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Source: *Limnology and Oceanography*, Vol. 49, No. 4, Part 1 (Jul., 2004), pp. 1084-1094
Published by: American Society of Limnology and Oceanography
Stable URL: <http://www.jstor.org/stable/3597659>
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Metabolic poise in the North Atlantic Ocean diagnosed from organic matter transports

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Abstract

Recently there has been discussion about the metabolic state of the ocean, with arguments questioning whether the open ocean is net autotrophic or net heterotrophic. Accurately determining the metabolic balance of a marine system depends on fully defining the system being evaluated and on quantifying the inputs and outputs to that system. Here, a net northward transport of dissolved organic carbon (DOC) (across 24.5°N) of 3.3 ± 1.9 Tmol C yr⁻¹ was determined using basin-wide transport estimates of DOC. This flux, coupled with DOC inputs from the Arctic Ocean (2.2 ± 0.8 Tmol C yr⁻¹), the atmosphere (0.6 ± 0.08 Tmol C yr⁻¹), and rivers (3.1 ± 0.6 Tmol C yr⁻¹), indicates net heterotrophy in the North Atlantic (full depth, 24.5–72°N) of 9.2 ± 2.2 Tmol C yr⁻¹. This rate is small (<2%) compared to autochthonous production (~494 Tmol C yr⁻¹) and consumption (production:respiration of 0.98), indicating that the North Atlantic is essentially metabolically balanced and that autochthonous production is remineralized within the basin. The upper layer of the subtropical gyre has previously been reported to exhibit high rates of net heterotrophy, but our analysis does not support those findings. Instead, allochthonous inputs of organic carbon to the upper subtropical gyre are an order of magnitude less than required by the elevated rates of net heterotrophy reported. We find, too, that net mineralization of allochthonous DOC within the basin could account for 10% of the preindustrial inorganic carbon exported from the basin to the south. Two factors, the import of organic matter and the unique thermohaline circulation pattern of the North Atlantic, are primary in ensuring net heterotrophy in the basin.

The ocean carbon cycle, a primary regulator of atmospheric carbon dioxide (CO₂) and thus the global climate (Hanson et al. 2000; Houghton et al. 2001), is a key component of the earth system, yet its current biogeochemical state is not well understood (Falkowski et al. 2000). The

metabolic state of the oceans, defined as the balance between in situ primary production and total respiration (Smith and Hollibaugh 1993), is intimately tied to inputs of organic matter and nutrients from land (Ver et al. 1999). Prior to the industrial revolution, the global ocean was a net source of CO₂ to the atmosphere, with CO₂ evasion to the atmosphere and carbon burial in the sediments balancing the input of fixed carbon from land (Smith and Mackenzie 1987). The current state of the global ocean may be different, depending on the relative importance of terrestrial inputs of inorganic nutrients (fueling primary production) and organic matter (supporting respiration). Inorganic nutrient inputs have approximately doubled, whereas organic matter inputs have increased by about 30% in the past three centuries (Ver et al. 1999).

The current metabolic state of the oceans, at basin to global scales, is a subject of debate. Most conclusions are based on budget calculations in which key terms (i.e., organic carbon production, respiration, and burial) have large uncertainties (Smith and Hollibaugh 1993), or on indirect assessments derived using empirical relationships of regional-scale process measurements having limited spatial or temporal coverage (del Giorgio et al. 1997; Hoppe et al. 2002). Recent direct assessments using discrete, local-scale measurements

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Acknowledgments

We thank the scientists and crew who participated on this cruise of the NOAA Ship Ron Brown in 1998. Through their hard work and dedication, co-Chief Scientists Dave Bitterman and Kitack Lee ensured a successful cruise. Rachel Parson and Amy Ritchie expertly analyzed the water for DOC. We thank Greg Johnson and Kristie McTaggart for their tireless efforts to calibrate the CTD data that were essential for the mass transport analysis. The field work was supported by the NOAA. The carbon portion of this work was supported by NOAA grant NA86GPO114 to D.A.H. The inverse modeling effort was funded through the Cooperative Institute of Marine and Atmospheric Studies (CIMAS), a joint institute of the University of Miami and NOAA, cooperative agreement NA67RJ0149. AMM was also funded through the Cooperative Institute of Climate and Ocean Research (CICOR), a joint institute of Woods Hole Oceanographic Institution and NOAA, cooperative agreement NA17RJ1223. H.W.D. was supported by NSF OCE 0095223.

of net oxygen production and respiration disagree on the sign of the balance for the subtropical gyres, the largest of ocean ecosystems (Duarte and Agusti 1998; Williams 1998; Williams and Bowers 1999; Serret et al. 2001). Most studies using geochemical tracers or spatially and temporally integrating sediment flux observations conclude that nearly all the global upper ocean is net autotrophic, annually producing and exporting more organic matter than it consumes (Emerson et al. 1997; Antia et al. 2001; Lee 2001). Unquantified in this debate is a critical term in the overall budget: the total inputs and outputs of dissolved organic carbon (DOC) to a given ocean basin, material that is transported in the ocean circulation and constitutes a substantial resource for total water column respiration balancing in situ production (Hansell 2002). In a steady state, the balance of transports of organic carbon across the boundaries of an ocean basin is an unambiguous measure of the metabolic state of that basin: net import indicates net heterotrophy, while net export indicates net autotrophy.

Here we evaluate the metabolic balance of the North Atlantic by estimating net transports of allochthonous organic carbon across the system boundaries. The North Atlantic Ocean exchanges water that is enriched with organic carbon at its northern and southern boundaries with the Arctic Ocean and the tropical Atlantic/Southern Hemisphere, re-

spectively (Fig. 1). Two other modes of organic carbon transport into the basin are atmospheric deposition and fluvial input. The balance of these inputs defines the metabolic state of the system.

Methods

Data to assess net organic carbon transport across the southern boundary became available during a cruise in January/February 1998, when DOC was measured on 24.5°N along with other hydrographic variables (McTaggart et al. 1999). The National Oceanic and Atmospheric Association (NOAA) Ship Ronald Brown made a high-density hydrographic transect across the North Atlantic to obtain measurements of carbon and related chemical species. One hundred and thirty conductivity-temperature-depth (CTD) stations were occupied, with ≈55-km spacing in the open ocean and ≈20-km spacing in the Florida Strait. Sampling was to the bottom of the water column at 24 depths. DOC samples (872) taken at 41 stations (locations shown in Figs. 2, 3) were analyzed at sea using a high-temperature combustion technique (Hansell and Carlson 2001). The water taken for DOC analysis was unfiltered and so included particulate organic carbon (1–3% of the total organic carbon). Quality assessment of the analyses was done using consen-

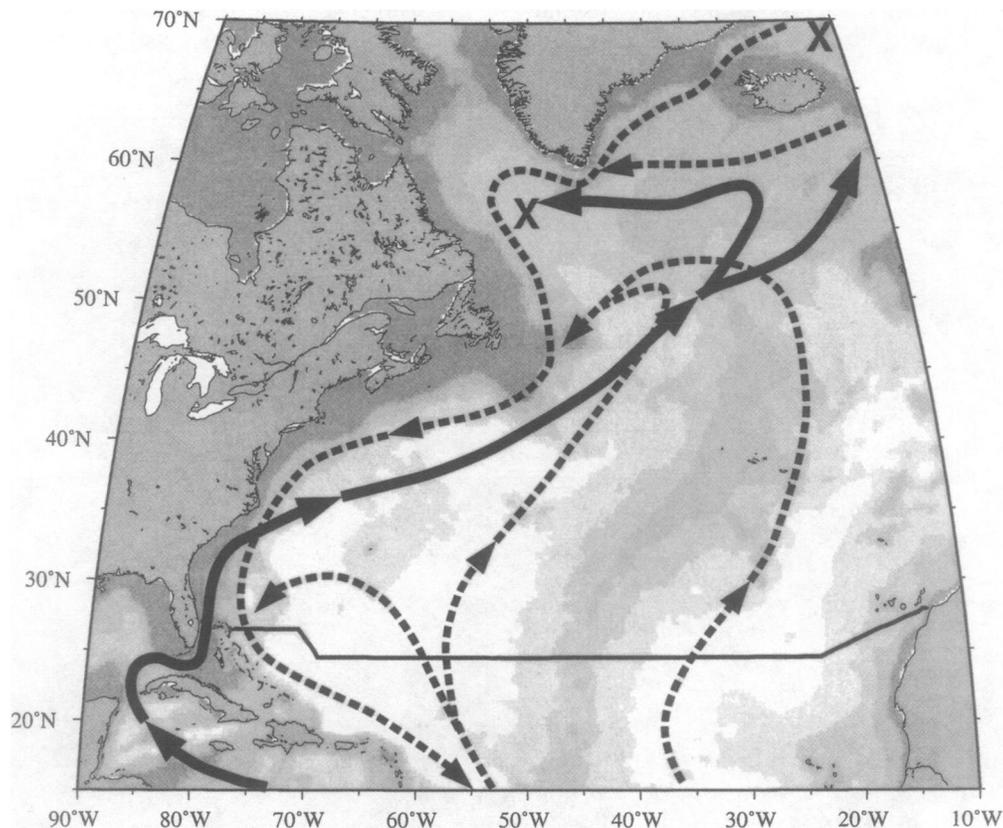


Fig. 1. Map of the North Atlantic Ocean showing the location of the 1998 hydrographic section nominally along 24.5°N (thin solid line), with a schematic of the upper layer (upper 500 m; solid arrows) and lower layer (>2,000 m; dashed arrows) meridional overturning circulation (adapted from Schmitz [1996]), including regions of important deep water-mass formation (X). The DWBC is represented by the westernmost dashed arrow.

