Spatial and temporal changes in the partitioning of organic carbon in the plankton community of the Sargasso Sea off Bermuda

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Abstract—The vertical distribution of plankton (bacteria, nanozooplankton, microzooplankton, mesozooplankton, macrozooplankton and salps) biomass in the photic zone near the JGOFS time series station off Bermuda was examined during 2–3 week periods in August 1989 and in March/April 1990. The amount of phytoplankton carbon in the photic zone was lower in August as compared to March/April (398 and 912 mg C m^{-2}, respectively). Total heterotrophic biomass in the photic zone was also lower in August as compared to March/April (1106 and 1795 mg C m^{-2}, respectively). Taken together, bacteria and nanozooplankton constituted approximately 70% of the total heterotrophic carbon in the photic zone on both cruises. Considering their high weight-specific carbon demand relative to micro-, meso-, and macrozooplankton, it is clear that most of the carbon in the surface waters of the Sargasso Sea near Bermuda cycles through bacteria and flagellates—the "microbial loop". However, both seasonal (August vs. March/April) and within-cruise variations in the vertical flux of organic material were related to the biomass of macrozooplankton. Macrozooplankton biomass was lower in August than March/April (93 and 267 mg C m^{-2}, respectively). There was more non-living carbon (detritus) than living carbon in the photic zone during the August cruise (70% of total organic matter) but about equal amounts of detritus and living carbon in March/April.

INTRODUCTION

Recent models of carbon and nitrogen fluxes in the ocean depend on estimates of the biomass of phytoplankton, bacteria, and nano-, micro- and mesozooplankton (Pace *et al.*, 1984; Fasham *et al.*, 1990; Moloney and Field, 1991). The amount of organic material which is either recycled in the photic zone or is sequestered below the pycnocline is related to the relative abundance or biomass partitioning among these plankton groups (Frost, 1984; Michaels and Silver, 1988; Longhurst and Harrison, 1989; Peinert *et al.*, 1989). In spite of the obvious importance of obtaining these biomass estimates, there have been relatively few attempts to simultaneously measure all of the major producer and consumer groups in oceanic food-webs (e.g. Grice *et al.*, 1980; Holligan *et al.*, 1984). Instead,

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investigators have tended to focus on particular biological components of the plankton rather than simultaneous measurements of the full complement of autotrophs and heterotrophs.

One reason for the general lack of data on the absolute abundance and relative importance of plankton groups is the discovery that heretofore unknown or undersampled taxa can be major trophic constituents. For example, cyanobacteria (Johnson and Sieburth, 1979) and prochlorophytes (Chisholm *et al.*, 1988), now recognized as ubiquitous in the ocean and at times a dominant biomass component of the plankton (Waterbury *et al.*, 1987), were not measured in early studies. Improved sampling and preservation techniques have allowed us to assess the importance of protozoa, usually the major consumer of bacteria and phytoplankton in the ocean (Fenchel, 1986; Sherr and Sherr, 1988). Gelatinous zooplankton, which are typically not sampled adequately by nets, also can be important consumers of phytoplankton and, through their production of rapidly sinking fecal material, facilitate the flux of carbon to the deep sea (Wiebe *et al.*, 1979).

Due to these refinements, our view of plankton has evolved rapidly in recent years from the more classical view of phytoplankton/copepod/fish food-chains to one of increasingly complex food-webs. We now know that much of the carbon passes through the microbial community (Pomeroy, 1974; Azam *et al.*, 1983; Sherr and Sherr, 1988). Thus to adequately account for losses of phytoplankton, a complete description of microbial populations is required. However, if one is concerned about the losses of carbon from the photic zone, one must study meso- and macrozooplankton. Through their production of rapidly sinking fecal pellets, these larger zooplankton contribute substantially to the flux of biogenic material (Fowler and Knauer, 1986; Small *et al.*, 1989; Altabet and Small, 1990). Therefore in order to understand the consumption, recycling and export of carbon in epipelagic waters, it is necessary to study the full range of heterotrophic organisms.

Cognizant of the paucity of data on both the structure and function of the epipelagic plankton community, a study was conducted at the JGOFS time-series station off Bermuda. The goals of the project (ZOOSWAT) were to: concurrently measure the biomass of all the autotrophic and heterotrophic plankton in the photic zone; analyse the flows of carbon between the plankton; quantify the flux of carbon out of the photic zone. The biomass and production of phytoplankton and bacteria was measured, and the biomass and grazing rates of flagellates, ciliates, crustacean zooplankton and salps. Hydrographic data, phytoplankton productivity, mesozooplankton biomass and grazing, and particle export have been reported (Malone *et al.*, 1993; Roman *et al.*, 1993; Dam *et al.*, 1995). Analysis of the microbial populations and the conversion factors used to estimate their carbon biomass are presented in Caron *et al.* (1995). This paper compares the vertical distribution of carbon biomass of the microbial (pico-, nano-, micro-) plankton with meso- and macrozooplankton during 2–3 week periods in August 1989 and March/April 1990 in relation to hydrographic conditions. A future paper will describe the relative importance of the plankton groups in the flow of carbon within the photic zone and how the structure and function of the plankton community influences carbon flux from the photic zone.

METHODS

Cruises were undertaken to the JGOFS time-series station off Bermuda (31°50′N, 64°10′W) during August 1989 and March/April 1990. Process studies were initiated near

the time-series station with subsequent stations conducted by following free-drifting sediment traps and primary productivity moorings (24 h incubations). Upon recovery of the moorings the ship returned to the original station. Measurements of conductivity, temperature, depth and chlorophyll fluorescence were made with a Seabird CTD and Seatech fluorometer. Incident photosynthetically active radiation (PAR) was recorded with a LiCor solar monitor. Water for inorganic nutrients, plankton and particulate analysis was collected with 30 l Niskin bottles (0.1 N HCl acid washed and equipped with teflon-coated springs) attached to a rosette sampler. In order to collect enough water for the various analyses, two bottles were filled at each depth (usually 6), and upon return to the ship, the contents of the two replicate bottles were combined into a single, acid washed 50 l polyethylene carboy.

Phytoplankton and particulate carbon

Particulate organic carbon (POC) and particulate organic nitrogen (PN) were measured in duplicate on precombusted Whatman GF/F glass fiber filters. POC and PN were determined with a Controlled Equipment C–H–N Elemental Analyser after fuming over HCl (March/April cruise only). Chlorophyll-*a* (Chl) concentrations were determined from duplicate samples collected on Whatman GF/F and 2 μm Nuclepore filters. The samples were extracted in 90% acetone and measured in a Turner Designs Fluorometer (Parsons *et al.*, 1984). Phytoplankton productivity was determined by ^{14}C uptake into two size fractions (GF/F and 2 μm Nuclepore) in dawn to dawn *in situ* incubations (Malone *et al.*, 1993).

