VARIABILITY IN ZOOPLANKTON BIOMASS DISTRIBUTION IN THE NORTHERN SARGASSO SEA: THE CONTRIBUTION OF GULF STREAM COLD CORE RINGS[1]

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ABSTRACT

The scale and frequency of physical variability resulting from incursion of Gulf Stream cold core rings into the northern Sargasso Sea makes this faunal province more heterogeneous than previously recognized. At any one time such rings may cover between 6 and 13% of the surface area of the northern Sargasso Sea. They are more productive than the surrounding Sargasso Sea and have a zooplankton biomass intermediate between the Sargasso Sea and the slope water. Cold core rings may augment by 3 to 7% the primary productivity and by 8 to 16% the zooplankton standing crop of the northern Sargasso Sea. Compared with either the surrounding Sargasso Sea or their parent slope water, an unusually large percentage of the 0-800 m biomass in rings is found at depths greater than 200 m. This distribution may be related to hydrographic and biological changes associated with ring decay. Because of their higher productivity, differences in vertical biomass structure, and the possibility that ring food chain efficiency is lower than that of the Sargasso Sea, rings may provide a disproportionately large fraction of the total supply of organic matter to the northern Sargasso deep Sea.

A number of papers have characterized the zooplankton biomass of the northern Sargasso Sea (Menzel and Ryther 1961; Grice and Hart 1962; Bé et al. 1971; Deevey 1971; Deevey and Brooks 1971; and others). Because of the variety of methods employed in both sampling and processing, the results of these studies are not readily comparable. In general, previous authors have portrayed the Sargasso Sea as a remarkably homogeneous faunal province. The scale and frequency of regional variability resulting from incursions of cold core rings into the Sargasso Sea have not been generally appreciated. Cold core rings are mesoscale hydrological features 150 to 300 km in diameter and up to several thousand meters in depth. They form when southerly directed Gulf Stream meanders become so accentuated as to separate from the Stream and move south, enclosing a core of cold and relatively fresh slope water within a remnant of the Gulf Stream (Parker 1971; Fuglister 1972; Richardson 1976). It is likely that in the northern Sargasso Sea, at any one time, there are 10 to 15 such rings (Lai and Richardson 1977). Estimating the surface area of the northern Sargasso Sea as 32.9×10^5 km² (Jahn 1976), cold core rings may cover between 6 and 13% of this surface. (Throughout the ensuing sections, unless otherwise indicated, the terms ring, slope water, and Sargasso Sea denote hydrographic, not geographic, entities.)

An overview of the phytoplankton, zooplankton, and midwater fish populations inhabiting cold core rings has been given by Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). The results of that study indicated that mean zooplankton biomass in the upper 750-800 m of rings between 3 and 10 to 12 mo of age was consistently higher than that in the surrounding Sargasso Sea. In these preliminary data the fraction of biomass below 250-300 m in depth was particularly large while the near surface was more similar to the Sargasso Sea. We have now taken vertically stratified hauls in the same ring 3 mo apart. The data from these hauls confirm our initial interpretation.

The objective of this paper is twofold. First, we describe the zooplankton biomass distributions characteristic of the northern Sargasso Sea, of a cold core ring, and to a lesser extent of the slope water—the source of ring water. Second, we will attempt to relate the patterns observed to systematic variations in phytoplankton standing

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crop, primary productivity, and water temperature, and to explore the significance of ring biomass distribution.

METHODS

The major portion of the data to be presented in this paper was collected on RV *Chain* cruise 125 (August 1975) and on RV *Knorr* cruise 53 (November 1975). The ring sampled (designated Ring-D by the Naval Oceanographic Office), was formed in February 1975. It was, therefore, about 6 mo old when first sampled and 9 mo old when sampled again in November. In November the slope water was hydrographically complex. It is likely that some of our intended slope water tows (MOC 39 and MOC 40) may have been taken in the vicinity of a warm core ring (Saunders 1971). The upper 200 m of the water column at that station was warmer and more saline than is typical for the slope water. In addition, infrared satellite photographs clearly show the presence of this warm ring during the period of sampling. Other slope water stations may have been influenced by the passage of a warm core ring. In analyzing the data, MOC 39 and 40 are considered separately and designated warm core ring tows. Data corroborating specific points or conclusions have been drawn from collections made on RV *Atlantis* cruise 71, RV *Chain* cruise 111, and RV *Knorr* cruises 35 and 38 (Table 1).

Collections in Gulf Stream cold core rings, the northern Sargasso Sea, and slope water were made with three types of sampling gear: on the early cruises 1-m diameter ring nets or modified opening/closing 70-cm diameter bongo nets (McGowan and Brown 1966), on the two most recent cruises a multiple opening/closing net and environmental sensing system—MOCNESS (Wiebe, Burt, Boyd, and Morton 1976)—with a mouth area of 1 m × 1.4 m (effective area is 1 m²). All nets were constructed from 0.333-mm Nitex[3] gauze; depth recorders and flow meters were used on all tows.

The 1-m nets were hauled obliquely, ideally to a depth of 800 m. On some cruises a second haul was taken to a depth of 300 m. Bongo nets were towed obliquely within the depth intervals 0-250, 250-500, and 500-750 m. With occasional exceptions, the MOCNESS sampled both from 800 m to the surface in 100-m intervals, and from 200 m to the surface in 25-m intervals. Sampling with 1-m and bongo nets was almost always done at night, while at most MOCNESS stations samples were taken both day and night. The types of tows taken on the five cruises are given in Table 1. All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium tetraborate. In the vicinity of all plankton hauls, hydrographic casts were made yielding nearly concomitant vertical profiles of temperature, salinity, oxygen, chlorophyll, nutrients, primary productivity, and phytoplankton species (see Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox 1976 for methods).

Zooplankton biomass was measured by the method of Ahlstrom and Thrailkill (1963) after removal of all organisms greater than 5 cm³. Displacement volumes were measured 5 to 9 wk after a cruise. No attempt has been made in this paper to partition the biomass according to taxa. The species composition of those samples already examined appears similar to that reported for the region by Grice and Hart (1962), Deevey (1971), and Deevey and Brooks (1971).

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of slope water, ring, and Sargasso Sea zooplankton sample stations.

