

# Macrozooplankton Biomass in Gulf Stream Warm-Core Rings: Spatial Distribution and Temporal Changes

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The vertical and horizontal distribution of macrozooplankton biomass was measured at four time points in warm-core ring 82B. Samples were also collected in two other warm-core rings, the Slope Water, nine cold-core rings, and the Sargasso Sea. Biomass in newly formed warm-core rings was 1.5–2 times lower than that of the surrounding Slope Water but increased within 3–4 months to levels found in the adjacent waters, a rate 4 times faster than the biomass in cold-core rings reaches levels found in the Sargasso Sea. A mixing model is used to show that for the period March through June the increase in biomass at the center of ring 82B was largely the result of in situ production. Half of the macrozooplankton biomass in the upper 1000 m of warm- and cold-core rings, the Slope Water, and the Sargasso Sea was usually below 200 m at night and 300 m by day. Biomass shoaled during periods of high concentrations of near-surface plant biomass associated with spring restratification of the upper ocean. Diel vertical shifts in median biomass depth in the upper 1000 m showed significant regional differences; the order of the values averaged for all cruises was ring 82B = 76 m < Slope Water = 115 m < cold-core rings = 149 m < Sargasso = 212 m.

## INTRODUCTION

In the northwestern Atlantic there is little detailed information concerning vertical and horizontal distributions of zooplankton biomass in relation to water mass structure or seasonal changes. Earlier studies by *Clarke* [1940] and *Grice and Hart* [1962] provide some seasonal information for the upper 100–300 m of the northern Sargasso Sea and Slope Water; *Be et al.* [1971] have provided the most recent comprehensive summary of the zooplankton biomass in the upper 300 m for the entire North Atlantic Ocean. Interpretation of these studies is difficult, however, since some samples may have been taken in both warm- and cold-core Gulf Stream rings, which were largely unrecognized until recently [*Sanders*, 1971; *Fuglister*, 1972, 1977; *Parker*, 1971], and because diel and ontogenetic migrations to depths greater than 300 m were not taken into consideration. On the whole the broad outline of geographic variation in biomass structure of the North Atlantic Ocean presented by *Be et al.* is probably a reasonable reflection of the long-term average for the near-surface zooplankton. These geographic averages, however, cannot be expected to hold for specific seasons or hydrographic regimes (i.e., Slope Water, Gulf Stream, and Sargasso Sea) because of mesoscale variability induced by Gulf Stream rings [*Ortner et al.*, 1978; *Haurv et al.*, 1978; *Wiebe*, 1981] and because the true seasonal cycle and vertical distribution of zooplankton biomass in this region have yet to be adequately described.

In general the Sargasso Sea and Gulf Stream are characteristically more oligotrophic than the Slope Water; consequently, biological gradients occur across the boundaries of newly formed Gulf Stream rings. The standing crop of macrozooplankton (those animals caught by 0.335-mm mesh nets) in the upper 800–1000 m of the Sargasso Sea is, on the average, 2 to 3 times lower than the Slope Water [*Wiebe et al.*, 1976a; *Ortner et al.*, 1978]. Furthermore, data from cold-core rings shows that

the decrease in total integrated zooplankton biomass and the change in vertical biomass distribution and migration patterns from Slope Water to Sargasso Sea conditions occur over an extended period of time (6–12 months; *Wiebe et al.*, [1976a]). It appears that the changes observed in cold-core rings result largely from in situ biological transformations rather than lateral physical exchange [*Wiebe and Flierl*, 1983].

From these observations we would expect that (1) the integrated macrozooplankton biomass in a newly formed warm-core ring should be a factor of 2 to 3 times lower than the Slope Water, (2) the macrozooplankton biomass in warm-core rings should increase in magnitude and shift vertically from Sargasso Sea to Slope Water conditions over a period of 6–12 months, and (3) the changes in warm-core ring biomass should be largely due to in situ processes.

At present, little is known about the distribution of biomass in warm-core rings, its change as a ring ages, or the heterogeneity in Slope Water biomass resulting from the presence of rings. During 1981–1982, as part of a multidisciplinary program to study the physics, chemistry, and biology of Gulf Stream warm-core rings [*Warm-Core Rings Executive Committee*, 1982; *Joyce and Wiebe*, 1983], we mapped the distribution and abundance of macrozooplankton in warm-core rings and the adjacent North Atlantic Slope Water. Complementing this work is that of *Roman et al.* [1985] on the distribution and abundance of epipelagic micro and mesozooplankton in warm-core ring 82B.

In this paper we will present the results of the biomass measurements made on an extensive set of stratified oblique macrozooplankton samples taken on four cruises to ring 82B and single cruises to rings 81D and 82H. Our objectives are (1) to describe the time-series changes that occurred in the upper 1000 m of ring 82B and the Slope Water with respect to (a) the total standing crop of macrozooplankton, (b) the gross vertical structure of biomass, and (c) the pattern of diel shifts in biomass as a result of vertical migration; (2) to compare results from 1 to the patterns observed in the other warm-core rings, the Sargasso Sea, and Gulf Stream cold-core rings; (3) to examine the processes responsible for the observed changes in biomass in rings.

In a companion paper [*Davis and Wiebe*, this issue], time series changes in the vertical distribution of total biomass of macrozooplankton in ring 82B is examined as a function of

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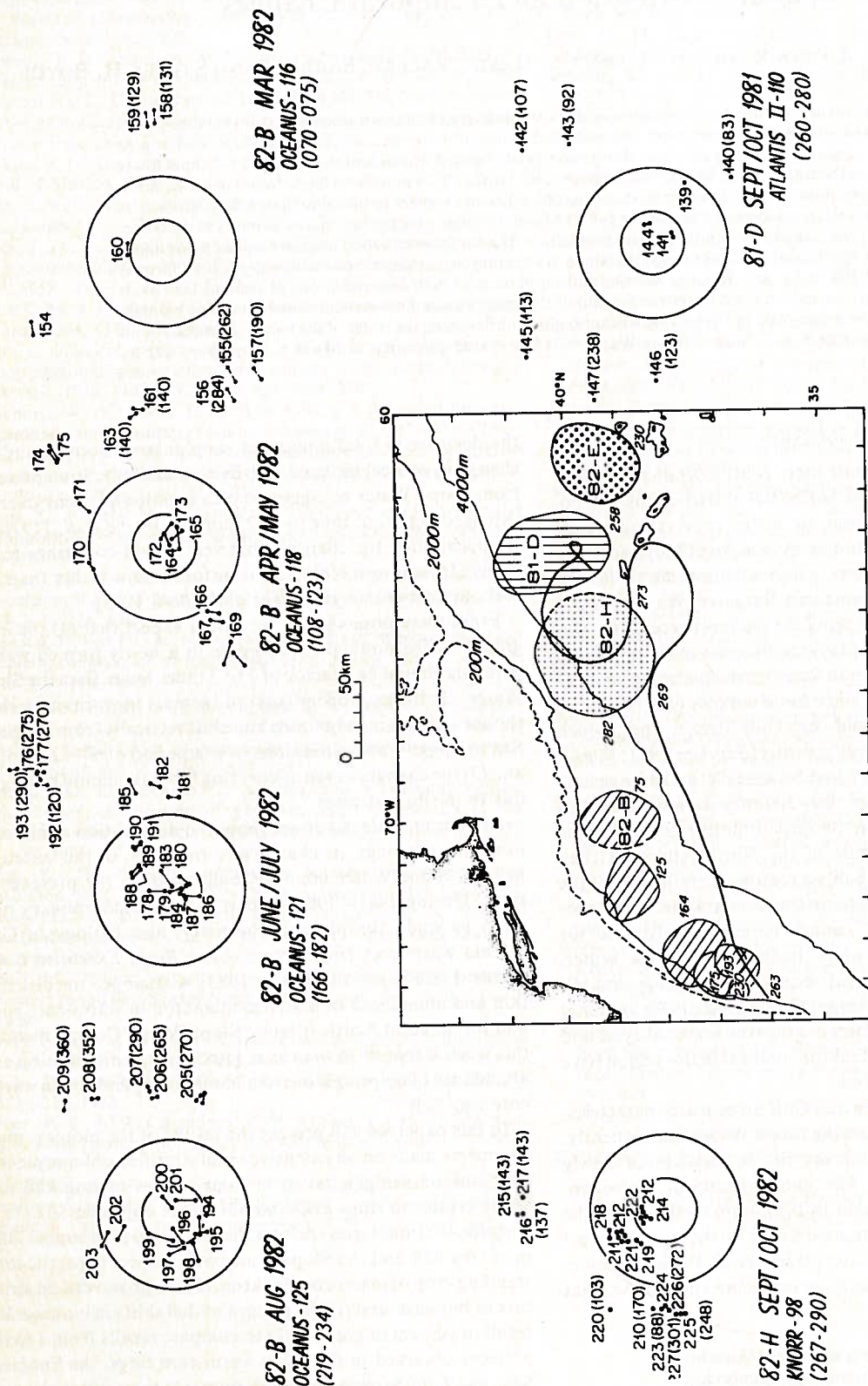