Phytoplankton carbon biomass for the March/April cruise data was estimated by converting measured Chl concentrations to carbon using C/Chl ratios. The C/Chl ratios were determined from the incorporation of ^{14}C into Chl based on *in situ*, 24 h incubations (Malone *et al.*, 1993). The estimated C/Chl ratios for March/April were: 60 for 0–30 m; 40 for 30–60 m; 30 for >60 m (Malone *et al.*, 1993). Direct measurements of C/Chl were not made for the August cruise. For these samples, phytoplankton biomass was calculated from the abundances of phototrophic populations and biomass conversions estimated from the March/April data set (Caron *et al.*, 1995). As a test of the appropriateness of these conversion factors, we then calculated C/Chl ratios from these carbon biomass values and the measured Chl values from the August cruise. The resulting estimated C/Chl ratios for August were: 101 at 3 m; 73 at 15 m; 60 at 30 m; 42 at 50 m; 25 at 100 m. These values are similar to the summertime Sargasso Sea C/Chl ratios measured by Goericke and Welschmeyer (1993) using rates of ^{14}C incorporation into Chl (Redalje and Laws, 1981).

Bacteria

Bacterial abundance was determined from whole water samples preserved with 1% glutåraldehyde and stored in the dark at 4°C until stained, filtered and counted. Bacteria were stained with DAPI and counted by epifluorescence (Porter and Feig, 1980). Bacterial production was estimated by the incorporation of [methyl-^3H] thymidine (TdR) into cold trichloroacetic acid (TCA)-insoluble material, specifically DNA (Fuhrman and Azam, 1980). Phenol-chloroform extractions (Wicks and Robarts, 1987) were run to isolate bacterial DNA. TdR incorporation rates were used to derive estimates of bacterial

production by employing conversion factors based on shipboard bacterial growth experiments and TdR incorporation in diluted "cultures" of bacteria (Kirchman *et al.*, 1982).

The carbon biomass of bacteria (BACT) was estimated from abundances and a carbon cell^{-1} conversion factor. We used measurements of Chl, POC, PN, C/N and C/Chl ratios to "constrain" the bacterial biomass conversion factor (Caron *et al.*, 1995). The factor which resulted from this analysis was 15 fg C bacterium^{-1}. This value is intermediate between the commonly used values of 10–20 fg C bacterium^{-1} (Van Duyl *et al.*, 1990).

Heterotrophic nanoplankton

This planktonic assemblage (primarily protozoa 2–5 μm, hereafter referred to as nanozooplankton = NANO) of protozoa was preserved in 1% glutaraldehyde and stored in the dark at 4°C until analysis. Within 24 h of preservation, the cells were stained with DAPI (25 μg ml^{-1}, Sherr *et al.*, 1993) and counted and sized by epifluorescent microscopy. Phototrophic (chloroplast-bearing) nanophytoplankton were distinguished from nanozooplankton (NANO) by the autofluorescence of Chl. We used the "constrained" conversion of 183 fg C μm^{-3} to convert NANO volume to carbon biomass (Caron *et al.*, 1995). This value is intermediate in the range (80–220 fg C μm^{-3}) of published conversion values (Strathman, 1967; Borsheim and Bratback, 1987; Choi and Stoecker, 1989; Putt and Stoecker, 1989).

Heterotrophic microplankton

This assemblage (predominantly ciliates and heterotrophic dinoflagellates 5–200 μm, hereafter referred to as microzooplankton = MICRO) was enumerated from two types of samples. A whole water sample (220 ml) was stained with DAPI (5 μg ml^{-1}; Porter and Feig, 1980) and proflavin (2 μg ml^{-1}; Haas, 1982) and filtered onto a 2 μm blackened Nuclepore filter, which was then placed on a glass slide and stored frozen. In order to enumerate the larger and more robust MICRO, a second sample (10–30 l) from each depth was gently reverse-flow concentrated on a 20 μm screen. Subsamples of the concentrated sample were stained with DAPI and placed in small settling chambers. Both types of MICRO samples were counted and sized by epifluorescent microscopy. Phototrophic microplankton were distinguished from heterotrophic microplankton (MICRO) by the autofluorescence of chlorophyll. Plastidic ciliates (other than *Mesodinium rubrum* (*Myrionecta rubra*)) were classified as heterotrophs as they are primarily phagotrophs (e.g., Stoecker *et al.*, 1988), and their contribution to integrated chlorophyll standing stock was estimated to be relatively small on average (< 8%, Lessard and Murrell, submitted). Large heterotrophic dinoflagellates that harbored phytosymbionts (e.g., *Ornithocercus* spp.) were also classified as heterotrophs, as their estimated chlorophyll contribution was very small (<1%). The plastidic ciliate, *Mesodinium rubrum*, was classified as a phototroph, as it is thought to be an obligate autotroph (Lindholm, 1985). Sarcodines were enumerated from the 30 l concentrates but were not included in the MICRO biomass, as radiolarians and foraminiferans were probably not quantitatively sampled with the 30 l Niskin bottles. Sarcodines (mainly acantharians) were relatively rare in these samples, ranging from 0 to 11 l^{-1}. Their integrated biomass was very low (<1 to *ca* 8 mg m^{-2}, based on the Michaels (1991) carbon to volume conversion of 2.9 fg μm^{-1}), making their biomass contribution relative to other groups insignificant. Biovolumes of MICRO were calculated

from linear dimensions and taxa-specific geometric formulas. We used the "constrained" conversion of 183 fg C μm^{-3} to convert MICRO volume to carbon biomass (Caron *et al.*, 1995).

Meso- and macrozooplankton

These groups were composed primarily of crustaceans and are distinguished by size: 64–200 μm (MESO) and >200 μm (MACRO). During the August cruise, zooplankton >64 μm were sampled with a pumping system (Roman *et al.*, 1993) and zooplankton >200 μm were sampled with a 1.0 m^2 MOCNESS (Wiebe *et al.*, 1985). During the March/April cruise a 0.25 m^2 MOCNESS was used instead of the pump to collect >64 μm zooplankton because the mixed layer was deeper, and pump collections were not practical. We had previously compared zooplankton caught with the pump and 0.25 m^2 MOCNESS and did not find any significant differences (Roman *et al.*, 1986).

Biomass of 64–200 μm zooplankton (MESO) was determined by taking duplicate aliquots from catches and measuring the carbon and nitrogen content with a Model 440 Control Equipment C–H–N Elemental Analyzer. The 64 μm catch from either the pump (August) or 0.25 m^2 MOCNESS (March/April) was wet-sieved through 200 μm mesh to determine the biomass of MESO. Biomass of the >200 μm zooplankton (MACRO) collected with the 1.0 m^2 MOCNESS was estimated from aliquots of preserved samples. Carbon loss during preservation was estimated by comparing the carbon content of aliquots from freshly frozen samples to preserved aliquots of the same sample measured with a Carlo Erba Model 1106 Elemental Analyzer. The comparison gave conversion factors of: carbon (sample) = 0.45 × (preserved dry weight) − 46.16 ($N = 13$, $r^2 = 0.59$, std. error slope = 0.11) for August: carbon (sample) = 0.44 × (preserved dry weight) − 94.53 ($N = 15$, $r^2 = 0.60$, std. error slope = 0.10) for March/April.

