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# Temporal dynamics of dissolved combined neutral sugars and the quality of dissolved organic matter in the Northwestern Sargasso Sea

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ABSTRACT

The dynamics of dissolved combined neutral sugars (DCNS) were assessed in the upper 250 m at the Bermuda Atlantic Time-series Study (BATS) site between 2001 and 2004. Our results reveal a regular annual pattern of DCNS accumulation with concentrations increasing at a rate of 0.009–0.012 μmol C $L^{-1}$ $d^{-1}$ in the surface 40 m from March to July and reaching maximum mean concentrations of 2.2–3.3 μmol C $L^{-1}$. Winter convective mixing (between January and March) annually exported surface-accumulated DCNS to the upper mesopelagic zone (100–250 m), as concentrations increased there by 0.3–0.6 μmol C $L^{-1}$. The exported DCNS was subsequently removed over a period of weeks following restratification of the water column. Vertical and temporal trends in DCNS yield (% of DOC) supported its use as a diagenetic indicator of DOM quality. Higher DCNS yields in surface waters suggested a portion of the DOM accumulated relatively recently compared to the more recalcitrant material of the upper mesopelagic that had comparably lower yields. DCNS yields and mol% neutral sugar content, together, indicated differences in the diagenetic state of the surface-accumulated and deep pools of DOM. Seasonally accumulated, recently produced DOM with higher DCNS yields was characterized by elevated mol% of galactose and mannose+xylose levels. Conversely, more recalcitrant DOM from depths >100 m had lower DCNS yields but higher mol% of glucose. Lower DCNS yields and elevated mol% glucose were also observed in the surface waters during winter convective mixing, indicating an entrainment of a diagenetically altered DOM pool into the upper 100 m. A multivariate statistical analysis confirms the use of DCNS as an index of shifts in DOM quality at this site.



## 1. Introduction

Dissolved organic matter (DOM) is the largest pool of reduced carbon in the ocean, and its redistribution during convective overturn (Carlson et al., 1994; Hansell and Carlson, 2001) or along ventilated isopycnals (Doval and Hansell, 2000; Abell et al., 2000) makes it an important form of carbon exported into the ocean interior (Hansell et al., 2002). DOM is also important ecologically as a substrate for heterotrophic bacterioplankton production (BP) (Azam and Hodson, 1977), a process that can rapidly metabolize ~50% of recently produced DOM over the timescale of minutes to hours (Ducklow, 1999). Many factors can control BP, including temperature (Hoppe et al., 2002), inorganic nutrient availability (Cotner et al., 1994; Thingstad et al., 1997; Obernosterer et al., 2003), and microbial community structure (Carlson et al., 2004; Morris et al., 2005; Giovannoni and Stingl, 2005). However, for any of these factors to be important controls of BP, ambient DOM has to be sufficiently bioavailable to be assimilated by bacterioplankton.

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Carbohydrates account for a large fraction of DOM in the surface ocean ($\leqslant$40%; Pakulski and Benner, 1994), and neutral sugars are biologically available sub-components within this pool (Cowie and Hedges, 1994; Skoog and Benner, 1997; Kirchman et al., 2001; Amon et al., 2001; Amon and Benner, 2003). Though neutral sugars are considered bioavailable, the range of removal rates of these compounds can be broad. For example, free monosaccharides are extremely labile and are removed on the timescales of seconds to hours (Rich et al., 1996, 1997; Kirchman et al., 2001), whereas portions of the dissolved combined neutral sugar (DCNS) pool are removed on the timescales of days (Amon et al., 2001; Hama et al., 2004) to months (Kirchman et al., 2001).

The enhanced overall reactivity of DCNS and comparison of the size and composition of the DCNS pool relative to bulk DOM has led to their utility as diagenetic indicators of DOM quality (Cowie and Hedges, 1994; Skoog and Benner, 1997). Changes in DCNS yields (% of DOC; Cowie and Hedges, 1994) reveal the effects of diagenesis on the DOM pool whereby higher yields indicate more bioreactive and less diagenetically altered material (Cowie and Hedges, 1994; Skoog and Benner, 1997; Meon and Kirchman, 2001). The concentration of DCNS and DCNS yield decrease with depth in the ocean (Skoog and Benner, 1997), and surface water DOC can become enriched with DCNS during the progression of a phytoplankton bloom (Kirchman et al., 2001). Compositional shifts of individual sugars within DCNS (i.e. molar fractions, mol% DCNS) have also been used to assess DOM diagenetic patterns, as one or more sugars may be utilized preferentially (Skoog and Benner, 1997; Kirchman et al., 2001; Amon et al., 2001; Amon and Benner, 2003). These patterns, in combination with radiocarbon analysis of carbohydrates in HMW-DOM (Repeta and Aluwihare, 2006), have been interpreted to indicate that surface derived DOM has been more recently produced and is less diagenetically altered than deep DOM (Skoog and Benner, 1997). While DCNS yield provides insight to the relative diagenetic state, yield alone does not constrain turnover rates of the accumulated DOM pool.

DCNS concentrations, DCNS yields, and mol% DCNS values vary systematically during the degradation of fresh DOM produced by algal sources (Aluwihare et al., 1997; Biersmith and Benner, 1998; Amon et al., 2001; Hama et al., 2004). Rapid turnover of fresh DCNS on the timescale of days to weeks can coincide with decreased DCNS yields and elevated molar fractions of glucose (Amon et al., 2001), suggesting that spatial and temporal gradients in these parameters in the ocean may serve as indices of DOM quality and diagenetic state. Supporting evidence for this hypothesis has been obtained through studies of the reactivity of the DOM pool in vertical profiles (Skoog and Benner, 1997), across spatial gradients of primary productivity (Amon and Benner, 2003), and through experimental and radiocarbon analysis of HMW-DOM (Amon and Benner, 1994, 1996; Repeta and Aluwihare, 2006). However, there is a paucity of data with regard to the seasonal dynamics of the DOM and DCNS pools.

Here we analyze the temporal and vertical variability of DCNS, DCNS yields, and the molar fractions of specific neutral sugars over the upper 250 m at the Bermuda Atlantic Time-series Study (BATS) site between 2001 and 2004 in the context of the larger seasonal DOC dynamics. A regular annual pattern of DOC accumulation in the euphotic zone, redistribution during convective mixing and remineralization in the upper mesopelagic zone has been documented in detail in several studies at the BATS site (Carlson et al., 1994; Hansell and Carlson, 2001; Lomas and Bates, 2004), and provide a reference for interpreting seasonal changes in the distribution and composition of the DCNS pool. We use empirical orthogonal function (EOF) analysis of the organic carbon constituents (i.e. DOC, DCNS, individual aldoses) to evaluate the dominant modes of variability explaining the organic carbon data. The dominant modes are correlated to DOM quality and stratification indices and reveal systematic seasonal changes in the accumulation, consumption, and diagenesis of the DCNS pool that are tightly coupled to the seasonal pattern of water column stratification.

## 2. Methods

### 2.1. Study site

The BATS site is located at 31°40′N, 64°10′W in the Northwestern Sargasso Sea. There, the surface layer of the water column is thermally stratified during summer and autumn months and concentrations of macronutrients are generally below limits of detection (Steinberg et al., 2001). Sub-tropical mode water (STMW), formed to the north before subducting with subsequent southerly flow, lies below the surface layer at the BATS site, occupying the 18 °C thermostad between 150 and 400 m (Worthington, 1976; Palter et al., 2005). Deep convective mixing that occurs during winter months can entrain STMW, with elevated nutrient concentrations, into the surface layer, supporting the annual winter/spring phytoplankton bloom.

### 2.2. Sample collection

Samples for DOC and DCNS were collected monthly to bimonthly between 2001 and 2004 at the BATS study site aboard the R/V *Weatherbird II*. Seawater was collected in 12 L Niskin bottles using a conductivity, temperature, and depth (CTD) profiler. Each sample was gravity filtered through an inline 47 mm glass fiber filter (GF/F filters, Whatman) housed in an acid cleaned polycarbonate cartridge (Gelman) and attached directly to the Niskin bottle spigot using silicone tubing. Filtrate was collected in 40 mL combusted glass EPA vials, frozen immediately, and stored at −20 °C until analysis at University of California Santa Barbara. For long-term storage, 4 mL aliquots of sample were transferred into 5 mL glass ampoules, dried in a Savant Speed Vac, sealed with Teflon tape, and stored in sealed polyethylene bags at −20 °C. All plasticware was washed with 10% hydrochloric acid (HCl; Fisher) and flushed thoroughly with UV oxidized Nanopure® water (Barnstead Thermoline). Glass fiber (GF/F)

filters and borosilicate vials were combusted at 450 °C for 2–3 h prior to use. All samples were analyzed between October 2004 and July 2006.

To ensure run-to-run comparability, surface (1 m) and deep (200 m) seawater references (same batch) were incorporated in each run. A large batch of reference seawaters were collected during the summer of 2004 from the Santa Barbara Channel, filtered, dried and stored in 5 mL glass ampoules as described above.