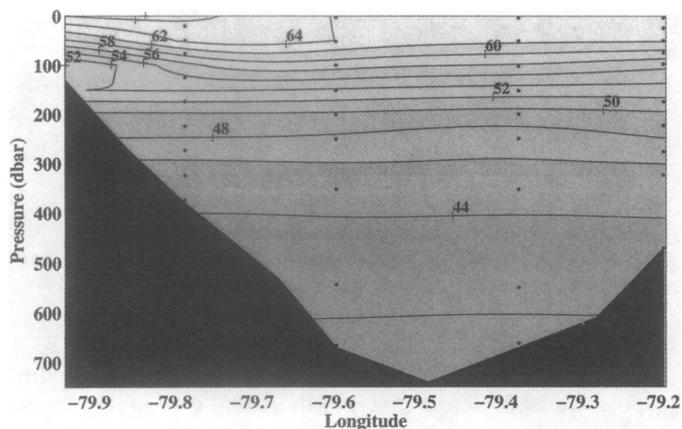


Fig. 2. Objectively mapped section of DOC ($\mu\text{mol L}^{-1} \text{C}$) across Florida Strait at 27°N . Locations (four stations) and depths of sampling for DOC are shown with small filled circles.

reference water distributed by the Hansell Laboratory (University of Miami, Rosenstiel School of Marine and Atmospheric Science; <http://www.rsmas.miami.edu/groups/organic-biogeochem/crm.html>), consisting of deep (2,600 m) Sargasso Sea water ($44\text{--}46 \mu\text{mol L}^{-1} \text{C}$) and low-carbon reference water, both of which are broadly distributed to the international community of DOC analysts.

To calculate DOC transport across 24.5°N , an absolute velocity field was obtained through the use of an inverse

model that conserved mass and salt within the basin and included constraints on the flow through the Florida and Bering Straits, Ekman transport, and freshwater input (Macdonald et al. 2003). DOC concentrations, linearly interpolated in neutral density space onto a 2-dbar grid in the vertical, were used along with the absolute velocity field to obtain the meridional DOC flux. This technique, described briefly below, estimates ocean circulation based on hydrographic observations and a set of physical constraints and is explained more fully in Macdonald et al. (2003).

Temperature and salinity observations allow for the calculation of geostrophic velocities relative to a reference surface. The model physics (here a set of conservation equations) were used to constrain the possible solutions for the unknowns in a least-squares sense. The constraints were based upon the baroclinic flow field described by the hydrographic transect, initial order of magnitude estimates of velocity at the reference surfaces, and estimates of the solution and data covariances. The inverse model was defined by 21 neutral density interfaces in the vertical and the observed station spacing in the horizontal. Relative geostrophic velocities were computed between station pairs on 2-dbar pressure intervals and are integrated vertically to produce the estimates of water and property transport used to define the constraints. Solutions (i.e., estimates of velocities at the reference surface and corrections to the initial Ekman component estimates) were found using a tapered-weighted least-squares (Gauss–Markov type) technique (Wunsch 1996;

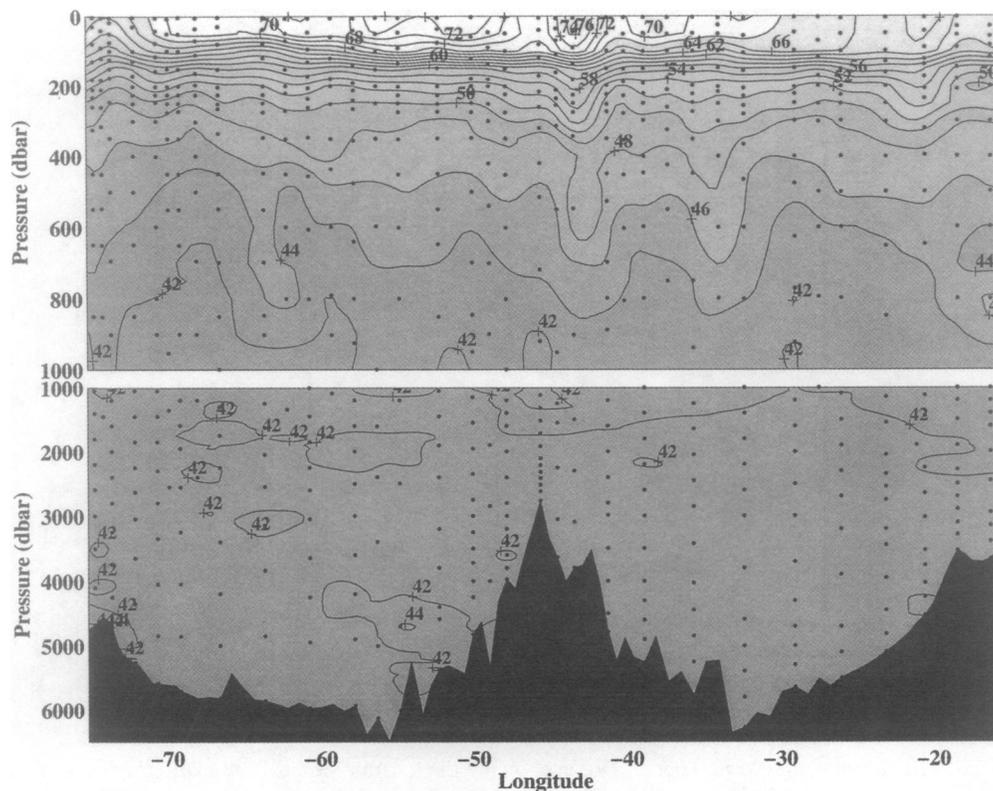


Fig. 3. Objectively mapped sections of DOC ($\mu\text{mol L}^{-1} \text{C}$) across the North Atlantic basin interior at 24.5°N . Upper plot is of the upper 1,000 m; lower plot is from 1,000 m to the sea floor. Locations (37 stations) and depths of sampling for DOC are shown with small filled circles.

Macdonald 1998). This technique weights the system only by a priori estimates of the uncertainty in constraints and unknowns. The inverse model transport uncertainties quoted in the text are based on the model estimated solution covariance, which is, in turn, related to the input estimates of the uncertainty in the constraints and solutions (*see* Wunsch [1996] and Macdonald et al. [2003] for further details).

Results and discussion

Mass and DOC transports—Surface layer (upper 50 m) DOC concentrations on the section varied from mostly $<64 \mu\text{mol L}^{-1} \text{C}$ in the Florida Strait (Fig. 2) to largely $>74 \mu\text{mol L}^{-1} \text{C}$ in the central gyre (Fig. 3). These central gyre values are $10\text{--}15 \mu\text{mol L}^{-1} \text{C}$ higher than surface values found near Bermuda during the same season (Hansell and Carlson 2001), likely reflecting greater vertical stability and DOC accumulation at the lower latitudes. DOC concentrations in the deeper layers ($>800 \text{ m}$) were $<44 \mu\text{mol L}^{-1} \text{C}$, about $1 \mu\text{mol L}^{-1} \text{C}$ less than values found near Bermuda at $32^\circ\text{N } 64^\circ\text{W}$ (Hansell and Carlson 2001). There was no evidence of zonal gradients in the deep-layer DOC concentrations across the gyre.

