides, humic acids, and microsporine-like amino acids. If CDOM is a by-product of microbial production, then this production in combination with the redistribution of CDOM by mixing could reduce the impact of UV exposure to organisms living near the surface, and potentially decrease light availability for photosynthesis. More work is needed to verify a link between bacterial processes and CDOM dynamics.

Seasonal composites of integrated bacterioplankton stocks and rates across the euphotic zone exhibit little variability during the spring phytoplankton bloom period (February–April) (Fig. 20), despite up to a five-fold increase in primary production variability (Fig. 19a) and significant seasonal accumulation in DOC in the surface 250 m (Carlson et al., 1994, 1998; Hansell and Carlson, 1998). Bacterial biomass, production, and specific growth rates (μ) are highest after the spring-bloom period (Fig. 20). The existence of a large, non-living (or dormant) subpopulation (Kirchman et al., 1982) could mask the response to a growing population and result in underestimation of μ . Thus these estimates represent the lower bounds of the bacterial-specific growth rate at BATS. Integrated bacterial production rates, a measurement that only assesses production of active cells, also exhibited a lag of several weeks to months after peaks in primary production in five of the seven years monitored (Fig. 19b). This apparent lag suggests that bacterioplankton growth is limited even in the presence of elevated primary production and DOC accumulation in the upper 250 m. Some studies suggest that the quality of the DOM produced during the spring period may not be available to bacterioplankton on short time scales (Carlson and Ducklow, 1996; Carlson et al., 1998). In addition, in some oceanic systems bacterioplankton are limited by availability of labile organic carbon and are thus energy-limited (Kirchman et al., 1990; Kirchman, 1990). Others suggest that bacterioplankton production is limited by the availability of inorganic nutrients such as phosphate (Cotner et al., 1997; Rivkin and Anderson, 1997).

Size structure and composition of the plankton community may largely control the quality of DOM produced and could affect production of bacterioplankton biomass. The plankton community at BATS is dominated by picoplankton and thus a microbial food web. Within the surface 100 m bulk DOC stocks accumulate as the water column stratifies, and remain high and relatively constant throughout the summer and early fall (Hansell and Carlson, 2001). The DOC that accumulates in the upper euphotic zone is resistant to microbial degradation and thus becomes available for export out of the euphotic zone during deep-mixing events (Carlson et al., 1994). These observations of a picoplankton-dominated system and sequestration of carbon as semi-labile DOC support the hypothesis of Legendre and Le Fevre (1995), which states that production and processing of organic material through the microbial food web (picoautotrophs as well as micrograzers and bacterioplankton) could play a significant role in the sequestration of DOC via the production of refractory DOC. However, the mechanisms associated with this phenomenon are not fully understood.