### 2.3. Sample processing

All DCNS samples were analyzed in triplicate following the methodology of Borch and Kirchman (1997) with slight modification of the hydrolysis time (see recovery tests below). Prior to hydrolysis, dried samples were resuspended to the initial volume with Nanopure® water. Samples were then flame sealed and hydrolyzed with $H_2SO_4$ (0.85 M; Fisher) for 21 h at 100 °C. Samples were cooled then pipetted into 30 mL polycarbonate tubes that had been pre-cleaned with successive rinses of methanol (Fisher), 0.5 M HCl, 0.5 M NaOH (Fisher), and Nanopure® water. Samples were neutralized with 1.2 Meq $CaCO_3$ that had been precombusted at 450 °C for 2–3 h and vortexed until a pH of ~6 was achieved (Skoog and Benner, 1997). Samples were then placed in a centrifuge and spun at 28,760*g* for 30 min at room temperature. The supernatant was dispensed by pipette into 7 mL combusted glass scintillation vials equipped with Teflon lined caps and refrigerated (4 °C no longer than 72 h) in the dark prior to desalting. The desalting protocol was conducted according to the methods of Mopper et al. (1992) in 20 mL BioRad (Hercules, CA) HDPE columns that were cleaned with full bed volumes of NaOH (0.5 M), HCl (0.5 M), and Nanopure® water prior to resin loading. Columns were loaded with 7 mL of mixed anion (AG 2-X8, 20–50 mesh, Bio-Rad) and cation (AG 50W-X8, 100–200 mesh, Bio-Rad) exchange resin that were then flushed 3 × with two bed volumes of Nanopure® water and dried by purging with ultra high purity He gas. Resin was primed 3 times with 400 μL of sample and purged immediately. Then, 900 μL of sample was added to the resin and let stand for 7 min before collection in 20 mL combusted glass scintillation vials. Sample salinity was randomly checked with a refractometer. Only one lot of mixed anion and cation exchange resin was used throughout this study and was regenerated over the extended period of analysis to ensure consistency in sugar recovery, as demonstrated with reference water runs.

### 2.4. HPLC analysis

DCNS were analyzed via pulsed amperometric detection high performance liquid chromatography (PAD-HPLC) using a Dionex (Sunnyvale, CA) Bio-LC 600 equipped with a GS-50 pump, ED-50 detector, and AS-50 autosampler. Chromeleon 6.2 integration software was used for data integration. Sugars were isocratically eluted at 18 mM NaOH (50% w/w, Fisher) and separated with Dionex CarboPac PA-10 analytical and guard columns. The electrochemical detector was equipped with an Au working electrode and an Ag/Cl pH reference electrode. A 200 mM NaOH wash (10 min) was used to minimize $CO_3$ buildup on the columns and was performed after each sample. A known Dionex mono-standard (100 nM) of 6 sugars (fucose, galactosamine, glucosamine, galactose, glucose and mannose) was analyzed every 8th sample to assess variability associated with the electrodes and PA-10 columns. This standard was also used to determine if the PAD-HPLC system was stable for each analytical run. Runs were aborted when the decrease in sensitivity approached 20% of initial standard values. A mono-standard mix of 7 sugars including fucose, rhamnose, arabinose, galactose, glucose, mannose, and fructose (Absolute Standards Inc., Hamden, CT) was used for standardization via a 4-point standard curve (10, 75, 125, 250 nM). Desalting and hydrolysis recoveries for aldoses in the quantification standard were within the range of 70–90% and 55–60%, respectively, for all neutral sugars. The values for DCNS in field samples were normalized to hydrolyzed and desalted quantification standards, similar to Kirchman et al. (2001). Concentrations reported have been corrected for blank levels measured with hydrolyzed Nanopure® water. Fructose is degraded or destroyed during acid hydrolysis, and is therefore not reported. Similar to other studies of DCNS in oceanic settings (Borch and Kirchman, 1997; Rich et al., 1997; Kirchman et al., 2001), the peaks for mannose and xylose co-eluted and are referred to as mannose+xylose hereafter.

Vials containing surface and deep reference seawater material processed with every batch of samples were analyzed to track total analytical variability over time. Surface and deep reference waters were analyzed in triplicate at the beginning, middle, and end of each run to assess protocol efficiency, cleanliness and consistency within and between runs.

### 2.5. Ancillary data

Supporting data such as DOC concentration, primary production (PP), temperature, and sigma–theta were provided by the BATS time-series program and are available at (http://bats.bbsr.edu/). DOC concentrations were determined according to the method of Farmer and Hansell (2007), and the analytical variability was $<2\%$ for field (Hansell and Carlson, 2001; Carlson et al., 2004) and seawater culture samples. There is minimal contribution of particles to TOC at the BATS site (Hansell and Carlson, 2001), and DOC concentrations reported herein reflect values determined from unfiltered samples. The methods used to make the remaining ancillary measurements are described in Knap et al. (1997).

### 2.6. Data analyses

Multivariate statistical analysis (EOF) was performed to assess vertical and temporal variability of organic carbon constituents including concentrations of bulk DOC, bulk DCNS, and individual neutral sugars (i.e. fucose, rhamnose, arabinose, galactose, glucose, and mannose+xylose) measured from 2001 to 2004 ($n = 228$ time

points) over the upper 250 m at the BATS study site. All data were mean centered and normalized to their standard deviation at each sampling depth (i.e. 0, 40, 80, 100, 140, 250 m). Correlation coefficients and *p*-values between EOF modal amplitudes, mol% DCNS values, DCNS yield, temperature, and sigma–theta were calculated with Statview 5.0 (SAS). Figures were made using Deltagraph and Matlab and all contour plots were generated using Ocean Data View (Schlitzer, 2007).

### 2.7. Seawater cultures

Seawater culture experiments using natural assemblages of heterotrophic bacterioplankton followed the methods of Carlson et al. (2004). They were designed to assess the turnover of DCNS and DOC that accumulated in the stratified surface seawater at or in the vicinity of the BATS study site. Seawater was collected at BATS in September of 2005 aboard the R/V *Weatherbird II* and along the A20 (30°54′N, 52°20′W) US CLIVAR Repeat Hydrography transect in October of 2003 aboard the R/V *Knorr*. Upon recovery of the CTD, a filtrate of surface seawater was collected in a clean polycarbonate carboy by gravity filtration through a 0.2 μm pore size 142 mm Costar Membra-Fil filter housed in a 142 mm plastic filter holder. Costar Membra-Fil filters leach DOC upon initial use (Carlson et al., 2004), and so were flushed with >2 L of Nanopure® water and >0.5 L of seawater prior to collecting the filtrate to prevent organic contamination. Whole surface seawater was diluted by 70% with the 0.2 μm filtrate for all experimental treatments, and final volumes were 10 and 8 L respectively for the BATS and A20 experiments. All cultures were incubated at *in situ* temperatures in the dark in Precision laboratory incubators for 8–31 days. Bacterioplankton samples for cellular abundance were collected and fixed with 0.2 μm filtered 10% formalin (final concentration 3.5%; Fisher). These samples were stored at 4 °C until slides were prepared (within 48 h of collection). Cells were filtered onto 0.2 μm polycarbonate filters pre-stained with Irgalan black that were subsequently stained with 4′-6′-diamidino-2-phenylidole (DAPI) according to the methods of Porter and Feig (1980). An Olympus AX70 or BX-51 epifluorescence microscope was used to enumerate DAPI stained cells.

## 3. Results

### 3.1. Neutral sugar hydrolysis tests and recoveries

Hydrolysis time was decreased from 24 to 21 h for logistical reasons to maintain high sample throughput while easing the burden of labor over the extended period of analysis. No significant difference in DCNS recovery was observed between these hydrolysis times. The yields for the 24 and 21-h hydrolysis of DCNS from surface reference seawater were 5.7 μmol C $L^{-1}$ (±0.2; $n=15$) and 5.9 μmol C $L^{-1}$ (±0.2 $n=20$) respectively. These results suggest that DCNS recoveries are comparable for the 24 and 21-h hydrolysis times.

Seawater reference material has been used by the DOC analytical community to reduce variability between laboratories and analytical runs and has led to improved analytical capability (Hansell, 2005). We adopted a similar approach of using seawater reference materials to accurately assess run-to-run variability of DCNS and mol% DCNS analyses for this time-series. The same surface and deep reference materials were analyzed several times during each run and throughout the entire analytical period. Average DCNS concentrations were 5.9±0.2 and 0.6±0.1 μmol C $L^{-1}$ for surface and 200 m deep reference seawaters, respectively ($n=20$). The coefficient of variation for all of the surface and deep DCNS references runs were 3% and 16%, respectively, over 20 runs. Variation for triplicate analyses of DCNS was 1–16% and <20% for surface and deep waters, respectively. Coefficients of variation were <11% for all individual neutral sugars except arabinose (~20%) in surface seawater material and were 6–18% for all individual neutral sugars except glucose (<35%) in deep seawater. Analytical variability for triplicate analysis of DCNS and individual neutral sugars in natural samples was within the range described for surface and deep reference seawater material.