Cruise	Date	Age of ring (mo)	Number of samples (stations)			Type of net
			Ring	Sargasso Sea	Slope water	
Atlantis II 71[1]	21 Sept.-14 Oct. 1972	10-12	8(4)	28(15)	4(2)	1 m
Chain 111[1]	7 Feb.-18 1973	3.5	6(2)	5(2)	2(2)	1 m and bongos
Knorr 35[1]	23 Nov.-3 Dec. 1973	3.0	8(4)	1(1)	5(3)	1 m and bongos
Knorr 38[1]	12 Feb.-3 Apr. 1974	10-12				1 m
Chain 125[2]	4 Aug.-17 1975	6.0	48(1)	32(2)	48(2)	MOCNESS
Knorr 53[3]	17 Nov.-1 Dec. 1975	9.0	48(1)	40(2)	64(3)	MOCNESS

[1]Positions of stations illustrated in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976).
[2]Sargasso Sea: MOC 1,2 (35°37', 68°31'), MOC 3,4 (35°22', 68°17'), MOC 12 (34°11', 71°40'), MOC 13,14,15 (34°10', 71°34'); ring: MOC 5,11 (34°29', 69°56'), MOC 6,7 (34°34', 69°52'), MOC 8 (34°31', 69°49'), MOC 10 (34°33', 69°53'); slope water: MOC 16,17 (38°02', 69°59'), MOC 18,19 (38°05', 70°02'), MOC 20,21 (39°05', 70°12'). All positions are north latitude and west longitude.
[3]Sargasso Sea: MOC 23,24,25 (32°44', 71°10'), MOC 26 (32°52', 71°08'), MOC 34 (34°12', 70°30'); ring: MOC 27, 28, 29 (33°49', 71°54'), MOC 31 (35°50', 71°48'), MOC 32 (33°56', 71°54'), MOC 33 (34°03', 71°56'); warm core ring: MOC 39,40 (40°04', 68°05'); slope water: MOC 35,36 (38°51', 67°47'), MOC 37,38 (38°55', 67°46'), MOC 41,42 (39°59', 69°00'). All positions are north latitude and west longitude.

RESULTS

Regional Biomass

The biomass collections obtained in the same ring 3 mo apart in August and November 1975 corroborate differences already noted in 0-800 m zooplankton biomass between the Sargasso Sea, cold core rings, and slope water (Figures 1, 2). In both months the slope water 0-800 m biomass was larger than either the Sargasso Sea or ring 0-800 m biomass (Mann-Whitney U-test, $P < 0.01$). In August, the contrast between slope water and the two other regions was particularly marked with average concentration in the upper 800 m approximately 10-12 times larger than in the Sargasso Sea and ring (Table 2, top). At several depths in the August slope water stations the zooplankton biomass was dominated by *Salpa aspera*.[4] Differences in abundance of this salp accounted for a large part of the variation between slope water stations. The high water content of these animals undoubtedly caused our estimate of biomass by displacement volume to be considerably higher than had we measured dry weight or organic carbon content. It is clear, nonetheless, that the standing stock of zooplankton was exceedingly large.

Relative to the Sargasso Sea, 0-800 m ring biomass was on the average 1.36 times larger in August and 1.33 times larger in November (Table

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[4]The significant biomass contribution of *S. aspera* is discussed in Wiebe, P. H., L. P. Madin, G. R. Harbison, L. R. Haury, and L. M. Philbin. 1977. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. Submitted to Mar. Biol.

TABLE 2.—Comparison of slope water, ring, and Sargasso Sea zooplankton biomass (cm³/m²) based on weighted averages of day and night samples collected at 0-800, 200-800, and 0-200 m depth intervals. Number of tows used to make average given in parenthesis.

Region	August 1975			November 1975		
	0-800	200-800	0-200	0-800	200-800	0-200
Sargasso Sea	16.6(4)	8.8(4)	8.1(8)	10.2(2)	5.6(2)	6.0(4)
Ring fringe				9.1(1)	4.3(1)	4.8(1)
Cold core ring	22.5(3)	15.6(3)	6.4(6)	13.6(4)	11.4(4)	3.4(5)
Slope water	256.2(4)	95.6(4)	121.8(6)	33.8(4)	23.0(4)	12.8(6)
Warm core ring				27.9(2)	17.2(2)	10.8(2)

	Ratio ring/Sargasso Sea		
Month	0-800	200-800	0-200
August	1.36	1.77	0.79
November	1.33	2.03	0.56

2, bottom). These differences are consistent with data from previous cruises; using paired regional biomass averages observed on all cruises to date (Table 3) we see that the mean zooplankton biomass in rings and in the Sargasso Sea is significantly different (Sign test, $P < 0.05$).

In November zooplankton standing crop was consistently lower than in August with the most pronounced change occurring in the slope water. Although *S. aspera* was still present at the slope water stations, it no longer dominated the biomass. Comparing August and November 0-800 m biomass averages, segregating day and night samples for each region, we see that the overall seasonal decline is statistically significant (Sign test, $P < 0.05$, computed using cubic centimeters per square meter in Figures 1 and 2). Indeed only one November 0-800 m biomass value was as large as the smallest 0-800 m biomass in the same region in August.

TABLE 3.—Average zooplankton biomass in slope water, ring, and Sargasso Sea—dry weight (mg/m³) in column ≈750 m deep. Numbers of stations per area and range of biomass values (after colon) given in parenthesis. This table is an expanded version of table 3 in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). Note that the biomass units in the original table were incorrectly presented as milligrams per square meter.

Cruise	Slope water		Ring		Sargasso Sea		Ring age (mo)	Ring ÷ Sargasso	Slope ÷ Sargasso
Atlantis II 71	7.43	(1)	2.24	(4:2.06-2.60)	1.68	(4:1.34-2.05)	10-12	1.33	4.42
Chain 111	4.21	(1)	4.95	([1]2:2.21-7.68)	2.70	([2]3:1.99-3.96)	3.5	1.83	1.56
Knorr 35	6.06	([3]4:3.60-7.74)	3.67	([4]3:3.15-4.33)	2.47	(1)	3.0	1.49	2.45
Knorr 38[5]	5.74	(4:2.2-9.14)	3.10	(6:2.56-4.98)	2.34	(4:1.76-3.21)	10-12	1.32	2.45
Chain 125[5]	9.10	([6]2:6.85-11.35)	2.26	(3:1.73-2.57)	1.49	(4:0.90-1.97)	6	1.52	6.11
Knorr 53[5]	3.43	(4:2.77-4.03)	1.09	(4:0.72-1.35)	0.83	(2:0.80-0.86)	9	1.31	4.13
Mean							7.3	1.47	3.52