Fig. 1. Position of the beginning and ending of double MOCNESS-I tows taken during the 1981-1982 warm-core rings cruises. Tow positions are plotted relative to the center of the ring; ring center positions, provided by Don Olson of the University of Miami, were based on satellite observations of sea surface temperature, XBT surveys of the ring, and acoustic-Doppler velocity measurements of the surface currents of the ring environments. Tows numbered 204-209 were taken on *Oceanus* cruise 125. Beyond the outer 50 km circle, distance from ring center is given in parentheses for those tows not plotted according to the scale. Duration of the cruise in Julian days is also given in parentheses with each cruise legend. Inset shows positions and corresponding Julian day of observation of four rings sampled during the study; note, the position of 82B in August 1982 is given for six different Julian day periods. The solid line traces the path of a satellite-tracked drogue placed in ring 82B in August 1982 and entrained into the Gulf Stream when 82B coalesced with the Gulf Stream off Cape Hatteras on day 263. This drogue entered 82H on day 273 while it was still a meander of the Gulf Stream. Ring 82H was formed as the drogue reached the northeast sector of the meander.



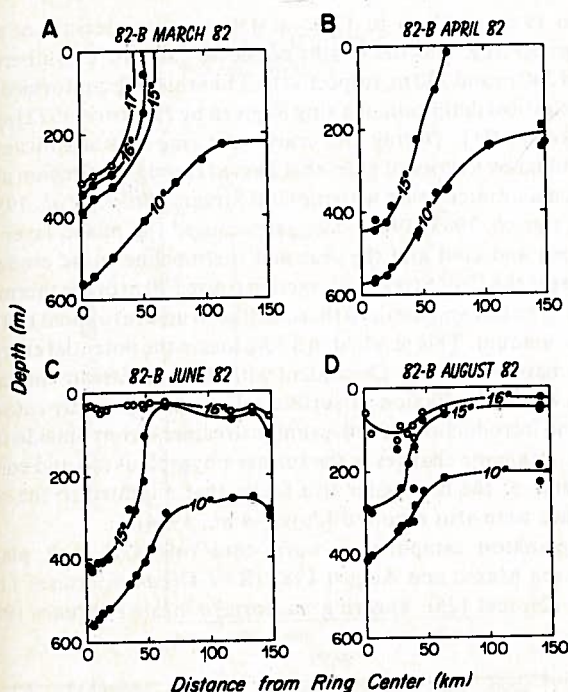


Fig. 2. Temporal pattern in warm-core ring 82B vertical temperature structure. Composite sections of the 10°, 15°, and 16°C isotherms versus distance from ring center, based on temperature profiles from MOCNESS-I tows and supplemented with data from XBT's. The 15° and 16°C isotherms define the ring thermostat.

taxonomic composition and size frequency. Subsequent papers will consider patterns in species abundance and community composition.

#### SAMPLING AREA AND METHODS

Warm-core ring and Slope Water data were collected on six cruises between September 1981 and October 1982 (Figure 1; Barber and Wiebe [1985]). The Sargasso Sea, cold-core rings, and additional Slope Water data sets were collected on a series of cruises between 1972 and 1977 [Ortner et al., 1978; Wiebe and Flierl, 1983]. In some of the analyses below, biomass will be plotted versus depth of the 10°C isotherm, and in others the arrangement of stations will have been determined in part by the 10°C depth. In the northwestern Atlantic Ocean the depth of the 10°C isotherm is a good measure of the hydrographic affinity of the water mass being sampled. The 10°C isotherm in the Slope Water is shallow (<250 m), while in the northern Sargasso Sea it is quite deep (>850 m). In the Gulf Stream this isotherm (and others) form a sharp gradient between the Slope Water and the northern Sargasso Sea. Thus in a warm-core ring with core water from the Gulf Stream and Sargasso Sea, the deeper the 10°C isotherm, the closer the observation to the ring's hydrographic center. It is also important to note that as a warm-core ring ages the 10°C depth shoals, although the change is not necessarily linearly related to ring age (Figure 2; also see Joyce and Wiebe [1983, Figure 9]).

#### Description of the Rings

Since the principal focus of this paper is on warm-core rings, we provide the following summary of the physical structure of these rings at the times of zooplankton sampling:

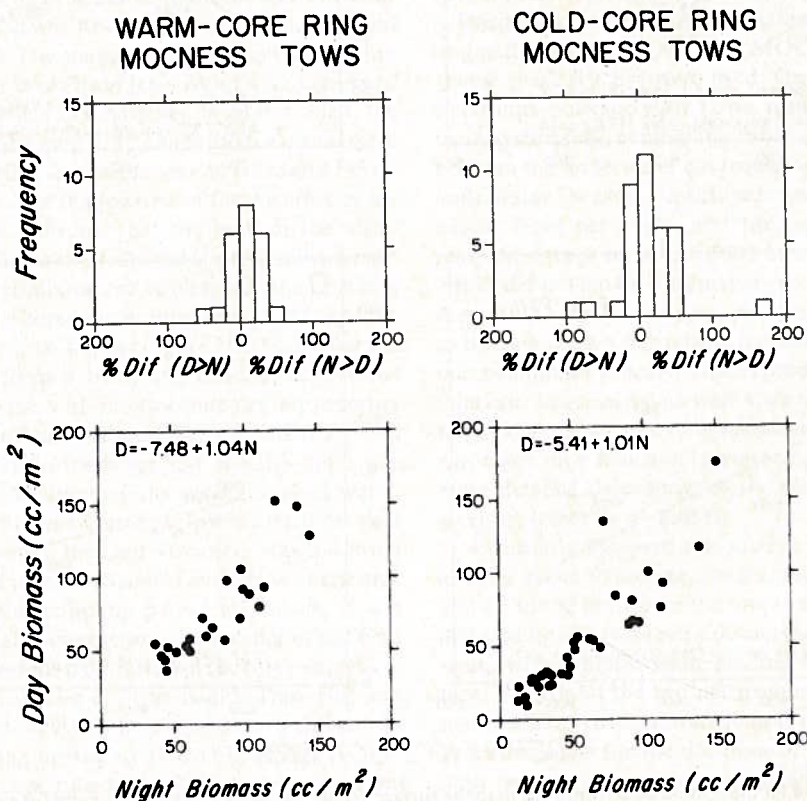


Fig. 3. Comparison of the integrated biomass (0–1000 m) for the pairs of day and night MOCNESS-I tows taken during the warm-core rings cruises of 1981–1982 and the cold-core rings cruises of 1975–1977. Individual observations are plotted below; their frequency distribution as a percent deviation away from equal day/night biomass is plotted above. Functional regression equations are given with each plot.