### 3.2. Primary production

Maximum levels in integrated PP over the surface 80 m were observed during the winter/early spring coincident with or just after deep convective mixing events at the BATS site. Maximum integrated values for PP ranged from 807 to 1183 mg C $m^{-2}$ $d^{-1}$ during spring months, and decreased to mean values of 238–457 mg C $m^{-2}$ $d^{-1}$ from May to October. Lower values of PP within summer coincided with enhanced mean DCNS concentrations within the surface 40 m at this site (see below).

### 3.3. Temporal variability of DOC

Regular annual patterns in DOC concentrations within the upper 250 m were observed throughout the time period of this study from 2001 to 2004 (Fig. 1a), and are provided as context for DCNS dynamics. Accumulation of DOC occurred annually within the suface 40 m shortly after stratification in late spring, and stable concentrations of 67–69 μmol C $L^{-1}$ were achieved by June (Fig. 1a). Elevated DOC concentrations persisted in the surface 40 m until convective mixing events reduced these concentrations in late autumn, early winter (Fig. 1a). As a result of winter mixing, a portion of the surface-accumulated DOC pool was exported into the upper mesopelagic zone (100–250 m) where it was subsequently removed in the weeks following stratification (Fig. 1a). The annual pattern in DOC concentrations at the BATS site during this study period are similar to those described and detailed elsewhere for previous years (Carlson et al., 1994; Hansell and Carlson, 2001; Carlson et al., 2002).

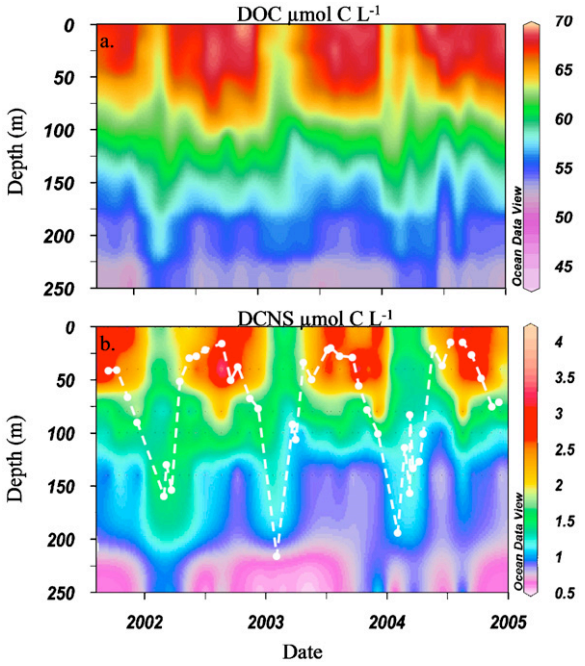


**Fig. 1.** Contour plot of DOC concentrations ($\mu mol\,C\,L^{-1}$) (a) and DCNS concentrations ($\mu mol\,C\,L^{-1}$) (b) over the surface 250 m at the BATS site between 2001 and 2004. DCNS concentrations are overlaid by maximum mixed layer depth (dashed line).

### 3.4. Temporal variability and dynamics of DCNS and DCNS yields

The seasonal dynamics in DCNS concentrations was similar to that of DOC, with a regular annual pattern of accumulation in the surface 100 m during the summer, redistribution and export into the upper mesopelagic during winter convective overturn, and subsequent removal in the upper mesopelagic after the water column stratification (Fig. 1b). During stratified periods (between May and October) DCNS concentrations were greatest in the surface 40 m. These concentrations ranged from 2.1 to 4.2 $\mu mol\,C\,L^{-1}$ compared to $<1\,\mu mol\,C\,L^{-1}$ at 250 m (Fig. 1b, Table 1). During periods of winter mixing (between January and March), DCNS concentrations were reduced to $<2\,\mu mol\,C\,L^{-1}$ in the euphotic zone and enhanced in the upper mesopelagic to 0.8–1.5 $\mu mol\,C\,L^{-1}$ (Fig. 1b, Table 1). After restratification of the water column in the late spring, the enhanced DCNS concentration within the upper mesopelagic zone was removed over the timescales of weeks to months (Fig. 1b).

Systematic changes in DCNS yields (% of DOC) over depth and through time were also observed with some interannual variability related to the magnitude of convective mixing (Table 1). DCNS yield in the upper 40 m ranged from ~3% to 6% during summer months, decreasing to ~2–4% during periods of winter mixing when diagenetically altered deeper water was entrained into the surface waters (Table 1; Supplemental Appendix A). Conversely, DCNS yields within the upper mesopelagic zone increased as much as two fold during and shortly after convective mixing compared to stratified periods (Table 1; Supplemental Appendix A).

### 3.5. DCNS dynamics within the surface 40 m

To examine temporal trends in DCNS concentration within specific depth horizons, we integrated each DCNS variable in the upper 40 m of the euphotic zone and the upper mesopelagic zone (100–250 m) and normalized each stock by the depth of integration to obtain mean DCNS concentrations for each depth horizon.

During convective overturn, between January and March, mesopelagic water with low DCNS concentrations and yields were entrained into the surface 40 m (Fig. 2a, b; Table 1). Over the entire DCNS time-series, the entrainment of deep water during mixing decreased mean DCNS concentrations and yields from December values of 2.6 $\mu mol\,C\,L^{-1}$ and 3.8%; to 1.3 $\mu mol\,C\,L^{-1}$ and 2.1% during mixing, respectively (Fig. 2a, b). As the water column restratified each year, DCNS concentrations increased systematically from March to June at rates of 0.009–0.012 $\mu mol\,C\,L^{-1}\,d^{-1}$ (Table 2). During stratified periods (MLD $<50$ m; May–October), mean DCNS concentrations and yields within the surface 40 m ranged from 2.5 to 2.8 $\mu mol\,C\,L^{-1}$ and 3.8–4.2%, respectively, with significant variability (Fig. 2a, b). The net accumulation of DCNS (0.7–1.2 $\mu mol\,C\,L^{-1}$) in the surface 40 m accounted for 13–33% of annual net DOC accumulation (Table 2).

### 3.6. DCNS dynamics within the upper mesopelagic (100–250 m)

During winter mixing, there was an annual DCNS flux out of the euphotic zone into the 100–250 m depth horizon, increasing the concentrations there from 0.3 to 0.6 $\mu mol\,C\,L^{-1}$ (Fig. 2c). DCNS exported from the surface 100 m was balanced by the enhanced mesopelagic DCNS concentrations each year (data not shown). A corresponding increase in DCNS yields was also observed in the upper mesopelagic zone as a result of this export, with yields as great as 2.5% during periods of deep mixing compared to summer stratified lows (Fig. 2d). Note that the extremely high value of DCNS and DCNS yield in August of 2004 (data point in parentheses) was not related to mixing and may be due to contamination or passage of a mesoscale feature (Fig. 2c, d). As the water column began to stratify, concentrations of DOC, DCNS and DCNS yields all systematically decreased from the time of winter convective mixing until late spring/early summer (Figs. 1 and 2; Table 2), indicating net remineralization of exported DOM within the mesopelagic zone. More specifically, net remineralization of DCNS resulted in the annual removal of 0.4–0.6 $\mu mol\,C\,L^{-1}$ within three months after mixing (Fig. 2c; Table 2) and accounted for 21–28% of the total annual DOC removal (Table 2). Additionally, removal of DCNS within the upper mesopelagic after mixing decreased DCNS yields to premixing levels by summer (Fig. 2c, d). Altogether, the decrease in DCNS and DCNS yields indicated that DOM became diagenetically altered as it was removed at depth.

**Table 1**
Mean concentrations of (±standard deviation) DCNS and DOC, DCNS yields (% DOC), and mol% DCNS during periods of stratification and mixing at the BATS site.