Mass transport across 24.5°N includes the interplay between two inseparable circulation elements: the wind-driven, near-surface subtropical gyre and the thermohaline-driven meridional overturning circulation. The near-surface northward Ekman flux (topmost three layers in Fig. 4c) contributes to the accumulation (convergence) of surface waters in the center of the subtropical gyre. This convergence in turn drives southward flow across the interior of the basin (above neutral density 27.16, or about 600 m). The wind-driven flow is mass balanced by the northward-flowing boundary current (the Florida Current) and by northward flow east of the Bahamas (the Antilles Current). Superimposed upon the wind-driven circulation is the thermohaline circulation, in which warm water is carried northward, cooled through air-sea fluxes, and transformed into cold, southward-flowing deep water, such as the Deep Western Boundary Current (DWBC; Fig. 1). In contrast to the surface layer, the deep circulation includes recirculating components with broad, slow northward-flowing deep and bottom waters within the basin interior that partially mass balance the southward DWBC (Figs. 1, 4c). Mass transport across 24.5°N in the Atlantic, as diagnosed herein, includes all of these components (Table 1, Fig. 4).

Transport across 24.5°N (Table 1) is dominated by the relatively warm flow through the Florida Straits ($31.4 \times 10^9 \text{ kg s}^{-1}$) and a compensatory net southward interior return flow ($32.4 \times 10^9 \text{ kg s}^{-1}$). The DWBC, which is a strong contributor to the southward return flow, is estimated by the model to carry $-43 \pm 21 \times 10^9 \text{ kg s}^{-1}$, and its strongest transport is found in the 27.92–27.98 neutral density layers (Fig. 4a) (designated upper North Atlantic Deep Water originating in the Labrador Sea; Fig. 1). A secondary maximum in southward flow is found in the 28.12–28.13 neutral density layer, characteristic of lower North Atlantic Deep Water originating in the Norwegian/Greenland Seas. The total DWBC transport computed here compares well to the mean

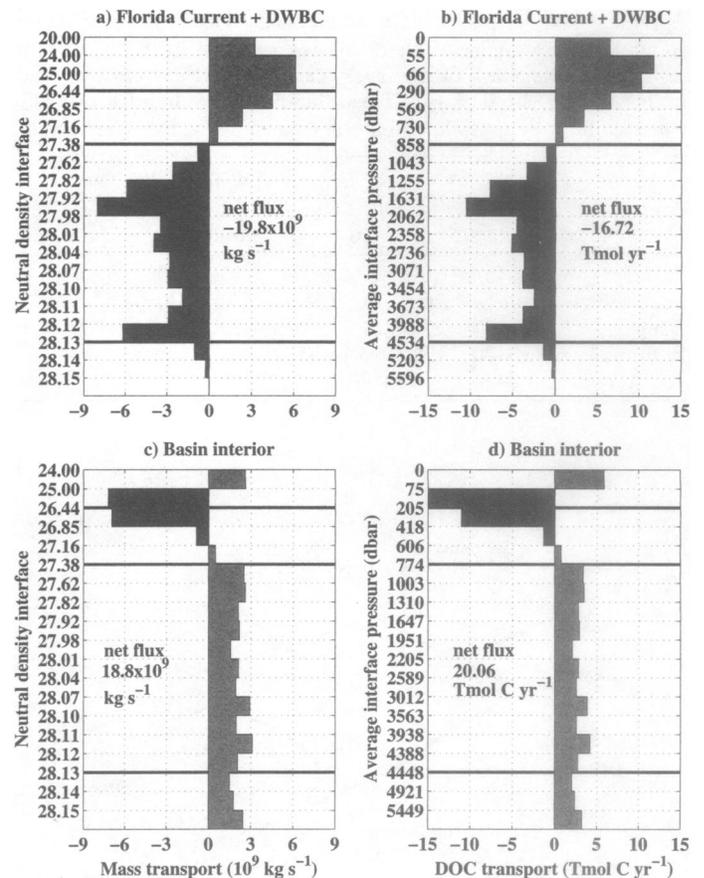


Fig. 4. Profiles of a) mass transport within the Florida Current and the stations including the deep western boundary current (DWBC) (from the western boundary to 70.23°W), b) the same for DOC, c) mass transport within the interior basin east of the DWBC (east of 70.23°W), and d) the same for DOC. Positive values are northward. The y-axes of the panels on the left are labeled by the neutral density of the interfaces and on the right by the average depth of the interfaces (20 layers). The water mass groupings defined according to neutral density in Table 1 are highlighted by dark horizontal lines. Note that the surface layer in the western boundary region is lower in density than the surface layer in the basin interior, so the surface-most neutral density interfaces differ (the uppermost two neutral density layers in the western zone do not exist in the eastern zone considered). Also, note that the Florida Strait and the Deep Western Boundary Current values are combined here because they encompass the major components of the meridional overturning circulation, and hence, these values differ relative to the data shown in Table 1.

and standard deviation of $-40 \pm 13 \times 10^9 \text{ kg s}^{-1}$ suggested by Lee et al. (1996) from their 4.7-yr time-series. In the interior, layers above neutral surface 25.0 ($\sim 75 \text{ m}$) carry $\sim 3 \times 10^9 \text{ kg s}^{-1}$ of DOC-enriched water northward within the Ekman layer. Just below this layer, the subtropical gyre carries $\sim 19 \times 10^9 \text{ kg s}^{-1}$ southward in the wind-driven layer ($<600 \text{ m}$). Deep mass transport in the basin interior, away from the DWBC ($>600 \text{ m}$), is mostly to the north, representing the broad recirculation noted above. Included in this interior flow is northward transport of the coldest water below 28.14 neutral density, the Antarctic Bottom Water layer.

Table 1. Water mass ($\times 10^9$ kg s^{-1}) and DOC ($Tmol$ C yr^{-1}) transports (\pm uncertainties) across the $24.5^\circ N$ section in the North Atlantic. Neutral density layers of water masses sampled in the water column and sectors (Florida [Fl] Strait, interior basin, and total basin) are resolved. Explanation of the layers can be found in Macdonald et al. (2003). These values are unique relative to the data shown in Fig. 4 in that Florida Strait and the ocean interior (including the DWBC) are separated here. The values in the bottom row are calculated for the water column as a whole and are not the sums of the other combined layers given.

Water mass	Layers	Neutral density surface range ($kg\ m^{-3}$)	Depth range of layer bottom (m)	Water mass transport			DOC transport		
				Fl Strait	Interior	Total	Fl Strait	Interior	Total
Surface	1–3	Surface to 26.44	130–270	18.9 ± 0.4	-8.0 ± 0.9	10.9 ± 0.9	34.7 ± 0.7	-15.6 ± 1.6	19.2 ± 1.9
Intermediate	4–6	26.44 to 27.38	700–870	11.6 ± 0.6	-11.5 ± 1.9	0.1 ± 1.9	16.6 ± 0.7	-17.5 ± 2.9	-0.9 ± 3.0
Deep	7–17	27.38 to 28.1295	4,200–4,500	0.8 ± 0.3	-17.2 ± 4.0	-16.4 ± 4.0	1.1 ± 0.3	-22.0 ± 5.2	-20.8 ± 5.2
Bottom	18–20	28.1295 to bot-	—	—	4.4 ± 3.5	4.4 ± 3.5	—	5.9 ± 4.6	5.9 ± 4.6
Top to bottom	1–20	tom	—	31.4 ± 1.0	-32.4 ± 1.3	-1.0 ± 0.9	52.4 ± 1.5	-49.1 ± 2.3	3.3 ± 1.9

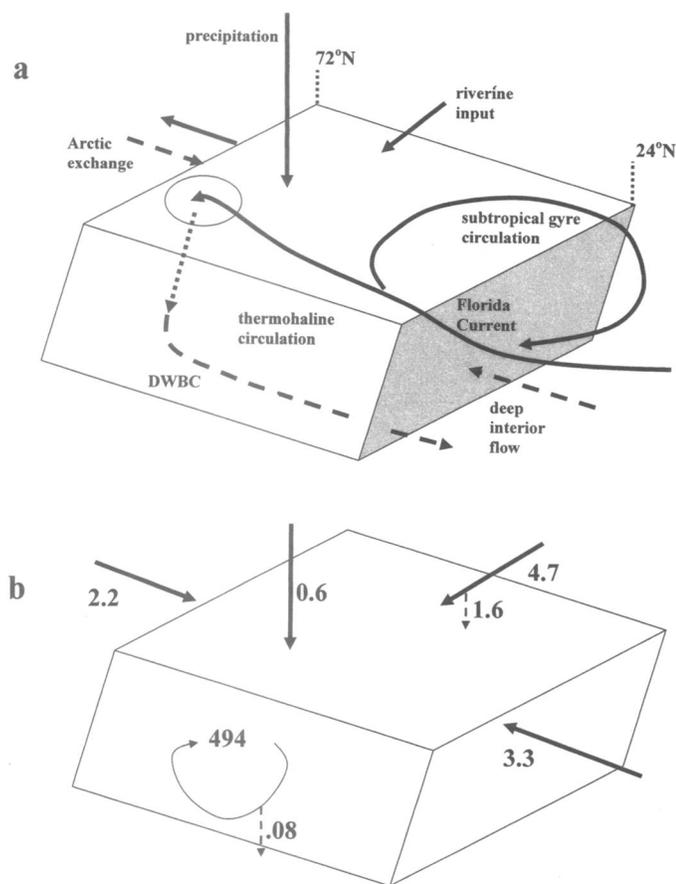


Fig. 5. a) Important basin boundary exchanges and circulations in the North Atlantic (vertical extent represents full water column depth). Shown schematically are exchanges with the Arctic Ocean, upper and deep ocean transports across the southern boundary at $24.5^\circ N$, including the gyre circulation and export within the deep western boundary current (DWBC), as well as input by rivers and precipitation. The circle represents the sites of water mass formation; solid and dashed lines represent upper- and deep-ocean circulation, respectively. b) Net transports ($Tmol$ C yr^{-1}) of dissolved organic carbon (solid arrows) in the North Atlantic (24.5 – $72^\circ N$). The estimated rate of in situ oceanic primary production and its remineralization are shown. Burial of fluvial POC as well as that produced by in situ primary production are shown as dashed arrows.

