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# Increased ocean carbon export in the Sargasso Sea is countered by its enhanced mesopelagic attenuation

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## Abstract

Photosynthetic $CO_2$ uptake by oceanic phytoplankton and subsequent export of particulate organic carbon (POC) to the ocean interior comprises a globally significant biological carbon pump, controlled in part by the composition of the planktonic community. The strength and efficiency of this pump depends upon the balance of particle production in the euphotic zone and remineralization of those particles in the mesopelagic (defined here as depths between 150 and 300 m), but how these processes respond to climate-driven changes in the physical environment is not completely understood. In the Sargasso Sea, from ~1996–2007, we have observed a decade-long >50% increase in euphotic zone integrated autotrophic biomass (estimated from chlorophyll *T*Chl-*a* from the surface ocean, prokaryotic phytoplankton, primary production and shallow (150 m) POC export coinciding with a shift in the mean phase of the winter North Atlantic Oscillation (NAO) from consistently positive to neutral but variable. During this same period mesopelagic POC flux attenuation has doubled such that carbon sequestration below 300 m, the maximum winter/spring ventilation depth, has not changed. The increased mesopelagic POC attenuation appears mediated by changes in plankton community composition and metabolic activity in both the euphotic and mesopelagic zones which are counter to extant hypotheses regarding inter-relationships between phytoplankton community composition, productivity and carbon export, and have significant impacts on how the Sargasso Sea ecosystem, at least, is modeled. Moreover, these time-series observations suggest that processes in the euphotic zone and mesopelagic are tightly coupled and should be considered together in future research.

## 1 Introduction

Marine phytoplankton are responsible for approximately 50% of global primary production (Field et al., 1998), most of which occurs in the oligotrophic ocean gyres, and so



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even small variations in primary production can have significant impacts on the global oceanic carbon cycle. A fraction of this production is sequestered in the ocean interior through both active and passive settling of particulate material and has been termed the biological carbon pump (Volk and Hoffert, 1985). Globally, the biological carbon pump sequesters ~2500 petagrams $y^{-1}$ from the surface ocean or ~3.5 times the atmospheric carbon pool (Gruber and Sarmiento, 2002). The strength and efficiency of the biological carbon pump in a given oceanic regime are controlled by a complex array of processes involving the production of particulate organic carbon (POC) in the euphotic zone and its remineralization with depth through the mesopelagic zone (Buesseler et al., 2007; Neuer et al., 2002) (here defined as 150–300 m). Phytoplankton diversity plays a central, but debated, role in POC production and carbon export efficiency. For example, mineral-ballasted phytoplankton like diatoms and coccolithophores are thought to disproportionately enhance the strength and efficiency of carbon export due to their mineral frustules which enhance sinking rates thereby reducing contact time in the upper ocean (e.g. Armstrong et al., 2002; Michaels and Silver, 1988). In contrast, it has been suggested that all phytoplankton, even picoplankton, contribute to carbon export in direct proportion to their contributions to primary production (Richardson and Jackson, 2007). A key point in reconciling these two disparate hypotheses is that the mechanisms of export differ; i.e. export of mineral phytoplankton is likely dominated by gravitational sinking while picoplankton are packaged into larger particles via grazing and/or aggregation. Resolving these two hypotheses is important to predicting future carbon sequestration in the oceans given that the oligotrophic gyres are dominated by non-mineral ballasted phytoplankton and account for ~60% of global carbon export.

In addition to complexities of phytoplankton diversity on the spatial scale, temporal variability needs to be considered given the non-steady state conditions characterized by the present-day increase of atmospheric $CO_2$ and accompanying increase of global ocean temperatures and stratification. Oligotrophic gyres previously considered "static" on a year-over-year basis, due largely to a lack of data, are now recognized to display substantial temporal variability (e.g. Karl et al., 2002; Maranon et al., 2003). Behrenfeld



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et al. (2006) show that global ocean net primary production and phytoplankton biomass (from 1997–2006), driven largely by changes within the oligotrophic gyres, decreased from 1999–2006 in response to increased water column stratification; evaluated as an increase in the multivariate El niño index. In contrast, or perhaps exemplifying the confounding temporal/spatial interactions, Karl et al. (2001) show that primary production and phytoplankton biomass in the North Pacific Subtropical Gyre, at the Hawaii Ocean Time-series and VERTEX sites, increased over the past three decades in response to a hypothesized increase in stratification, which was linked to a shift in the phase of the Pacific Decadal Oscillation (POD). Moreover, just within the two decades of the Hawaii Ocean Time-series (HOT) program, Corno et al. (2007) have observed a continued trend for increasing primary production that also has been linked to the ENSO/PDO and changes in stratification. Corno et al. (2007) also have observed that phytoplankton biomass (*T*Chl-*a*) and primary production increased in concert suggesting the increased primary production was due to increasing biomass rather than changes in the physiology of the resident autotrophs. This increase in primary production and biomass occurred with a shift from larger eukaryotes to smaller prokaryotes, but data are lacking for this site to evaluate consequent changes in the biological carbon pump on the same three decade timescale. Recent modeling activities have attempted to capture these trends in euphotic zone integrated primary production at both time-series sites (Saba et al., in review) with limited success, thus highlighting the need to gain better understanding of processes below the depths which satellites can see into the ocean.

For the past two decades biogeochemical measurements have been made in the northwestern Sargasso Sea as part of the Bermuda Atlantic Time-series Study (BATS; Steinberg et al., 2001). The Sargasso Sea, on an annual basis, is a net sink (net air-to-sea flux) for $CO_2$ due to the strength of biological carbon sink during the winter/spring period which offsets the strong $CO_2$ source in the summer (Bates, 2007). Using the Sargasso Sea as a natural laboratory, we examined temporal variability of phytoplankton abundance, primary production, carbon export and its attenuation below the euphotic zone to evaluate the strength and efficiency of the winter/spring biological



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carbon pump in response to a shift in the phase of the dominate climate mode for the North Atlantic, the North Atlantic Oscillation.

## 2 Materials and methods

### 2.1 Sampling scheme and biogeochemical rate and stock measurements

Monthly hydrographic and biogeochemical measurements have been collected at the BATS site since October 1988. Starting in January 1990, biweekly measurements have been made during the winter/spring bloom period (January to April) for all measurements except POC gravitational flux, which are measured just once monthly. This sampling scheme results in up to 4–6 data points during each annual winter/spring bloom period. The BATS data are available from the Bermuda Institute of Ocean Sciences/Bermuda Atlantic Time-series Study web page http://bats.bios.edu/. Specific details and information for all of the methods can be found on the web page as well under BATS Information/Methods, but a brief description of each method relevant to this particular work is given below.

Bulk phytoplankton biomass (*T*Chl-*a*) and specific accessory pigments were analyzed by HPLC (from 1990–2004 using the method of Bidigare (1991), and from 2005–2007 using the method of Van Heukelem (2001). For the sample volumes filtered, both methods have a detection limit of ~1 ng and compare favorably with each other. Whole water samples (4 L) were filtered onto 47 mm GF/F filters using polycarbonate in-line filter holders under a low vacuum pressure (<100 mm Hg) and then stored in liquid nitrogen until analysis on shore. In the laboratory, pigments were extracted by placing the filter in 5 ml of 100% acetone (the retention volume of the filter is approximately 0.8 ml resulting in a final acetone concentration of ~90% and, a final extraction volume of 5.8 ml) and allowed to extract overnight at −20°C. Samples (1 ml) were eluted on a reverse-phase C18 column (250×4.6 mm, 5 $\mu$m particle size, ODS-2 Spherisorb C18 column) using a three-step mobile phase program. The mobile phases are as



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follows: (a) Eluent A – 80:20 v:v, methanol: 0.5 M ammonium acetate, pH 7.2; (b) Eluent B – 90:10 v:v, acetonitrile: water, and; (c) Eluent C – ethyl acetate. Sample peak identities were determined based upon retention times of pure standards and algal extracts of known pigment composition. The HPLC system was calibrated with commercially obtained pigment standards where the concentrations were determined spectrophotometrically in the appropriate solvent using recommended extinction coefficients (e.g. Bidigare, 1991). Sample peaks were quantified using a response factor generated for each pure pigment standard.