TABLE 1. Average Percent Difference Between Day and Night Biomass (Integrated to 1000 m) of Zooplankton in Each Hydrographic Region Sampled During Warm- and Cold-Core Rings Cruises

Region	Warm-Core Rings Cruises		Cold-Core Rings Cruises	
	Percentage Night/Day Difference	N	Percentage Night/Day Difference	N
Slope Water	8.8	8	23.0	9
WCR 82B-CCR	7.6	12	14.6	16
Sargasso Sea	6.8	4	8.7	11

The first cruise in September/October 1981 (R/V *Atlantis II*, cruise 110) was to 81D, a ring approximately 3 months of age [Joyce et al., 1983, 1984; Joyce, 1984]. At the time of sampling it was located at 40°N, 64°W and had an elliptical shape with major and minor dimensions (as defined by the area enclosed by the 10°C isotherm at 300 m) of 190 and 144 km, respectively. Initially, there was a large thermostad of 18°C water (measured

from 19.0° at 99 m to 17.0° at 450 m) characteristic of the Sargasso Sea, and the depths of the 15° and 10°C isotherms were 540 m and 730 m, respectively. Thus this ring conformed to the classical definition of a ring as given by Fuglister [1972] and Parker [1971]. During the cruise, the ring was significantly modified by a series of gales that passed through the region and by a major interaction with the Gulf Stream [Brown et al., 1983; Joyce et al., 1983, 1984]. The gales caused the mixed layer to deepen and cool and the seasonal thermocline to be eroded, whereas the Gulf Stream interaction caused 90 m of the thermostad to be lost and the deep thermocline structure to shoal by the same amount. This resulted in a 30% loss in the potential energy and mass of the ring. Coincident with the Gulf Stream interaction was the reduction of surface salinities, apparently caused by the introduction of low-salinity streamers from outside the ring. Dramatic changes in the surface phytoplankton and components of the mid-water fish fauna that migrated to the sea surface were also reported [Joyce et al., 1984].

Zooplankton sampling in warm-core ring 82B took place between March and August 1982 (R/V *Oceanus*, cruises 116, 118, 121, and 125). This ring was formed in late February 1982

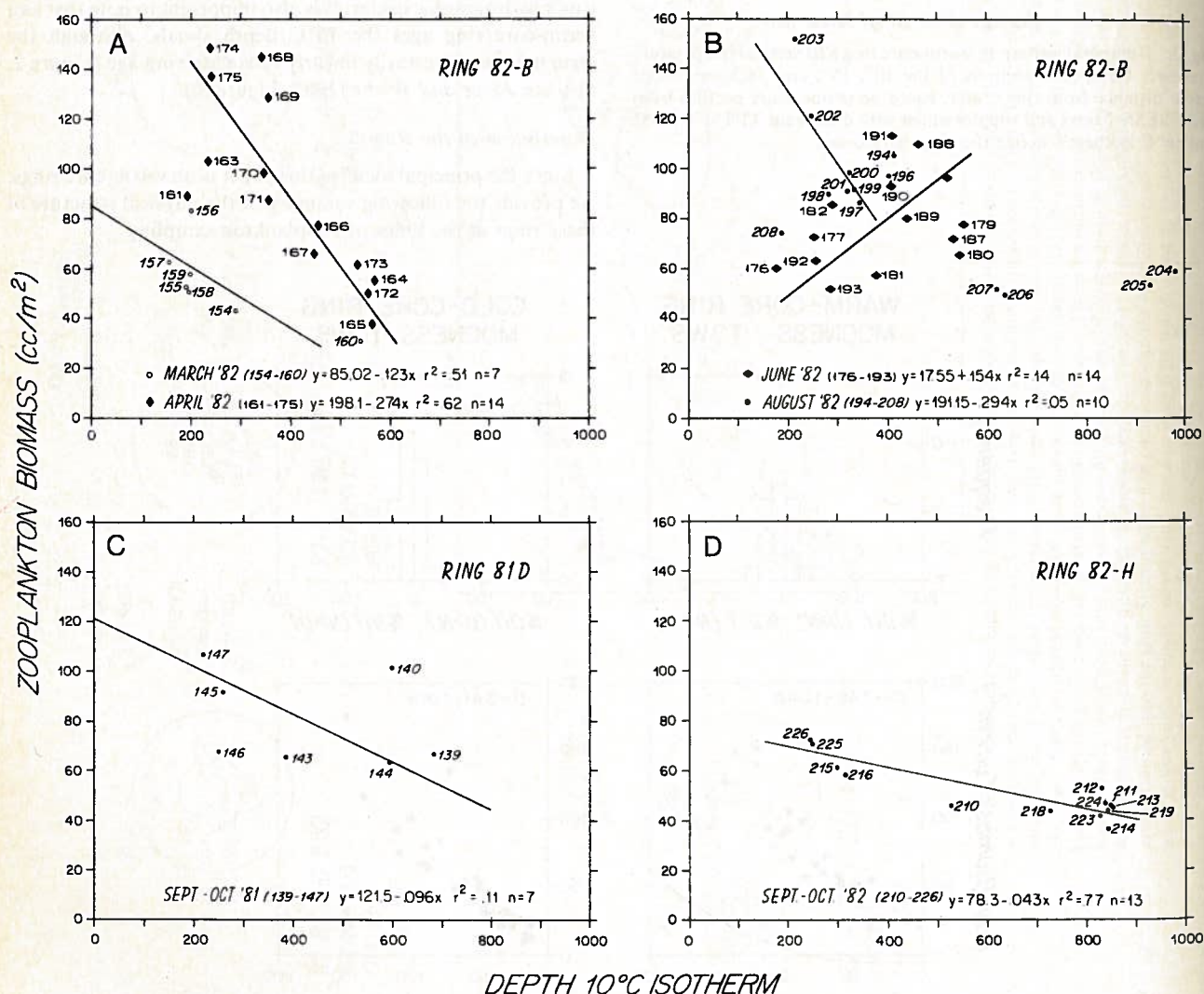


Fig. 4. Zooplankton biomass integrated from 1000 m to the surface versus the depth of the 10° isotherm for each of the four cruises to ring 82B. Regression lines in a and d are significant ( $p < 0.05$ ); those in b and c are not. Note that stations 206 and 207 were taken in the Gulf Stream, and 204 and 205 were taken in the Sargasso Sea; biomass values at these stations were not used in the 82B August regression of biomass versus depth of 10°C.

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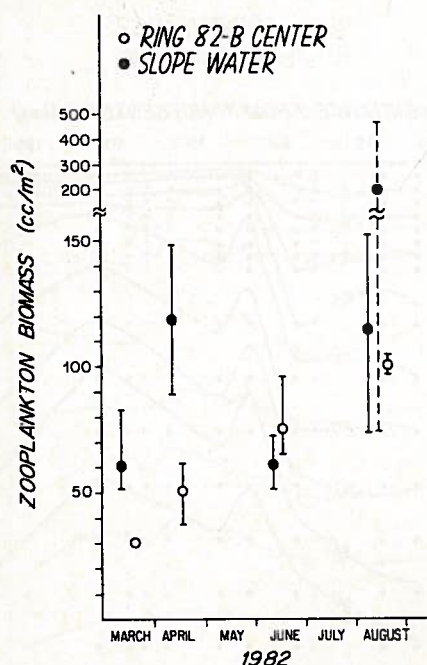


Fig. 5. Temporal changes in ring 82B and the Slope Water zooplankton biomass integrated to 1000 m. Mean and range denoted by circle and bar, respectively. The dashed line for the Slope Water in August includes the large catch of scyphomedusa discussed in the text. Note that the values in this plot have had a correction in volume filtered by the nets applied that was not applied to the data in Figure 12 of Joyce and Wiebe [1983], and thus these values are 10% to 15% larger.

by the pinch-off of a northward extending meander of the Gulf Stream centered along longitude  $68^{\circ}\text{W}$  between latitudes  $37^{\circ}$  and  $39^{\circ}\text{N}$ . Initially, 82B was 160 km in diameter, and when last sampled in August 1982, it was 40 km in diameter (see Joyce and Wiebe, 1983, Figure 11). The change in 82B's physical structure is described by Schmitt and Olson [this issue] and Joyce and Kennelly [this issue]. When first sampled in March 1982, the ring core was  $17.7^{\circ}\text{C}$  and about  $36.5\text{‰}$  salinity from the surface to 330 m. The  $15^{\circ}$  and  $10^{\circ}\text{C}$  isotherms were at 343 m and 545 m, respectively (Figure 2a). The shallowness of these isotherms for a ring of age 3 weeks indicates that the bulk of the water entrapped at ring formation was from the Gulf Stream and not the Sargasso Sea. Winter mixing and cooling modified the ring so that in April 1982 the core temperature was  $15.7^{\circ}\text{C}$  and the salinity was about  $36.4\text{‰}$  to 440 m (Figure 2b). Thereafter the seasonal thermocline, formed by spring heating, capped the ring, leaving a thermostad with intermediate depth properties matching the April conditions (Figure 2c; see also Joyce and Wiebe, [1983, Figure 9]. In the latter half of 82B's life it was substantially modified by interactions with the shelf water, Slope Water, and Gulf Stream. During July, the ring underwent at least one interaction with the Gulf Stream in which it lost a considerable portion of its mass [Schmitt and Olson, this issue]. At the beginning of the sampling period in August, it was undergoing another major interaction. A meander of the Gulf Stream was sweeping over part of the top of the ring to depths of at least 75–100 m [Evans et al., this issue]. Thus 82B was significantly smaller in both its horizontal and vertical extent by the time of last sampling in August 1982 (Figure 2d).