The recirculating components in both the upper and lower water columns lead to a small net southward mass transport associated with the flow from the Arctic and net inputs from river and surface freshwater fluxes.

DOC transports track mass transports, with net northward DOC flux in the upper western boundary region (dominated by the Florida Current) and net southward DOC flux in the deep western boundary current and the shallow, wind-driven basin interior (Fig. 4). Northward DOC transport in the narrow Florida Strait (at $27^\circ N$) is 52.4 ± 1.5 $Tmol$ C yr^{-1} , exceeding the net southward transport of 49.1 ± 2.3 $Tmol$ C yr^{-1} in the interior (Table 1). The overall net transport of DOC across $24.5^\circ N$ is to the north at 3.3 ± 1.9 $Tmol$ C yr^{-1} , dominated by the large northward transport of DOC in the Florida Current and the upper layers of the western basin (Table 1, Fig. 4b). This transport delivers DOC-enriched upper ocean water (Fig. 5) for recirculation in the subtropical gyre as well as for intermediate and deep-water formation via cooling and transformation at higher latitudes.

The character of the integrated meridional DOC transport differs most notably from the mass transport in the upper water column, where the horizontal variability of DOC concentrations are the highest. Above 26.44 neutral density (about 200 m), horizontal and vertical variations in DOC concentrations and mass transport variations are most important. The northward flow of the high-DOC waters in the surface Ekman layer in the interior (Figs. 3, 4d) can be thought of as a shallow recirculation cell, which is mass balanced at greater depths, where the DOC concentrations are lower (implying a net northward DOC transport). As noted above, the meridional overturning circulation also acts to send DOC toward the north, as near-surface Florida Current waters (high DOC values) are returned in the deep western boundary current (low DOC values). Some of the northward Florida Current transport is returned southward in near surface waters within the wind-driven circulation, where DOC concentrations are even higher than in the Florida Current (e.g., $DOC > 48 \mu mol\ L^{-1}\ C$ at 300 m in the interior, whereas $DOC < 46 \mu mol\ L^{-1}\ C$ at 300 m in the Florida Straits; Figs. 2 and 3). Thus, the wind-driven component of the circulation produces a small southward DOC transport, which is overshadowed by the much larger effects of the Ekman and meridional overturning circulations.

The meridional overturning circulation, whose magnitude is here defined as the maximum value in the vertical of the meridional mass transport stream function, carries $13\text{--}14 \times 10^9 \text{ kg s}^{-1}$ of mass and $21\text{--}24 \text{ Tmol C yr}^{-1}$ of DOC. The bulk of the mass transport of the Florida Current ($31.4 \times 10^9 \text{ kg s}^{-1}$) could therefore be considered to be made up of the wind-driven circulation ($17\text{--}18 \times 10^9 \text{ kg s}^{-1}$). This estimate would be similar to the Roemmich and Wunsch (1985) computed value for the wind-driven circulation of $19 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ ($1 \times 10^9 \text{ kg s}^{-1}$ is approximately $1 \times 10^6 \text{ m}^3 \text{ s}^{-1}$). The overturning circulation at $13\text{--}14 \times 10^9 \text{ kg s}^{-1}$ is somewhat less than the $17 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ estimated by Roemmich and Wunsch (1985), but this value is similar to more recent estimates, such as the $13.3 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ suggested by Dickson and Brown (1994). Thus, the wind-driven component drives a southward transport of DOC across the section, which only slightly reduces the effect of the dominant components: the meridional overturning circulation and the near-surface Ekman circulation.

Assessment of basin-wide metabolic balance—To determine the metabolic balance of the North Atlantic Ocean ($24.5^\circ\text{--}72^\circ\text{N}$, full water column), the various transports of DOC into or out of the basin must be quantified (Fig. 5). Net import of organic carbon to the basin would indicate a net heterotrophic system (sink for organic matter), whereas net export would indicate net autotrophy (source of organic matter). The major transport terms to consider for the basin are exchange in the north (with the Arctic Ocean), exchange in the south (with the southern hemisphere via the equatorial Atlantic), and import from the rivers and from atmospheric deposition. Transport of DOC across the southern boundary was determined above; each of the other transport terms is considered here from literature estimates. Where the published estimates did not have uncertainties provided, these were assigned for this analysis.

The North Atlantic exchanges water with the Arctic Ocean at its northern boundary. Because of the net transport of Pacific and river waters from the Arctic into the North Atlantic, there is a net transport of DOC in that direction as well. Anderson (2002) reported that the sum of DOC transports into the Arctic Ocean ($9.3 \pm 6.6 \text{ Tmol C yr}^{-1}$) is indistinguishable from the sum of transports from the Arctic into the North Atlantic ($8.9 \pm 0.3 \text{ Tmol C yr}^{-1}$), indicating that the Arctic Ocean itself appears to be neither a sink nor a source of organic carbon. There remains, however, an export of organic carbon from the Arctic to the Atlantic of $2.1\text{--}2.4 \text{ Tmol C yr}^{-1}$ (Wheeler et al. 1997; and Anderson 2002, respectively). This transport results from organic matter flux into the Arctic Ocean from the Pacific via the Bering Strait, plus fluvial inputs to the Chukchi, Beaufort, East Siberian, and Laptev Seas, minus net mineralization in the Arctic basin (Wheeler et al. 1997). Much of the DOC produced by primary production within the Arctic Ocean is thought to be mineralized there (Wheeler et al. 1997; Anderson 2002), so only carbon that conservatively transits the basin reaches the Atlantic. For this analysis, we assign a flux of $2.2 \pm 0.8 \text{ Tmol C yr}^{-1}$ (assumed uncertainty of approximately one third the flux) from the Arctic Ocean to the North Atlantic (Fig. 5).

Rivers add DOC and particulate organic carbon (POC) to the North Atlantic ($24.5\text{--}72^\circ\text{N}$, from Ludwig et al. 1996) at rates of $3.1 \pm 0.6 \text{ Tmol C yr}^{-1}$ and $1.6 \pm 0.3 \text{ Tmol C yr}^{-1}$, respectively (assumed errors of 20%). Loss of fluvial organic carbon to the lithosphere by burial in the coastal ocean is estimated at one third the total input (Smith and Mackenzie 1987; Smith and Hollibaugh 1993). Hence, of the $4.7 \text{ Tmol C yr}^{-1}$ organic carbon entering the North Atlantic, $\sim 1.6 \text{ Tmol C yr}^{-1}$ is lost to the lithosphere, a value approximating POC input. For this analysis we take the rate of carbon burial to be equal to the fluvial input of POC to the North Atlantic, removing it from the metabolic balance of the basin. Of the fluvial DOC input ($3.1 \text{ Tmol C yr}^{-1}$; Fig. 5), 15–30% is biologically and photochemically labile and rapidly mineralized in the coastal ocean (Spitzzy and Itekkot 1991; Ludwig et al. 1996; Vodacek et al. 1997; Sempéré et al. 2000). The balance is oxidized over a longer time scale following transport to the open ocean.

The rate of atmospheric deposition of organic carbon to the North Atlantic is not known because of the difficulties in collecting samples representative of the spatial and temporal variability inherent in the system. The global mean rainwater flux of DOC to the surface ocean, however, has been estimated to be $21.6 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ (Willey et al. 2002). If this value is characteristic of input to the North Atlantic, and with a surface area of $26 \times 10^{12} \text{ m}^2$ between 24.5°N and 72°N , the basin would receive DOC at $0.6 \pm 0.08 \text{ Tmol C yr}^{-1}$ (assumed uncertainty of 20%). Forty percent of the organic matter deposited ($0.24 \text{ Tmol C yr}^{-1}$) is resistant to microbial mineralization over a several-month time frame, with the balance respired more rapidly (Willey et al. 2002).