[1]Each of the two values is integrated for the water column based on three stratified bongo net tows.
[2]Two values are from oblique meter net tows; one is an integrated value based on three stratified bongo net tows.
[3]Two values are from oblique meter net tows; one is an integrated value based on three bongo net tows; one is an oblique bongo net tow.
[4]One value is an integrated value based on three stratified bongo net tows; two values based on two stratified bongo net tows.
[5]Cubic centimeters per cubic meter converted to milligrams per cubic meter using equation 4 table 2 in Wiebe et al. (1975). Note that this conversion affects the regional biomas ratios (see Figure 2) because the relationship between displacement volume and dry weight is not linear.
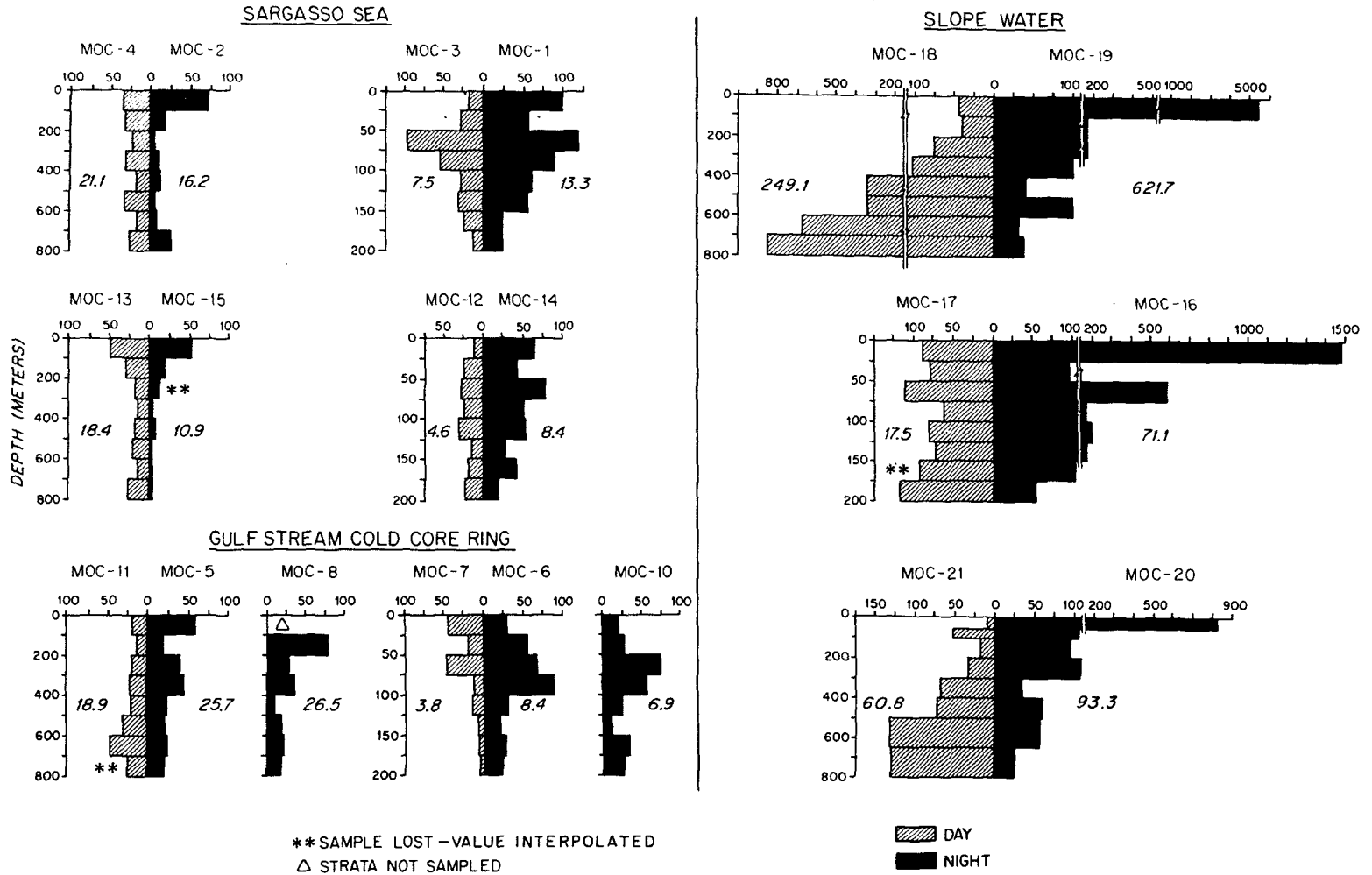[6]Salp-rich tows, MOC 39 and MOC 40, excluded.