Sampling in warm-core ring 82H (R/V Knorr, cruise 98) commenced on September 27, 1982, while it was still a very extended meander of the Gulf Stream oriented northwest-southeast and centered about  $39^{\circ}30'\text{N}$ ;  $64^{\circ}\text{W}$ . During the

period October 1–4, the meander closed off and formed 82H with a diameter of approximately 300 km. The ring then moved rapidly to the west, and when last sampled on October 12, it was centered about  $39^{\circ}05'\text{N}$ ;  $66^{\circ}\text{W}$ . At the time of formation, core water characteristics were very similar to the Sargasso Sea. Eighteen-degree water (measured from  $19.0^{\circ}$  at 160 m to  $17.0^{\circ}\text{C}$  at 545 m) had a thickness of about 390 m, and the  $15^{\circ}$  and  $10^{\circ}\text{C}$  isotherms were at 650 and 845 m, respectively. In addition, the seasonal pycnocline started between 55 and 60 m, and the "mixed layer" was nearly isothermal ( $26.8^{\circ}\text{C}$ ) and isohaline ( $36.08\text{‰}$ ). On October 9 and 10 a gale with sustained winds over 40 knots and gusts to 60 knots significantly altered the upper mixed layer such that on October 11, when work was resumed, the isothermal layer had deepened 30 m to approximately 90 m, the temperature of the surface layer was reduced to  $24.1^{\circ}\text{C}$ , and the salinity increased to  $36.29\text{‰}$ . Most of these changes can probably be accounted for by vertical mixing.

#### Methods of Sampling and Analysis

Sampling for macrozooplankton on the warm-core ring cruises was done with a double MOCNESS-1 (Multiple Opening/Closing Net and Environmental Sensing System) (with 20 1-m<sup>2</sup> nets), except in March 1982 (*Oceanus* 116), when we used the nine-net MOCNESS. The double MOCNESS-1 is similar to that described by Wiebe et al. [1976b], except that the frame width has been doubled to permit two independent sets of nets to be mounted side by side. Each set contains 10 nets and has its own net bar guides, net bar release indicator, and toggle release/motor drive. In addition, each set of nets had traps to keep the net bars from riding back up the guides after closure. The nets are constructed of 335- $\mu\text{m}$  Nitex nylon gauze in the pattern described by Wiebe et al. [1976b].

During the first cruise (R/V *Atlantis* II 110), the electronics originally developed for the MOCNESS and described in Wiebe et al. [1976b] were used. On the remaining cruises an electronics package with 12-bit resolution was used. Both of these systems use conducting cable as the communication link between the underwater electronics unit and the deck unit. The underwater sensors measured temperature, conductivity, depth, flow, net angle, and the passage of a net bar once released, except in March 1982 on *Oceanus* 116, when MOCNESS did not have a conductivity probe. The deck unit displays the sensor outputs and provides the means to send commands to operate the net bar release mechanism. A Commodore 8032 microcomputer processed data coming from the deck unit at 4-s intervals. Processed data were then printed out and stored on a floppy disk, and a plot of temperature and salinity versus depth was made on a Houston Instruments DMP-7 digital plotter. A more detailed description of the various sized MOCNESS' is given in Wiebe et al. [1985].

We usually deployed this system with the ship underway at about 2 knots by fishing one net from each side on the oblique section to the bottom of the tow and then sequentially opening and closing nets from one side and then the other so that oblique strata were sampled while hauling the system back to the surface. The top of the last net from each set of nets was permanently affixed to the net bar guides. Thus both sides of the frame had a net open for the duration of the tow. On each 1.5–3.5 hour haul we generally obtained eight samples integrating 100-m intervals from 1000 to 200 m and eight samples integrating 25-m intervals from 200 to 0 m. The samples were preserved in 10% formalin buffered to a  $\text{pH} > 8.0$  with sodium tetraborate.