HPLC pigment concentrations were converted to relative taxonomic phytoplankton distributions using the equations of Letelier et al. (1993), which have been shown to accurately reflect phytoplankton populations, as determined by electron microscopy, at all depths in this region of the Sargasso Sea (Anderson et al., 1996). The taxonomic groups and signature pigments used are as follows: Cyanobacteria (excluding Prochlorophytes, i.e. *Synechococcus*), zeaxanthin; Haptophytes, 19'-hexanoyloxyfucoxanthin; and Diatoms, fucoxanthin. These are the only groups that showed significant changes in absolute biomass and/or relative abundance and therefore are the only groups considered in this manuscript. Samples for picoplankton enumeration have been collected on each core BATS cruise from October 2001 to present. Samples are collected from 9 depths between 0 and 140 m, fixed with paraformaldehyde (0.5% final concentration), stored at ~4°C for 1–2 h, before long term storage in liquid nitrogen. Samples were analyzed on a Becton Dickinson (formerly Cytopeia Inc.) Influx cytometer using a 488 nm blue excitation laser, appropriate Chl-*a* (692+20 nm) and phycoerythrin (580+15 nm) bandpass filters, and was calibrated daily with 0.53 $\mu$m and 2.88 $\mu$m fluorescent microbeads (Spherotech Inc. Libertyville, Illinois, USA). Each sample was run for 4–6 min (~0.2–0.3 ml total volume analyzed), with log-amplified Chl-*a* and phycoerythrin fluorescence, and forward and right-angle scatter signals recorded. Data files were analyzed from two-dimensional scatter plots based on red or orange fluorescence and characteristic light scattering properties (e.g. DuRand and Olson, 1996) using FCS Express 3.0 (DeNovo Software Inc. Los Angeles, Califor-



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nia, USA). Pico-autotrophs were identified as either *Prochlorococcus* or *Synechococcus* based upon cell size and the presence or absence of phycoerythrin, respectively. Based upon these gating criteria, the number of cells in each identified population was enumerated and converted to cell abundances by the volume-analyzed method (Sieracki et al., 1993). Precision of triplicate samples was <5% for cell concentrations >200 cells $ml^{-1}$.

Samples for $NO_3^-$, $NO_2^-$ and $PO_4^-$ were gravity filtered through 0.8 $\mu$m Nuclepore polycarbonate filters using in-line polycarbonate filter holders, then frozen (−20°C) in HDPE bottles until analysis (Dore et al., 1996). Tests of frozen versus refrigerated samples have indicated no significant difference between storage methods (Dore et al., 1996). Nitrite concentrations were subtracted from combined $NO_3^-/NO_2^-$ concentrations to estimate $NO_3^-$concentrations. Nutrient samples prior to ~2003 were analyzed on a modified Technicon Autoanalyzer and samples post ~2003 were analyzed on an Alpkem Flow Solution IV; both instrumental setups have comparable sensitivity and method detection limits. During every sample run, several commercially available certified standards, Ocean Scientific International and Wako Chemical, were analyzed to maintain the generation of high quality data, as well as 'standard water' from 3000 m which is analyzed for QC/QA purposes and serves as an internal standard.

Rates of primary production were calculated from the autotrophic incorporation of $H^{14}CO_3^-$ into particulate organic matter (i.e. particles >0.7 $\mu$m) using an assumed ratio of total inorganic carbon present to radiocarbon added. For each sample depth, $H^{14}CO_3^-$ was added to triplicate light bottles, a single dark bottle and a single $T_0$ bottle with a sample for total added activity removed from the $T_0$ bottle. Samples were incubated in situ from local dawn to dusk (~12 h) at the depths from which they were originally collected. Rates of primary production were calculated from the mean light bottle value corrected for the dark bottle value, and integrated to a depth of 140 m.

Bacterial production (BP) was measured using [$^3$H-methyl] thymidine incorporation during a 2–3 h dark incubation at in situ temperatures. A median thymidine conversion factor of $1.63\times10^{18}$ cells $mol^{-1}$ thymidine and cell-specific C-biomass value of



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4.5 fg C cell$^{-1}$ (Carlson et al., 1996) were used to convert thymidine incorporation rates to carbon-based bacterial production estimates using standard equations (Carlson and Ducklow, 1996). Bacterial Carbon Demand (BCD) was estimated by dividing bacterial productivity by a bacterial growth efficiency of 0.14 (Carlson and Ducklow, 1996). Prior to 1998, only several years of bacterial productivity data are available (C. Carlson unpubl. data).

The POC sinking flux from the euphotic zone was quantified using a surface-tethered particle interceptor trap (Knauer et al., 1979). After manual removal of swimmers, samples were dried to constant weight at 65°C, fumed overnight in a desiccator saturated with HCl fumes, re-dried at 65°C, and then analyzed using Control Equipment Model 240XA CHN elemental analyzer (Knap et al., 1997). Carbon and nitrogen fluxes were calculated from the mass of material captured in the traps, its surface area and deployment length. ΔPOC was calculated as the difference in average POC fluxes at 150 and 300 m. Mesopelagic transfer efficiency was calculated as the ratio of POC fluxes at 300 m/150 m (Buesseler et al., 2007).

Zooplankton were collected using a vertically integrated (0–200 m) oblique tow (Madin et al., 2001). After collection, samples were fixed with buffered formalin (~10%), split using a Folsom Splitter, with one-half split sieved through sequential nitex screens to separate specific size fractions. Size-fractionated samples, were washed onto a smaller nitex screen, rinsed with buffered milli-Q water to remove salt and dried to constant weight.

Irradiance data were collected as part of the Bermuda BioOptics Project (BBOP). Underwater irradiance data were collected using the Multi-channel Environmental Radiometer (MER) from 1992 to 1999 and the Satlantic Profiling Multi-channel Radiometer (SPMR) from 2000 to 2007. PAR was computed using wavelength integration of irradiance ($E_d$) spectra using Planck's law to estimate spectral quantum flux from energy. The 1% PAR depth was interpolated from valid surface PAR and vertical profiles. Underwater irradiance data indicates that there have been only subtle changes in the average winter/spring 1% PAR (photosynthetically active radiation) depth between



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1992 and 2007; 86.6±10.4 m from 1992 to 1999 and 84.8±11.6 m from 2000 to 2007, suggesting light has not become less limiting over time.

### 2.2 Data processing

In this manuscript the winter/spring period is defined as the period from 1st January to 30th April in a given year. Generally there are 4–6 sampling efforts during this period each year and each is considered independently in estimates of biogeochemical changes over time based upon the observation that the de-correlation timescale is roughly 15 days in this region of the Sargasso Sea (Dickey et al., 2001). All profile data are integrated to 140 m which is ~0.1% PAR level (e.g. Siegel et al., 2001) and the deepest sampling depth that does not exceed the 150 m sediment trap depth. Where data are integrated over different depth ranges, this is stated. NAO data were downloaded from NCAR's Climate Analysis Section http://www.cgd.ucar.edu/cas/jhurrell/indices.html.