SARGASSO SEA

SLOPE WATER

MOC-4 MOC-2

MOC-3 MOC-1

MOC-18 MOC-19

21.1 16.2

7.5 13.3

249.1 621.7

MOC-13 MOC-15

MOC-12 MOC-14

MOC-17 MOC-16

18.4 10.9 **

4.6 8.4

17.5 ** 71.1

GULF STREAM COLD CORE RING

MOC-11 MOC-5

MOC-8

MOC-7 MOC-6

MOC-10

MOC-21 MOC-20

18.9 25.7 ** 26.5 △

3.8 8.4 6.9

60.8 93.3

** SAMPLE LOST — VALUE INTERPOLATED
△ STRATA NOT SAMPLED

▨ DAY
■ NIGHT

FIGURE 1.—Slope water, ring, and Sargasso Sea zooplankton biomass (cm³/1,000 m³). August 1975—*Chain* cruise 125. Values associated with each profile are cubic centimeters per square meter for the entire portion of the water column sampled. Note that 0-200 m profiles have an expanded vertical depth scale.
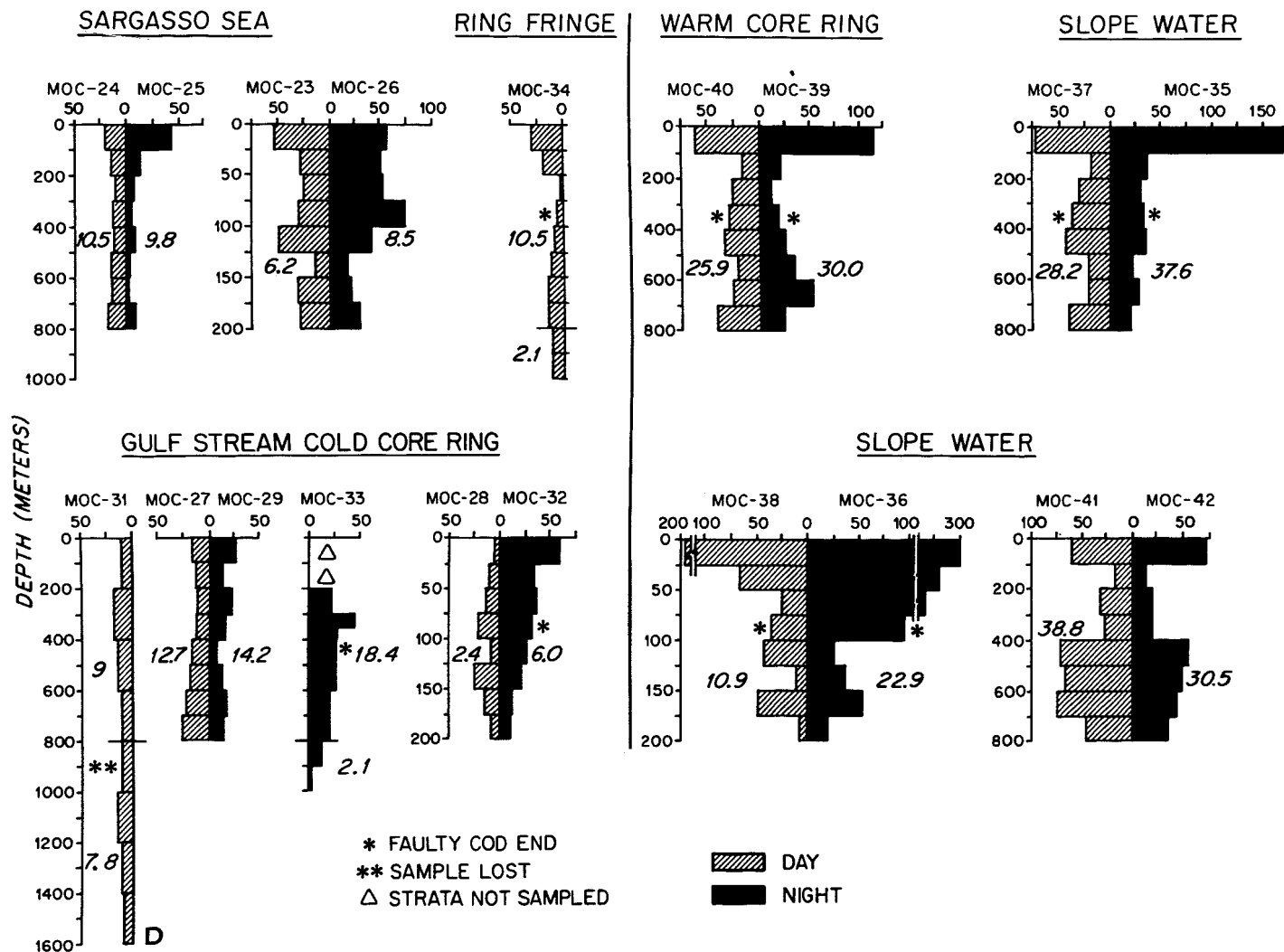
FIGURE 2.—Slope water, ring, and Sargasso Sea zooplankton biomass (cm³/1,000 m³). November 1975—*Knorr* cruise 53. Values associated with each profile are cubic centimeters per square meter for the water column sampled except for MOC-31, MOC-33, and MOC-34, where values have been calculated for above and below 800 m. Note that 0-200 m profiles have an expanded vertical depth scale.

Average Vertical Structure

Comparing Ring-D biomass partitioned according to depth, the upper 200 m in the ring contained, on the average, less biomass during both sampling periods than did the Sargasso Sea (Table 2, top). This was true both day and night during the August and November cruises. In contrast, ring biomass between 200 and 800 m was higher both day and night (Figures 1, 2). The range of 200-800 m biomass values in the ring and in the Sargasso Sea does not even overlap. The combination of lower average surface biomass and higher average subsurface biomass in the ring is highly significant (Sign test, $P < 0.01$, computed using sums of 0-200 m and 200-800 m cm^3/1,000 m^3 derived from Figures 1 and 2). The regional weighted averages of percent 0-800 m biomass present in the upper 200 m in August were 51%, 34%, and 27% in the Sargasso Sea, slope water, and ring, respectively. In November these averages were 45%, 32%, and 25% (Table 4). Although very different sampling systems and tow strategies were employed, data from *Atlantis II* cruise 71 corroborate the direction of difference of these observations in that the percentages of 0-800 m biomass found at night in the upper 300 m were 64% and 52% for the Sargasso Sea and ring, respectively (Table 5). In addition, the 300-800 m biomass was 1.73 times larger in this latter ring than in the surrounding Sargasso Sea.

Diel Migration

Complicating these general observations and contributing to sample variability are day/night differences in biomass distributions (Table 4). In all day/night sample pairs the fraction of 0-800 m biomass present in the 0-200 m interval is larger in the night sample (Sign test, $P < 0.01$). This results from either diel migration or day/night differences in avoidance within the comparatively well-illuminated surface layers. Avoidance does not appear to be an important factor because at some stations the day 0-800 m biomass exceeds the night 0-800 m biomass. This is true in all Sargasso Sea 0-800 m sample pairs and at one slope water station (Figures 1, 2). Furthermore, some species of zooplankton taxa already enumerated, e.g., euphausiids and pteropods, exhibit strong diel migration patterns in all three areas.

Since we believe diel migration to be the appropriate explanation, the data further suggest that while essentially the same percentage of 0-800 m biomass was migrating into the surface layers of the Sargasso Sea (24-30% during both sampling periods), there was a reduced percentage migrating in the ring in November (21% in August versus 9% in November—Table 4). Although a smaller proportion of the biomass may have been migrating in the ring relative to the Sargasso Sea, there was a significantly greater (Mann-Whitney U-test, $P < 0.05$) day/night biomass ratio in the

TABLE 5.—Ring and Sargasso Sea zooplankton biomass— *Atlantis II* cruise 71 (mg/m^2).