| Depth (m) | DCNS (μmol C $L^{-1}$) | DOC (μmol C $L^{-1}$) | DCNS yield (% DOC) | Mol% fuc | Mol% rham | Mol% arab | Mol% gal | Mol% gluc | Mol% mann+xyl |
|---|---|---|---|---|---|---|---|---|---|
| *2001 Stratified (May–October)* | | | | | | | | | |
| 0 | 2.7±0.3 | 67.5±0.2 | 4.0±0.4 | 15.6±0.4 | 12.7±0.3 | 5.3±0.3 | 26.0±1.3 | 12.8±2.1 | 27.5±1.1 |
| 40 | 2.8±1.0 | 66.4±0.6 | 4.3±1.5 | 14.1±1.6 | 9.9±1.4 | 6.3±0.6 | 25.1±0.3 | 15.0±3.7 | 29.7±0.2 |
| 80 | 1.5±0.3 | 62.7±0.0 | 2.5±0.4 | 13.0±0.7 | 12.3±1.1 | 8.8±0.4 | 24.2±1.6 | 16.5±1.2 | 25.2±1.8 |
| 100 | 1.4±0.4 | 61.0±0.2 | 2.3±0.6 | 12.3±3.4 | 12.5±3.6 | 8.8±1.3 | 18.1±5.3 | 29.7±17.4 | 18.7±3.7 |
| 140 | 1.1±0.3 | 57.2±0.2 | 1.9±0.6 | 9.5±2.4 | 8.6±0.3 | 6.8±2.0 | 12.9±3.6 | 35.9±5.3 | 26.3±2.9 |
| 250 | 0.6±0.0 | 52.3±0.5 | 1.2±0.0 | 13.8±0.1 | 10.2±2.4 | 5.0±0.3 | 18.7±0.9 | 33.4±2.6 | 18.8±1.0 |
| *2002 Stratified (May–October)* | | | | | | | | | |
| 0 | 2.3±0.4 | 67.2±0.2 | 3.4±0.5 | 14.7±1.2 | 11.2±1.7 | 5.9±1.2 | 27.1±1.0 | 14.1±1.1 | 27.0±1.9 |
| 40 | 2.7±0.8 | 67.5±1.0 | 4.1±1.0 | 12.6±2.2 | 9.1±1.5 | 5.6±1.3 | 25.5±2.3 | 18.7±8.4 | 28.5±2.5 |
| 80 | 1.6±0.6 | 64.4±1.6 | 2.5±0.9 | 14.1±1.2 | 9.5±1.3 | 7.8±1.6 | 25.0±1.5 | 17.3±1.6 | 26.4±1.5 |
| 100 | 1.6±0.2 | 63.0±1.1 | 2.6±0.4 | 11.3±3.0 | 9.2±2.8 | 7.2±2.6 | 18.6±6.0 | 27.1±19.9 | 26.6±12.6 |
| 140 | 1.0±0.3 | 59.5±0.9 | 1.7±0.5 | 12.6±2.4 | 9.2±2.2 | 7.6±1.9 | 15.2±3.5 | 32.4±8.8 | 23.1±1.3 |
| 250 | 0.6±0.1 | 53.5±0.7 | 1.2±0.2 | 12.8±3.0 | 10.0±1.3 | 5.9±0.7 | 18.3±3.6 | 29.5±8.5 | 23.5±1.5 |
| *2003 Stratified (May–October)* | | | | | | | | | |
| 0 | 2.5±0.3 | 68.2±.09 | 3.7±0.5 | 13.9±1.0 | 7.7±0.5 | 6.6±1.0 | 28.4±1.4 | 17.4±0.7 | 26.0±1.5 |
| 40 | 2.7±0.8 | 67.3±1.0 | 4.1±1.2 | 12.0±1.9 | 7.5±1.5 | 6.2±1.0 | 27.1±6.1 | 21.1±13.8 | 26.3±4.5 |
| 80 | 1.7±0.3 | 64.6±0.5 | 2.6±0.4 | 14.9±0.9 | 8.4±0.3 | 5.4±0.5 | 23.6±3.0 | 19.4±3.9 | 28.4±1.5 |
| 100 | 1.3±0.2 | 61.7±0.9 | 2.1±0.3 | 11.7±2.4 | 8.8±1.7 | 5.3±0.6 | 18.0±4.8 | 34.6±13.3 | 21.6±4.3 |
| 140 | 0.8±0.1 | 58.1±1.1 | 1.4±0.1 | 12.3±0.5 | 8.3±0.8 | 6.8±2.4 | 16.0±1.4 | 35.8±4.8 | 20.7±2.4 |
| 250 | 0.6±0.2 | 52.3±0.4 | 1.2±0.2 | 10.9±1.6 | 9.3±1.3 | 5.7±0.9 | 17.8±1.8 | 33.7±4.6 | 22.7±1.3 |
| *2004 Stratified (May–October)* | | | | | | | | | |
| 0 | 2.7±0.4 | 68.2±0.9 | 4.1±0.6 | 13.0±0.6 | 9.4±1.6 | 8.8±0.8 | 27.3±1.3 | 13.0±1.4 | 28.6±0.9 |
| 40 | 2.4±0.7 | 67.1±0.8 | 3.7±1.1 | 13.1±0.9 | 8.9±1.2 | 8.8±0.5 | 27.1±1.6 | 13.9±2.8 | 28.2±3.2 |
| 80 | 1.6±0.8 | 63.1±1.0 | 2.7±1.3 | 12.3±0.5 | 10.9±1.2 | 8.8±0.8 | 24.0±1.7 | 14.3±2.1 | 29.6±1.9 |
| 100 | 1.1±0.5 | 61.0±1.1 | 2.0±0.7 | 13.6±0.8 | 10.0±2.8 | 8.1±0.4 | 23.3±2.4 | 20.1±5.7 | 24.9±2.8 |
| 140 | 0.8±0.2 | 57.8±1.4 | 1.5±0.3 | 13.6±0.5 | 9.2±1.1 | 8.5±0.7 | 22.0±2.6 | 18.6±2.0 | 28.1±1.5 |
| 250 | 0.7±0.2 | 53.3±1.0 | 1.4±0.5 | 11.0±2.2 | 7.9±2.0 | 7.0±1.9 | 17.0±3.8 | 32.7±9.4 | 24.4±1.5 |
| *2002 Mixed (January–March)* | | | | | | | | | |
| 0 | 1.7±0.4 | 64.1±0.9 | 2.7±0.8 | 14.1±3.4 | 11.5±2.4 | 5.2±1.1 | 19.6±3.0 | 22.9±9.9 | 26.7±1.6 |
| 40 | 1.5±0.2 | 62.7±3.1 | 2.5±0.4 | 14.9±1.9 | 9.5±1.1 | 7.7±0.8 | 22.1±1.6 | 19.8±4.7 | 26.0±1.2 |
| 80 | 1.1±0.1 | 61.7±2.1 | 1.8±0.1 | 15.1±1.0 | 11.3±1.2 | 9.2±0.3 | 21.9±0.4 | 16.8±0.9 | 25.7±1.4 |
| 100 | 1.3±0.1 | 61.7±0.7 | 2.1±0.3 | 13.3±3.1 | 11.4±2.2 | 8.6±1.5 | 19.8±2.3 | 24.2±13.1 | 22.7±4.0 |
| 140 | 1.5±0.2 | 59.6±1.2 | 2.4±0.4 | 11.1±1.7 | 10.6±1.1 | 9.0±1.1 | 16.4±0.6 | 27.5±7.8 | 25.5±4.2 |
| 250 | 1.0±0.1 | 55.3±1.1 | 1.8±0.3 | 11.2±4.1 | 7.3±2.5 | 4.1±1.3 | 15.4±5.9 | 42.7±17.9 | 19.4±7.4 |
| *2003 Mixed (January–March)* | | | | | | | | | |
| 0 | 1.4±0.2 | 64.2±0.9 | 2.2±0.4 | 15.9±0.6 | 9.1±0.4 | 8.0±0.3 | 23.7±3.5 | 21.4±3.5 | 21.9±1.0 |
| 40 | 1.5±0.1 | 63.6±1.3 | 2.4±0.1 | 13.5±1.2 | 10.1±2.0 | 7.0±0.4 | 23.5±1.9 | 19.9±0.5 | 25.9±1.0 |
| 80 | 1.3±0.3 | 62.7±1.6 | 2.1±0.5 | 17.3±1.7 | 9.5±0.5 | 6.2±0.5 | 19.4±0.9 | 23.2±3.7 | 24.4±0.1 |
| 100 | 1.2±0.3 | 61.7±1.5 | 2.0±0.4 | 13.8±0.4 | 9.4±0.7 | 5.1±0.6 | 19.8±2.2 | 22.7±7.2 | 29.3±5.0 |
| 140 | 1.2±0.2 | 59.6±0.6 | 2.0±0.3 | 14.4±0.4 | 9.0±0.4 | 6.3±0.4 | 19.3±0.7 | 29.0±2.7 | 22.1±1.5 |
| 250 | 0.6±0.1 | 53.2±0.3 | 1.1±0.1 | 11.5±0.7 | 10.7±1.0 | 5.7±0.8 | 15.5±3.7 | 31.8±1.2 | 24.9±1.2 |
| *2004 Mixed (January–March)* | | | | | | | | | |
| 0 | 1.4±0.1 | 63.3±1.1 | 2.2±0.1 | 13.5±0.7 | 9.0±0.7 | 9.4±0.6 | 21.8±1.3 | 20.2±3.7 | 26.2±1.0 |
| 40 | 1.3±0.1 | 62.8±0.1 | 2.1±0.2 | 13.3±0.6 | 11.9±1.3 | 8.2±0.6 | 22.6±4.0 | 17.9±2.7 | 26.1±1.3 |
| 80 | 1.4±0.1 | 61.9±0.9 | 2.3±0.1 | 12.5±0.9 | 12.3±1.1 | 8.8±0.4 | 24.2±1.6 | 16.2±3.3 | 28.2±1.6 |
| 100 | 1.2±0.1 | 61.7±1.6 | 2.0±0.1 | 14.4±0.5 | 10.4±2.7 | 9.3±0.7 | 22.4±1.1 | 15.2±1.7 | 28.2±1.5 |
| 140 | 1.1±0.1 | 59.0±1.8 | 2.0±0.3 | 12.9±1.0 | 7.8±0.9 | 5.8±0.1 | 20.9±1.5 | 25.8±4.5 | 26.8±1.3 |
| 250 | 0.8±0.2 | 53.4±1.3 | 1.4±0.6 | 10.0±2.7 | 6.5±1.7 | 5.3±1.1 | 14.4±3.1 | 41.2±11.1 | 22.5±3.7 |

Means and standard deviations were calculated from triplicate means at each nominal depth for 7 stratified and 3 mixed time-points each year.