We find that, on balance, the North Atlantic serves as a DOC sink for the several transports considered and is, then, net heterotrophic. The rate of net heterotrophy (the sum of the net allochthonous inputs of organic carbon minus fluvial POC burial; $9.2 \pm 2.2 \text{ Tmol C yr}^{-1}$ or $0.3 \text{ mol C m}^{-2} \text{ yr}^{-1}$) is very small (<2%) compared to autochthonous production and consumption. Primary productivity in the North Atlantic basin (north of the equator) averages $19 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (Longhurst et al. 1995). We take this value to be a reasonable estimate for mean primary productivity over the area considered here (north of 24.5°N), resulting in production of $\sim 494 \text{ Tmol C yr}^{-1}$. Burial of organic carbon in the open North Atlantic sediments is $\sim 5 \times 10^{-3} \text{ mol C m}^{-2} \text{ yr}^{-1}$ ($0.08 \text{ Tmol C yr}^{-1}$ in the study area; Jahnke 1996), or <0.03% of primary productivity. Because the basin is slightly net heterotrophic, we conclude that the North Atlantic is metabolically balanced in terms of in situ production; there is a high rate of carbon fixation in the North Atlantic, but on balance, this material is consumed internally and not exported to other ocean basins. The resulting production/respiration ratio (P:R) is $0.98 (= [494/(494 - .008 + 9.2)])$, similar to the P:R of 0.99 determined by Smith and Mackenzie (1987) for the whole ocean.

We assume that the transports calculated here reflect steady-state conditions and that storage of DOC in the North Atlantic is not changing. If storage is increasing, then the rate of net heterotrophy is an overestimate. Our estimate for DOC flux across 24.5°N does not account for uncertainty

Table 2. Estimates of net community production (NCP) from experimental work in the subtropical gyre of the North Atlantic and resulting organic carbon deficits. Negative values for NCP indicate net heterotrophy.

Net community production		Carbon deficit	Reference
(mmol O ₂ m ⁻² d ⁻¹)	(mmol C m ⁻² d ⁻¹)	(mol C m ⁻² yr ⁻¹)	
-76	-60.8*	22.2	Robinson et al. (2002)
-130†	-103*	37.7	Serret et al. (2001)
-57 to -129	-52.5 to -108‡	19.4 to 37.2§	Gonzalez et al. (2001)
-38	-21.7‡	7.9§	Duarte et al. (2001)

* Calculated using a respiratory quotient of 0.8.

† Estimated mean from their fig. 7a.

‡ Calculated from annual carbon deficit given in Gonzalez et al. (2001).

§ Calculated from carbon deficits given in reference.

|| Daily rate extrapolated to annual.

due to seasonal changes in the upper ocean DOC stocks. For example, if during summer the DOC concentrations were elevated by 5 $\mu\text{mol L}^{-1}$ C in the upper three density layers across the entire basin, relative to the values found during this winter-time occupation, then the northward transport of DOC would increase by 1.7 Tmol C yr⁻¹, making the system more heterotrophic.

Evaluating findings of net heterotrophy in the upper subtropical North Atlantic—Recent studies have determined that the upper layer of the subtropical gyre of the North Atlantic Ocean are in a state of negative net community production, or net heterotrophy (del Giorgio et al. 1997; Duarte and Augusti 1998; Duarte et al. 2001; Gonzalez et al. 2001; Serret et al. 2001; Robinson et al. 2002). Countering arguments have been that large regional metabolic imbalances do not exist (Williams 1998), and discussions have ensued on the form of data analyses required to correctly determine the balance (Duarte et al. 1999; Williams and Bowers 1999). Others have suggested that net heterotrophy in the gyre results from temporal or spatial separation of organic carbon consumption and production processes (Hansell et al. 1995; Hoppe et al. 2002), perhaps with net inputs from mesoscale features such as eddies and net consumption outside the features.

Here we evaluate if the proposed net carbon mineralization rates can be matched by allochthonous inputs of organic carbon to the gyre. Input terms for DOC include horizontal

Table 3. Rates of organic carbon input (mmol C m⁻² yr⁻¹) to the surface layer in the northern sector of the North Atlantic subtropical gyre (24.5°N to the Gulf Stream) from allochthonous sources. Shown as well is the range for the estimated carbon deficit from Table 2. Refer to text for details.

Net DOC transport from the south	333
Net DOC transport from the north	17
Oxidation of refractory DOC	255
Precipitation	22
Input from margins	
Western	60
Eastern	25
Total inputs	712
Estimates of deficit	7,916–37,666

transport of DOC from the south (from the tropics) and from the north (across the subtropical front) via surface Ekman currents, geostrophic flow, and geostrophic eddies. Deposition of organic matter occurs with precipitation, and there is vertical input (via convective overturn) of deep, refractory organic carbon made biologically labile with ultraviolet light. Transport of both fluvial and shelf-produced organic matter from the continental margins to the upper gyre, particularly via filaments, is the final input term.

The published rates of net heterotrophy at issue are summarized in Table 2. Based on these daily rates of net community production (ranging from -38 to -130 mmol O₂ m⁻² d⁻¹ and assuming a respiratory quotient of 0.8), the apparent annual rates of the organic carbon deficit range from 7.9 to 37.7 mol C m⁻² yr⁻¹. As net community production, these carbon deficits are in excess of inputs from primary production, estimated at 10.1 mol C m⁻² yr⁻¹ in the northeast gyre (Longhurst et al. 1995) and 12.8 mol C m⁻² yr⁻¹ in the western gyre (Steinberg et al. 2001). Gonzalez et al. (2001) and Duarte et al. (2001) estimated organic carbon deficits of 81.7–156 Tmol C yr⁻¹ and 41.7 Tmol C yr⁻¹, respectively, for the eastern portion of the subtropical gyre.

In order to determine if the estimates for net heterotrophy in the gyre (Table 2) are approximately matched by allochthonous inputs (Table 3), we evaluate these latter terms in the northern sector of the subtropical gyre (here defined as north of 24.5°N and south of the subtropical front (region of the Gulf Stream), comprising the western and eastern North Atlantic Subtropical biogeographical regimes of Longhurst et al. (1995), and with a total surface area of 10×10^{12} m²). Some of the allochthonous inputs to this system, such as transport of organic carbon from the margins to the gyre, cannot be estimated with certainty. Our goal is to test for an approximate balance of DOC inputs with net heterotrophy, so in this evaluation we take a liberal approach that maximizes the inputs. For example, we allow all of the net northward transport of DOC across 24.5°N (calculated above at 3.3 ± 1.9 Tmol C yr⁻¹) to be consumed in the surface layer of the northern sector of the gyre. With this allowance, net DOC transport from the south will distribute DOC across the northern sector at a rate of 333 ± 190 mmol C m⁻² yr⁻¹ (Table 3). It is unlikely that the entirety of the net transported DOC is actually mineralized in the northern sector, but this

allowance sets an upper limit on the contribution to heterotrophy in the system by this input term.

Transport of organic matter into the gyre from the north, across the subtropical front, is less well known. Westerly winds over subpolar waters induce a net southward volume transport across the subtropical/subpolar boundary of ~ 5 Sv (Williams and Follows 1998) ($1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$). Surface-layer concentrations of DOC north of the boundary (near 43°N during May 2000; Hansell 2002) were $<70 \mu\text{mol L}^{-1}$, similar to summertime concentrations near Bermuda (Hansell and Carlson 2001). If $10 \mu\text{mol L}^{-1}$ C of the DOC to be available for biological oxidation is in the upper layer during southward transport into the gyre (approximately the DOC drawdown between surface and mode water depths in the region), and if the available DOC is fully utilized in the northern sector of the gyre, then this process would contribute $16.7 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ to the heterotrophs.

Refractory DOC from the deep ocean is mixed into the surface layer with convective events during winter and by vertical diffusion throughout the year. Mopper et al. (1991) measured the production of (presumably biologically labile) low-molecular weight carbonyl compounds in the surface waters of the Sargasso Sea at $4.1 \text{ nmol C L}^{-1} \text{ h}^{-1}$. Hansell et al. (1995), seeking to estimate the total contribution of labile organic carbon to microbes by this process, doubled the Mopper et al. (1991) rate to account for other low-molecular weight organic molecules not measured (e.g., organic acids). At this elevated rate, labile DOC would be introduced at $0.07 \mu\text{mol L}^{-1} \text{ d}^{-1}$ or $0.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ($255 \text{ mmol C m}^{-2} \text{ yr}^{-1}$) over the upper 10 m of water column. For comparison, Moran and Zepp (1997) estimated global ocean, zonally averaged rates of the photochemical production of biologically available C photoproducts from refractory DOM. In the latitudinal band of $20\text{--}40^\circ\text{N}$, $0.3\text{--}0.4 \text{ mol C m}^{-2} \text{ yr}^{-1}$ of DOM was photoaltered. Half of the photoproduct was CO , with the remainder (taken here to be $0.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$) being available to microbes as low-molecular weight organic compounds. We take the rate of $255 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ as the contribution of photo-oxidized organic carbon to heterotrophy in the northern sector (Table 3). As described above, precipitation is taken to introduce labile organic carbon at a rate of $21.6 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ (Willey et al. 2002).