Macronutrients consumed during the course of each winter/spring bloom period were calculated as the difference between measured concentrations averaged for November/December (before bloom initiation) and April/May (after bloom termination). November/December were chosen as the pre-bloom months as $N_2$-fixation is past its summer maximum (Orcutt et al., 2001) and mixed layer depths (MLDs) were shallower than the euphotic zone. Mesoscale eddies not withstanding, the balance between nutrient inputs, consumption and remineralization should be relatively stable and therefore a reasonable estimate of the pre-winter/spring bloom nutrient pool can be made. May was chosen as the post-bloom month as MLDs have shoaled to less than the euphotic zone depth and measured nutrient concentrations represent what was consumed, in a net sense, with minimal bias associated with new N inputs by $N_2$-fixation that increase throughout the summer. The depth horizon on which nutrient concentrations were estimated for this calculation was the $\sigma_\theta$=26.28–26.32 kg m$^{-3}$. This isopycnal range was chosen because it is shallower than the core of the 18°C mode water, and therefore minimally impacted by non-local productivity and nutrient consumption (Palter et al.,



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2005). These isopycnals, during months of active convection and mixed layer depths >200 m, are the source waters for nutrients in the winter/spring bloom.

Total community metabolism was estimated from the calculation of apparent oxygen utilization (AOU). AOU calculations are compromised by deep mixing and therefore are usually calculated on an annual basis, after seasonal stratification has occurred. In this manuscript, data collected on cruises between when the seasonal mixed layer shallowed to <200 m and the end of April were used and therefore do not include any heterotrophic metabolism during the period of deepest convection. For these cruises, AOU was calculated as follows. At 200, 250 and 300 m dissolved oxygen concentrations were determined using an automated Winkler titration (Williams and Jenkinson, 1982) and an oxygen anomaly was calculated assuming saturation at the observed sample temperature and salinity. The oxygen anomaly was integrated from 200–300 m and plotted as a function of day of the year. A Model I linear regression was applied to the data and the resulting slope and intercept were used to calculate the integrated AOU at the beginning of the shortened data record for each year and at 30 April (day of year 122). The difference between these two values was taken as the AOU associated with the material remineralized during the period of interest in this study.

Statistical analyses were done using the routines in Sigma-Stat 3.5 (Systat Software Inc, San Jose, California). Data streams used for correlation analyses were averaged by month so that each pair of variables had the same number of measurements.

## 3 Results

### 3.1 Particle production in the euphotic zone

Seasonality in Sargasso Sea biogeochemical processes is strong (Steinberg et al., 2001), yet underlying multi-year trends in biological carbon pump parameters are apparent and statistically robust. Over the entire 17-year data record presented here, euphotic zone (0–140 m) integrated stocks of (*T*Chl-*a*), suspended particulate organic





carbon (POC), rates of primary production and shallow (150 m) POC export all display significant (least squares Model 1 linear regression, $P<0.05$) increases in winter/spring values of >50% (Fig. 1, Table 1). Increases in time however, were not uniform over the entire record. Indeed, *T*Chl-a was the only parameter of those four that showed a significant increase from 1990–1996, albeit with a lower slope than the later part of the record (Table 1). Moreover, the *T*Chl-*a* data for winters of 1995 and 1996 contribute disproportionately to the increase observed for the entire 1990–1996 period. All four parameters displayed increases with time from 1996–2007 with slopes that were much higher than for the 1990–1996 period or the entire dataset (Table 1).

Integrated *T*Chl-*a*, primary production, and shallow POC export from 1996–2007, when the overall increase was greatest, were all significantly correlated with each other (Spearman Rank Order Correlation, all pairwise comparisons $P<0.05$, all data within a month were averaged so $n=4$ for each variable for each year), indicating a coherent euphotic zone response to a broader external forcing. As also observed by Corno et al. (2007) for the subtropical North Pacific, biomass normalized primary production (i.e. the assimilation number) remained virtually constant suggesting the increase in primary production was due almost exclusively to the increase in biomass and not a change in physiological condition. Supporting the observed increase in *T*Chl-*a*, primary production and POC export was increased consumption of $NO_3^-$ and $PO_4^-$ during the duration of the winter/spring period (Fig. 2). The net N:P drawdown ratio on these isopycnals ranged from 27 to 43 mol:mol, consistent with particulate bulk N:P ratios in this region (Ammerman et al., 2003) and N:P ratios of cyanobacteria (Bertilsson et al., 2003) that contribute substantially to total autotrophic carbon during the winter/spring (DuRand et al., 2001).

The increase in *T*Chl-*a* was not uniform across all taxonomic groups (Fig. 3, Table 2). Diatoms, an important mineral ballasted phytoplankton group, have been declining steadily with significant reductions (Mann-Whitney Rank Sum, $P<0.05$) in both absolute and relative abundance (Fig. 3a, Table 2). Absolute haptophyte biomass, dominated by the coccolithophore *Emiliania huxleyi* in this region (Haidar and Thierstein,




2001), has not significantly changed over time (Mann-Whitney Rank Sum, $P$=0.55; Fig. 3b, Table 2), but their relative contribution to *T*Chl-*a* has been reduced by approximately half due to increases in *Synechococcus* abundance over the past decade. Absolute pigment biomass of *Synechococcus* has increased ~40% over the past decade (Fig. 3c, Table 2) with an associated increase in relative abundance from ~25% to ~40% of *T*Chl-*a* (Fig. 3c, Table 2). Euphotic zone integrated *Synechococcus* cell abundance, determined by analytical flow cytometry, has increased 3-fold since 2002 supporting the HPLC data. Using published estimates of cell carbon quotas and C:Chl-*a* ratios for *Synechococcus* (Bertilsson et al., 2003), the increase in *Synechococcus* cell abundance accounts for >50% of the *T*Chl-a increase.

### 3.2 Particle remineralization in the mesopelagic

This shift in the relative abundance of specific phytoplankton groups after ca. 1996 appears to have altered the magnitude and biological lability of the exported particulate matter. The significant increase in shallow (150 m) POC export did not result in increased POC export to the deeper mesopelagic zone (>300 m). The ~60% increase in POC export at 150 m has been countered by a significant decrease in mesopelagic transfer efficiency (defined as $T_{eff}$; Fig. 4a) such that POC fluxes at 300 m remained statistically identical over the entire time-series (Fig. 4b, Table 1). This observation is not confounded by changes in the relative depths of the traps (where particles are captured) and euphotic zone (where some particles are produced) as there has only been a ~2 m shoaling of the 1% light depth over the past two decades (Fig. 5; Buesseler and Boyd, 2009). The coherence of increased primary production, POC flux at 150 m and attenuation of this flux ($T_{eff}$) with depth suggests that ecosystem pathways in the mesopelagic respond on similar timescales and proportionately with euphotic zone pathways (Spearman Rank Cross correlation, $P$<0.05 for all pairwise comparisons; Table 3).