Salps

Abundance estimates were derived from samples collected day and night with a 10 m^2 mouth-area, 3.0 mm-mesh trawl. Salps were identified, sized and counted. Size frequency data of salps was converted to carbon biomass based on established conversion factors (Madin *et al.*, 1981).

RESULTS

Hydrographic changes

During the August cruise the station had to be left when Hurricane Dean passed near the area (5/8–6/8). Records on Bermuda showed that wind speed increased to 28 m s^{-1} during this period (U.S. Naval Air Station Bermuda). The CTD profiles from before and after the hurricane showed that the mixed layer increased from 25 m to 50 m, the depth of the nitracline increased from 31 m to 71 m, and the Chl maximum eroded (Malone *et al.*, 1993; Roman *et al.*, 1993). Water temperature at different depths over the August cruise indicated that mixing occurred down to at least 100 m (Fig. 1). Surface water temperatures were cooler after the hurricane as a result of mixing, with a gradual warming for the duration of the cruise (Fig. 1).

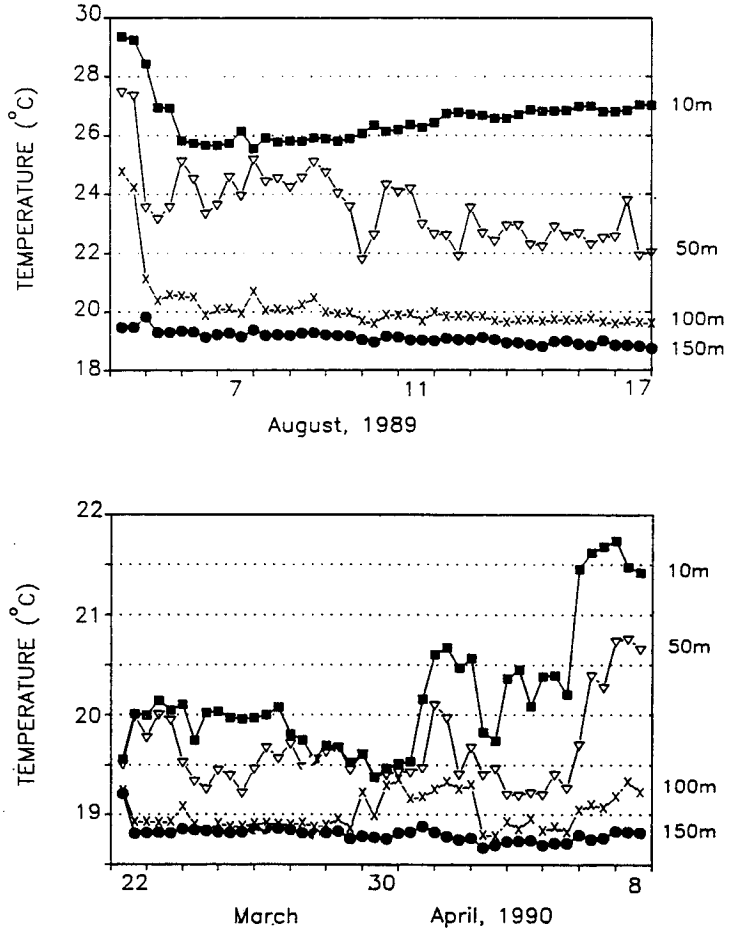

Fig. 1. Temperature at four depths during the August 1989 and March/April 1990 time-series.

The March/April cruise was characterized by different hydrographic regimes associated with water masses which moved through the study area (Malone *et al.*, 1993; Roman *et al.*, 1993). Initially weak stratification of the upper water column was apparent 23–29 March; a front appeared to pass through the study area 29–30 March; the advection of a warmer, fresher water mass through the area after 6/4 resulted in both higher nitrate and Chl in the water column (Malone *et al.*, 1993; Roman *et al.*, 1993). Water temperatures at different depths (Fig. 1) illustrate the periods of stratification, isothermal conditions to 100 m in the front, and the intrusion of warmer water at the end of the cruise (Fig. 1).

Vertical distribution of plankton biomass

There was no measurement of the carbon biomass of the various plankton groups before the passage of Hurricane Dean; the 8 August 1989, station was after this mixing event (Fig. 2). With the exception of 8/8, when the highest biomass of phytoplankton was found at the top of the thermocline (50 m), phytoplankton biomass was relatively constant with depth

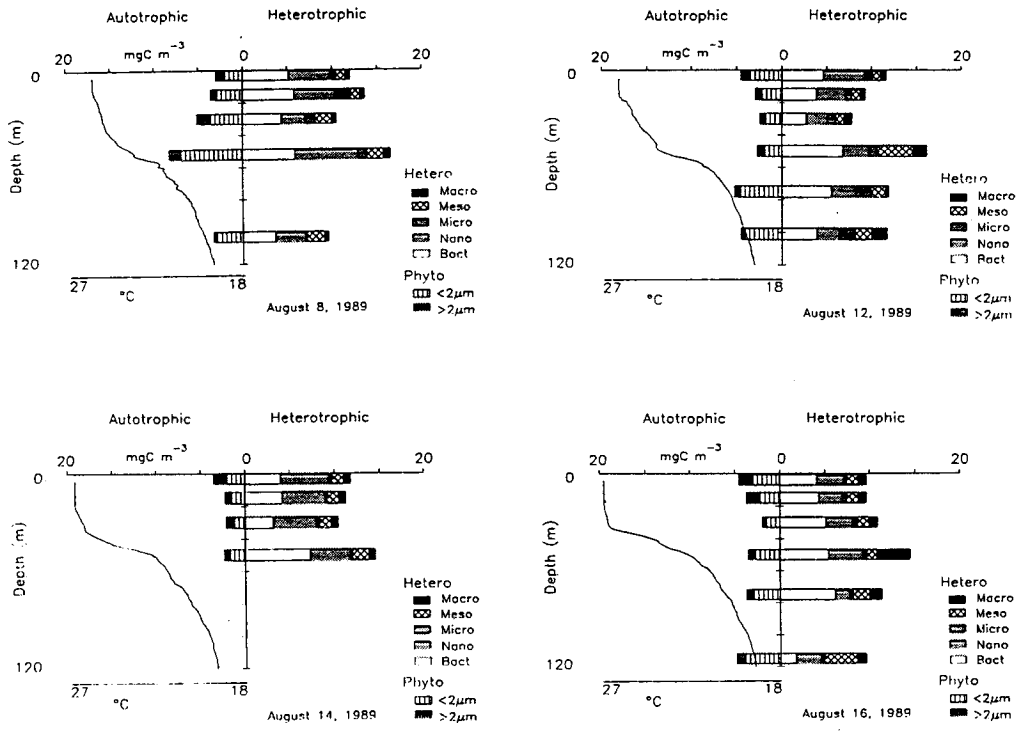

Fig. 2. Vertical profiles of temperature (solid line) and the biomass (mg C m^{-3}) of macrozooplankton, mesozooplankton, microzooplankton, nanozooplankton, bacteria, phytoplankton $<2\,\mu m$ and phytoplankton $>2\,\mu m$ on 8, 12, 14, 16 August 1989.