Inputs of biologically labile DOC from the margins to the northern sector are the least known of the input terms, but we use here the few estimates for carbon transport that exist in the literature for specific coastal filaments. On the western margin, much of the water that is exported as a filament at Cape Hatteras, North Carolina, is likely subducted beneath the Gulf Stream (Lillibridge et al. 1990; Churchhill et al. 1993), in which case this carbon would not contribute to the metabolic balance of the surface layer being evaluated here. Likewise, if the shelf water is entrained into the Gulf Stream on its outer boundary, then input to the gyre is unlikely; instead, subpolar waters would be the most likely destination. However, in order to set upper limits on the potential contribution of the process to heterotrophy in the gyre, we allow the net organic carbon export from the Mid-Atlantic Bight to transit into the northern sector of the gyre for mineralization. Bates and Hansell (1999) estimated net DOC ex-

port (including both riverine and shelf-produced organic carbon) from the shelf into the Gulf Stream to range from $0.25\text{--}2.6 \text{ Tmol C yr}^{-1}$, with the wide range largely resulting from the disparate estimates for volume transport off the shelf. Vlahos et al. (2002) estimated that $0.34\text{--}0.6 \text{ Tmol C yr}^{-1}$ of shelf-produced DOC is exported off the Mid-Atlantic Bight shelf. Estimates of POC export from the shelf (Olson 2001) are an order of magnitude less than the DOC fluxes, so POC is not considered here. Taking the high value of the Vlahos et al. (2002) estimates and distributing this carbon over the northern sector of the gyre results in a DOC input of $60 \text{ mmol C m}^{-2} \text{ yr}^{-1}$ from the western margin.

The input of organic carbon to the gyre from the eastern margin is unknown as well, but export in a major upwelling filament from the Northwest Iberian upwelling system has recently been reported. Alvarez-Salgado et al. (2001a) found that 20% of net ecosystem production on the Iberian shelf accumulates as DOC, which is exportable via the filaments. The major filament in the system, originating near 42°N , carries with it $0.03 \text{ Tmol C yr}^{-1}$, equally distributed between particulate and dissolved forms (Alvarez-Salgado et al. 2001b). The filament receives water from $3,400 \text{ km}^2$ of shelf area, so export from the shelf occurs at $8.3 \text{ mol C m}^{-2} \text{ yr}^{-1}$. This filament is one of several in the eastern boundary, so its contribution is an unknown fraction of the total. It sweeps carbon into the open ocean north of the gyre system being evaluated here, but for purposes of this analysis we presume that the carbon will be entrained into the southward-flowing Canary Current and, eventually, into the northern sector of the gyre. If so, then the organic carbon contribution to the northern sector of the gyre from this single filament would be $2.5 \text{ mmol C m}^{-2} \text{ yr}^{-1}$. We do not know what fraction this single filament represents of total transport from the eastern boundary, but for this analysis we will assume that it is 10%. So total transport to the northern sector from the eastern margin is assumed to be $25 \text{ mmol C m}^{-2} \text{ yr}^{-1}$.

If high rates of net heterotrophy are the norm in the surface gyre waters, then the allochthonous inputs addressed here must sum to a similar magnitude. The rates of net heterotrophy (the carbon deficits from Table 2) range from 7.9 to $37.7 \text{ mol C m}^{-2} \text{ yr}^{-1}$. The allochthonous inputs of carbon, estimated to total $0.7 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (Table 3) with high uncertainty, are an order of magnitude less than the demand. This imbalance indicates either that the estimates for the carbon demand are too high (overestimates for net heterotrophy) or that the estimates of the allochthonous inputs are too low. Any individual DOC input term in Table 3 would have to be in error by two orders of magnitude or more to make the sum of the inputs equal the carbon deficit. Input from the margins is the least well constrained, so that is where the error likely lies if we have underestimated the total allochthonous input so greatly.

Alternatively, the measured rates of net heterotrophy may be overestimated. One test of this is to evaluate the net DOC drawdown in gyre waters required by the reported net heterotrophy. First, we can evaluate the possibility of net heterotrophy in the western Sargasso Sea after assuming as valid the correlation between P:R ratios (here, depth-integrated primary production to community respiration ratios) and daily primary production, reported by Aristegui and Harrison

(2002) for the eastern and northern North Atlantic. Mean annual primary production at the BATS site was $12.8 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (Steinberg et al. 2001), or a mean daily rate of $35 \text{ mmol C m}^{-2} \text{ d}^{-1}$, from 1989 to 1997. The predicted P:R ratio at that rate of primary production is ~ 0.6 (Aristegui and Harrison 2002), thus requiring a community respiration rate of $58 \text{ mmol C m}^{-2} \text{ d}^{-1}$, or net heterotrophy of $25 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ($9.1 \text{ mol C m}^{-2} \text{ yr}^{-1}$), requiring a daily drawdown of $0.25 \text{ } \mu\text{mol L}^{-1}$ DOC over the upper 100 m. This drawdown would be measurable under controlled experimental conditions. Carlson et al. (2002) evaluated the bioavailability of DOC resident in the upper layer of the western Sargasso Sea (summer months) by isolating, without contamination, 0.2-micron filtered water and then exposing it to a natural, diluted population of microbes. With the incubation proceeding for up to 3 months, they found that the DOC was biologically refractory on that time scale (i.e., there was no measurable drawdown of DOC, given a measurement precision of $<1 \text{ } \mu\text{mol L}^{-1} \text{ C}$). This finding indicates that net heterotrophy based on DOC resident at that site was not occurring. Similar analyses must be performed in the eastern gyre to determine if the DOC is in fact mineralized at the rates required by the net heterotrophy measured there. Under similar experimental conditions to those utilized by Carlson et al. (2002), Hansell et al. (1995) found net DOC drawdown in the Sargasso Sea of $3\text{--}7 \text{ } \mu\text{mol L}^{-1} \text{ C}$ over a 3-month period, but that work did not confirm the absence of trace DOC contamination during the experimental setup because of limitations in DOC analytical capabilities at the time. The drawdown they reported, even if it is an accurate representation of nature, is too small to satisfy the demands of the reported net heterotrophy.

Second, the range of carbon deficit estimates from Table 2 ($7.9\text{--}39.7 \text{ mol C m}^{-2} \text{ yr}^{-1}$) would require daily DOC drawdown of $0.2\text{--}1.0 \text{ } \mu\text{mol L}^{-1} \text{ C}$. If the primary source of the allochthonous DOC is the margins, then over 1 month or 1 yr of time during transport into the gyre, concentration decreases of $6\text{--}30$ or $73\text{--}365 \text{ } \mu\text{mol L}^{-1} \text{ C yr}^{-1}$, respectively, should occur. These very large DOC concentration decreases are not found in the gyre (nor are the larger values possible); in fact, DOC increases in concentration from the gyre boundaries to its interior (Fig. 3). This latter finding is suggestive of net autotrophy in the upper gyre. These findings do not support the reported high rates of net heterotrophy in the system.