The absolute magnitude of POC attenuation in the mesopelagic zone (150–300 m) was greater after ca. 1996 than in the prior decade (Student's t-test with unequal vari-




ance, $P<0.01$; Fig. 4d). This increase in POC remineralization was associated with a significant (Student's t-test with unequal variance, $P<0.01$; Fig. 4d) increase in apparent oxygen utilization (AOU; Fig. 4d) suggesting that POC attenuation is due to increased mesopelagic metabolic activity (Steinberg et al., 2008b), although changes in trap collection efficiency can not be completely ruled out. Mesopelagic temperatures have been warming at $\sim 0.004^{\circ}C\,y^{-1}$, and while significant for stratification, this is too small a change, even over a decade, to significantly increase metabolic rates of individual organisms (which have a $Q_{10}$ of $\sim 2$ for many physiological processes; e.g. Eppley, 1972). Therefore the increase in metabolic activity is more likely associated with an increase in heterotrophic biomass or changes in its composition. Mesopelagic bacterial carbon demand (BCD) has decreased significantly (least squares Model 1 linear regression, $P<0.01$, Fig. 4d) due to decreases in bacterial productivity. This decrease in BCD is substantial as estimates have decreased from roughly twice the POC attenuation to one-half these values. As a result, the fraction of AOU associated with biota other than free-living bacteria must have increased; most probably particle-attached bacteria (which our method does not account for) and zooplankton. At this time there is no data to directly evaluate the former, although it is hypothesized that attached bacterial activity would increase with increased POC flux. Epipelagic mesozooplankton biomass in the Sargasso Sea, here only the data for the 200–500 $\mu$m size class is shown but it is representative of data in the other size classes, has increased significantly since 1994 (Steinberg et al., 2008a; Fig. 6). Too few data are available prior to 1994 to determine if there was a different trend in zooplankton biomass in the early 1990's. As mesozooplankton metabolic rates and production generally scale with biomass (e.g. Roman et al., 2002), the increased mesozooplankton biomass would equate to increased metabolic demand and support the observed increases in AOU. Some of the attenuation of POC flux may also be due to fragmentation of large aggregates into smaller particles with slower sinking rates by biological processes such as particle-attached microbial activity, zooplankton feeding, or zooplankton-induced shear (Steinberg et al., 2008b).



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## 4 Discussion

This analysis of the Sargasso Sea biological carbon pump over the past two decades suggests that this ecosystem is not static as perhaps previously thought. The decision to separate the nearly two-decade dataset between 1995 and 1996 was not arbitrary. The primary reason is the well documented change in the phase of the NAO in the mid 1990's. Prior to the winter of 1996 the wintertime NAO was consistently positive and after 1996 was variable but on average neutral (discussed later). Given the generally well established linkages between modes of climate forcing and marine planktonic processes (e.g. Chavez et al., 2003; Corno et al., 2007; Karl et al., 2002) and in particular the NAO in the North Atlantic (Irigoien et al., 2000; Oschlies, 2001), a change in planktonic response was hypothesized to occur coincident with the change in the NAO. If the transition timing is moved up to three years on either side of 1996 (e.g. 1990–1993 and 1994–2007 or 1990–1999 and 2000–2007), non-significant trends remain non-significant and significant trends remain significant (data not shown). This suggests that the correlations observed and discussed below are robust and not dependent on the exact date chosen. Furthermore, a transition set at 1996 also explains the most variance in both time periods (i.e. extending the 1990–1996 period forward in time to include more data only reduces the $r^2$ value, and extending the 1996–2007 period back in time to include more data also decreases the $r^2$ value). Regardless of the choice of transition time point, there have been increases in biological carbon pump parameters over time that have coincided with a decrease in wintertime NAO over the same timeframe.

### 4.1 Relationships between climate forcing and the Sargasso Sea biological carbon pump

Additional physical and biogeochemical data allow an assessment of possible triggers for the changing strength and efficiency of the biological carbon pump. The most obvious are changes in upper ocean stratification and nutrient inputs, given that primary



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production in the subtropical North Atlantic is limited by the nutrient supply rate (Maranon, 2005), and how these may change in response to multi-year climate oscillations. No significant changes in wintertime stratification were apparent between the near surface and 200 m (Fig. 7a) in contrast to changes in summer time stratification which were large enough to drive an annual increase in stratification from 1989 to 2003 (Krause et al., 2009). Estimated MLDs consistently reached depths of 150 to 200 m, with occasional mixing to 250 m (Fig. 7c); the depth of the 26.28 to 26.32 kg $m^{-3}$ isopycnals from which we observed increased nutrient drawdown during the course of the winter/spring bloom (Fig. 2). Underwater irradiance data indicates that there has only been a slight decrease in the depth of the winter/spring 1% isolume; 86.6±10.4 m from 1992 to 1999 and 84.8±11.6 m from 2000 to 2007, suggesting light has not become less limiting (Fig. 5). Despite the similarity in estimated MLDs and apparent upper ocean stratification, it is hypothesized that there have been changes in physical forcing between the two decades of the BATS dataset. The wintertime (December through March) North Atlantic Oscillation (NAO) index, the dominant climate mode in this region (Marshall et al., 2001), shifted from consistently positive to more neutral values starting with the winter of 1996 (Fig. 7b); negative NAO values result in intensified midlatitude westerlies (Marshall et al., 2001). While the depth of mixing has not changed, the frequency of mixing in this region may have increased, suggested by the reduction in month-to-month variability of estimated MLD (based upon calculated CV of $n$=4 monthly average MLDs) taken from cruise data during the duration of the winter/spring period (Fig. 7d). It is hypothesized that the change in the phase of the NAO has resulted in more continuous, but not necessarily deeper, mixing that enhances the supply of nutrients to the euphotic zone leading to more efficient and greater biological nutrient utilization (Fig. 2) and ultimately biomass accumulation (Fig. 1a). In support of this there are significant statistical correlations between the NAO index and all euphotic zone carbon pump parameters (Table 3), the strongest of which is a negative correlation (Spearman's Correlation, $r$=−0.58, $P$<0.02; Fig. 8) between euphotic zone integrated primary production and the wintertime NAO index (Fig. 8). This observation



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is consistent with previous findings based upon the BATS dataset (Bates, 2001; Lomas and Bates, 2004). In addition, the MLD coefficient of variation is negatively correlated with the biological carbon pump parameters (Table 3). These findings suggest a mechanism by which shifts in a dominant climate mode for the North Atlantic may lead to increased productivity.

If our hypothesis is correct, that negative anomalies in the NAO result in more continuous mixing of the upper ocean supporting the increase in primary production and biomass accumulation, then why are diatoms declining (alternatively, why is *Synechococcus* increasing)? There are several possible explanations. First, in the Sargasso Sea, silica uptake by diatoms may be chronically substrate limited (Brzezinski and Nelson, 1996) thereby restricting their ability to respond to enhanced mixing and nutrient inputs. Silicate gradients are lower in the upper 250 m of the Sargasso Sea than $NO_3^-$ gradients such that mixing to depth will entrain relatively more $NO_3^-$, thus exacerbating potential silica limitation. In contrast, *Synechococcus* populations in the Sargasso Sea have been shown to respond to nanomolar level $NO_3^-$ pulses by increasing net growth rates and most importantly for this discussion, accumulating biomass (Glover et al., 2007). Second, salinity normalized DIC concentrations in the Sargasso Sea have been increasing at $0.80 \pm 0.06\,\mu\text{moles}\,\text{kg}^{-1}\,\text{yr}^{-1}$ with a consequent acidification of the surface ocean (Bates, 2007). Recent $CO_2$ manipulation studies in other ocean regions show that under elevated $pCO_2$ conditions diatoms are out competed by pico- and nano-phytoplankton when macronutrients are depleted (Hare et al., 2007) but that diatoms out compete pico- and nano-phytoplankton when nutrients are replete (Riebesell et al., 2007). While, both diatoms and *Synechococcus* have enhanced growth rates under elevated $pCO_2$ (Fu et al., 2007; Riebesell et al., 1993) macronutrient limitation likely offsets these gains in diatoms, thus allowing *Synechococcus* to gain a competitive growth advantage. Lastly, common vertical migrators in the Sargasso Sea show a strong preference for grazing on diatoms relative to other co-occurring phytoplankton (Schnetzer and Steinberg, 2002b). Given the increase in daytime mesozooplankton biomass (Fig. 6), it is probable that grazing pressure on diatoms will also have in-



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creased from 1996–2007 potentially contributing to the decline in diatom abundance. A fraction of the mesozooplankton biomass increase is due to diel vertical migrators that are resident in the mesopelagic zone during the day (Madin et al., 2001; Steinberg et al., 2000), but active and passive POC fluxes attributed to vertically migrating mesozooplankton range from 3–18% (Schnetzer and Steinberg, 2002a) with a long-term average closer to 6% (Lomas et al., 2002). While they may be important in diatom population dynamics, their contribution to export flux appears insufficient to account for the observed 60% increase POC flux. Consequently a mechanistic understanding of the role of vertically migrating mesozooplankton is incomplete at this time.