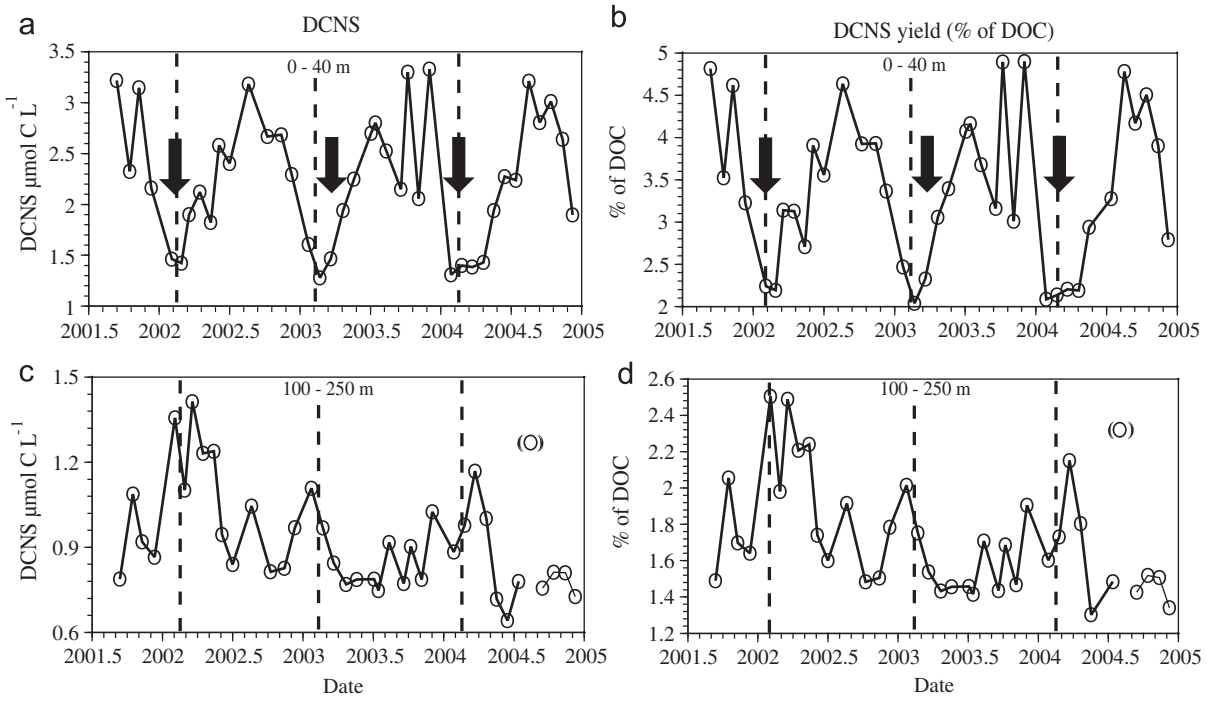


**Fig. 2.** Integrated and depth normalized DCNS (a,c) and DCNS yields (b,d) from 0 to 40 m (top panels) and 100 to 250 m (bottom panels). DCNS yields represent the percentage of integrated and depth-normalized DCNS means relative to DOC means. Vertical dashed lines represent the date when maximum mixed layer depths occurred and blackened arrows denote the time when maximum primary production values were observed. The high value in August of 2004 (denoted by parentheses) was not related to mixing and may be due to sampling error, contamination, or passage of a mesoscale feature. DCNS yield panels contain fewer points than the DCNS concentration panels due to missing DOC values for corresponding time-points.

**Table 2**
Depth normalized rates of net-production and net-remineralizaton of DCNS within the surface 40 m and 100–250 m depth horizons at the BATS site.

| Year | Months | Duration (days) | ΔDCNS ($\mu$mol C L$^{-1}$) | %ΔDOC | DCNS ($\mu$mol C L$^{-1}$ d$^{-1}$) | $R^2$ | $n$ |
|---|---|---|---|---|---|---|---|
| *Net DCNS production 0–40 m* | | | | | | | |
| 2002 | March–July | 73 | 0.7 | 13 | 0.009 | 0.35 | 4 |
| 2003 | March–July | 100 | 1.2 | 33 | 0.012 | 0.99 | 4 |
| 2004 | March–July | 83 | 0.9 | 19 | 0.011 | 0.91 | 4 |
| *Net DCNS remineralization 100–250 m* | | | | | | | |
| 2002 | March–July | 103 | 0.6 | 21 | 0.006 | 0.91 | 5 |
| 2003 | January–April | 90 | 0.4 | 25 | 0.004 | 0.98 | 4 |
| 2004 | March–June | 83 | 0.6 | 28 | 0.007 | 0.96 | 4 |

The start of production was considered to be in March of each year; net production rates were estimated from March to July.
The onset of remineralization between 100 and 250 m varied, and corresponded to maximum DCNS values that were coincident with winter mixing.
% ΔDOC represents percentage of DCNS produced or removed relative to the amount of DOC produced or removed.

### 3.7. DCNS composition

Vertical and temporal variability of glucose, galactose, and mannose+xylose concentrations, when translated to mol% DCNS values, revealed qualitative diagenetic trends. All neutral sugar concentrations were enhanced in the upper 40 m during stratified periods (Fig. 3; Table 1). Fucose, rhamnose, and arabinose made smaller contributions to DCNS of 12–16%, 8–13%, and 5–9%, respectively, within the upper 40 m during stratified periods (Table 1). Less variability was observed for the molar fractions of fucose, rhamnose, and arabinose throughout the entire time-series study (Table 1), and although the trends of these neutral sugars will not be discussed further, all data has been provided (Supplemental Appendix A). Concentrations of galactose, mannose+xylose and glucose were greatest in the upper 40 m during stratification (Fig. 3a–c; Table 1), and galactose and mannose+xylose each contributed 25–30% to total DCNS while glucose accounted for 13–21% (Fig. 3d–f; Table 1). The enrichment in mol% of

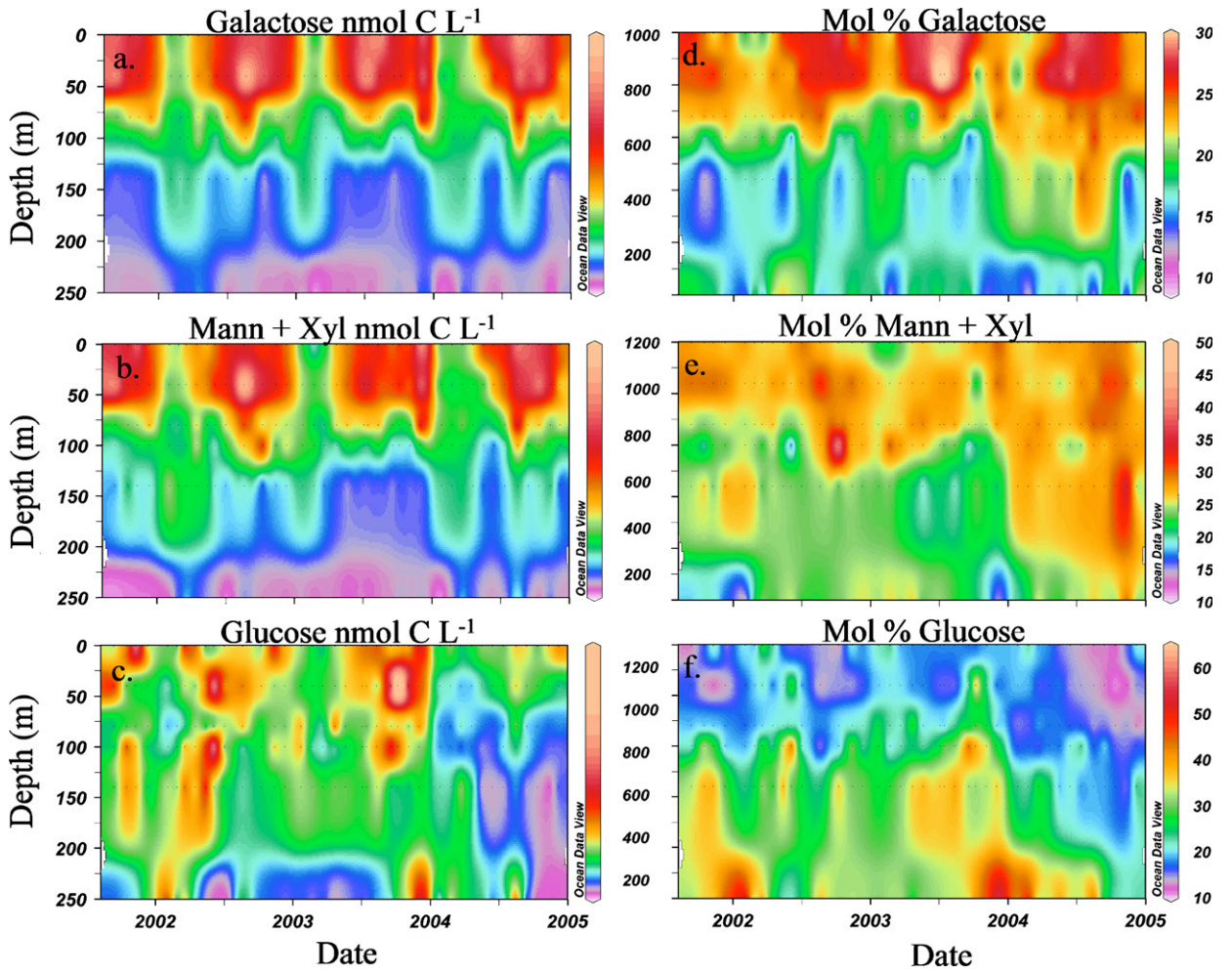


**Fig. 3.** Contour plots of galactose (a), mannose+xylose (b), and glucose (c) concentrations (nmol C $L^{-1}$); and mol% galactose (d), mol% mannose+xylose (e), and mol% glucose (f) values over the upper 250 m at BATS between 2001 and 2004. Maximum concentrations were $<2100$ nmol C $L^{-1}$.