Area	0-300 m	0-800 m	$\frac{0\text{-}300}{0\text{-}800} \times 100$	
Ring	954	1,648	58%	
	963	2,080	46%	52%
	930	1,704	55%	
	828	1,728	48%	
Sargasso Sea	858	1,344	64%	
	798	1,072	74%	64%
	765	1,640	47%	
	921	1,304	71%	

TABLE 4.—Percent of 0-800 m slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m (800 m tows only). D = Day; N = Night.

Region	August 1975					November 1975				
	Percentages of individual tows	D	N	N–D	(D + N)/2	Percentages of individual tows	D	N	N–D	(D + N)/2
Sargasso Sea	$D_1 = 32$	39	63	24	51	$D_1 = 30$	30	60	30	45
	$N_1 = 57$					$N_1 = 60$				
	$D_2 = 41$									
	$N_2 = 69$									
Ring fringe						$D_1 = 46$	46			
Cold core ring	$D_1 = 16$	16	37	21	27	$N_1 = 29$	20	29	9	25
	$N_1 = 32$					$D_1 = 21$				
	$N_2 = 42$					$D_2 = 19$				
Slope water	$^1D_1 = 3$	7	61	54	34	$D_1 = 32$	23	41	18	32
	$^1N_1 = 93$					$N_1 = 55$				
	$D_2 = 7$					$D_2 = 13$				
	$N_2 = 61$					$N_2 = 27$				
Warm core ring						$D_1 = 30$	30	46	16	38
						$N_1 = 46$				

[1]On this tow series, MOC 18 and 19, salps were extremely dominant. These tows are excluded from averages.

upper 200 m in the ring (Table 6). This apparent contradiction results from the fact, already noted, that the percentage of 0-800 m biomass present in the upper 0-200 m was very much greater in the Sargasso Sea. Day/night ratio of biomass in the upper water column is often used to measure intensity of diel migration; clearly the meaning of this ratio is highly dependent upon average vertical biomass distribution.

Slope water day/night sample pairs may be interpreted as documenting diel migration, but the data are extremely variable both within and between cruises (Table 4). There may have been a less well-developed migration in the fall, but the generality of this is questionable.

TABLE 6.—Day/night differences in slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m.

| Region | Ratio night/day | | | |
	August 1975		November 1975	
Sargasso Sea	[1]1.78	[2]1.37	[1]1.37	[2]1.86
	[1]1.84	[2]0.99		
Cold core ring	[1]2.01	[2]3.10	[1]2.48	[2]1.86
Slope water	[1]4.06	[2,3]68.33	[1]2.10	[2]2.27
		[2,3]14.82		[2]1.70

[1]Based on 0-200 m tows.
[2]Based on 0-800 m tows.
[3]Ratio affected by extreme salp dominance.

Shallow Biomass Structure

In the 0-200 m biomass profiles, an intermediate biomass peak occurred between 50 and 100 m depth at nearly every station in August 1975 (Figure 1: MOC 1, 3, 6, 7, 10, 16, 17). At all but one of the Sargasso Sea and ring stations this intermediate peak is the highest observed value in the 0-200 m tows. At slope water stations of the same cruise this intermediate peak is the second highest observed value. If we rank each interval in a profile in order of zooplankton abundance, we can test the significance of this observation. For instance, the individual summer tows in the ring and the Sargasso Sea exhibit significant concordance as to which depth intervals have the larger and which the smaller zooplankton biomass (Friedman 2-way analysis of variance on ranks, $P < 0.005$). Given this result, the best estimate of the differences between intervals is the order of their summed ranks (i.e., 50-75 m > 75-100 m > 100-125 m > 25-50 m > 0-25 m > 150-175 m > 125-150 m > 175-200 m). Applying a procedure for testing differences between individual depth intervals (Nemenyi 1963), we see that concordance results from the fact that the 50-75 m biomass is significantly greater than the biomass

in the intervals 125-150, 150-175, and 175-200 m, and the 75-100 m biomass is greater than the 175-200 m biomass ($P < 0.05$). An intermediate peak is not a notable feature of any of the 0-200 m profiles taken on the fall cruise with the exception of the Sargasso Sea sample pair (Figure 2: MOC 23, 26).

DISCUSSION

Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have discussed the formation and decay of an idealized cold core ring. Initially conditions inside a ring core are identical to those in the slope water just northward of the Gulf Stream at the time of ring formation. Through time the ring decays; the isotherms deepen, the water becomes more saline, the O_2 minimum deepens, and the constituent flora and fauna either die off or become diluted by populations from the surrounding Sargasso Sea. Because zooplankton populations are generally suited to the environmental conditions they encounter within their normal range, this decay process may be viewed as the gradual imposition of a complex environmental stress upon an entire community. Wiebe, Hulbert, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have documented some of the intermediate stages in this idealized process. In fact, this process can be aborted when a ring is reabsorbed by the Gulf Stream (Fuglister 1972; Richardson et al. 1977). All biological and physical properties are not equally conservative so their decay rates would not be the same.

Regional Contribution of Cold Core Rings

PRIMARY PRODUCTIVITY.—It is well known that slope water is more productive than the Sargasso Sea. Ryther (1963) estimated that slope water is about twice as productive on an annual basis (120 g C/m^2 per yr versus 60 g C/m^2 per yr). Although our own data are scanty, rings on the average are intermediate between slope water and the Sargasso Sea (Table 7). A few simplifying assumptions permit budgetary computations to be made regarding the overall effect of rings on the carbon budget of the northern Sargasso Sea. Let us assume an average ring life of 1 yr and a linear rate of decay of productivity (i.e., that annual ring production is the arithmetic mean of annual Sargasso Sea and slope water production). Allowing 6 to 13% as the areal contribu-

TABLE 7.—Summary of slope water, ring, and Sargasso Sea primary productivity (mg C/m² per day), phytoplankton carbon[1] (mg/m²), and chlorophyll a (mg/m²) measurements.