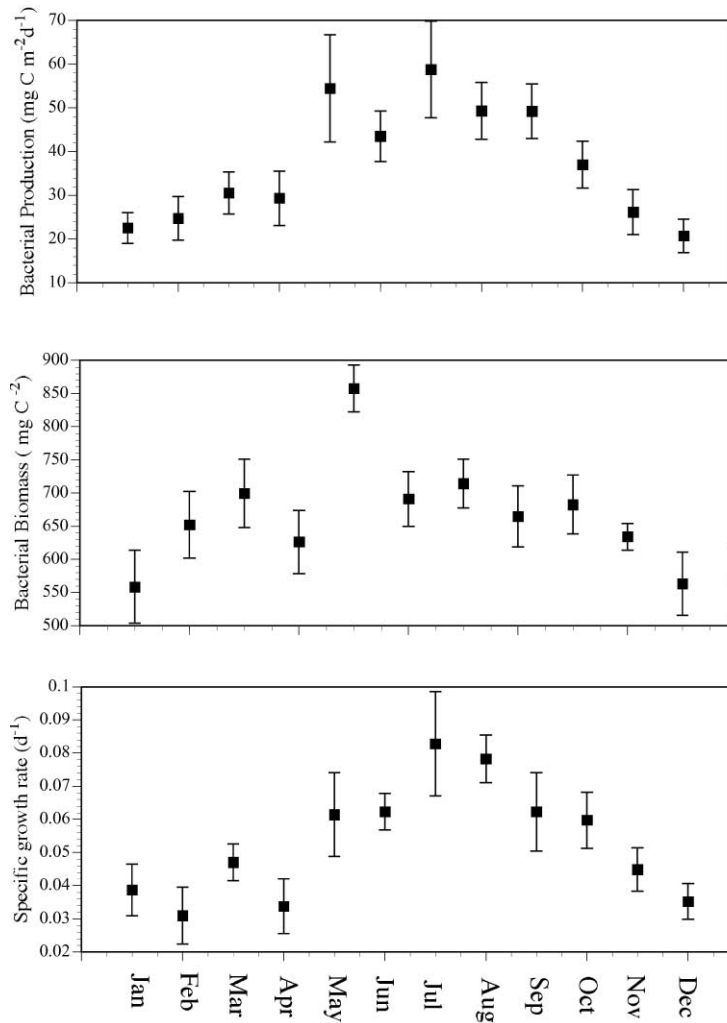


Fig. 20. Seasonal composites of integrated bacterioplankton stocks and rates over the euphotic zone. Error bars = 1 standard error.

While the supply of organic or inorganic nutrients ultimately may limit bacterioplankton production in the Sargasso Sea, we still observe a 2–3 fold increase in integrated bacterial production (May–September; Figs. 19a and 20a) and specific growth rates (Fig. 20c) during the summer relative to winter–spring. During summer, DOC stocks appear to resist rapid microbial degradation in the upper euphotic zone. This indicates that bacterioplankton production is supported by a rapidly overturning and freshly produced labile DOM pool rather than a slowly degraded, semi-labile pool. In an oceanic system this labile material must come from autochthonous sources such as direct phytoplankton exudation (Lignell, 1990; Bronk et al., 1994; Karl et al., 1998), zooplankton sloppy feeding and excretion (Banse, 1992; Nagata and Kirchman, 1992), particle solubilization (Smith et al., 1992, 1995), viral lysis (Proctor and Fuhrman, 1990, 1991), and

nitrogen fixation (Karl et al., 1997). The increase in summertime bacterioplankton production may result from a shift in the supply rate of labile DOM, perhaps from a rarely sampled portion of the phytoplankton community. Large phytoplankton such as *Pyrocistis* sp., *Halosphaera* sp., *Rhizosolenia alata*, and *Ethmodiscus rex* are ubiquitous in oligotrophic regions, including the Sargasso Sea (Villareal and Lipschultz, 1995) but are rarely sampled for ^{14}C incubation (via Niskin or GO-Flo bottles). Goldman et al. (1992) demonstrated that large diatoms release DOC during stationary growth. The previously discussed diatom bloom in summer 1995 resulted in elevated bacterioplankton production in the surface 60 m, but no DOC accumulation was observed. This suggests that the diatom bloom produced DOM of a quality amenable to rapid bacterioplankton utilization. Nitrogen fixers such as *Trichodesmium* are also abundant in the Northwestern Sargasso Sea (Orcutt et al., 2001) and may contribute to increased labile carbon flux during periods when the water column is most stable. An alternative explanation may be that the summer bacterial population uses labile DOM at a greater efficiency than the winter population.

Ratios of bacterioplankton production (BP) to primary production (PP) are often used to estimate how much of the carbon fixed into organic particles eventually is processed by bacterioplankton. These ratios calculated on a seasonal basis from 1991 to 1998 range from 0.01 to 0.06 in winter (December–February), 0.02 to 0.1 in spring (March–May), 0.04 to 0.23 in summer (June–August), and 0.04 to 0.18 in fall (September–November). These values are similar to values of 0.02–0.15 previously reported for the Sargasso Sea (Carlson et al., 1996). While the BP:PP ratio is significantly lower at the BATS site compared to the global BP:PP ratio of 0.31 (Cole et al., 1988), one must consider the bacterioplankton growth efficiency (BGE) in order to estimate the flux of carbon through bacterioplankton, or bacterial carbon demand (BCD; essentially gross bacterial production, calculated by dividing BP by BGE). Studies that compare changes of bacterial biomass with changes in substrate concentration or respiratory by-products have demonstrated that BGE is lower than the often-cited 50% (Jahnke and Craven, 1995; Carlson and Ducklow, 1996; delGiorgio et al., 1997). In the present analysis we used a BGE of 14% as determined by Carlson and Ducklow (1996) for the Sargasso Sea to calculate BCD. In Fig. 19a, integrated BCD is overlaid estimates of integrated primary production. In summer the BCD is most closely coupled to primary production. However, there are periods of significant uncoupling between net primary production and BCD, as in winter and spring-bloom events when primary production is greater than BCD. There are also periods in the timeseries wherein BCD exceeds PP (e.g., summer 1993, 1994), indicating that bacterial respiration and production are supported by previously accumulated labile DOM, an observation also made by del Giorgio et al. (1997) in oceanic systems. In order to support a higher BCD (when BCD is a greater percentage of net PP), either a greater portion of gross primary production is partitioned as DOC (Hansell et al., 1995; Karl et al., 1998) or the bacterial carbon demand is over-estimated due to the use of an inappropriately low bacterial growth efficiency in the calculation of BGE. These are questions presently being addressed at the BATS site.