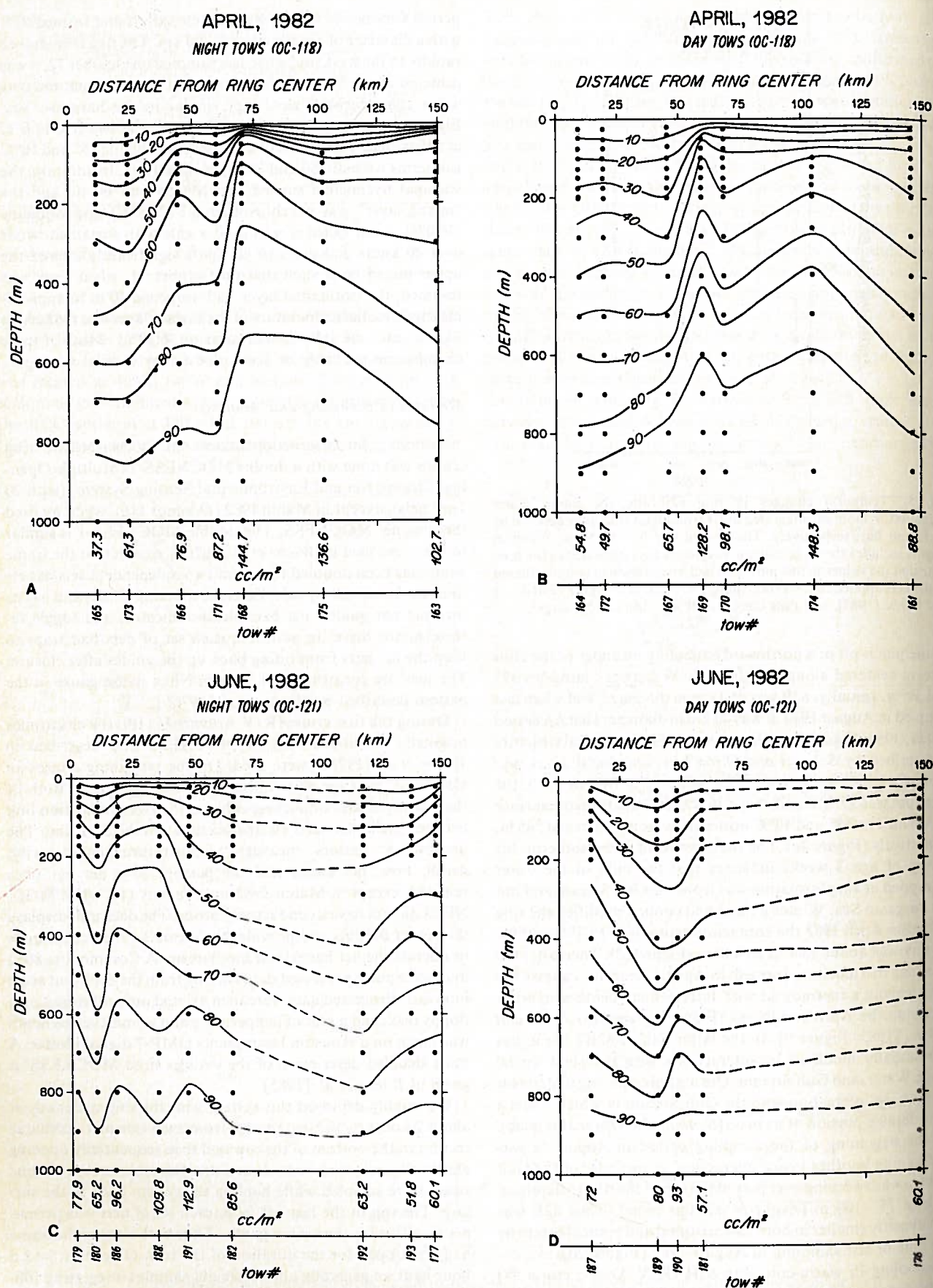


Fig. 6. (a-f) Temporal pattern in warm-core ring 82B vertical zooplankton biomass structure. Composite sections prepared by using cumulative percent of biomass with increasing depth and distance of tow from ring center. Integrated displacement volumes are given at the bottom of each section to the right of the MOCNESS number. Note that in Figure 6e tow 207 was taken in the Gulf Stream and tow 204 was taken in the Sargasso Sea and similarly in Figure 6f, tow 206 was taken in the Gulf Stream and tow 205 was taken in the Sargasso Sea.

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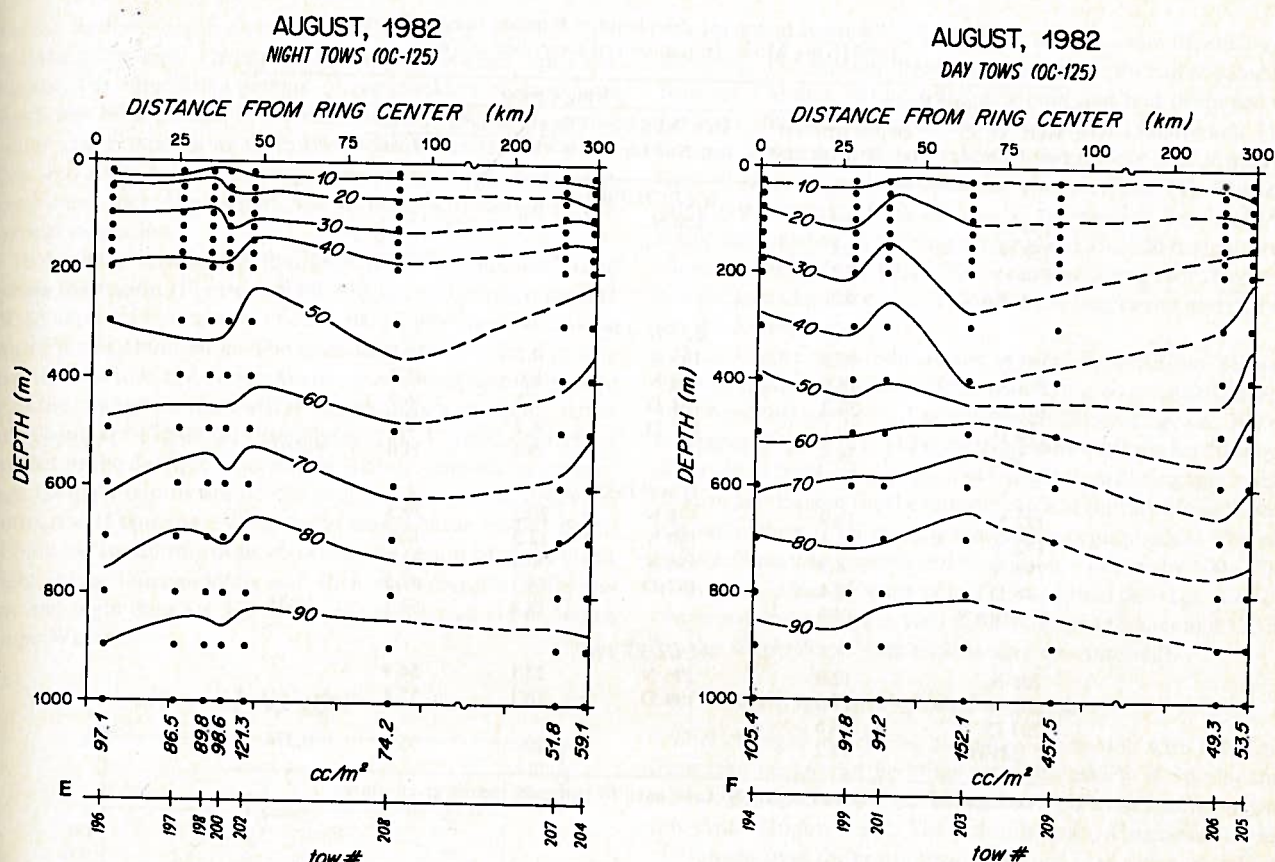


Fig. 6(e, f)

The nondestructive technique of measuring zooplankton displacement volume [Alhstrom and Thraill, 1963; Wiebe et al., 1975] was used to estimate zooplankton biomass. Almost all of the displacement volumes reported were measured 4–6 weeks after sample collection in order to assure that biases that are possibly introduced by shrinkage of samples in the preserving liquid are similar for all cruises. The volume of water filtered by each net was used to standardize the displacement volumes to cubic centimeters per 1000 m³.

The estimates of biomass in each stratum were integrated to give the biomass per square meter in the upper 1000 m [Barber and Wiebe, 1985]. The vertical distribution of biomass will be presented in terms of the cumulative percent of biomass in each stratum, beginning with the stratum closest to the surface. Thus a cumulative percent of 0 is at the surface and 100% is at 1000 m. The term depth of median biomass refers here to the depth at which the cumulative percent equals 50. Individual vertical profiles of biomass and cumulative percent of biomass are given in Barber and Wiebe.

#### Effects of Avoidance

The effects of diel vertical migration on the vertical biomass distribution is examined below by using night/day pairs of tows taken as near as possible to the same station location within a hydrographic regime and having similar depths of the 10°C isotherm. In doing this the assumption is made that differential night/day avoidance is negligible. A plot of all the night/day pairs of tows taken on the warm-core rings cruises (Figure 3) shows that eight had higher day biomass and 15 had higher night biomass. While the trend is not significant ( $p > 0.1$ ; chi-square test), it is an indication that some avoidance may be taking place. The trend is enhanced by the fact that on the June

cruise, *Oceanus* 121, all the night tow pairs had higher biomass than the day pairs. Taxonomically, these tows had a larger proportion of large animals such as euphausiids than tows on other cruises [Davis and Wiebe, this issue], and they were less abundant in the day tows. It appears that net avoidance with the double MOCNESS-1 may only have been a problem on this one cruise. On average, night tow biomass was 7.8% larger than day tow biomass. In contrast, for the cold-core rings cruises (described by Wiebe and Flierl [1983] and Ortnier et al. [1978]), average night tow biomass was significantly ( $p < 0.05$ ) larger than day tow biomass by 14.9%. The zooplankton biomass of 12 day tows was larger than the paired night tows (Figure 3), whereas biomass in 24 night tows was larger than in the corresponding day tows.

The regional averages of integrated biomass presented below are affected by the bias from the differential night/day avoidance of the MOCNESS, but this error is relatively small and does not affect conclusions we have reached about differences between the regions. There is the possibility, however, that the bias is a significant factor influencing the estimates of diel shifts in depth of median biomass. If the differential daytime avoidance of the net were concentrated in the near-surface waters, this bias would give the appearance of diel vertical migration, even if it were not taking place [Wiebe et al., 1982]. If this bias were uniform across the sampling area, then we would expect the largest error where the apparent diel vertical migration was largest. When the night/day difference is averaged according to regions and sampling periods (where  $N$  is the number of night/day pairs), the values in Table 1 reflect the results.