(Fig. 2). Although the amount of Chl was highest at the base of the photic zone (100 m), this depth did not represent a maximum in phytoplankton biomass. Phytoplankton $<2\,\mu m$ dominated the autotrophic biomass. The percentage of $<2\,\mu m$/total phytoplankton carbon ranged from 57 to 95% at the various depths during the August study. In general the contribution of $<2\,\mu m$ phytoplankton was greater at depth: the average % of total phytoplankton carbon was 90% at the base of the photic zone and 70% at the surface (N = 5).

The carbon biomass of total heterotrophic plankton in August was highest at the top of the thermocline (Fig. 2). The heterotrophic carbon found at each depth of the August study was dominated by BACT and NANO. BACT and NANO were similar in magnitude, with less biomass of MICRO, MESO and MACRO. These are daytime profiles and therefore do not account for diel migration by the zooplankton. Often over two times more MACRO was caught in the surface waters at night as compared to day samples (Roman *et al.*, 1993).

As a result of the changing hydrographic conditions and increased productivity, both the vertical distribution and the amount of plankton biomass were less variable in August as compared to March/April. At the beginning of the study (27 March) the biomass of phytoplankton was highest at the top of the thermocline (Fig. 3). When the front passed the station and the water was isothermal to >100 m (31 March), phytoplankton biomass was highest in surface waters. On 2 April, the biomass maximum of phytoplankton

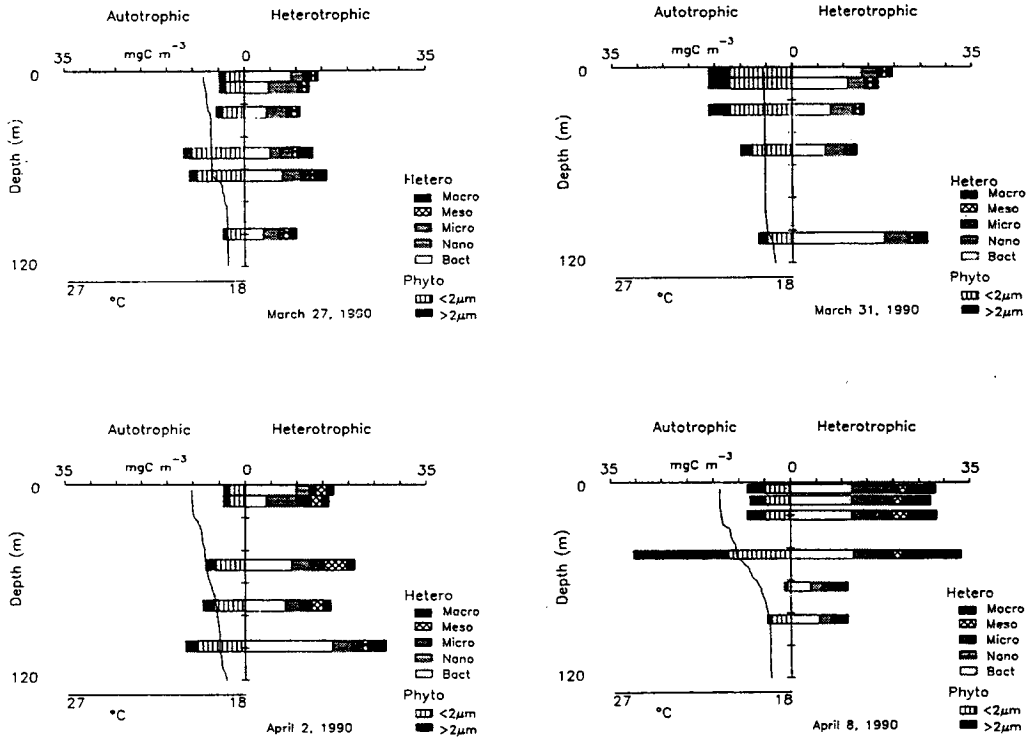

Fig. 3. Vertical profiles of temperature (solid line) and the biomass (mg C m^{-3}) of macrozooplankton, mesozooplankton, microzooplankton, nanozooplankton, bacteria, phytoplankton <2 μm and phytoplankton >2 μm on 27, 31 March, 2, 8 April 1990.

coincided with the subsurface Chl maximum at the base of the photic zone. The highest amount of phytoplankton biomass occurred on 8 April, when warmer, fresher water was advected into the study area. At 44 m we measured 2 μM nitrate and 0.9 μg Chl litre^{-1}. The phytoplankton assemblage of this Chl maximum was dominated by diatoms (Malone *et al.*, 1993).

In general, the depths of highest heterotrophic biomass in March/April were coincident with maxima in autotrophic biomass. At the beginning of the cruise (27 March) the maximum heterotrophic biomass was found at the top of the thermocline. When the front passed the study area, peaks were found in heterotrophic biomass both at the surface as well as at the top of the thermocline (100 m), primarily the result of greater BACT. The highest amount of heterotrophic biomass was found on 8 April, when the warmer, fresher water advected through the study area. At this station, the largest increase in heterotrophic carbon occurred in the MACRO. These daytime profiles underestimate the biomass of MACRO. During the March/April cruise more MACRO was caught in the surface waters at night (Roman *et al.*, 1993).

Biomass comparisons

The amount of phytoplankton carbon in the photic zone was lower in August as compared to March/April (398 and 912 mg C m^{-2}, respectively). A lower amount (72 vs

295 mg C m^{-2}) and % of total (18% vs 28%) of the phytoplankton were >2 μm in August as compared to March/April (Table 1, Fig. 4). The highest phytoplankton biomass was found on 8 April when the warmer, fresher water mass passed through the region. On this day over 50% of the phytoplankton biomass (predominately diatoms) in the photic zone was >2 μm. The coefficient of variation (standard deviation/mean) for integrated (100 m) <2 μm phytoplankton biomass was similar for the August (19%) and March/April (18%) cruises. The variability was greater for the larger (>2 μm) standing crop (24% in August and 58% in March/April) especially during the March/April cruise when different water masses passed through the study area.