Region	March 1974 Productivity	March 1974 Chlorophyll	August 1975 Productivity	August 1975 Chlorophyll	Phytoplankton carbon	November 1975 Productivity	November 1975 Chlorophyll	Phytoplankton carbon
Sargasso Sea	228.5	46.4	[2]207	13.3	33.4	86.5		21
			100			252.2	12.0	
Cold core ring	440.1					483.2		
		73.0	83	17.3	45			28.2
	333.1		106			155.5	10.3	
						186.5		
Slope water	1,025.5		175			1,302.2		
		70.4		50.5				
	368.4		270		280	824.0	39	287
						376.2		
						363.7		

[1]Based on counts of cells larger than 4-5 μm.
[2]The high value in average mg C/m² per day observed at this station is a consequence of one unusually high surface value.

tion of rings to the northern Sargasso Sea as explained earlier, and Ryther's estimate of a twofold difference in annual production, the net annual production of the geographic northern Sargasso Sea is then 3 to 7% higher than if it contained no rings (i.e., $6 \times 1.5 = 9, 9 + 94 = 103$ and $13 \times 1.5 = 20, 20 + 87 = 107$). Our assumption of linear decay is most certainly an oversimplification. In November 1975, the ring water column, like the slope water, began its winter overturn before the surrounding Sargasso Sea. Mixing eroded the seasonal thermocline that had been observed in Ring-D in August 1975. The decay we have assumed was reversed, and ring productivity was enhanced (Table 7).

ZOOPLANKTON STANDING CROP.—Similar calculations can be made regarding the relative contribution of rings to the mean zooplankton biomass of the geographic northern Sargasso Sea. Neglecting one station which had anomalously high values due to extreme salp dominance, the average of slope water biomass values is 3.5 times the observed Sargasso Sea biomass (Table 3). Given this ratio and the same linear [i.e., $(3.5 + 1) \div 2 = 2.25$] and areal assumptions made earlier, rings may augment the zooplankton standing crop of the geographic northern Sargasso Sea by 8 to 16% (i.e., $6 \times 2.25 = 14, 14 + 94 = 108$ and $13 \times 2.25 = 29, 29 + 87 = 116$). Our ratio of slope water to Sargasso Sea biomass may be compared with that of Grice and Hart (1962), who reported the slope water standing crop as three to four times that of the Sargasso Sea. They also excluded extremely salp-rich samples in making this comparison. Our assumption of 2.25 as an annual mean ring/Sargasso biomass ratio (i.e., linear decay) may be an overestimate considering the average biomass ratio obtained on all cruises to date

and the average ring age sampled (Table 3). On the other hand some rings do last longer than a year and the lowest ring:Sargasso Sea ratios that we have observed are approximately 1.3 (i.e., >1.0).

We have noted a highly significant decline in 0-800 m biomass from August to November in slope water, ring, and Sargasso Sea both in data presented here and in data more recently collected.[5] This observation is consistent with those of Grice and Hart (1962) with respect to the slope water. They noted, however, no such decline in the Sargasso Sea. Neither is there a summer-to-fall decline in the Sargasso Sea data of Deevey (1971). The Sargasso Sea and slope water data of Fish (1954) exhibit irregular fluctuations in biomass throughout the summer and fall. Moore (1949) presented some Sargasso Sea data indicating a progressive decline of biomass from a spring maximum to a fall minimum. Their data substantiate that interseasonal fluctuations in the Sargasso Sea are less marked than in the slope water.

Vertical Structure

We have pointed out that, compared with either the Sargasso Sea or slope water, an unusually small percentage of 0-800 m biomass is present in the upper 200 m of a ring. We found a relatively large fraction of the 0-800 m zooplankton biomass above 200 m in the northern Sargasso Sea. The netting employed by Leavitt (1935, 1938) was relatively coarse (1.0 mm) so it is difficult to compare our results with his. Nonetheless, at his two Sargasso Sea stations (2462, 2463) the percentages of

0-800 m biomass present in the upper 200 m were 42 and 49% which corresponds closely to our values (Table 3). Both of our results are virtually identical with those obtained by Menzel and Ryther (1961). From their table 1 we can calculate the percentages of 0-500 m biomass and 0-1,000 m biomass present above 200 m. Averaging the results, we find 44% of the 750-m biomass was present during the day above 200 m. Iashnov (1961) presented data for the Sargasso Sea in which 90% of the 0-1,000 m plankton was present above 200 m, but he used a relatively fine mesh net (0.180 mm). Unfortunately, Deevey and Brooks (1971) characterized 500-m depth intervals with horizontal tows at the midpoint of each interval to 2,000 m, while Grice and Hart (1962) sampled only the upper 100-200 m.

Several authors suggest that a vertical biomass structure similar to our slope water and Sargasso Sea observations is to be expected in temperate or subtropical oceanic environments relatively free of advective inputs. Vinogradov (1968: figure 47 and stations 3206 and 3829 in table 18) gave examples of oceanic regions with such a distribution. Zenkevich and Birstein (1956) agreed that zooplankton biomass in the North Pacific rather steadily decreases from the surface downwards, although the most marked reduction they discuss might be below our lowest standard sampling depth. The one very deep tow series we obtained in a ring, however, gave no indication of such a reduction (Figure 2, MOC 31).

Zooplankton biomass profiles obtained by Murano et al. (1976) in the northwest Pacific above the Sagami Trough exhibit the expected decrease with depth. Reanalyzed in our manner, the data of Marlowe and Miller (1975) for Station P in the North Pacific support the above generalization; the percentage of their 0-500 m biomass found at night in the upper 200 m was 57%. If one extrapolates their 500-m values as approximately applicable to the 500-800 m interval—a conservative approach for this argument—the resulting percentage becomes 49% (N). This is not unlike our average slope water percentage of 51% (N) and quite distinct from the average ring percentage of 33% (N) (Table 4). Station P is very different from Ring-D in respect to its vertical biomass distribution.

In slope water, the intermediate biomass peak in the upper 200 m approximately coincides with the depth of a nitrite maximum of the type discussed by Vaccaro and Ryther (1960). Our results and those of Marlowe and Miller (1975) appear to differ: they felt that the shallow nitrite peak of Station P was avoided by zooplankton. Since the levels of nitrite we have observed at the maximum are only slightly lower than those reported by Marlowe and Miller (0.2-0.5 μg A-N-NO$_2$/l versus 0.64 μg A-N-NO$_2$/l), our findings cast doubt on their speculation that nitrite toxicity might have been involved in the maintenance of the biomass minima they observed.

Explanations for Ring Biomass Structure

Given the relatively high zooplankton biomass of the slope water, it is clear why cold core rings have a higher average zooplankton biomass than the Sargasso Sea. Further, their higher average primary productivity appears responsible for this differential persisting 10-12 mo after ring formation. Our data suggest the decline in ring biomass takes place rather slowly; the oldest rings sampled (10-12 mo) had ring/Sargasso biomass ratios only 20% smaller than the same ratios in the newest rings sampled (3.0 and 3.5 mo, Table 3). Although physically and chemically intermediate between slope water and Sargasso Sea, rings appear to be unique in their vertical distribution of biomass.