In fact the Sargasso Sea, with the largest average night/day shift in median depth of biomass in the upper 1000 m (as described below), has the smallest average night/day difference



TABLE 2. Values of Integrated Zooplankton Biomass Used to Evaluate the Mixing Model (Equation (1)) Described in Text

Slope Water		Ring Center			f
MOCNESS Tow Number	Depth Interval 0—50 m, cc/m <sup>3</sup>	MOCNESS Tow Number	Depth Interval, cc/m <sup>3</sup> 0—50 m      0—10°C		
MARCH 1982					
154 N	7.0	160 N	3.0	17.5	0.171
158 N	8.1				
159 D	2.1				
MEAN	4.8				
APRIL 1982					
163 N	48.2	165 N	4.2	26.5	0.167
175 N	40.4	173 N	8.0	42.3	
161 D	30.2	164 D	6.2	36.7	
174 D	39.1	172 D	4.7	32.8	
MEAN	39.5		5.8	34.6	
JUNE 1982					
177 N	19.9	179 N	20.2	59.3	0.345
192 N	9.5	180 N	12.5	42.9	
193 N	8.3	186 N	30.8	74.9	
176 D	12.6	187 D	15.7	47.5	
MEAN	12.6		18.4	53.3	
AUGUST 1982					
208 N	12.0	196 N	23.1	54.9	0.374
202 N	17.5	194 D	18.1	55.1	
203 D	23.6				
MEAN	19.2		20.6	55.0	

Averages of day (D) and night (N) tows used to compute means given above.

in both data sets, and the Slope Water region, with a much smaller diel shift, has the largest. We require, then, another explanation of these differences. We suggest that the biases may be more strongly influenced by the differences in sizes of the organisms in different regimes and also the migration of the larger organisms. Since the Slope Water organisms are generally larger [Grice and Hart, 1962] and thereby better avoiders, the night/day differences in biomass would be increased over those in the Sargasso Sea. In addition, avoidance by the larger migrators would decrease the catch rate in the deep water during the day, giving a shallower apparent depth of median biomass. Thus the diel shifts observed in the Slope Water are probably conservative.

#### TIME SERIES OBSERVATIONS IN 82B

Zooplankton biomass progressively increased in ring 82B over the sampling period (March to August), while in the Slope Water it was highest in April and August. Biomass was shallowest in the Slope Water in April and in the ring in June, with diel vertical shifts most pronounced in the high-velocity region.

#### Vertically Integrated Biomass

During the first two periods of sampling warm-core ring 82B, total integrated biomass per square meter was significantly lower in the ring center than in adjacent hydrographic regimes, ( $p < 0.001$  in March and  $p < 0.01$  in April; linear regression analysis of variance, ANOVA). This gave rise to a negative relationship between biomass and the depth of the 10°C isotherm (Figure 4a). Between March and April, biomass increased in both ring 82B and in the Slope Water. In the ring it increased by about 50% and in the Slope Water it increased by about a factor of 2.

By June a major change had occurred (Figure 4b); zooplank-

ton biomass was higher in the ring than in the Slope Water. Because the biomass in the high-velocity region (the region of highest upper ocean currents located 40–60 km from ring center in June [Joyce and Kennelly, this issue]) had a somewhat higher standing crop than adjacent regions, the positive relationship between biomass and depth of the 10°C isotherm was not significant ( $p > 0.05$ , Figure 4b). This variation across the ring differs substantially from both March and April, when the gradient of increasing biomass relative to the 10°C depth was linear.

The August biomass in ring 82B, while higher than in June, was nonsignificantly ( $p > 0.05$ ) lower than in the Slope Water (Figure 4b). Variability in the Slope Water was extreme, however, with the scyphomedusa *Pelagia pelagia* dominating one Slope Water station (MOC-1D-209) and strongly affecting the estimates of the Slope Water mean state. During August, we also sampled the Sargasso Sea and Gulf Stream. Slope Water and ring 82B biomass was substantially higher (factors of 2 to 4) than at either of these locations (Figure 4b).

These results may be summarized in a plot of biomass/m<sup>2</sup> versus time for the four sampling periods (Figure 5). Ring 82B had lower biomass/m<sup>2</sup> than the Slope Water during the first 2–3 months of its existence but had an integrated biomass that exceeded the Slope Water in June. While maximum values in the ring core in August were higher than in June, Slope Water values were even higher (whether or not the station dominated by *P. pelagia* is included).

#### Vertical Distribution of Biomass

Significant changes took place in the vertical distribution of zooplankton biomass as 82B evolved. A single nighttime tow in 82B in March showed over one half of the biomass in the upper 1000 m was deeper than 400 m, whereas in the Slope Water the

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median biomass depth was 175–250 m at night and about 350 m during the day. To illustrate changes between April and August, the cumulative percent of zooplankton biomass with depth has been plotted in section form, beginning at the ring center and extending out into the Slope Water (Figure 6 a-f). Day and night tow data are portrayed separately because in some cases there were significant vertical shifts caused by diel vertical migration.

In April the vertical distribution of nighttime biomass varied across the region (Figure 6a). At ring center the night median (50%) depth of biomass was below 300 m, whereas in the Slope Water it was about 80 m. The transition between the ring core distribution and the Slope Water was abrupt and coincided with the changes in the vertical temperature and salinity structure (compare Figure 6a with Figure 2b). A similar pattern is evident in the daytime data, except that the cumulative percentage biomass depths are on the order of 50–100 m deeper in both areas (Figure 6b). Weighted averages of the median depth of biomass (weighting done by taking the means of the day and night values independently and then averaging them) for the day and night data are 343 m for ring center and 111 m for the Slope Water.

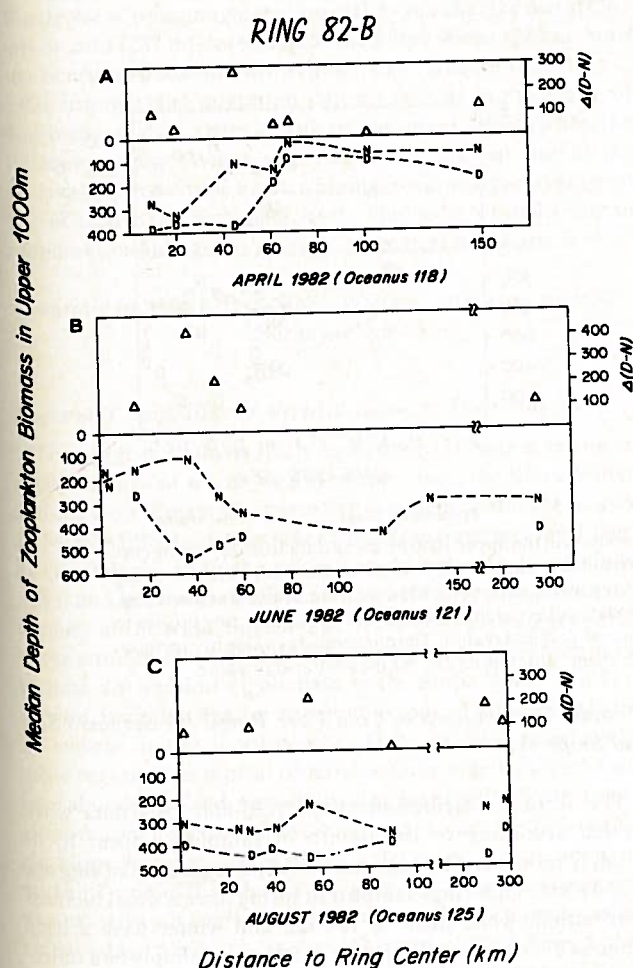


Fig. 7. Plots of the median depth (50th percentile in cumulative percent of biomass with depth) of zooplankton biomass in the upper 1000 m and the difference in daytime and nighttime median depth in paired tows versus distance from ring center. Note that in Figure 7c the day value of the pair of samples at 90 km was strongly affected by a large catch of scyphomedusa at the surface and that the two rightmost pairs of tows were taken in the Gulf Stream (250 km) and Sargasso Sea (300 km).

June data (both night and day) show that a dramatic shift had occurred. The median nighttime biomass depth had shoaled to between 100 and 200 m in the ring core and had deepened to between 300 and 400 m in the Slope Water (Figure 6c). The latter shift was due in part to the downward ontogenetic migration of species such as *Calanus finmarchicus* (T. Cowles, unpublished data, 1985). Similarly, the median depth of the single daytime tow in the ring center was 150–250 m shallower than elsewhere (Figure 6d). The weighted average for the combined day and night data is 225 m for the ring center and 379 m for the Slope Water.