BACT were the largest fraction of the integrated photic zone heterotrophic carbon on both cruises (39% in August, 46% in March/April; Fig. 5), with half as much BACT in the photic zone in August as compared to March/April (430 vs 833 mg C m^{-2}, respectively). Integrated BACT in the photic zone exhibited the lowest coefficient of variation of all the plankton groups during the two cruises (13% in August and 15% in March/April). The next largest component of heterotrophic carbon biomass were NANO which comprised on average 30% and 24% of the total heterotrophic biomass in August and March/April, respectively (Fig. 5). Averaged over the cruise, there were less NANO in the photic zone in August as compared to March/April (332 vs 430 mg C m^{-2}, Table 1). MICRO were the most variable component of the microorganisms, the coefficient of variation for their integrated photic zone biomass, 50% and 52% in August and March/April, respectively (Table 1, Fig. 4). MICRO were the smallest component of total heterotrophic carbon biomass (6% in August and 8% in March/April). The coefficient of variation for biomass estimates generally increased with the size of the plankton group during March/April, suggesting a closer coupling as size decreases.

In contrast to the other heterotrophic groups, the average amount of MESO (nauplii and small copepodites) was slightly higher during August as compared to March/April (183 vs 126 mg C m^{-2}, Fig. 4). As mentioned previously however, the variability in heterotrophs in March/April was higher than August (coefficient of variation in MESO 17% in August and 57% in March/April). Day/night differences in MESO biomass were not significant. However on average, twice as much MACRO was caught in the photic zone at night during both cruises (Roman *et al.*, 1993). Thus the daytime heterotrophic biomass comparisons underestimate the role of MACRO in relation to the other heterotrophic groups. The relative increase in MACRO between the August and March/April cruises (average 93 vs 267 mg C m^{-2}) was the greatest of the heterotrophic groups (Table 1, Fig. 4). MACRO comprised 8% and 15% of total daytime heterotrophic biomass in August and March/April, respectively.

Salps were a minor component of heterotrophic biomass during the cruises. The average biomass of salps in the upper 200 m was 0.07 and 0.50 mg C m^{-2} for day and night trawl collections in August and 0.11 and 0.70 mg C m^{-2} for day and night collections in March/April. Even if it is assumed that all of this biomass is in the photic zone (100 m), salp biomass would contribute < 0.01% of total heterotrophic biomass during the day and approximately 0.04% of heterotroph biomass using the salp biomass estimates from nighttime collections during both the August and March/April cruises.

The plankton biomass distribution on the two cruises was not a broad-based pyramid where phytoplankton ≫ heterotrophs. The steep-sided biomass distribution (Fig. 6) implies that there is a rapid turnover of the smaller plankton components and that trophic relationships are likely complex. The ratio of integrated heterotroph/phytoplankton

Table 1. *Biomass* (mg C m^{-2} *integrated to* 100 m) *of phytoplankton, particulate organic carbon (POC), detritus (DET), bacteria (BACT), nanozooplankton (NANO), microzooplankton (MICRO), mesozooplankton (MESO) and macrozooplankton (MACRO). Averages (Avg), Standard deviations (Std) and Coefficient of variation (Cv = Std/Avg) given for each cruise*

	Phytoplankton			Heterotrophs								
Date	<2 μm	>2 μm	Total	POC	DET	BACT	NANO	MICRO	MESO	MACRO	Total	Hetero/Phyto
						August 1989						
8/8	431	96	527	5493	3930	486	463	87	166	57	1259	2.4
10/8	361	56	417	4932	3775	354	320	66	228	108	1076	2.6
12/8	299	67	366	3464	2218	474	285	121	189	90	1159	3.2
14/8	261	54	315	3461	2418	376	325	27	141	56	925	2.9
16/8	274	87	361	3538	2409	461	265	40	193	154	1114	3.1
Avg	325	72	397	4178	2950	430	332	68	183	93	1106	2.8
Std	63	17	73	864	742	54	69	34	29	36	109	0.3
Cv	19%	24%	18%	21%	25%	13%	21%	50%	16%	39%	10%	11%
						March/April 1990						
27/3	628	123	751	3807	2041	530	337	147	86	168	1269	1.7
29/3	564	142	706	4403	2605	667	348	75	102	296	1488	2.1
31/3	826	283	1109	4262	1676	1024	391	62	62	155	1695	1.5
2/4	540	183	723	4715	2510	858	382	241	258	177	1917	2.6
6/4	612	241	853	5086	2795	723	607	108	67	125	1631	1.9
8/4	537	625	1168	4960	2270	893	420	209	140	582	2244	1.9
Avg	616	295	912	4685	2371	833	430	139	126	267	1795	2.0
Std	109	172	193	315	386	127	92	72	72	168	264	0.4
CV	18%	58%	21%	7%	16%	15%	21%	52%	57%	63%	15%	20%

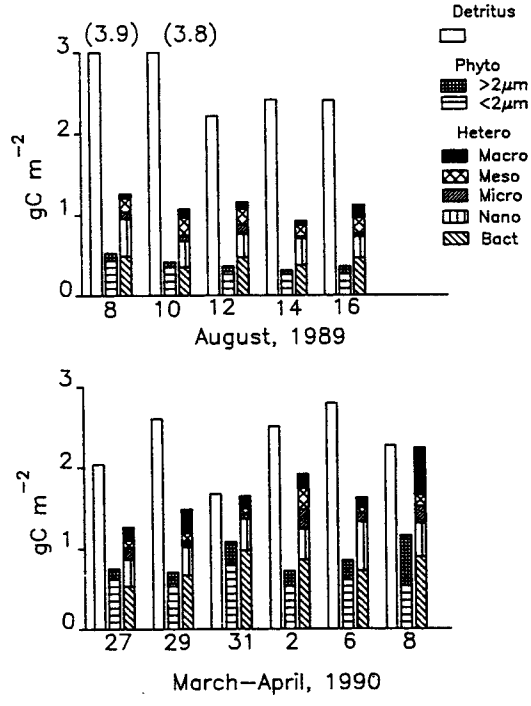

Fig. 4. Integrated photic zone (100 m) carbon biomass (g C m^{-2}) of detritus, macrozooplankton, mesozooplankton, microzooplankton, nanozooplankton, bacteria, phytoplankton <2 μm and phytoplankton >2 μm during the August 1989 and March/April 1990 time-series.

biomass (Hetero/Phyto) was higher during August as compared to March/April (Table 1). During August the Hetero/Phyto ratio ranged from 2.4 to 3.2 (average = 2.8) and in March/April the ratio ranged from 1.7 to 2.6 (average = 2.0). Thus a greater phytoplankton turnover rate or more detrital carbon supported the biomass of heterotrophs in August as compared to March/April.