In contrast to some model predictions (Bopp et al., 2005; Laws et al., 2000), data presented here for the Sargasso Sea shows that shallow POC export increases with a shift to smaller phytoplankton. This observation, in conjunction with the discussion of zooplankton in the previous paragraph, suggests that particle aggregation in relatively low biomass environments may be an underappreciated process in the "packaging" of particles as they leave the euphotic zone in the oligotrophic North Atlantic (Jackson et al., 2005). Indeed, these ideas are at the heart of two competing ideas linking phytoplankton community composition and POC export. It is a long-held belief that regions of efficient and high absolute POC export rates are dominated by diatoms and coccolithophores and that these groups contribute disproportionately to these high fluxes. This is in part due to the mineral tests encasing these groups that act to increase settling rate, and therefore decrease contact time in the biological active upper ocean (Armstrong et al., 2002). As a result model predictions of the future strength of the biological carbon pump appear to be inextricably linked to changes in the abundance of diatoms. Interestingly, Emerson et al. (2001) suggest that per unit area oligotrophic systems, which are dominated by the biomass of small cells not diatoms, can have annual POC export rates similar to subpolar regions due to a longer growing season. This supports the recent hypothesis that all phytoplankton contribute to carbon export rates in proportion to primary production, although specific export mechanisms may differ (Richardson and Jackson, 2007). If aggregation were a significant process in

the Sargasso Sea biological carbon pump, it would explain both the increase in POC flux with smaller phytoplankton and enhanced remineralization. Unfortunately data on aggregate abundance, or other descriptive characterizations of flux material, are not available at this time for the Sargasso Sea that would allow a more complete evaluation of this hypothesis.

## 5 Global implications

The findings presented here suggest there may be long time-scale, climate-related shifts in phytoplankton community composition in the subtropical North Atlantic that have significant, and perhaps unanticipated, implications for the production and export of POC in this oligotrophic gyre. A similar climate-related shift in phytoplankton community composition and increase in *T*Chl-*a* and primary production has been observed in the North Pacific (Karl et al., 2001), suggesting the possibility of observed biological responses to climate forcing in the broader subtropical oceans. However, there is a difference in that stratification was not shown to increase in the Sargasso Sea as it did in the North Pacific along with the increase in primary production, and therefore the exact physical mechanism may differ between the two oligotrophic gyres. The data presented here suggests that in the oligotrophic North Atlantic there is a tight coupling between enhanced biological production and carbon export from the euphotic zone and its attenuation in the mesopelagic such that they increase in concert following a shift in the wintertime NAO index that enhances vertical mixing.

Regional variability of $T_{eff}$ within the mesopelagic is not well constrained (Buesseler et al., 2007), and in no model that we are aware of does $T_{eff}$ change temporally with euphotic and mesopelagic zone processes. If the data at the HOT (Karl et al., 2001) and BATS are representative of the broader oligotrophic gyres, and assuming they contribute ~60% of the global shallow export production of 11 Pg C $yr^{-1}$ (Laws et al., 2000), not accounting for the decrease in $T_{eff}$ would result in an overestimation of POC sequestration below 300 m of 2.3 Pg C $yr^{-1}$. For reference, global anthropogenic $CO_2$



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emissions are 6–7 Pg C $yr^{-1}$. While the uncertainties on this calculation are quite large, it highlights that not accounting for tight coupling between metabolic activities in the euphotic and mesopelagic zones, or assuming that the oligotrophic gyre biological carbon pumps are static, can have a substantial impact of our understanding of the oceans role in carbon sequestration.

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**Table 1.** Rates of change in biogeochemical parameters in the Sargasso Sea. Statistics provided for the entire period, as well as divided up into the two periods of interest as defined by the phase of the winter NAO index. n/s=no significant change. Data in the "Period Change" column are given as the absolute change, in appropriate units, from the beginning of the time period.

| Parameter | Time period | Slope & Std. Error | Period Change [§] | P-value | $r^2$ | $n$ |
|---|---|---|---|---|---|---|
| Int. *T*Chl-*a* (0–140 m; mg $m^{-2}$) | 1990–1996 | 1.34±0.51 | +8.04 (~34%) | 0.01 | 0.11 | 50 |
| | 1996–2007 | 1.71±0.47 | +18.7 (~62%) | < 0.01 | 0.59 | 58 |
| | 1990–2007 | 1.13±0.16 | +19.2 (~82%) | <0.01 | 0.33 | 108 |
| Int. Suspended POC (0–140 m; mmol C $m^{-2}$) | 1990–1996 | 0.20±0.33 | n/s | 0.56 | 0.01 | 58 |
| | 1996–2007 | 0.87±0.05 | +8.6 (~35%) | < 0.01 | 0.60 | 51 |
| | 1990–2007 | 0.64±0.10 | +10.9 (~44%) | < 0.01 | 0.26 | 109 |
| Int. Primary Production (0–140 m; mmol C $m^{-2}d^{-1}$) | 1990–1996 | 0.01±0.06 | n/s | 0.79 | 0.01 | 53 |
| | 1996–2007 | 2.95±0.76 | +32.5 (~98%) | < 0.01 | 0.63 | 56 |
| | 1990–2007 | 0.85±0.42 | +14.5 (~44%) | 0.04 | 0.04 | 109 |
| POC flux @ 150 m (mmol C $m^{-2}d^{-1}$) | 1990–1996 | 0.01±0.12 | n/s | 0.97 | 0.01 | 36 |
| | 1996–2007 | 0.18±0.08 | +1.95 (~66%) | 0.05 | 0.38 | 36 |
| | 1990–2007 | 0.12±0.04 | +2.1 (~71%) | < 0.01 | 0.12 | 72 |
| POC flux @ 300 m (mmol C $m^{-2}d^{-1}$) | 1990–1996 | 0.00±0.06 | n/s | 0.99 | 0.00 | 36 |
| | 1996–2007 | −0.03±0.06 | n/s | 0.62 | 0.01 | 36 |
| | 1990–2007 | 0.02±0.02 | n/s | 0.47 | 0.01 | 72 |



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**Table 2.** Rates of change in phytoplankton composition parameters in the Sargasso Sea. Statistics provided for the entire period, as well as divided up into the two periods of interest as defined by the phase of the winter NAO index. n/s=no significant change. Data in the "Period Change" column are given as the absolute change in appropriate units and as percent increase from the beginning of the time period.