We offer two logically distinct explanations for the small fraction of the 0-800 m biomass found within the upper 200 m of a ring. They are not mutually exclusive and the relative importance of these explanations is species dependent. The simpler argument stresses the importance of a physical factor—temperature. If a slope water animal were physiologically restricted to a particular temperature range, its habitat would descend as the ring decayed and isotherms sank. To the extent that the zooplankton population in the slope water exhibited this behavior, ring biomass distributions would deepen. This could apply only to a species which in its home range—the slope water—remains beneath the seasonal thermocline (i.e., moderately deep-living and exhibiting limited diel migration). Such a species would most likely have to be either carnivorous or omnivorous. Wiebe and Boyd (1978) have documented such a phenomenon for the slope water euphausid species, *Nematoscelis megalops*.

A more complex explanation stresses the importance of a biological factor—food resources. The kinds of changes that accompany ring decay must have a substantial effect upon zooplankton-phytoplankton interactions. Using unpublished

data obtained in August 1975 from 5 nine bottle hydrocasts, the number of phytoplankton cells per liter averaged 10,000 in the slope water, 2,500 in the ring, and 2,000 in the Sargasso Sea. Cells smaller than 4-5 μm were not enumerated and were, therefore, excluded from these computations. Values were integrated from 0 to 200 m—a conservative procedure tending to reduce slope water versus ring or Sargasso Sea differences. The species composition of the ring, while distinct, was more like that of the Sargasso Sea than that of the slope water. Again, considering the 0-200 m depth interval, the number of different phytoplankton species an animal would have encountered in a liter of water would, on the average, have been 6.0 (slope water), 9.6 (ring), and 10.4 (Sargasso Sea). Converting the mean cell volume of each species to carbon (Strathmann 1967) and multiplying by the number of individuals present, yielded values of average phytoplankton carbon of 1,400, 200, and 140 ng C/l. Thus, to acquire the same ration of food, a herbivore would have had to filter more than five times more water in the ring than in the slope water, and even more in the Sargasso Sea. In addition, the evenness of species' carbon equivalence was 0.46, 0.75, and 0.76. That is, the total carbon per liter was more evenly distributed among different species in the ring and the Sargasso Sea than in the slope water. (Evenness equals H/H_{max} (Pielou 1966) where H is the Shannon-Weaver diversity index computed upon species carbon equivalence rather than abundance and $H_{max} = \log_e S$ where S = number of species.) This last result implies that a herbivore capable of selecting by carbon content (i.e., particle size) would have found it less advantageous to concentrate on a particular species in the Sargasso Sea and the ring than in the slope water.

These properties of the phytoplankton population, i.e., species composition, carbon concentration, cell concentration, and cell carbon distribution, have profound effects on a filter-feeding herbivore's harvesting ability. We believe that early in ring evolution herbivorous slope water species are deleteriously affected and, therefore, may be replaced by Sargasso Sea forms more quickly than deeper living carnivorous or omnivorous slope water species. If we are correct, ring biomass distribution may deepen in part because a ring's 0-200 m biomass declines more rapidly than does its 200-800 m biomass.

Identification of some of the taxa in August 1975 samples, although limited, support the argument

that in Ring-D epizooplanktonic herbivores were replaced before epizooplanktonic carnivores or omnivores. The species list of Ring-D thecosomatous pteropods, a largely herbivorous group, was quite similar to that of the surrounding Sargasso Sea.[6] Grice and Hart (1962) found that chaetognaths, a purely carnivorous group, were considerably more abundant in the Sargasso Sea than they are in slope water. In 6 nine-net fine-mesh tow series (12.5 cm diameter, Clarke-Bumpus nets with 67 μm mesh) taken in August, chaetognaths were five to ten times more abundant in the surrounding Sargasso Sea than they were in Ring-D. Other epizooplanktonic carnivores, e.g., *Stylocheiron suhmii* and *S. abbreviatum*, which are routinely found in the Sargasso Sea were not found in Ring-D August MOCNESS tows.

Organic Flux to Deep Sea

Rings may contribute a disproportionate fraction of the utilizable organic material available to the northern Sargasso deep sea. We feel this is likely both because of their generally higher productivity and because of their unique zooplankton biomass distribution and the factors that have resulted in that distribution. Ring zooplankton biomass below 200 m, in that it exceeds Sargasso Sea biomass and ultimately declines to a similar level, contributes to this augmentation. Differential seasonal mixing processes could also increase downward particulate flux. For example, in November 1975 we observed that winter mixing had proceeded further in Ring-D than in the surrounding Sargasso Sea water column. Herbivorous ring zooplankton (i.e., Sargasso forms) may have been unable to fully capitalize upon the sudden opportunity afforded by the increased primary production that accompanied the mixing (Table 7). If so, a larger fraction of this enhanced phytoplankton production would sink into the aphotic depths. Physical evidence obtained on two cruises undertaken to study rings during the summer has suggested to us that the seasonal thermocline may often be less stable in rings than in the Sargasso Sea.

Finally, there is a possibility of enhanced contribution of organic matter into the deep sea due to a lower overall trophic efficiency within the upper 200 m of rings (and slope water). If we divide

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[6]John Wormuth, unpubl. data; cited with permission.

average 0-200 m zooplankton biomass (milligrams of carbon per square meter calculated using equation 4, table 2 in Wiebe et al. 1975) by 0-200 m phytoplankton carbon (milligrams of carbon per square meter from Table 5), excluding salp-rich MOC 18 and 19, we obtain the following ratios:

	Sargasso Sea	Ring	Slope water
Aug. 1975	253	138	84
Nov. 1975	332	131	28

Ratios in the ring are low, as are those in the slope water. Lower ratios suggest to us lower overall trophic efficiency within the upper 200 m. Although biased in that many cells are quite small, particularly in the Sargasso Sea, phytoplankton carbon of cells >5 μm is probably a reasonable estimate of the food available at the time of sampling to many of the herbivorous animals caught by our 0.333-mm mesh nets. The direction of difference noted above conforms with ideas expressed by Menzel and Ryther (1961), Heinrich (1962), and others who argued that especially close phytoplankton-zooplankton coupling may characterize oceanic tropical-subtropical waters.