The amount of detritus was calculated by subtracting the estimated biomass of phytoplankton, BACT, NANO and MICRO from particulate carbon measured on filters (Table 1). The amount of detritus in August was highest on 8 August sampling (3.9 g C m^2) and decreased over the cruise (Fig. 4). The amount of detritus in the photic zone averaged 3.0 g C m^{-2} in August and 2.4 g C m^{-2} in March/April. This represents an average % detritus/particulate carbon of 70% and 51%, respectively. Detrital carbon accounted for a larger fraction of POC in August when the Hetero/Phyto ratio was highest, suggesting that heterotrophs contributed to the detrital pool. As mentioned in the Methods section, POC samples collected on the August cruise were not fumed with acid prior to analysis, potentially biasing the estimates of detritus. However, low C/N ratios in both surface waters (6.6) and the subsurface Chl maximum (5.5) in August were not statistically different from C/N ratios determined during March/April (Malone *et al.*, 1993). Thus inorganic carbon probably did not contribute to higher August estimates of detritus.

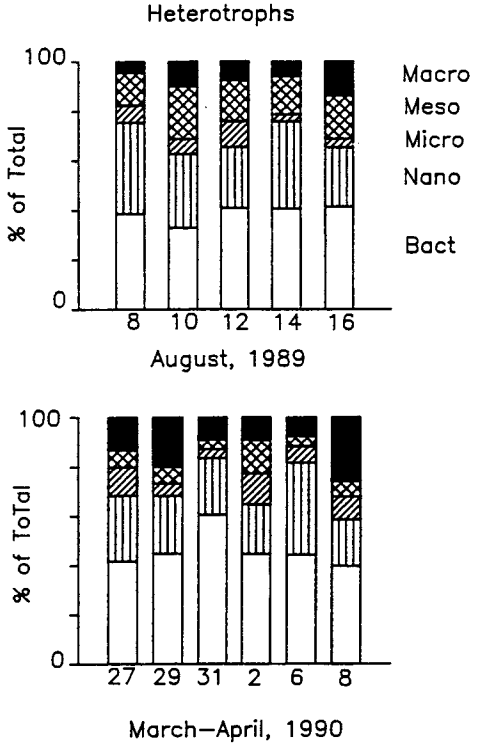

Fig. 5. The percent composition of integrated (100 m) heterotrophic carbon contributed by macrozooplankton, mesozooplankton, microzooplankton, nanozooplankton and bacteria.

DISCUSSION

Past work in the Sargasso Sea off Bermuda has shown that chlorophyll, primary production, zooplankton biomass and the vertical flux of organic material exhibit a seasonal cycle related to the depth of the mixed layer (Menzel and Ryther, 1961a,b; Deevey, 1971; Deuser, 1986; Altabet, 1989; Lohrenz *et al.*, 1992). Cooling of surface waters and increased winds result in deepening of the mixed layer and the input of nitrate into the photic zone. Although there are year-to-year variations in the extent and duration of this deep mixing, in general the winter injection of nutrients results in maximum phytoplankton and zooplankton stocks in March/April. After shoaling of the mixed layer and depletion of nitrate, the standing stocks of phytoplankton and zooplankton decrease to annual minima in summer and early fall. Thus the two cruises provide a contrast with respect to both plankton biomass and vertical flux of organic material.

The data set allows estimates of the amount of detrital organic carbon in the photic zone. Both the estimated amount of particulate organic detritus and the percent of POC that was detritus was higher in August as compared to March/April (Fig. 6). The plankton community in the northern Sargasso Sea receives a nitrate input in the winter/spring as a result of deep mixing which results in enhanced phytoplankton production. With shoaling of the thermocline, the phytoplankton rely more on recycled nitrogen, total plankton biomass decreases, and the ratio of Hetero/Phyto increases. Increased recycling may result

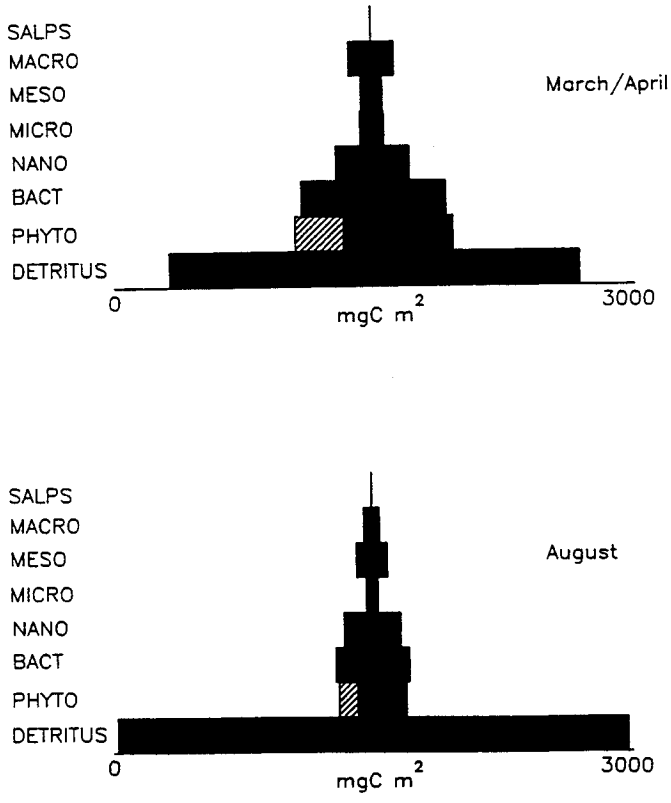

Fig. 6. Average integrated (100 m) biomass of detritus and plankton groups during the August and March/April cruises. Width of histogram represents biomass (mg $C \cdot m^{-2}$). Hatched bar = phytoplankton >2 μm with solid bar = phytoplankton <2 μm.

in the build-up of detritus in the photic zone. This detrital material has a variety of sources (e.g. phytoplankton exudates, bursting bubbles, zooplankton egesta, molts and gelatinous houses). Previous studies using microscopic examination suggested that detritus (primarily organic aggregates) is the dominant component of POC in the Sargasso Sea (Riley *et al.*, 1965; Gordon, 1970). Even during March/April, a period of maximum plankton biomass in the Sargasso Sea, approximately half of the suspended organic carbon was non-living detritus! Efforts to model carbon flow in pelagic systems must take into account this large particulate organic pool. Unfortunately, little is known about the rates of detritus formation, consumption and degradation. Most of the detrital carbon is in small particles and organic aggregates which likely have slow settling velocities and therefore a relatively long residence time in surface waters.

Previous work on the partitioning of plankton biomass in the Sargasso Sea has included only microbial groups (Fuhrman *et al.*, 1989; Li *et al.*, 1992). These studies showed that bacterial biomass could be greater (Fuhrman *et al.*, 1989) or equal (Li *et al.*, 1992) to phytoplankton biomass. Based on our "constrained" conversion factors we (Caron *et al.*, 1995; Table 1) found that the average integrated photic zone biomass ratio of bacteria/phytoplankton was 1.08 and 0.91 in August and March/April, respectively.