| Parameter | Time period | Slope & Std. Error | Period Change (%)[§] | P-value | $r^2$ | $n$ |
|---|---|---|---|---|---|---|
| Chl$a_{dino}$(mg m$^{-2}$) | 1990–1996 | 0.03±0.01 | +0.18 (~104%) | 0.01 | 0.12 | 58 |
| | 1996–2007 | 0.03±0.02 | n/s | 0.17 | 0.05 | 42 |
| | 1990–2007 | 0.03±0.01 | +0.40 (~215%) | 0.01 | 0.35 | 100 |
| Chl$a_{diatom}$(mg m$^{-2}$) | 1990–1996 | −0.03±0.01 | −0.15 (~74%) | 0.05 | 0.07 | 58 |
| | 1996–2007 | −0.03±0.01 | −0.24 (~110%) | 0.03 | 0.11 | 42 |
| | 1990–2007 | −0.02±0.00 | −0.34 (~113%) | <0.01 | 0.53 | 100 |
| Chl$a_{pelago}$(mg m$^{-2}$) | 1990–1996 | 0.12±0.07 | n/s | 0.10 | 0.05 | 58 |
| | 1996–2007 | 0.18±0.06 | +1.26 (~45%) | <0.01 | 0.27 | 42 |
| | 1990–2007 | 0.1±0.02 | +1.7 (~54%) | <0.01 | 0.51 | 100 |
| Chl$a_{hapto}$(mg m$^{-2}$) | 1990–1996 | 0.72±0.27 | +5.06 (~56%) | <0.01 | 0.12 | 58 |
| | 1996–2007 | −0.28±0.12 | n/s | 0.05 | 0.09 | 42 |
| | 1990–2007 | −0.07±0.11 | n/s | 0.55 | 0.02 | 100 |
| Chl$a_{Pro}$(mg m$^{-2}$) | 1990–1996 | −0.03±0.08 | n/s | 0.70 | <0.01 | 58 |
| | 1996–2007 | 0.07±0.09 | n/s | 0.43 | 0.02 | 42 |
| | 1990–2007 | 0.06±0.05 | n/s | 0.25 | 0.08 | 100 |
| Chl$a_{Syn}$(mg m$^{-2}$) | 1990–1996 | −0.10±0.15 | n/s | 0.50 | 0.07 | 58 |
| | 1996–2007 | 1.11±0.27 | +7.78 (~120%) | <0.01 | 0.30 | 42 |
| | 1990–2007 | 0.34±0.10 | +5.78 (~64%) | <0.01 | 0.42 | 100 |
| Int. *Prochlorococcus* ×10$^{11}$ cells m$^{-2}$ | 2002–2007 | 1.77±1.6 | n/s | 0.28 | 0.04 | 30 |
| Int. *Synechococcus* (×10$^{11}$ cells m$^{-2}$) | 2002–2007 | 5.09±1.36 | +26.5 (~170%) | 0.01 | 0.33 | 30 |



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**Table 3.** Spearman Rank Correlation table of selected biogeochemical and environmental parameters. Within each cell, first row = correlation coefficient and second row = *P*-value. For each correlation, N=15 to 17. $\delta NO_3^-$ and $\delta PO_4^-$ are $NO_3^-$ and $PO_4^-$ drawn down during the course of the winter/spring bloom; PProd=euphotic zone integrated primary production; $\delta\sigma_T$=difference in $\sigma_T$ between 200 m and 5 m values. All other parameters as defined in the text.

| | MLD | $\delta NO_3^-$ | $\delta PO_4^-$ | $T_{eff}$ | PProd | *T*Chl-*a* | POCflux | MLD-CV | $\delta\sigma_\theta$ |
|---|---|---|---|---|---|---|---|---|---|
| NAO | 0.06 | −0.37 | −0.33 | 0.17 | −0.48 | −0.61 | −0.42 | 0.25 | 0.08 |
| | 0.81 | 0.17 | 0.20 | 0.51 | 0.05 | <0.01 | 0.08 | 0.32 | 0.75 |
| MLD | | 0.34 | 0.26 | −0.39 | −0.00 | 0.22 | 0.08 | 0.05 | −0.21 |
| | | 0.22 | 0.32 | 0.10 | 0.99 | 0.38 | 0.76 | 0.86 | 0.44 |
| $\delta NO_3^-$ | | | 0.62 | −40.11 | 0.36 | 0.58 | 0.63 | −0.67 | −0.28 |
| | | | 0.01 | 0.71 | 0.21 | 0.03 | 0.01 | <0.01 | 0.33 |
| $\delta PO_4^-$ | | | | −0.52 | 0.41 | 0.65 | 0.28 | −0.34 | −0.42 |
| | | | | 0.03 | 0.10 | <0.01 | 0.29 | 0.18 | 0.10 |
| $T_{eff}$ | | | | | −0.44 | −0.61 | −0.46 | 0.06 | 0.00 |
| | | | | | 0.08 | <0.01 | 0.07 | 0.82 | 0.99 |
| PProd | | | | | | 0.51 | 0.60 | −0.49 | −0.33 |
| | | | | | | 0.04 | 0.01 | 0.05 | 0.23 |
| *T*Chl-a | | | | | | | 0.56 | −0.48 | −0.17 |
| | | | | | | | 0.02 | 0.05 | 0.63 |
| POCflux | | | | | | | | −0.65 | −0.29 |
| | | | | | | | | <0.01 | 0.28 |
| MLD-CV | | | | | | | | | 0.23 |
| | | | | | | | | | 0.40 |



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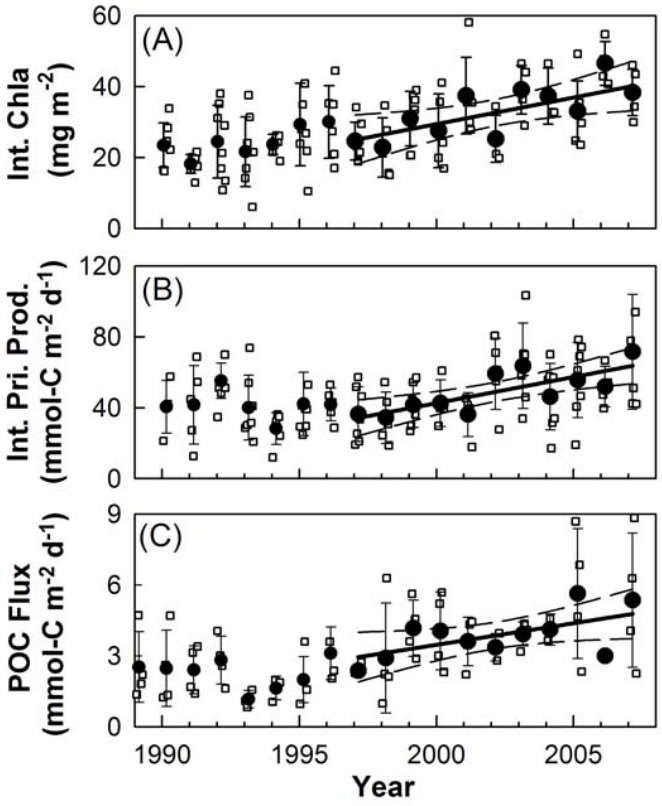


**Fig. 1.** Time-series of biological carbon pump components in the Sargasso Sea. **(A)** Integrated (0–140 m) HPLC *T*Chl-*a*, **(B)** integrated (0–140 m) in situ primary production and **(C)** sediment trap POC flux at 150 m. In all panels, open squares are data for January through April of each year. The filled symbols are the mean (±std. dev.) of the data for each winter/spring period. The solid lines in each panel are the least squares Model 1 linear regression and 95% confidence intervals (dashed line). All linear regressions are significant, $P<0.05$.