Contributions of the mineralized product of net DOC transport to net DIC transport in the North Atlantic—Net transport of DOC into the North Atlantic results in the addition of dissolved inorganic carbon (DIC) to the basin via the mineralization of the imported DOC. This DIC will in turn be exported from the North Atlantic, thus contributing to the net export of DIC from that system. At the time of occupation of the 24.5°N line in 1998, the North Atlantic was exporting DIC to the south at a rate of $61.7 \pm 75.8 \text{ Tmol C yr}^{-1}$ (Macdonald et al. 2003). This flux can be compared to earlier estimates of net DIC transport southward at that latitude of $132 \text{ Tmol C yr}^{-1}$ (Roson et al. 2001; data collected in 1992) and $107 \text{ Tmol C yr}^{-1}$ (Brewer et al. 1989; DIC data collected in 1988; corrected for net mass transport

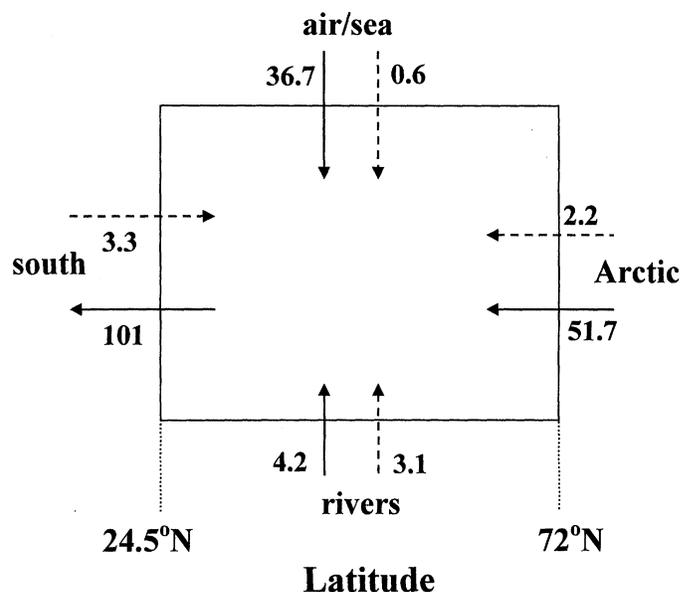


Fig. 6. Preindustrial fluxes (Tmol C yr^{-1}) of carbon across boundaries of the North Atlantic between 24.5°N and 72°N . Organic carbon fluxes on the dashed lines; inorganic carbon fluxes on the solid lines. Fluxes included fluvial and atmospheric inputs. Inorganic carbon fluxes are from Macdonald et al. (2003) (their fig. 3c). The northern boundary used by Macdonald et al. (2003) is 80°N , while that used in this analysis is 72°N , yet we used their estimate for air–sea exchange of CO_2 . We assume that the ocean surface area between those two latitudes is small enough, and the uncertainty in the air–sea flux estimate of Macdonald et al. (2003) large enough, to allow this. Likewise, fluvial inputs of carbon by rivers between 72°N and 80°N is small (Ludwig et al. 1996), so we did not adjust the Macdonald et al. (2003) estimate for DIC input by that process.

through Bering Strait by Macdonald et al. 2003). Macdonald et al. (2003) reevaluated the Roson et al. (2001) data for DIC transport in 1992, but they did so using their own methods. This effort reduced the estimate for 1992 to $109 \pm 82 \text{ Tmol C yr}^{-1}$, an estimate that is more in line with the adjusted Brewer et al. (1989) flux but still higher than the transport estimated using the data collected in 1998.

Net transports of DIC (taken from Macdonald et al. 2003) and DOC (from above) across the boundaries and relevant interfaces of the North Atlantic are shown in Fig. 6. Macdonald et al. took the average of the 1998 and 1992 values (i.e., $101 \text{ Tmol C yr}^{-1}$) as the best estimate for net DIC southward transport across 24.5°N . Inputs of DIC to the North Atlantic include that from rivers ($4.2 \text{ Tmol C yr}^{-1}$), air–sea exchange ($36.7 \text{ Tmol C yr}^{-1}$), and flux from the Arctic Ocean ($51.7 \text{ Tmol C yr}^{-1}$; Lundberg and Haugen 1996). The preindustrial value for the air–sea exchange of DIC in Macdonald et al. was $46 \text{ Tmol C yr}^{-1}$, but they did not account for the DIC added through the mineralization of DOC. This process requires reduction of their air–sea flux value to $36.7 \text{ Tmol C yr}^{-1}$, the value we used in Fig. 6. Net mineralization of DOC within the basin (at $9.2 \text{ Tmol C yr}^{-1}$), if the mineralization product CO_2 is not lost to the atmosphere, could account for 10% of the inorganic carbon exported ($101 \text{ Tmol C yr}^{-1}$) to the south.

We find that two factors, the import of organic matter and

the unique thermohaline circulation pattern of the North Atlantic, are primary in ensuring net heterotrophy in the basin. The overturning component of the total circulation delivers DOC-enriched surface waters to great depths, where heterotrophic processes dominate the metabolism, creating a heterotrophic trap for organic matter, whether this matter is transported into or produced within the basin. Ocean basins without similarly strong overturning circulation will not have such traps and may, therefore, exhibit metabolic neutrality or net autotrophy. If, for example, we hypothesize that the South Atlantic Ocean is characterized by low DOC concentrations entering from the high southern latitudes and high DOC concentrations leaving northward across the equator, that system would be net autotrophic in the upper layers. Changes in ocean basin circulation patterns—for example, through changes in overturning circulation (Clark et al. 2002) or through variability in the wind fields driven by climatic oscillations—should affect the regional metabolic balances in the ocean.

References

- ÁLVAREZ-SALGADO, X. A., M. D. DOVAL, A. V. BORGES, I. JOINT, M. FRANKIGNOULLE, E. M. S. WOODWARD, AND F. G. FIGUEIRAS. 2001b. Off-shelf fluxes of labile materials by an upwelling filament in the NW Iberian upwelling system. *Prog. Oceanogr.* **51**: 321–337.
- , J. GAGO, B. M. MÍGUEZ, AND F. F. PÉREZ. 2001a. Net ecosystem production of dissolved organic carbon in a coastal upwelling system: The Ria de Vigo, Iberian margin of the North Atlantic. *Limnol. Oceanogr.* **46**: 135–147.
- ANDERSON, L. G. 2002. DOC in the Arctic Ocean, p. 665–683. *In* D. A. Hansell and C. A. Carlson [eds.], *Biogeochemistry of marine dissolved organic matter*. Academic Press.
- ANTIA, A. N., W. KOEVE, G. FISCHER, AND OTHERS. 2001. Basin-wide particulate carbon flux in the Atlantic Ocean: Regional export patterns and potential for atmospheric CO₂ sequestration. *Global Biogeochem. Cycles* **15**: 845–861.
- ARISTEGUI, J., AND W. G. HARRISON. 2002. Decoupling of primary production and community respiration in the ocean: Implications for regional carbon studies. *Aquat. Microb. Ecol.* **29**: 199–209.
- BATES, N., AND D. A. HANSELL. 1999. Hydrographic and biogeochemical signals in the surface ocean between Chesapeake Bay and Bermuda. *Mar. Chem.* **67**: 1–16.
- BREWER, P. G., C. GOYET, AND D. DRYSEN. 1989. Carbon dioxide transport by ocean currents at 25°N in the Atlantic Ocean. *Science* **246**: 477–479.
- CARLSON, C. A., S. J. GIOVANNONI, D. A. HANSELL, S. J. GOLDBERG, R. PARSONS, M. P. OTERO, K. VEGIN, AND B. R. WHEELER. 2002. The effect of nutrient amendments on bacterioplankton growth, DOC utilization, and community structure in the northeastern Sargasso Sea. *Aquat. Microb. Ecol.* **30**: 19–36.
- CHURCHILL, J. H., E. R. LEINE, D. N. CONNORS, AND P. C. CORNILLON. 1993. Mixing of shelf, slope and Gulf Stream water over the continental slope of the Middle Atlantic Bight. *Deep-Sea Res.* **40**: 1063–1085.
- CLARK, P. U., N. G. PISIAS, T. F. STOCKER, AND A. J. WEAVER. 2002. The role of the thermohaline circulation in abrupt climate change. *Nature* **415**: 863–869.
- DEL GIORGIO, P. A., J. J. COLE, AND A. CIMBERLIS. 1997. Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems. *Nature* **385**: 148–151.
- DICKSON, R. R., AND J. BROWN. 1994. The production of North Atlantic Deep Water: Sources, rates and pathways. *J. Geophys. Res.* **99**: 12319–12342.
- DUARTE, C. M., AND S. AGUSTÍ. 1998. The CO₂ balance of unproductive aquatic ecosystems. *Science* **281**: 234–236.
- , J. ARISTEGUI, N. GONZÁLEZ, AND R. ANADÓN. 2001. Evidence for a heterotrophic subtropical northeast Atlantic. *Limnol. Oceanogr.* **46**: 425–428.
- , P. A. DEL GIORGIO, AND J. J. COLE. 1999. Regional carbon imbalances in the ocean: Response. *Science* **284**: 1735b.
- EMERSON, S., P. QUAY, D. KARL, C. WINN, L. TUPAS, AND M. LANDRY. 1997. Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature* **389**: 951–954.
- FALKOWSKI, P., R. J. SCHOLLES, E. BOYLE, AND OTHERS. 2000. The global carbon cycle: A test of our knowledge of earth as a system. *Science* **290**: 291–296.
- GONZÁLEZ, N., R. ANADÓN, B. MOURIÑO, E. FERNÁNDEZ, B. SINHA, J. ESCÁNEZ, AND D. DE ARMAS. 2001. The metabolic balance of the planktonic community in the North Atlantic Subtropical Gyre: The role of mesoscale instabilities. *Limnol. Oceanogr.* **46**: 946–952.
- HANSELL, D. A. 2002. DOC in the global ocean carbon cycle, p. 685–715. *In* D. A. Hansell and C. A. Carlson [eds.], *Biogeochemistry of marine dissolved organic matter*. Academic Press.
- , N. BATES, AND K. GUNDERSEN. 1995. Mineralization of dissolved organic carbon in the Sargasso Sea. *Mar. Chem.* **51**: 201–212.
- , AND C. A. CARLSON. 2001. Biogeochemistry of total organic carbon and nitrogen in the Sargasso Sea: Control by convective overturn. *Deep-Sea Res.* **48**: 1649–1667.
- HANSON, R., H. W. DUCKLOW, AND J. G. FIELD. 2000. The changing carbon cycle in the oceans. Cambridge Univ. Press.
- HOPPE, H.-G., K. GOCKE, R. KOPPE, AND C. BEGLER. 2002. Bacterial growth and primary production along a north–south transect of the Atlantic Ocean. *Nature* **416**: 168–171.
- HOUGHTON, J. T., Y. DING, D. J. GRIGGS, M. NOGUER, P. J. VAN DER LINDEN, X. DAI, K. MASKELL, AND C. A. JOHNSON. 2001. *Climate Change 2001: The Scientific Basis Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge Univ. Press.
- JAHNKE, R. A. 1996. The global ocean flux of particulate organic carbon: Areal distribution and magnitude. *Global Biogeochem. Cycles* **10**: 71–88.
- LEE, K. 2001. Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. *Limnol. Oceanogr.* **46**: 1287–1297.
- LEE, T. N., W. E. JOHNS, R. J. ZANTOPP, AND E. R. FILLENBAUM. 1996. Moored observations of Western Boundary Current variability and thermohaline circulation at 26.5°N in the Subtropical North Atlantic. *J. Phys. Oceanogr.* **26**: 962–983.
- LILLIBRIDGE, J. L., G. HITCHCOCK, T. ROSSBY, E. LESSARD, M. MORK, AND L. GOLMEN. 1990. Entrainment and mixing of shelf/slope waters in the near-surface Gulf Stream. *J. Geophys. Res.* **95**: 13065–13087.
- LONGHURST, A., S. SATHYENDRANATH, T. PLATT, AND C. CAVERHILL. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *J. Plankton Res.* **17**: 1245–1271.
- LUDWIG, W., P. AMIOTTE-SUCHET, AND J.-L. PROBST. 1996. River discharges of carbon to the world's oceans: Determining local inputs of alkalinity and of dissolved and particulate organic carbon. *Comptes Rendus Acad. Paris Ser. II* **323**: 1007–1014.
- LUNDBERG, L., AND P. M. HAUGAN. 1996. A Nordic Seas-Arctic