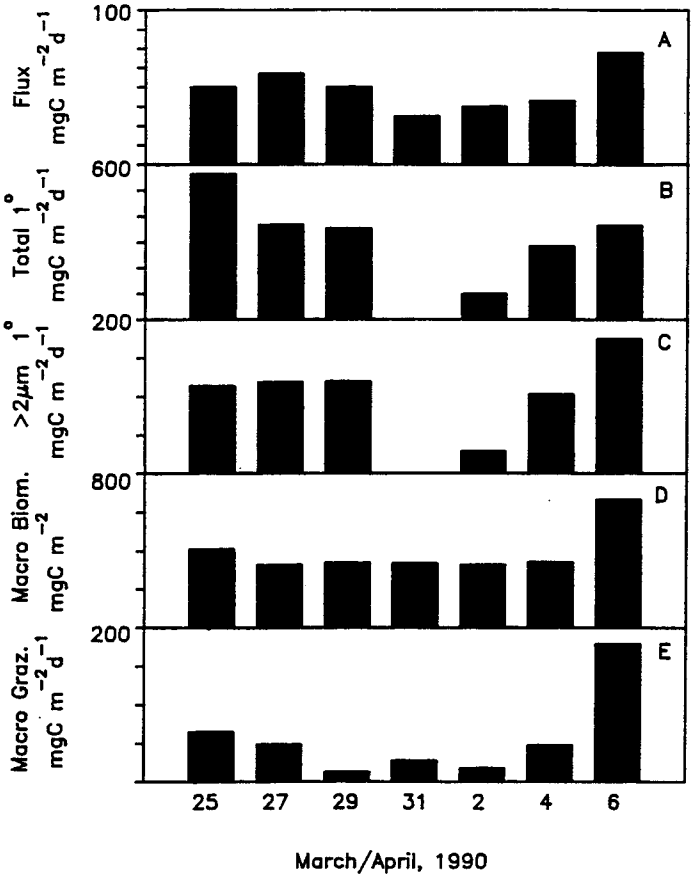

Fig. 7. (A) Gravitational flux at 150 m; (B) Total (GFF) phytoplankton production; (C) >2 μm phytoplankton production; (D) Average of night and day macrozooplankton biomass integrated to 150 m; (E) Macrozooplankton grazing integrated over the photic zone.

Bacterial production averaged 126 mg C m^{-2} d^{-1} (range = 94–258) in August and 76 mg C m^{-2} d^{-1} (range = 50–108) in March/April; phytoplankton production averaged 141 mg C m^{-2} d^{-1} (range = 56–395) in August and 333 mg C m^{-2} d^{-1} (range = 285–368) in March/April (Malone *et al.*, 1993). We can assess the amount of production per unit substrate produced (DOC from phytoplankton) by comparing the ratio of bacterial production/phytoplankton production on individual days on the two cruises. This ratio averaged 0.94 (range = 0.36–2.32) in August and 0.20 (range = 0.14–0.24) in March/April. Thus in general, a greater proportion of phytoplankton production may serve to support bacteria and the microbial loop in August as compared to March/April.

Taken together, BACT and NANO represented an average of 69% and 70% of total heterotrophic carbon in the photic zone in August and March/April, respectively. The remaining heterotrophs, MICRO, MESO and MACRO averaged 6%, 17% and 8% of total heterotrophic biomass in August and 8%, 7% and 15% in March/April. As noted previously, these are daytime measurements, and MACRO biomass would be roughly

twice as much at night. Holligan *et al.* (1984), conducted a comparison of the biomass of various plankton groups (phytoplankton, protozoa [NANO and ciliates], 80–200 μm and >200 μm zooplankton) in the English Channel. Although their methods of estimating the carbon biomass were different than the methods employed here, the general proportion of carbon in the various plankton groups provides an interesting comparison of a neritic and oceanic food-web. Holligan *et al.* found that the contribution of bacteria to total heterotrophic biomass was 34%, 28% and 8% at a front, mixed and stratified station, respectively. With the exception of the front, the relative proportion of bacteria to total heterotrophs was less than we found in the Sargasso Sea (averages of 39% in August and 46% in March/April). Taken together, bacteria and protozoa (NANO + ciliates) in the English Channel study constituted 89%, 53% and 12% of total heterotrophic carbon at the front, mixed and stratified station with MESO and MACRO contributing 11%, 56% and 88%, respectively. In contrast to the Sargasso Sea, the English Channel had a greater proportion of carbon in larger zooplankton. Higher phytoplankton standing stocks and a greater average cell size of phytoplankton may be responsible for this difference. Whereas the ratio of heterotrophs/phytoplankton biomass averaged 2.83 (August) and 1.96 (March/April) in the Sargasso Sea, this ratio was 0.06, 0.47 and 2.68 at the front, mixed and stratified stations in the English Channel. It appears as though small phytoplankton cells with a high growth rate (Malone *et al.*, 1993) can support a heterotrophic biomass which is greater than autotrophic biomass in the Sargasso Sea. At both the front and mixed stations in the English Channel, the biomass of autotrophs is larger than heterotrophic biomass, resulting in a more classical biomass "pyramid".

Most of the heterotrophic carbon in the Sargasso Sea plankton was in BACT and NANO. Considering their high weight-specific carbon demand relative to the MICRO, MESO and MACRO, a carbon flow analysis would further emphasize the importance of BACT and NANO. For example, using Williams (1981) estimation of respiration from biomass for microheterotrophs and mesozooplankton and an R.Q. of 0.85, we estimate that although BACT and NANO constituted roughly 70% of total heterotrophic biomass on the two cruises, they could potentially contribute over 90% of the total heterotrophic carbon demand. Clearly, most of the carbon in the surface waters of the Sargasso Sea is cycling through the "microbial loop", especially during August when the biomass of >2 μm phytoplankton and MACRO are small.

Our conclusions concerning the relative importance of autotrophic vs heterotrophic biomass, and the relative importance of the various microbial assemblages within these categories, are dependent on several conditions. Chief among these conditions are the correct choice of conversion factors used to convert microbial abundances to carbon content, and the clear distinction between autotrophic and heterotrophic microorganisms in analyses. The derivations of our conversion factors for each microbial assemblage are detailed in a companion paper (Caron *et al.*, 1995). The existence of symbiont-bearing or "mixotrophic" protists could also confound the clear distinction of producer and consumer microbial assemblages in the samples. The determination of autotrophic and heterotrophic biomass in the study was based on the presence or absence of autofluorescing chlorophyll as detected by epifluorescence microscopy. We recognize that this commonly-employed convention is somewhat artificial for marine plankton communities because of the presence of protists that are capable of combining phototrophic and heterotrophic nutrition. For example, several species of ciliates retain functioning chloroplasts and thus are both phagotrophic and photosynthetic (Stoecker *et al.*, 1989).