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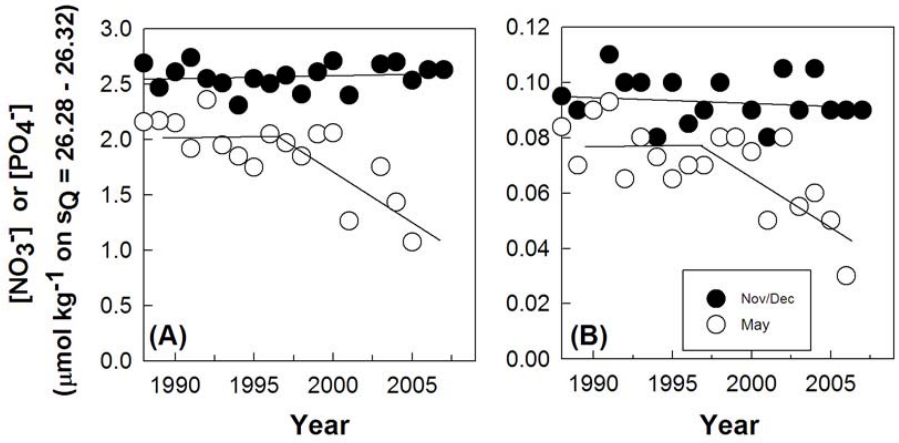


**Fig. 2.** Time-series plots of **(A)** [$NO_3^-$] and **(B)** [$PO_4^{-3}$] concentrations before (November/December, filled circles) and after (May, open circles) the winter/spring period on isopycnal band $\sigma_\theta$=26.28–26.32 kg m$^{-3}$. Lines are drawn to the data to depict trends and are not statistical fits.



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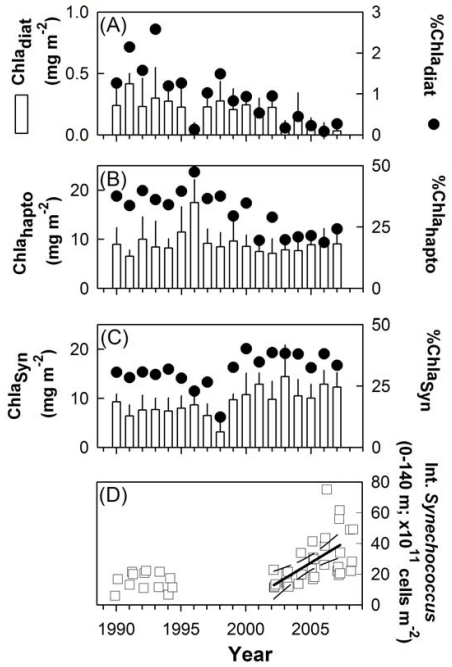


**Fig. 3.** Time-series of phytoplankton taxonomic groups determined from HPLC pigment analysis as described in the text. **(A)** diatoms, **(B)** haptophytes, and **(C)** *Synechococcus*. Phytoplankton group biomass estimates (0–140 m; mg m$^{-2}$; open bars) are given as the mean (+std. dev.) for January to April of each year and their percent contribution to *T*Chl-*a* (filled circles). **(D)** Integrated *Synechococcus* abundances (0–140 m; $\times 10^{11}$ cells m$^{-2}$) as determined by direct analytical flow cytometric counts. The solid line through data from 2002 to 2007 is the least squares Model 1 regression, significant at the $P<0.01$ level, and predicted 95% confidence intervals (dashed lines). Data from 1991 to 1994 were taken from DuRand et al. (2001), as available on the CD that accompanied the Deep Sea Research II volume 48, issue 8/9 in which that data were originally published.



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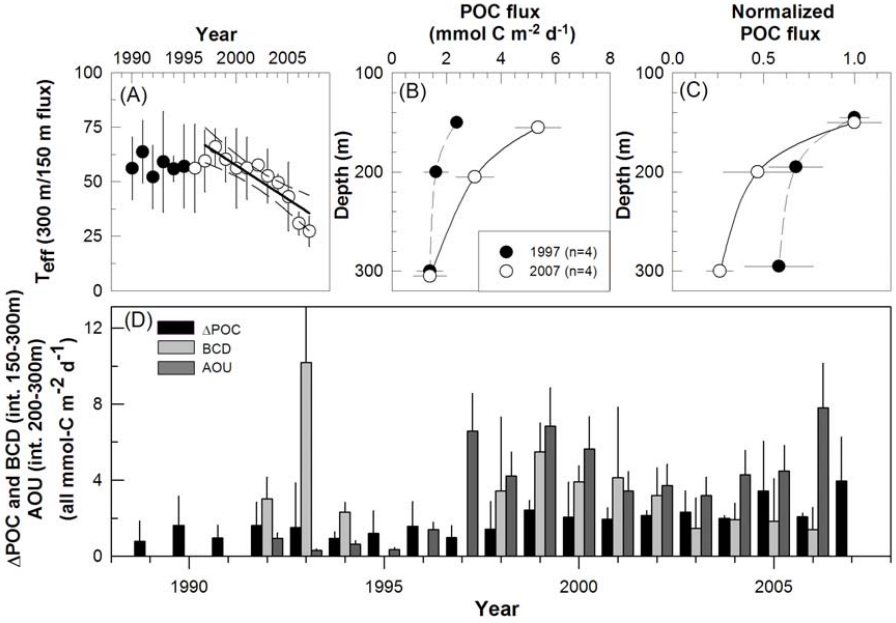


**Fig. 4.** Remineralization of sinking particulate organic carbon in the Sargasso Sea. **(A)** time-series of mean (+std. dev.) winter/spring (January to April) mesopelagic transfer efficiency ($T_{eff}$). Filled circles denote data from 1990 to 1996, and open circles denote the 1996 to 2007 period. **(B)** Absolute POC flux profiles for January to April of 1997 (filled circles) and 2007 (open circles) are plotted as an example of the change in attenuation during this period. **(C)** POC flux profiles normalized to 150 m fluxes for January to April of 1997 (filled circles) and 2007 (open circles). **(D)** Time-series of sinking particulate organic carbon loss between 150 and 300 m (ΔPOC; black bars), 150 to 300 m integrated bacterial carbon demand (light grey bars), and 200 to 300 m apparent oxygen utilization (dark grey bars).



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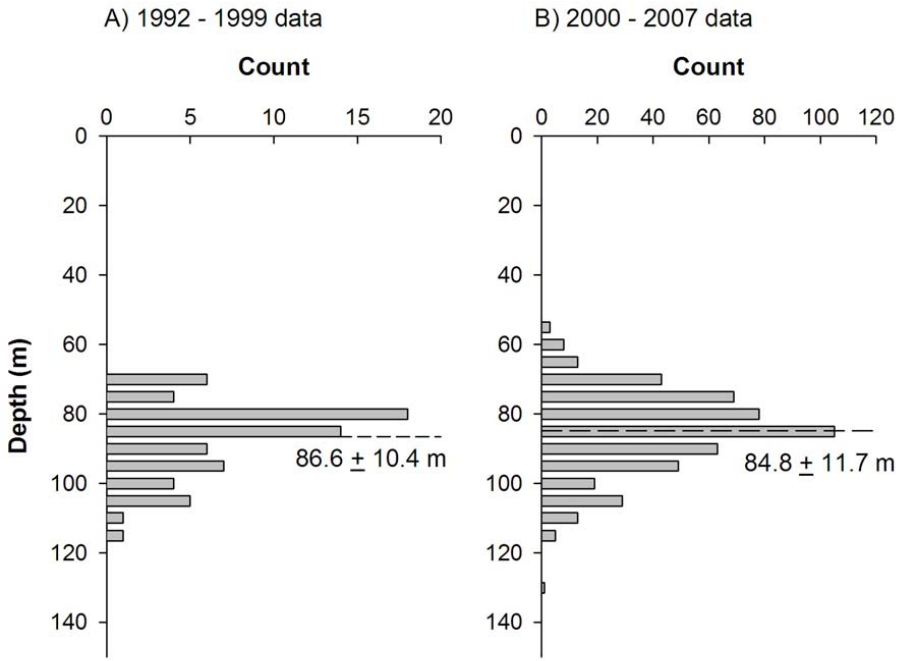


**Fig. 5.** Histograms of computed 1% PAR depths in the Sargasso Sea for the periods **(A)** 1992 to 1999 and **(B)** 2000 to 2007. The data in these two periods was collected by different, but intercalibrated underwater radiometers.