The August data indicate the vertical distributions of biomass at night in the Slope Water and ring were quite similar, and the median depths of biomass were fairly deep, i.e., 300 m or deeper (Figure 6e). These distributions were similar to those observed in the Sargasso Sea and Gulf Stream during this cruise (Figure 6e). Except for the notable catch at the day Slope Water station farthest from the ring where the scyphomedusa *Pelagia pelagia* dominated, daytime distribution is deeper by 100–200 m in both areas (Figure 6f). The weighted average for the combined day and night data is 346 m for ring center and 372 m for the Slope Water (anomalous day tow omitted).

#### Diel Changes in Depth of Median Biomass

Diel changes in vertical biomass distribution with distance from ring center can be observed more clearly if we plot the median depth of the biomass versus tow position relative to the ring center (Figure 7 a-c). The diel shift upward in median depth of biomass over the entire region in April is an average of 96 m (range 6–275 m; Figure 7a). This average diel shift is considerably smaller (65 m) if the one sizable shift of 275 m observed in the high-velocity region is omitted. In June (Figure 7b) there also were large vertical day/night biomass shifts (423 and 209 m) in the high-velocity region. In ring center and the Slope Water, diel differences in median biomass depth were smaller, and deltas varied between 100 and 111 m. Diel shifts in August were similar in the ring and Slope Water, averaging 141 m (range 80–217 m; Figure 7c).

#### PATTERNS IN OTHER WARM- AND COLD-CORE RINGS, SARGASSO SEA, AND SLOPE WATER

##### Biomass Distribution in Warm-Core Rings 81D and 82H

Integrated zooplankton biomass in warm-core ring 81D averaged slightly higher than that present in the adjacent Slope Water, even though this ring was only about 3 months old (Figure 4c). This gave rise to a nonsignificant ( $p > 0.1$ ; linear regression ANOVA) positive relationship between biomass and the depth of the 10°C isotherm. The effects of diel migration on the biomass distribution in this ring are difficult to assess. Only one day/night pair of tows was obtained, and these tows were taken when the biological components of the ring surface (upper 50 m) and deepwater structure (>500 m) were being strongly affected by a massive interaction between the ring and the Gulf Stream [Joyce et al., 1984]. The median depth of biomass was about 50 m at night and 600 m during the day. On a second day tow, taken several days later, the median depth of biomass was 300 m. There was a substantial change in the absolute biomass in the ring water column over this period, and thus it is not clear whether the day/night shifts in biomass reflect vertical migration or horizontal advection (Figure 4c). Within the Slope Water the single day/night pair showed the



## Median Depth of Zooplankton Biomass in Upper 1000m

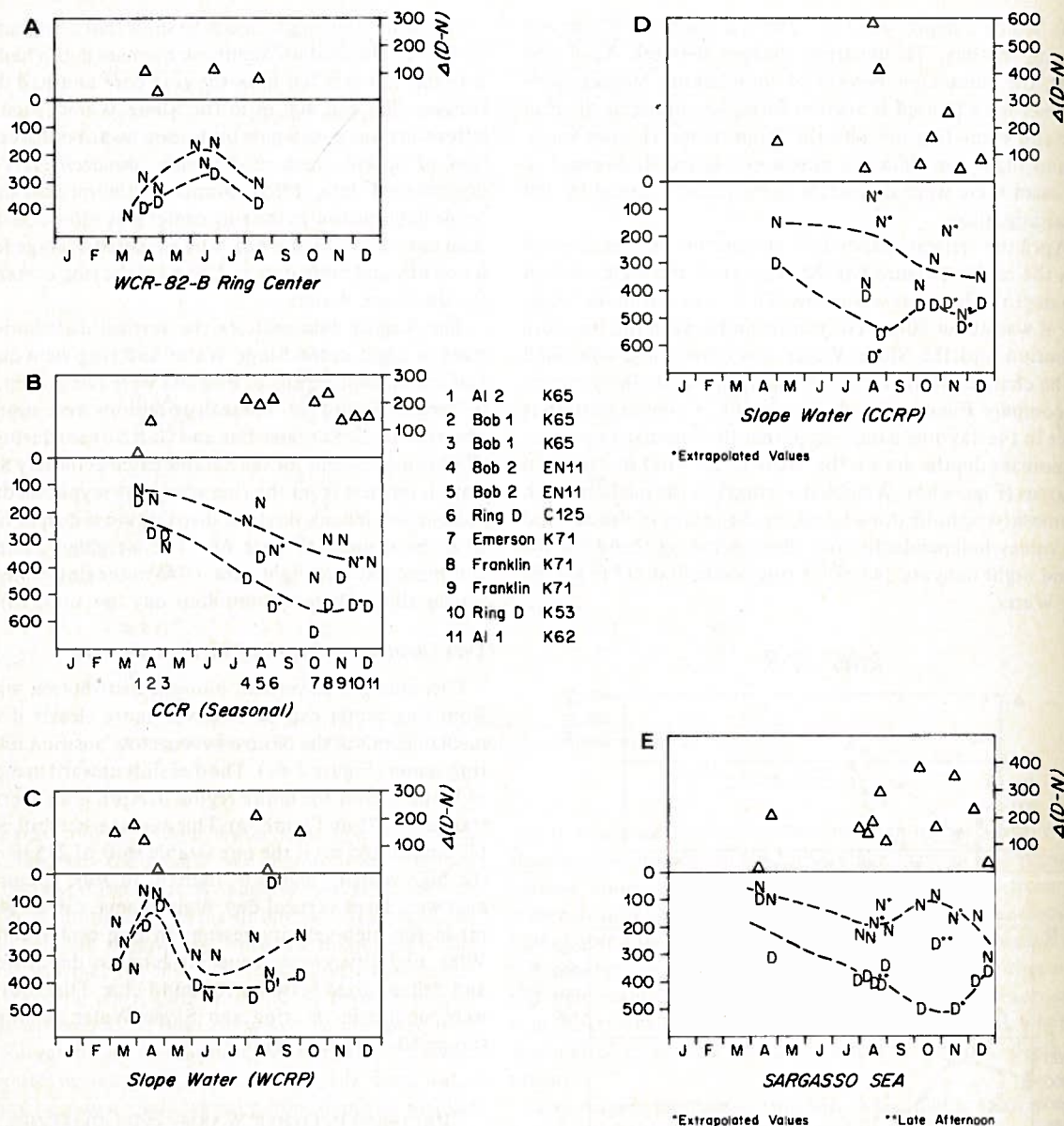


Fig. 8. Temporal variation in the median depth of zooplankton biomass in the upper 1000 m, using data from (a) warm-core ring 82B center, (b) cold-core rings (numbers on the abscissa correspond to rings listed to right of plot), (c) warm-core ring cruise Slope Water, (d) cold-core ring cruise Slope Water, and (e) warm-core and cold-core ring cruise Sargasso Sea. Asterisk values in b, d, and e include extrapolation of 0–800 m data collected in the first year of cold-core ring cruises to 1000 m, using other cold-core ring cruise tows taken at the same time of year and region. The daggered day value in e includes the scyphomedusa, *Pelagia pelagia*; the day value below excludes them; difference (D–N) uses latter-day value.

median biomass depth to be 403 m at night and 459 m during the day.

Warm-core meander/ring 82H contained significantly ( $p < 0.001$ ) lower integrated biomass levels than the adjacent Slope Water (Figure 4d); the ratios of Slope Water to ring biomass ranged from 1.3 to 2.0 (mean, 1.61). During the day, median biomass depth varied between 283 and 437 m; during the night, it varied between 194 and 355 m. For a given day/night pair of tows the day depth was always deeper than the night depth. In this ring, as in 81D, substantial changes in ring structure were taking place as the meander pinched off to form the ring, and it is not clear how much of the variation in diel pattern in the vertical biomass distribution is due to migration versus advection. Species data, when available, may help to resolve this issue. In the Slope Water a similar distribution was observed (day depth, 375 m; night depth, 220 m).