- Ocean carbon budget from volume flows and inorganic carbon data. *Global Biogeochem. Cycles* **10**: 493–510.
- MACDONALD, A. M. 1998. The global ocean circulation: A hydrographic estimate and regional analysis. *Prog. Oceanogr.* **41**: 281–382.
- , M. O'NEIL BARINGER, R. WANNINKHOF, K. LEE, AND D. W. R. WALLACE. 2003. A 1998–1992 comparison of inorganic carbon and its transport across 24.5°N in the Atlantic. *Deep-Sea Res. II* **50**: 3041–3064.
- MCTAGGART, K. E., G. C. JOHNSON, C. I. FLEURANT, AND M. O. BARINGER. 1999. CTC/O₂ measurements collected on a climate and global change cruise along 24°N in the Atlantic Ocean (WOCE Section A6) during January–February 1998. NOAA DR ERL PMEL-68, Pacific Marine Environmental Laboratory.
- MOPPER, K., X. ZHOU, R. J. KIEBER, D. J. KIEBER, R. J. SIKORSKI, AND R. D. JONES. 1991. Photochemical degradation of dissolved organic carbon and its impact on the oceanic carbon cycle. *Nature* **353**: 60–62.
- MORAN, M. A., AND R. G. ZEPP. 1997. Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. *Limnol. Oceanogr.* **42**: 1307–1316.
- OLSON, D. B. 2001. Biophysical dynamics of western transition zones: a preliminary synthesis. *Fish. Oceanogr.* **10**: 133–150.
- ROBINSON, C., P. SERRET, G. TILSTONE, E. TEIRA, M. V. ZUBKOV, A. P. REES., E. MALCOLM, AND S. WOODWARD. 2002. Plankton respiration in the Eastern Atlantic Ocean. *Deep-Sea Res. I* **49**: 787–813.
- ROEMMICH, D., AND C. WUNSCH. 1985. Two transatlantic sections: Meridional circulation and heat flux in the subtropical North Atlantic Ocean. *Deep-Sea Res. I* **32**: 619–664.
- ROSÓN, G., A. F. RIOS, A. LAVÍN, AND H. L. BRYDEN. 2003. Carbon distribution, fluxes and budgets in the subtropical North Atlantic Ocean (24.5°N). *J. Geophys. Res.* **108**: 10.1029/1999JC000047.
- SCHMITZ, W. J., JR. 1996. On the world ocean circulation. V. I. Woods Hole Oceanographic Institution Technical Report WHOI-96-03.
- SEMPÉRÉ, R., B. CHARRIÈRE, F. V. WAMBEKE, AND G. CAUWET. 2000. Carbon inputs of the Rhône River to the Mediterranean Sea: Biogeochemical implications. *Global Biogeochem. Cycles* **14**: 669–681.
- SERRET, P., C. ROBINSON, E. FERNANDEZ, E. TEIRA, AND G. TILSTONE. 2001. Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. *Limnol. Oceanogr.* **46**: 1642–1652.
- SMITH, S. V., AND J. T. HOLLIBAUGH. 1993. Coastal metabolism and the oceanic organic carbon balance. *Rev. Geophys.* **31**: 75–89.
- , AND F. T. MACKENZIE. 1987. The ocean as a net heterotrophic system: Implications from the carbon biogeochemical cycle. *Global Biogeochem. Cycles* **1**: 187–198.
- SPIITZY, A., AND V. ITTEKOT. 1991. Dissolved and particulate organic matter in rivers, p. 5–17. *In* R. F. C. Mantoura, J. M. Martin, and R. Wollast [eds.], *Ocean margin processes in global change*. Wiley.
- STEINBERG, D. K., C. A. CARLSON, N. R. BATES, R. J. JOHNSON, A. F. MICHAELS, AND A. H. KNAP. 2001. Overview of the US JGOFS Bermuda Atlantic Time-Series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Res. II* **48**: 1405–1447.
- VER, L. M. B., F. T. MACKENZIE, AND A. LERMAN. 1999. Carbon cycle in the coastal zone: Effects of global perturbations and change in the past three centuries. *Chem. Geol.* **159**: 283–304.
- VLAHOS, P., R. F. CHEN, AND D. J. REPETA. 2002. Dissolved organic carbon in the Mid-Atlantic Bight. *Deep-Sea Res. II* **49**: 4369–4385.
- VODACEK, A., N. V. BLOUGH, M. D. DEGRANDPRE, E. T. PELTZER, AND R. K. NELSON. 1997. Seasonal variation of CDOM and DOC in the Middle Atlantic Bight: Terrestrial inputs and photooxidation. *Limnol. Oceanogr.* **42**: 674–686.
- WHEELER, P. A., J. M. WATKINS, AND R. L. HANSING. 1997. Nutrients, organic carbon and organic nitrogen in the upper water column of the Arctic Ocean: Implications for sources of dissolved organic carbon. *Deep-Sea Res. II* **44**: 1571–1592.
- WILLEY, J. D., R. J. KIEBER, M. S. EYMAN, AND G. B. AVERY. 2002. Rainwater dissolved organic carbon: Concentrations and global flux. *Global Biogeochem. Cycles* **14**: 139–148.
- WILLIAMS, P. J. L. 1998. The balance of plankton respiration and photosynthesis in the open oceans. *Nature* **394**: 55–57.
- , AND D. G. BOWERS. 1999. Regional carbon imbalances in the oceans. *Science* **284**: 1735b.
- WILLIAMS, R. G., AND M. J. FOLLOWS. 1998. The Ekman transfer of nutrients and maintenance of new production over the North Atlantic. *Deep-Sea Res. I* **45**: 461–489.
- WUNSCH, C. 1996. *The ocean circulation inverse problem*. Cambridge Univ. Press.

Received: 19 August 2003

Accepted: 11 February 2004

Amended: 12 March 2004