galactose and mannose+xylose in the euphotic zone DOM during stratified periods was coincident with higher DCNS yields (Fig. 3d, e; Table 1), indicating that these neutral sugars were recently produced and less diagenetically altered. Conversely, higher mol% glucose content, coupled with lower DCNS yields in the deeper waters ($>100$ m), revealed the presence of a more recalcitrant and diagenetically altered DOM pool (Fig. 3f; Table 1).

Regular annual patterns in depth-normalized mean concentrations and the mol% contributions of galactose, mannose+xylose, and glucose also revealed qualitative diagenetic trends within the surface 40 m at BATS (Fig. 4). The DCNS that accumulated in the surface 40 m after stratification was enriched in galactose and mannose+xylose relative to glucose, and reached maximum concentrations of 600–950 nM C during summer months (Fig. 4a). Concentrations of these three neutral sugars decreased to levels ranging from 200 to 550 nM C during winter mixing (Fig. 4a). The diagenetically altered signature of mol% glucose enrichment combined with low DCNS yield was expressed in the surface waters during winter convection as a result of entrainment of diagenetically altered mesopelagic DOM into the surface layer (Fig. 4b, Table 1). During these times, glucose levels reached 22–30% of DCNS while mannose+xylose and galactose were 23–25% and 20%, respectively (Fig. 4b). Mean glucose concentrations and mol% of glucose were uncharacteristically high in June of 2002 and October of 2003, and could be related to sample contamination (Fig. 4; points in parentheses).

### 3.8. *Seawater cultures*

The dark seawater culture experiments were designed to assess the fraction of the accumulated DCNS and DOC available to heterotrophic bacterioplankton on the timescales of days to weeks. Concentrations of DOC and DCNS at the initial time point of the experimental treatments were not significantly different from *in situ* surface concentrations, indicating no resolvable contamination of these variables as a result of experimental set

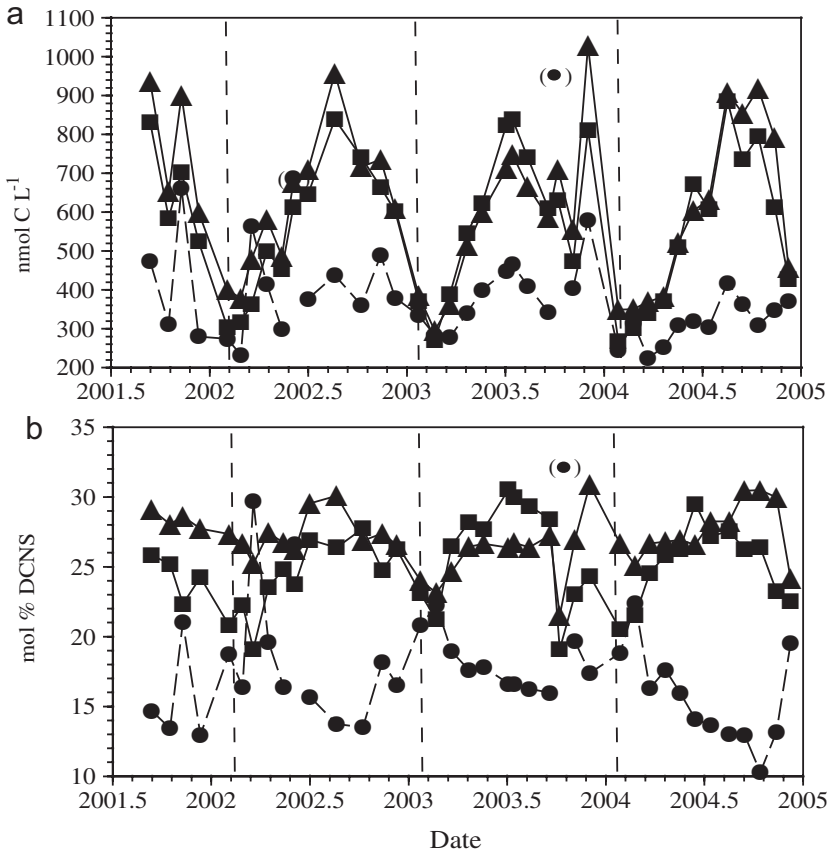


**Fig. 4.** Integrated and depth normalized concentrations (a) and mol% DCNS values (b) for glucose (closed circles, dashed lines), galactose (closed squares), and mannose+xylose (closed triangles) in the upper 40 m between 2001 and 2004 at the BATS study site. Vertical dashed lines indicate the date when maximum mixed layer depths were observed. Uncharacteristically high mean glucose concentrations and mol% of glucose observed in June of 2002 and October of 2003 are enclosed in parentheses (see text).

**Table 3**
Variables for seawater culture experiments conducted at the BATS study-site and the A20 transect site in the subtropical North Atlantic Ocean.

| Expt (date) | Lat. long. | Duration (days) | Inc temp (°C) | ΔBact (μmol C L$^{-1}$) | Ambient DOC (μmol C L$^{-1}$) | Experimental DOC (μmol C L$^{-1}$) | | Experimental DCNS (μmol C L$^{-1}$) | | Experimental DCNS yield (% of DOC) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Initial | Final | Initial | Final | Initial | Final |
| A20E2 10/03 | 30°54′N 52°20′W | 8 | 26 | 0.15 | 68.4 | 69.6±0.6 | 69.1±1.0 | 3.3±0.2 | 3.5±0.1 | 5 | 5 |
| BATS 9/05 | 31°40′N 64°10′W | 31 | 26 | 0.09 | 67.5±0.4 | 68.4±0.2 | 67.5±0.4 | 4.2±0.2 | 3.9±0.2 | 6 | 6 |

Ambient and experimental means (±standard deviation of triplicate samples) for DOC, DCNS, and DCNS yields are reported.
Ambient DOC concentrations correspond to the surface 10–20 m.
A conversion factor of $1\times10^{-14}$ g C cell$^{-1}$ (Fuhrman, 1981) was used to convert cell abundances to bacterial carbon.

up (Table 3). Experimental results demonstrated minimal change in bacterial biomass over the course of 8 days (Table 3) with no resolvable change in DOC, DCNS, or DCNS yields over the course of 8 or 31 days ($p>0.05$). In all, the values reported for DCNS concentrations and yields were within the ranges observed within the surface 40 m (2.1–4.2 μmol C L$^{-1}$ and 3–6%, respectively) throughout the entire time-series study (see Supplemental Appendix A).

### 3.9. EOF modes

The EOF statistical technique decomposes a data set into a set of modes of variability (Emery and Thomson, 1997) analogous to the axes in principle component analysis. The analysis produces an amplitude time-series for each mode that indicates its relative importance to overall variability at each point in time. Comparison of the amplitude time series of each mode is useful for

diagnosing how the contribution of each mode to total variance changes in time or space (Emery and Thomson, 1997). We used EOF analysis to assess the variability of the concentrations of DOC, fucose, rhamnose, arabinose, galactose, glucose, mannose+xylose, and DCNS relative to one another. The aforementioned trends in DCNS composition, specifically the relationship between mol% of galactose, mannose+xylose, and glucose, were confirmed by EOF analysis. The first two EOF modes describe 82% of the variance within the organic carbon pool (Fig. 5). The remaining 6 modes each explain a minor fraction of the remaining 18% of variance and will not be discussed further.