Similarly, many oceanic heterotrophic dinoflagellates retain photosynthetic symbionts (Taylor, 1990), and most surface-dwelling planktonic sarcodines (Acantharia, Radiolaria and Foraminifera) harbor endocytoplasmic symbiotic algae (Caron and Swanberg, 1990). The inclusion of these organisms in the "heterotrophic" biomass categories could have underestimated the autotrophic biomass in those situations in which cell counts were used to estimate phytoplankton biomass (i.e. for the August data set). Conversely, most algal classes contain chloroplast-bearing genera that also feed phagotrophically on bacteria and other small protists (Sanders and Porter, 1988). The exclusion of these algae from the heterotrophic microbial categories because of the presence of chloroplasts in these specimens may have resulted in underestimations of the importance of nanoplanktonic consumers in our samples.

Based on our examinations, inclusion of symbiont-bearing and mixotrophic organisms should not substantially change our conclusions in this study. Obviously mixotrophic ciliates (i.e., the plastidic ciliates other than Mesodinium and symbiont-bearing dinoflagellates) were classified as heterotrophs because they are primarily phagotrophs (e.g. Stoecker *et al.*, 1988). Some underestimation of phototrophic biomass as a consequence of this generalization may have occurred in the August data set where microscopical counts were used to estimate phytoplankton biomass (chlorophyll measurements were used in March). However, the contribution of these ciliates to integrated chlorophyll standing stock was estimated to be relatively small (on average <9%, Lessard and Murrell, submitted). The plastidic ciliate, *Mesodinium rubrum*, was classified as a phototroph because it is thought to be an obligate autotroph (Lindholm, 1985). This classification would avoid an underestimation of autotrophic biomass due to the presence of this ciliate. Planktonic sarcodines were rare in the samples, ranging from 0 to 11 l^{-1}. Their integrated biomass was insignificant relative to other groups (<1 to *ca* 8 mg m^{-2} using the conversion factor of Michaels, 1991) and therefore should not have significantly affected the calculation of phototrophic biomass.

The contribution of nanoplanktonic, phagotrophic phytoplankton to total nanophytoplankton was highly variable, and it was therefore more problematical to estimate the potential contribution of these microorganisms to the microbial assemblages. For example, we estimated that phagotrophic algae ranged from undetectable up to 50% of the chloroplast-bearing nanoplanktonic protists in the samples (based on the ingestion of fluorescently labeled bacteria by chloroplast retaining nanoplankton; approximate limit of detection = 5% of NANO abundance; Arenovski *et al.*, 1995). However, average abundances of phagotrophic algae in this study and a subsequent study in April 1992 near our sampling site were less than 5% of the chloroplast-bearing nanoplanktonic protists (Arenovski *et al.*, 1995). It is therefore unlikely that the number of phagotrophic algae were substantially underestimated in our study. If we did significantly underestimate the importance of phagotrophic algae, however, it would only strengthen our conclusions concerning the important contribution of heterotrophic microbial biomass to total biomass in this ecosystem, and the predominance of this component of the food web in energy and elemental flow in surface waters of this region of the Sargasso Sea.

In the Sargasso Sea off Bermuda flux rates of organic material measured at the base of the photic zone as well as at 3200 m are less in August as compared to March/April (Deuser, 1986; Altabet, 1989; Lohrenz *et al.*, 1992). This greater flux rate at the time of annual maxima in total and >2 μm phytoplankton biomass, production and macrozoop-

lankton biomass is the result of enhanced flux of sinking phytoplankton, organic aggregates and zooplankton fecal pellets. Since MACRO were approximately three times more abundant in March/April as compared to August, one would expect that MACRO fecal pellet production of a similar magnitude would also be greater. In fact, the actual increase in fecal pellet production is likely more than the increase in MACRO biomass because greater phytoplankton biomass and the larger size spectrum of the phytoplankton community in March/April (Malone *et al.*, 1993) would result in greater weight-specific MACRO ingestion and egestion rates.

MACRO ingestion rates increased from an average of 2 mg C m^{-2} d^{-1} (1% of daily primary production) in August to 57 mg C m^{-2} d^{-1} (17% of daily primary production) in March/April (Roman *et al.*, 1993). If one assumes that 70% of the ingested phytoplankton is assimilated and 30% is egested as fecal pellets (Small and Ellis, 1992), the potential fecal carbon flux in August would average 1 mg C m^{-2} d^{-1} (range <1–2) and 17 mg C m^{-2} d^{-1} (range 4–54) in March/April. These potential pellet production rates underestimate actual fecal production because they assume that MACRO only consume phytoplankton. Most copepods are omnivores, consuming phytoplankton, protozoa and small metazoans (e.g. Corner *et al.*, 1976; Landry, 1981; Roman, 1984; Stoecker and Egloff, 1987). We consistently found high C:Chl ratios in MACRO fecal pellets (>500) which would suggest that MACRO consumed mostly non-phytoplankton (detritus, protozoa, metazoans) carbon (Small and Ellis, 1992). Assuming that 50% of the MACRO diet is non-phytoplankton carbon, the carbon flux of MACRO pellets would double to an average of 2 mg C m^{-2} d^{-1} in August and 34 mg C m^{-2} d^{-1} in March/April. Fecal pellet production by salps would add to these estimates.

The flux of particulate organic carbon at 150 m estimated with free-drifting sediment traps by Lohrenz *et al.* (1992) was approximately 20 and 45 mg C m^{-2} d^{-1} in August 1989 and April 1990, respectively. Flux measurements conducted during our March/April 1990 cruise (Fig. 7) ranged from 25–58 mg C m^{-2} d^{-1} (average 39). Thus our average estimated flux rates due to MACRO fecal pellets of 34 mg C m^{-2} d^{-1} (50% of ingestion as non-phytoplankton carbon) in March/April was 87% of the carbon flux at 150 m. These flux estimates illustrate that although MACRO constituted only 15% of total heterotrophic biomass in March/April, their contribution to the vertical flux of organic material is much greater. Short-term changes in the sinking of organic matter during March/April, when different water masses passed through the study area, were consistent with increases/decreases in MACRO biomass and grazing (Fig. 7).

These results support previous evidence that most of the carbon flow in the open ocean is through microbial communities. Relatively high phytoplankton growth rates and constant phytoplankton standing stocks during the cruises (Malone *et al.*, 1993) suggest that phytoplankton production and consumption were in balance. Bacterial production and consumption also appeared to be in balance. Previous gravitational flux estimates as well as flux estimates conducted during March/April cruise suggest that export increases with the biomass >2 μm phytoplankton and MACRO. Thus the composition of the planktonic food-web can directly influence the amount of carbon which is exported from surface waters.

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