3.5. Protozoan and zooplankton dynamics

Previous work on partitioning of plankton carbon biomass in the Sargasso Sea and subtropical North Atlantic has shown that most of the carbon must be cycling through the microbial loop.

Bacterial biomass has been found approximately equal to or greater than phytoplankton biomass (Li et al., 1992; Caron et al., 1995a; Fuhrman et al., 1989; Buck et al., 1996; Carlson et al., 1996). Most of the heterotrophic carbon biomass at BATS is contained within the bacteria and nanozooplankton (protozoa 2–5 μm), which average about 70% of heterotrophic carbon in the euphotic zone (Roman et al., 1995; Caron et al., 1995a). Studies of the microbial food web near BATS suggest that carbon is recycled efficiently within the microbial loop; thus little energy is passed on as food for metazoa (Caron et al., 1999). However, models of the effects of biological community structure on export predict that large organisms are more important than small in export because of the high sinking rates of large cells and the short food webs that lead from large suspended organisms to large sinking particles (e.g., Michaels and Silver, 1988). Thus the larger heterotrophic plankton play an integral role in the flux of material out of the euphotic zone.

Protozoans are abundant at BATS, including the relatively large planktonic sarcodines (acantharia, radiolaria, and foraminifera), which form a conspicuous component of the plankton community (Michaels et al., 1995). Many of these sarcodines are symbiont-bearing (mixotrophic) and exhibit high rates of primary production compared to equivalent volumes of surrounding seawater (Caron et al., 1995b). Production within sarcodine symbioses constitutes a significant fraction of primary production of organisms $> 70 \mu\text{m}$, yet total symbiont production contributes little (generally $< 1\%$) to total primary production at BATS. Despite this, sarcodine fluxes are a significant component of sinking flux at BATS, averaging 15.5% of the organic C flux (Michaels et al., 1995). Occasionally, a single species dominates (e.g., the foraminifera *Globorotalia truncatoides*, reaching 40% of the total trap flux (Michaels et al., 1995). On average, fecal pellets constitute 8.5% of the flux, with the largest component being marine snow (detritus — including discarded larvacean houses and many other aggregate types), which on average constitutes 73.6% of the flux (Michaels et al., 1995).

Time-series studies of zooplankton seasonal dynamics at BATS date back several decades (Menzel and Ryther, 1961b; Deevey, 1971; Deevey and Brooks, 1977), as do other zooplankton studies (e.g., Moore, 1949, 1950; Sutcliff, 1960; Beers, 1966). More recently, the ZOOSWAT project compared zooplankton in the spring-bloom period (March/April) with the summer period (August) (Roman et al., 1993, 1995). The most comprehensive time-series study of seasonal and interannual variation in zooplankton biomass at BATS is presented in this issue (Madin et al., 2001). A maximum in zooplankton biomass occurs in March/April generally following peaks in primary production (after injection of nutrients from deep winter mixing), although there is significant interannual variation. After shoaling of the thermocline and reduction of phytoplankton stocks, zooplankton stocks decrease, although occasional summer zooplankton biomass peaks occur (Madin et al., 2001). Zooplankton biomass is reported to be as much as 4–6 times greater (Deevey, 1971; Menzel and Ryther (1961b) — for upper 500 m), and more than 3 times greater (Roman et al., 1993; Madin et al., 2001; for upper 200 m) in March/April compared to August. Roman et al. (1995) report that micro-, meso-, and macrozooplankton together average about 30% of the integrated heterotrophic carbon biomass at BATS in spring and summer. While the macrozooplankton biomass was more than 3-fold higher in spring than summer, the mesozooplankton biomass was approximately 3-fold higher in summer than spring (Roman et al., 1993). Thus, smaller zooplankton dominate in the summer, and may be more efficient at utilizing the small phytoplankton and protozoa that also dominate that time of year (Roman et al., 1993). Average estimated flux due to