Mode 1 accounts for 68% of the variance within the organic carbon data set, revealing that all of the variables fluctuated in relative unison throughout this time series. All concentrations of DOC, DCNS, and neutral sugars increased when amplitudes were more positive and decreased when amplitudes were more negative (Fig. 5a). Correlations between the first mode and each of the variables in the organic carbon data set were significantly positive, with greater values indicating stronger contribution to modal variance (Fig. 5a). The strongest positive correlations were between Mode 1 and fucose ($r^2 = 0.87$), rhamnose ($r^2 = 0.72$), arabinose ($r^2 = 0.64$), galactose ($r^2 = 0.87$), mannose+xylose ($r^2 = 0.88$), and DCNS ($r^2 = 0.89$) while the contribution of DOC ($r^2 = 0.33$) and glucose ($r^2 = 0.16$) to the variance was significantly less (Fig. 5a). Visualization of the modal amplitudes reveals distinct temporal and vertical patterns (Fig. 5b). In the euphotic zone, amplitudes are more positive during periods of seasonal DCNS accumulation in the summer and autumn and more negative during winter convective mixing. Negative amplitudes that occurred annually within the upper 100 m are due to dilution with lower DOM concentrations from the upper mesopelagic during winter mixing. Within the upper mesopelagic, the changes from positive to negative are due to the interannual variability of maximal mixed layer depths (Fig. 5b) that influence the amount of DOC and DCNS annually exported into this depth horizon (Fig. 5b). Though the number of sample points available within the upper mesopelagic zone limits our analysis, the empirical trends are both repeatable and consistent with those established for bulk DOC at this site (see above).

Pearson pair-wise correlation analysis between mode 1 amplitude time-series, DOM quality indices, and stratification indices (temperature and sigma-theta) reveals significant positive correlations with DCNS yields and temperature, and a significant negative correlation with sigma–theta (Table 4). This finding reinforces our observations that the seasonal accumulation of DOM occurs

**Table 4**
Pearson's correlation coefficients ($R$) for association for mol% DCNS, DCNS yield (% of DOC), temperature, and sigma–theta against EOF Modes 1 and 2.

| Variable | EOF Mode 1 ($R$) | EOF Mode II ($R$) | ($n$) |
|---|---|---|---|
| % Fucose | −0.13 | 0.23 | 216 |
| % Rhamnose | −0.06 | 0.29 | 216 |
| % Arabinose | −0.04 | 0.30 | 216 |
| % Galactose | 0.21 | **0.58** | 216 |
| % Glucose | −0.16 | **−0.67** | 216 |
| % Mannose+xylose | 0.26 | **0.53** | 216 |
| DCNS yield | **0.89** | **0.50** | 216 |
| Temperature | **0.68** | **0.52** | 207 |
| Sigma–theta | **−0.64** | **−0.47** | 207 |

Numbers in bold are significant at $p<0.01$ level. Sample size, ($n$), is the number of samples compared.

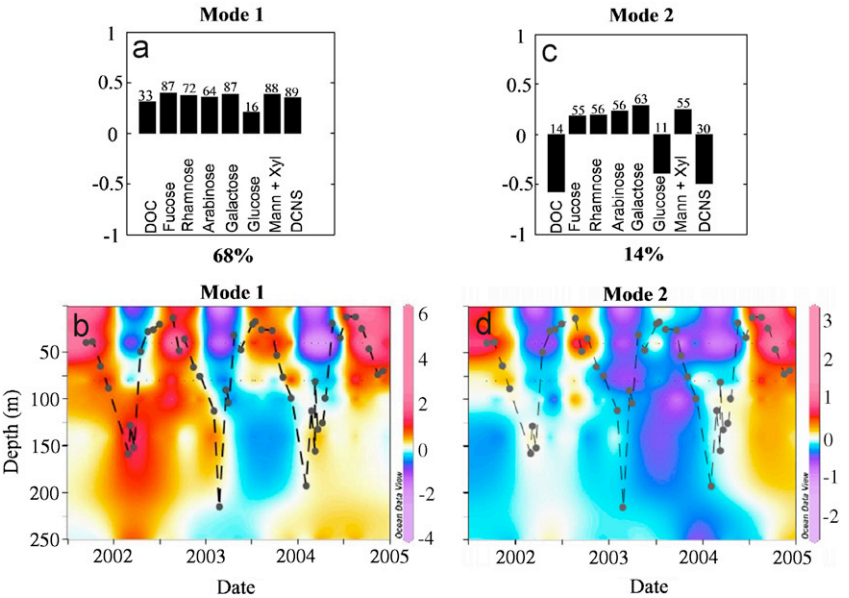


**Fig. 5.** EOF Modes 1 and 2 (a,c) for DOC, fucose, rhamnose, arabinose, galactose, glucose, mannose+xylose, and DCNS. Emboldened values describe the amount of variance explained by each mode and the numbers above each bar are the $r^2$ values between each organic carbon measurement and the corresponding mode. Contour plots represent the distribution of EOF time amplitude functions from Mode 1 (b) and Mode 2 (d) between 2001 and 2004. Dashed line represents maximum mixed layer depth.

during the summer and autumn within the upper 100 m where temperatures are warmer, the DCNS yield is high, and seawater density is lower. The inverse of these relationships define periods of winter mixing when time-amplitude functions are negative.

Mode 2 describes 14% of the variance within the organic carbon pool and appears related to the differences in organic carbon constituents between surface waters and the upper mesopelagic (Fig. 5c). The patterns of fucose, rhamnose, arabinose, galactose, and mannose+xylose were inversely correlated with those of DOC, glucose, and DCNS. Positive modal amplitudes reflect the increase in the concentrations of all of the organic carbon variables; however, variability is driven by the changes of fucose, rhamnose, arabinose, galactose, and mannose+xylose relative to DOC, glucose, and DCNS. Negative amplitudes demonstrate the decrease in the concentrations of all the organic carbon variables, indicating an enhanced contribution of DOC, glucose, and DCNS concentrations to the variance compared to the remaining variables. Significant correlations were observed between Mode 2 and all of the organic carbon constituents analyzed (Fig. 5c). Strongest positive correlations were observed between Mode 2 and fucose ($r^2 = 0.55$), rhamnose ($r^2 = 0.56$), arabinose ($r^2 = 0.56$), galactose ($r^2 = 0.63$), and mannose+xylose ($r^2 = 0.55$) (Fig. 5c). Within the euphotic zone, periods of seasonal DOM accumulation were more positive than those of winter mixing (Fig. 5d). This result indicates that the increase in the concentrations of fucose, rhamnose, arabinose, galactose, and mannose+xylose during seasonal DOM accumulation contributes more to the variance than the increase of DOC, glucose, and DCNS within upper 100 m during these times (Fig. 5c, d). Higher concentrations of DOC, glucose, and DCNS relative to the 5 other neutral sugars are predominantly indicative of the upper mesopelagic, with the exception of the latter part of 2004 (Fig. 5d). Thus, the presence of negative amplitudes within the upper 100 m throughout periods of winter mixing traced a DOM pool originating from the upper mesopelagic zone.

Correlation analysis revealed strong positive correlations between Mode 2 time-amplitude series and mol% galactose and mol% mannose+xylose, DCNS yields and temperature, but significant negative correlations with mol% glucose and sigma–theta (Table 4). These correlations suggest that positive amplitudes observed during stratified periods are coincident with a DCNS pool enriched in mol% galactose and mannose relative to glucose, higher DCNS content, warmer temperatures, and lower seawater densities that define periods of seasonal DOM accumulation within the euphotic zone. Negative amplitudes are consistent with a DCNS pool enriched in glucose, lower temperatures, and higher seawater densities such as those present in the upper mesopelagic and euphotic zone during winter mixing.

## 4. Discussion

The recovery of known standards from the hydrolysis and desalting procedure was comparable to Borch and Kirchman (1997) and Kirchman et al. (2001). The BATS DCNS time-series was analyzed over the course of 21 months (20 separate runs). Our recovery and replication results, including the replicate variability of glucose (<35%), are consistent with those observed for coastal and open ocean samples (Borch and Kirchman, 1997; Skoog and Benner, 1997; Rich et al., 1997; Amon et al., 2001; Kirchman et al., 2001). The consistent recovery of DCNS in reference material lends support to the trends observed for DCNS concentrations, DCNS yields, and mol% DCNS that will be discussed below.

Changes in DCNS concentrations, DCNS yields (% of DOC), and the molar fractions of DCNS indicated systematic shifts in DOM quality at the BATS study site. The seasonal dynamics of DCNS concentrations and DCNS yield were similar to that of DOC observed from 2001 to 2004 (Fig. 1; Table 1) and for DOC dynamics that have been previously detailed for this site (Carlson et al., 1994; Hansell and Carlson, 2001; Carlson et al., 2002). DOM with higher DCNS concentrations and yields accumulated in the euphotic zone shortly after stratification, and a portion of this surface-accumulated pool was exported into the upper mesopelagic during winter mixing (Figs. 1 and 2). This exported DCNS and DOC was utilized within the upper mesopelagic in the weeks following convective overturn. DCNS yields tracked both the export of recently produced DOM into the upper mesopelagic and the ensuing diagenetic alteration that accompanied DOM and DCNS remineralization (Fig. 2; Table 1).

### 4.1. DCNS accumulation in relation to primary productivity

Carbohydrates account for a large fraction of the DOM released by phytoplankton (Ittekot et al., 1981; Ittekot, 1982; Eberlein et al., 1985; Obernosterer and Herndl, 1995; Biddanda and Benner, 1997; Borsheim et al., 1999; Meon and Kirchman, 2001). Our results reveal that the production of DCNS at BATS was temporally offset relative to the peak in primary productivity, and that DCNS production was not directly related to the magnitude of primary production (Fig. 2a). However, the exact DOM production mechanisms that resulted in the production of DCNS remain unclear. There are many mechanisms by which DOM is produced, including phytoplankton extracellular release, zooplankton sloppy feeding and excretia, viral and bacterial lysis of cells, particle solubilization, and bacterial transformation and release (Carlson, 2002 and citations within). A large fraction (10–60%) of DOM release can occur during bloom senescence phases (Myklestad, 2000) upon the onset of nutrient depletion (Mopper et al., 1995; Obernosterer and Herndl, 1995). Additionally, phytoplankton community structure may influence DOM release (Lomas and Bates, 2004), which might also help to explain some of the temporal offset between peak bloom primary production and DCNS accumulation.