The biomass data presented here illustrate the fact that geographic demarcation of oceanic faunal provinces is not sufficient. Hydrographic as well as faunal mapping is essential in explaining that portion of station-to-staion variability associated with mesoscale hydrographic variability resulting from phenomena like Gulf Stream cold core rings.

ACKNOWLEDGMENTS

LITERATURE CITED

AHLSTROM, E. H., AND J. R. THRAILKILL.
1963. Plankton volume loss with time of preservation. Calif. Coop. Oceanic Fish. Invest. Rep. 9:57-73.

BÉ, A. W. H., J. M. FORNS, AND O. A. ROELS.
1971. Plankton abundance in the North Atlantic Ocean. In J. D. Costlow, Jr. (editor), Fertility of the sea, Vol. 1, p. 17-50. Gordon and Breach Sci. Publ., N.Y.
DEEVEY, G. B.
1971. The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. I. The upper 500 m. Limnol. Oceanogr. 16:219-240.
DEEVEY, G. B., AND A. L. BROOKS.
1971. The annual cycle in quantity and composition of the zooplankton of the Sargasso Sea off Bermuda. II. The surface to 2000 m. Limnol. Oceanogr. 16:927-943.
FISH, C. J.
1954. Preliminary observations on the biology of boreo-arctic and subtropical oceanic zooplankton populations. In Symposium on marine and fresh-water plankton in the Indo-Pacific, Bangkok, p. 3-9. Diocesan Press, Madras.
FUGLISTER, F. C.
1972. Cyclonic rings formed by the Gulf Stream 1965-66. In A. L. Gordon (editor), Studies in physical oceanography. A tribute to George Wüst on his 80th birthday, Vol. 1, p. 137-168. Gordon and Breach, N.Y.
GRICE, G. D., AND A. D. HART.
1962. The abundance, seasonal occurrence, and distribution of the epizooplankton between New York and Bermuda. Ecol. Monogr. 32:287-309.
HEINRICH, A. K.
1962. The life histories of plankton animals and seasonal cycles of plankton communities in the oceans. J. Cons. 27:15-24.
IASHNOV, V. A.
1961. Vertikal'noe respredelenie massy zooplanktona tropicheskoi oblasti Atlanticheskogo Okeana (Vertical distribution of the mass of zooplankton throughout the tropical zone of the Atlantic). Dokl. Akad. Nauk. SSSR 136:705-708.
JAHN, A. E.
1976. On the midwater fish faunas of Gulf Stream rings, with respect to habitat differences between Slope water and Northern Sargasso Sea. Ph.D. Thesis, Woods Hole Oceanogr. Inst., Woods Hole, 172 p.
LAI, D. Y., AND P. L. RICHARDSON.
1977. Distribution and movement of Gulf Stream rings. J. Phys. Oceanogr. 7:670-683.
LEAVITT, B. B.
1935. A quantitative study of the vertical distribution of the larger zoöplankton in deep water. Biol. Bull. (Woods Hole) 68:115-130.
1938. The quantitative vertical distribution of macrozoö-plankton in the Atlantic Ocean basin. Biol. Bull. (Woods Hole) 74:376-394.
MARLOWE, C. J., AND C. B. MILLER.
1975. Patterns of vertical distribution and migration of zooplankton at Ocean Station "P". Limnol. Oceanogr. 20:824-844.
MCGOWAN, J. A., AND D. M. BROWN.
1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23:1-56.
MENZEL, D. W., AND J. H. RYTHER.
1961. Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production. J. Cons. 26:250-258.
MOORE, H. B.
1949. The zooplankton of the upper waters of the Bermuda area of the North Atlantic. Bull. Bingham Oceanogr. Collect., Yale Univ. 12(2), 97 p.

MURANO M., R. MARUMO, T. NEMOTO, AND Y. AIZAWA.
    1976. Vertical distribution of biomass of plankton and micronekton in the Kuroshio water off Central Japan. Bull. Plankton. Soc. Jap. 23:1-12.
NEMENYI, P. B.
    1963. Distribution-free multiple comparisons. Ph.D. Thesis, Princeton Univ., Princeton, 127 p.
PARKER, C. E.
    1971. Gulf Stream rings in the Sargasso Sea. Deep-Sea Res. 18:981-993.
PIELOU, E. C.
    1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13:131-144.
RICHARDSON, P.
    1976. Gulf Stream rings. Oceanus 19(3):65-68.
RICHARDSON, P. L., R. E. CHENEY, AND L. A. MANTINI.
    1977. Tracking a Gulf Stream ring with a free drifting surface buoy. J. Phys. Oceanogr. 7:580-590.
RYTHER, J. H.
    1963. Geographic variations in productivity. In M. N. Hill (editor), The sea. Ideas and observations on progress in the study of the seas, Vol. 2, p. 347-380. Interscience Publ., Lond.
SAUNDERS, P. M.
    1971. Anticyclonic eddies formed from shoreward meanders of the Gulf Stream. Deep-Sea Res. 18:1207-1219.
STRATHMANN, R. R.
    1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr. 12:411-418.

VACCARO, R. F., AND J. H. RYTHER.
    1960. Marine phytoplankton and the distribution of nitrite in the sea. J. Cons. 25:260-271.
VINOGRADOV, M. E.
    1968. Vertical distribution of the oceanic zooplankton. [In Russ.] Isdatel'stvo Nauka, Moskva, 319 p. (Isr. Prog. Sci. Transl., 1970, 339 p.)
WIEBE, P. H., AND S. H. BOYD.
    1978. Limits of *Nematoscelis megalops* in the Northwestern Atlantic in relation to Gulf Stream cold core rings. Part I. Horizontal and vertical distributions. J. Mar. Res. 36:119-142.
WIEBE, P. H., S. BOYD, AND J. L. COX.
    1975. Relationships between zooplankton displacement volume, wet weight, dry weight, and carbon. Fish. Bull., U.S. 73:777-786.
WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
    1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313-326.
WIEBE, P. H., E. M. HULBURT, E. J. CARPENTER, A. E. JAHN, G. P. KNAPP, III, S. H. BOYD, P. B. ORTNER, AND J. L. COX.
    1976. Gulf Stream cold core rings: large-scale interaction sites for open ocean plankton communities. Deep-Sea Res. 23:695-710.
ZENKEVICH, L. A., AND J. A. BIRSTEIN.
    1956. Studies of the deep water fauna and related problems. Deep-Sea Res. 4:54-64.