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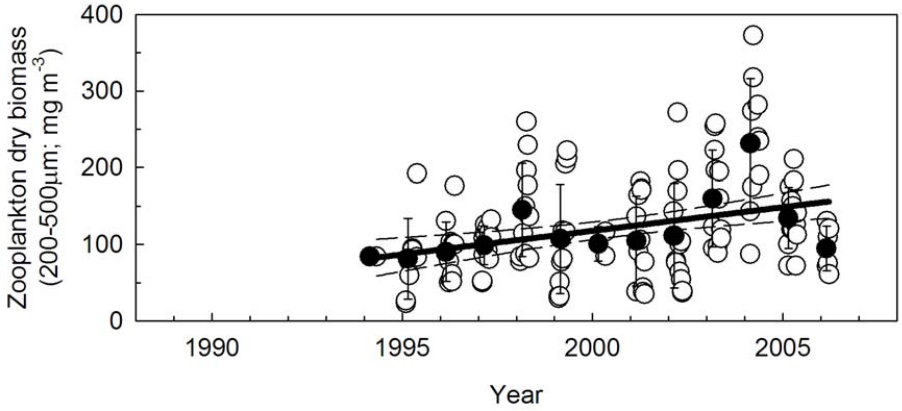


**Fig. 6.** Time-series of daytime zooplankton biomass (mg dry weight $m^{-2}$) in the 200–500 $\mu$m size class in the Sargasso Sea.



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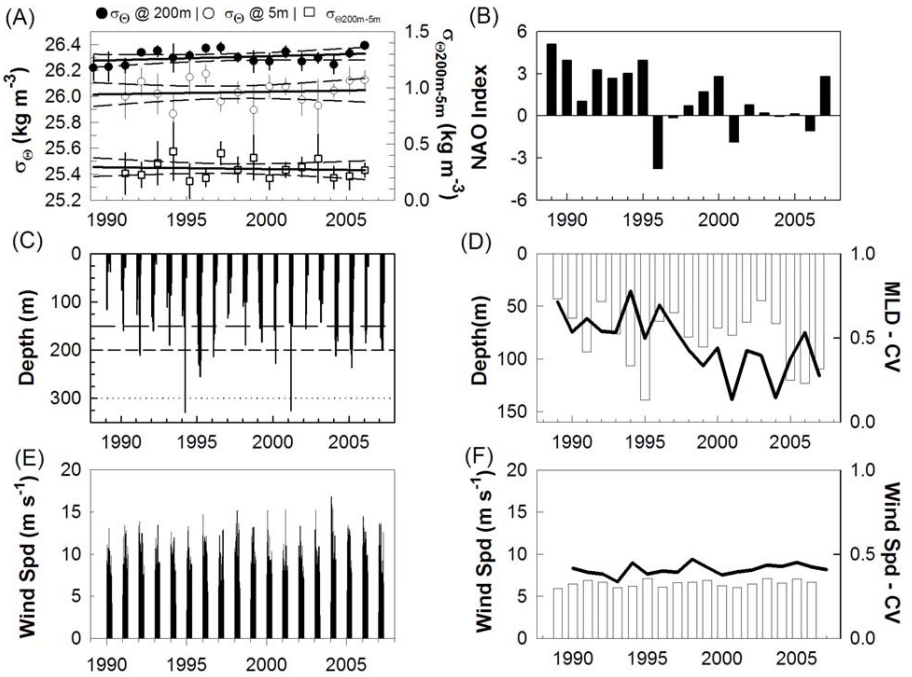


**Fig. 7.** Time-series of upper ocean physical forcing at BATS. **(A)** Mean (±std. dev.) $\sigma_\theta$ (k m$^{-3}$) for near surface water (~5 m; open circles) and 200 m (filled circles), and the difference between the two (open squares). Solid lines are the least square Model 1 linear regression and dashed lines are the 95% confidence intervals. **(B)** winter (December through March) index of the NAO. **(C)** Estimated mixed layer depths using a variable $\sigma_T$ difference criterion of 0.02 kg m$^{-3}$ difference from the surface (~5 m) value. Horizontal lines denote the depths of the BATS sediment traps at 150, 200 and 300 m. **(D)** Mean mixed layer depth (bars) and the coefficient of variation within each winter (solid line). **(E)** daily winter/spring wind speeds recorded at the Bermuda Airport. (E) Same as (C) but for wind speed.



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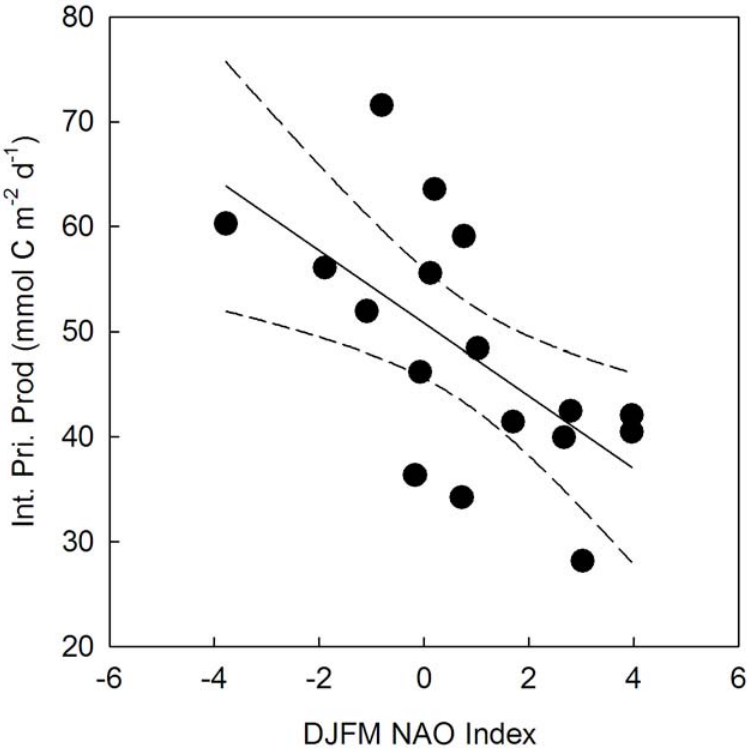


**Fig. 8.** Bivariate plot of euphotic zone integrated primary production (mmol C $m^{-2}$ $d^{-1}$) vs. winter NAO index. Solid line is the least squares Model II regression and the dashed lines are the are 95% confidence intervals. Correlation is significant at the $P<0.02$ level.



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