### 4.2. DCNS yields, DOM quality, and turnover

The most labile components of the DOC pool include compounds such as dissolved free neutral sugars (DFNS),

dissolved free amino acids (DFAA) and some unknown portion of their combined pools. These labile components cycle very rapidly (Fuhrman, 1987; Suttle et al., 1991; Rich et al., 1997; Keil and Kirchman, 1999) and fuel a significant fraction of bacterial production in the euphotic zone of some systems (Rich et al., 1997; DFNS, and Suttle et al., 1991; Kirchman et al., 2001: DFAA). As a result of this tight coupling, the most labile components of organic matter do not accumulate and are kept at very low concentrations (<3 nM). By only measuring concentrations of DCNS without associated flux measurements, one will underestimate the contribution of labile DCNS to carbon cycling. Additional tracer (stable or radioisotopic) approaches would be necessary to accurately account for the flux and contribution of labile compounds to carbon cycling. Thus, care must be taken when interpreting the concentrations of specific compounds, such as the accumulated DCNS pool, relative to bulk DOC. The objectives of this study were to (1) assess the dynamics of the accumulated DCNS pool that can be readily resolved by measuring concentrations, and (2) normalize DCNS concentrations to those of bulk DOC to help infer DOM quality. Higher DCNS yields measured in the euphotic zone at BATS are indicative of less diagenetically altered organic matter compared to deeper DOM and is consistent with studies conducted in the Pacific, Southern and Arctic oceans (Skoog and Benner, 1997; Kirchman et al., 2001; Amon and Benner, 2003). Several studies have demonstrated the rapid cycling of freshly produced DCNS in both HMW-DOM (Aluwihare and Repeta, 1999) and bulk DOM (Janse et al., 1999; Amon et al., 2001; Hama et al., 2004), while others studies have shown that a portion of the newly produced DCNS and DCAA pools resists rapid removal and withstands degradation over longer timescales (Fry et al., 1996; Keil and Kirchman, 1999; Kirchman et al., 2001; Meon and Kirchman, 2001). In the present study, DOM remineralization experiments were conducted to evaluate the fraction of the surface-accumulated DCNS and DOC pool that may turnover on time scales of days to weeks at the BATS site. These experiments were designed to "shut off" photoautotrophic DOM production and force the heterotrophic bacterioplankton to utilize surface-accumulated DOM (Carlson and Ducklow, 1996).

At the time these experiments were conducted, changes in the concentrations of DCNS and DOC were below our limits of detection and such changes could not be resolved over the time scale of one to four weeks (Table 3). The lack of resolvable change in DCNS and DOC concentrations in these experiments was consistent with previous studies conducted at this site that employed the same experimental design. These earlier studies were unable to resolve DOC removal at the BATS site when initial experimental concentrations were within the climatological range of 67–69 $\mu mol\,C\,L^{-1}$, characteristic of the summer mixed layer (Carlson and Ducklow, 1996; Carlson et al., 2002, 2004; Repeta per. com). However, it is important to note the large variability in DCNS concentrations and yields in the surface 40 m during summer stratified periods at BATS (Fig. 2a, c). Such variability suggests aperiodic uncoupling between DOM source-sink mechanisms resulting in short-term accumulation of labile compounds. Consistent with this hypothesis, other experimental studies have attributed the removal of labile DOC to the observed changes in respiratory gases ($CO_2$ or $O_2$) measured over timescales of days to months at this site (Hansell et al., 1995; Obernosterer et al., 2003). Because DOC concentrations were not measured directly in the experimental treatments conducted by Hansell et al. (1995) and Obernosterer et al. (2003), it is difficult to evaluate how initial experimental conditions compared to BATS mixed layer DOC concentrations. Nonetheless, we do not rule out the likelihood of short-term transient accumulation of labile DCNS at the BATS site. Our experimental results are important because they suggest that the presence of high DCNS concentrations and yields, which was observed within the seasonally accumulated pool of DOM in the surface waters at the BATS site, may not always equate to rapid microbial removal as portions of the DCNS pool can, at times, survive degradation over longer timescales (Kirchman et al., 2001; Meon and Kirchman, 2001). Similar dynamics have been proposed for the DCAA pool at the BATS site, as discussed by Keil and Kirchman (1999).

### 4.3. Neutral sugar contribution to DCNS: relating EOF modes to DOM quality

DCNS yield provides insight into the reactivity of the bulk DOM pool. Examination of the contribution of individual neutral sugars within DCNS provides information about the accumulation or preferential utilization of these compounds and the quality of the DCNS pool. We used EOF analysis to assess the variability of DOC, DCNS, and neutral sugars and related this variability to indices of DOM quality and stratification. EOF analysis revealed that concentrations of DOC, DCNS, and the suite of 6 neutral sugars covaried and accounted for 68% of the Mode 1 variance and was significantly correlated to aldose yields but not to any of the individual mol% fractions of DCNS (Fig. 5a, b; Table 4). Although Mode 1 describes the general dynamics of the DOM pool, changes in the composition of DCNS (i.e. mol% neutral sugars) cannot be related to shifts in DOM quality tracked by changes in DCNS yields. At face value, these results are consistent with studies suggesting that the composition of DCNS is relatively uniform over depth in both HMW (McCarthy et al., 1996; Aluwihare et al., 1997) and total DOM (Borch and Kirchman, 1997).

However, results from Mode 2 of our EOF analysis accounted for a smaller yet significant portion of the variance (14%) and demonstrated an inverse relationship between the concentrations of DOC, DCNS, glucose and the 5 remaining neutral sugars (Fig. 5c, d). Mode 2 was significantly correlated with DCNS yields, mol% galactose, mol% mannose+xylose, and mol% glucose indicating that these specific mol% fractions of DCNS could be used to infer changes in DOM quality in this mode (Table 4). More diagenetically altered DOM with a lower DCNS yields was enriched with glucose (Table 1). Conversely, diagenetically fresher DOM with relatively higher yields was enriched with galactose and mannose+xylose (Table 1). This finding

suggests that there were clear differences in the mol% DCNS content of recently produced and older, more diagenetically altered DOM at the BATS site. Elevated mol% galactose, mol% mannose+xylose, and low mol% glucose indicated less diagenetically altered DOM compared to DOM enriched with glucose and low DCNS yield. This result is consistent with studies that have related DCNS composition to DOM diagenetic state in bulk DOM (Skoog and Benner, 1997; Kirchman et al., 2001), HMW-DOM (Amon and Benner, 2003), LMW-DOM (Skoog and Benner 1997), and recalcitrant DOM (Engbrodt and Kattner, 2005).

### 4.4. Potential implications of DCNS dynamics in the upper mesopelagic zone

DOM exported from the surface waters into the upper mesopelagic zone during convective mixing was elevated in DCNS concentrations and yields (Fig. 2c, d; Table 1), indicating the flux of some recently produced DOM into this depth horizon. At the BATS site, a marked increase in mesopelagic bacterial biomass has been observed shortly after convective overturn and DOM export (Steinberg et al., 2001; Morris et al., 2005), and specific lineages of bacterioplankton (i.e. OCS116, SAR11 subgroup II, marine Actinobacteria, and SAR202) respond and account for a portion of this increase (Morris et al., 2005; Carlson et al., 2008). Morris et al. (2005) hypothesized that the flux of surface organic matter into the upper mesopelagic may be a factor governing the observed community structure shift. The introduction of diagenetically fresher DOM into the mesopelagic that has been demonstrated herein is consistent with this hypothesis and may help to explain some of this community structure response. Further studies are required to verify this hypothesis.

## 5. Conclusions

We have shown that the annual pattern of DCNS accumulation within the euphotic zone, export into the mesopelagic zone, and net removal within the mesopelagic zone seems to parallel that of DOC dynamics. There were clear differences in the DCNS yield and the mol% contribution of neutral sugars to total DCNS between new and older more recalcitrant DOM. The surface-accumulated DOM pool had greater DCNS yields and elevated mol% galactose and mannose+xylose levels, indicating the accumulation of some recently produced DOM. Prior to deep convective mixing, deeper waters were characterized by lower DCNS yields and the DOM was enriched in glucose. After convective overturn and export of DOM into the upper mesopelagic zone, DCNS concentrations and DCNS yields increased significantly within this depth horizon. In the weeks proceeding stratification, DCNS concentrations and yields systematically decreased in the mesopelagic, lending support to the claim that DOC removal at depth was a result of biological remineralization. Finally, while DCNS yields are indicative of overall DOM bioreactivity potential, DCNS yield alone does not constrain the timescales of its turnover.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2008.12.013.

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