macrozooplankton fecal pellets at BATS in the spring was 65% of carbon flux at 150 m (estimated from a single cruise, Roman et al., 1993). Thus, while macrozooplankton are only a small part of the biomass, they are likely to contribute significantly to carbon flux from the euphotic zone by production of rapidly sinking fecal pellets (Fowler and Knauer, 1986; Small et al., 1989; Altabet and Small, 1990).

Another mechanism by which zooplankton contribute to carbon and nutrient cycling and fluxes at BATS is via active transport of biogenic material by vertical migration. Zooplankton biomass in the upper 200 m at BATS on average nearly doubles at night due to vertically migrating zooplankton (Madin et al., 2001). As elsewhere, studies in the Sargasso Sea show that vertically migrating zooplankton can actively transport a substantial amount of dissolved inorganic carbon and nitrogen to deep water (via respiration and excretion), which can be significant relative to the passive flux of sinking particulate organic matter measured with sediment traps (Longhurst et al., 1989, 1990; Dam et al., 1995; Steinberg et al., 2001). Estimates of active transport due to vertical migration in these studies range from 8 to 70% of the sinking POC flux, and from 8% to more than 80% of the sinking PON flux at 150 m. Recently, Steinberg et al. (2001) demonstrated that active transport of dissolved organic carbon by migrators is also significant at BATS. They suggest that during most of the year when deep mixing does not occur, diel migration by zooplankton makes a significant supply of DOC available for use by the microbial community at depth. New estimates of active transport by migrants may help resolve observed imbalances in the C budget at BATS (Michaels et al., 1994a), but the magnitude depends highly on the biomass of the migrating community.

3.6. Conclusion and a challenge for the future

Oceanographic time series provide an integral tool for investigating ocean biogeochemistry and its effects on the carbon cycle. A decade of measurements at BATS clearly illustrates the structure of the biological community and its effect on biogeochemical cycling, and also shows that the biogeochemistry of the upper ocean at BATS is highly variable on seasonal, annual, and interannual timescales. This biogeochemical variability is linked to physical forcing, which in turn is ultimately tied to larger-scale climatic changes. Climatological forcing of ocean ecosystems by ENSO has been demonstrated in the Pacific Ocean (Karl et al., 1995). Likewise, in the deeper ocean of the Sargasso Sea, relationships between physics and climate can be clearly demonstrated (e.g., Curry et al., 1998). However, in the upper ocean, the inherent mesoscale variability of the Sargasso Sea potentially masks the impact of atmospheric forcing over shorter timescales. Despite these problems, modes of climate variability, such as the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO), have been shown to impact the interannual variability of hydrography and biogeochemistry at BATS (Bates, 2001). For example, anomalies of temperature, integrated primary production, mixed-layer depth, and CO₂ concentrations at BATS are strongly coupled to variability of NAO, whereas anomalies of salinity and alkalinity are strongly linked to ENSO phenomena (Bates, 2001). As the BATS time-series record extends, our ability to observe the relationship between climate and biogeochemistry improves. One of our future challenges, through modeling and other efforts underway at BATS, is to increase our ability to understand the role of the oceans in the global carbon budget and improve our ability to predict the effects of climate change on ecosystems.

3.7. Data availability

All of the data from the BATS program and many of the data from the Hydrostation S program are made available publicly over the internet and through the National Ocean Data Center (NODC). The public release of the data is generally within 12 months of collection and frequently much sooner. The BATS data can also be accessed via the World-Wide-Web by starting at the BBSR home page (URL: <http://www.bbsr.edu>) and following the links to the BATS data repository, or can be received from the NODC office at Woods Hole Oceanographic Institution. Hard copies of the data reports and the methods manual are available from the US JGOFS Planning Office at Woods Hole Oceanographic Institution or through the authors. After 1998, annual data reports are available as Adobe Acrobat PDF files.

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