#### Biomass Distributions in Cold-Core Rings, the Sargasso Sea, and Slope Water

The vertical distribution of the cold-core ring data when plotted according to the month of sampling appear to be strongly influenced by seasonal variation regardless of ring age (Figure 9b). Thus rings sampled in spring have a shoal biomass distribution, while those in the fall and winter have a deep biomass distribution. While this pattern may simply be a reflection of seasonal changes taking place in the surrounding or parent water masses, there is another explanation, which involves the cold-core ring aging process. Young rings can start out with a relatively shallow median biomass, which then proceeds to deepen with increasing age [Ortner et al., 1978]. More than half of the cold-core rings making up this data set were formed in the spring. The data, when plotted according to ring

age, support the seasonal pattern. The seasonal pattern in Slope Water (Figure 9c) is similar to the late summer pattern in the deeper meander structure in the spring-for-

The difference in biomass between the cold-core rings and the Slope Water is significantly larger in the cold-core rings.

The Slope Water biomass is deeper in the cold-core rings. The Slope Water biomass is deeper in the cold-core rings. The Slope Water biomass is deeper in the cold-core rings.

Nighttime biomass is deeper in the cold-core rings. Nighttime biomass is deeper in the cold-core rings. Nighttime biomass is deeper in the cold-core rings.

warm-

#### Regional

The regional pattern in the cold-core rings is similar to the pattern in the Slope Water. The regional pattern in the cold-core rings is similar to the pattern in the Slope Water. The regional pattern in the cold-core rings is similar to the pattern in the Slope Water.



age, support this second view. However, it should be clear from the seasonal pattern of vertical biomass shifts in the Slope Water (Figure 9c and 9d) that a cold-core ring formed during late summer, fall, and winter is likely to start out with a much deeper median biomass depth. Evolution of vertical biomass structure in such a ring might vary considerably from that of a spring-formed ring.

The diel shift in biomass in these cold-core rings (average difference between day and night medians, 149 m) is significantly larger ( $p < 0.05$ ; Mann-Whitney  $U$  test) than in warm-core ring 82B (average, 87 m; Figure 9a).

The Slope Water data from the warm-core rings cruises (Figure 9c) is similar to the Slope Water data obtained on the cold-core rings cruises (Figure 9d). The April median biomass depth is usually shallowest, and for most other times the median is deeper. Exceptions occur, however, when animals such as the salp, *Salpa aspera* [Wiebe et al., 1979], or the scyphomedusa, *P. pelagia* noted above, dominate the biomass. Furthermore, the diel shifts in Slope Water biomass are also quite similar, averaging 116 m for the cold-core rings cruises and 115 m for the warm-core rings cruises when the exceptional periods of biomass domination by salps or scyphomedusa are omitted.

Nighttime biomass in the Sargasso Sea (median, 173 m; Figure 9e) is, on average, shallower than in either the warm (267 m)- or cold (287 m)-core rings or the Slope Water (264 m; both sets of cruises pooled). Furthermore, there is a significantly ( $p < 0.02$ ) stronger diel migration pattern evident in the Sargasso Sea biomass data than in any of the other areas (when the infrequent Slope Water salp migrations are left out of the analysis), with daytime median biomass occurring an average of 212 m below the nighttime level. The order of diel shifts in zooplankton biomass as a result of vertical migration is

warm-core ring 82B < Slope Water < cold-core rings < Sargasso Sea

#### Regional Composites of Vertical Biomass Distributions

The range in biomass likely to be observed within the upper 1000 m strata of warm- and cold-core rings, the Slope Water, and the Gulf Stream/Sargasso Sea is seen in composite plots of all MOCNESS-1 samples taken thus far in these regions (Figure 8). Greatest variability occurs in the cold-core ring data set (nine rings) and least in the warm-core ring set (three rings), probably because of the wide range in age of the cold-core rings and the lower number of warm-core rings available. Differences in the vertical distribution of biomass in the Slope Water and Gulf Stream/Sargasso Sea are apparent in spite of the large variability evident at nearly all depths. These profiles deviate from those regarded as typical of most oceanic regions where absolute abundance and variability decreases with depth [Vinoogradov, 1968]. Occasionally, very large values are observed in the Slope Water at depths of 300–500 m, as occurred on a tow north of ring 82B in August (Figure 8a). This particular case was caused by a nearly monospecific catch of *Calanus finmarchicus* (stage V's). This species is typical of the copepod community in the Slope Water and throughout the temperate North Atlantic and ontogenetically migrates to these depths during mid-spring to summer [Longhurst and Williams, 1979; T. Cowles, unpublished data, 1985]. However, such concentrations in the Slope Water on the periphery of a warm-core ring could result from interaction between the mesoscale convergence zone associated with the ring/Slope Water front and the

species maintaining a preferred depth [Olson and Backus, 1985].

#### PROCESSES AFFECTING BIOMASS DISTRIBUTION

We now examine processes affecting the biomass changes in 82B and compare these changes with similar observations made in cold-core rings and in the Sargasso Sea during the mid-1970's. Also included are data from a MOCNESS tow made in warm-core ring N on R/V *Endeavor*, cruise 11 (August 1977). We focus on seasonal changes in vertical distribution, ring initial conditions, rates of decrease in biomass gradients, and the relative importance of in situ versus lateral processes affecting these gradients.

#### Seasonal Shifts in Vertical Distributions and Initial Conditions

The median depth of biomass in ring 82B at night was about 400 m in March, and it progressively shoaled through June (Figure 9a); these changes in vertical distribution may have been a response to changes in the vertical distribution of plant biomass as indicated by chlorophyll *a*. A uniform chlorophyll distribution (about 0.3 mg/m<sup>3</sup>) was observed in the upper 100 m in 82B in March; the fact that the ring core was isothermal to 330 m suggests that similar chlorophyll concentrations probably extended to 200 m or deeper. April data, extending deeper in the water column, support this view; chlorophyll (about 0.4 mg/m<sup>3</sup>) was nearly uniformly mixed to 200 m or deeper [Smith and Baker, this issue; Hitchcock et al., 1985; P. Wiebe, unpublished data, 1985] paralleling the vertical temperature structure which was isothermal to nearly 400 m. Satellite Coastal Zone Color Scanner (CZCS) data for the late winter/early spring period reveal that during April, the spring bloom was occurring in the Slope Water (but not in ring 82B [Evans et al., this issue; Brown et al., 1985]), and the Slope Water MOCNESS tows show that the zooplankton were strongly concentrated near the surface (Figures 6a, 6b, 9c), whereas they were not a month earlier (Figure 9a). Although ring chlorophyll concentrations were low compared to the Slope Water (<0.5 mg/m<sup>3</sup> versus >2.0 mg/m<sup>3</sup>), ring values in April, when integrated to 200 m, were about equal to that in the Slope Water. CZCS images also show that shortly after the ring stratified in early May, surface concentrations of chlorophyll peaked in the ring while declining in the Slope Water. While the June shoaling of zooplankton biomass in the ring appears to have been a response to increasing concentrations of plant material at the surface, it could be argued that the zooplankton were reacting to the development of the seasonal thermocline. This did not, however, appear to be the case in the Slope Water, where a near-surface (upper 100 m) mixed layer and thermocline was present throughout the study period, yet large vertical shifts in zooplankton biomass still occurred. Furthermore, in August, with maximal development of the seasonal thermocline, the depth of median biomass occurred deeper in the ring because of an approximate 50% increase in biomass between 200 and 1000 m; biomass concentrations in the upper 200 m remained about what they were in June. Day biomass was distributed generally less than 100 m deeper than at night.

Our data show that a newly formed warm-core ring does not consistently have an integrated biomass level 2–3 times lower than the Slope Water. At the time of first sampling in ring 82B, about 3 weeks after formation, integrated biomass was 1.6–2.7 times lower (mean, 2.1) than adjacent Slope Water. Somewhat lower ratios of 1.3–2.0 (mean, 1.6) were observed for samples from the core of meander/ring 82B. The lower-than-expected ratios indicate that Gulf Stream and adjacent Sargasso Sea



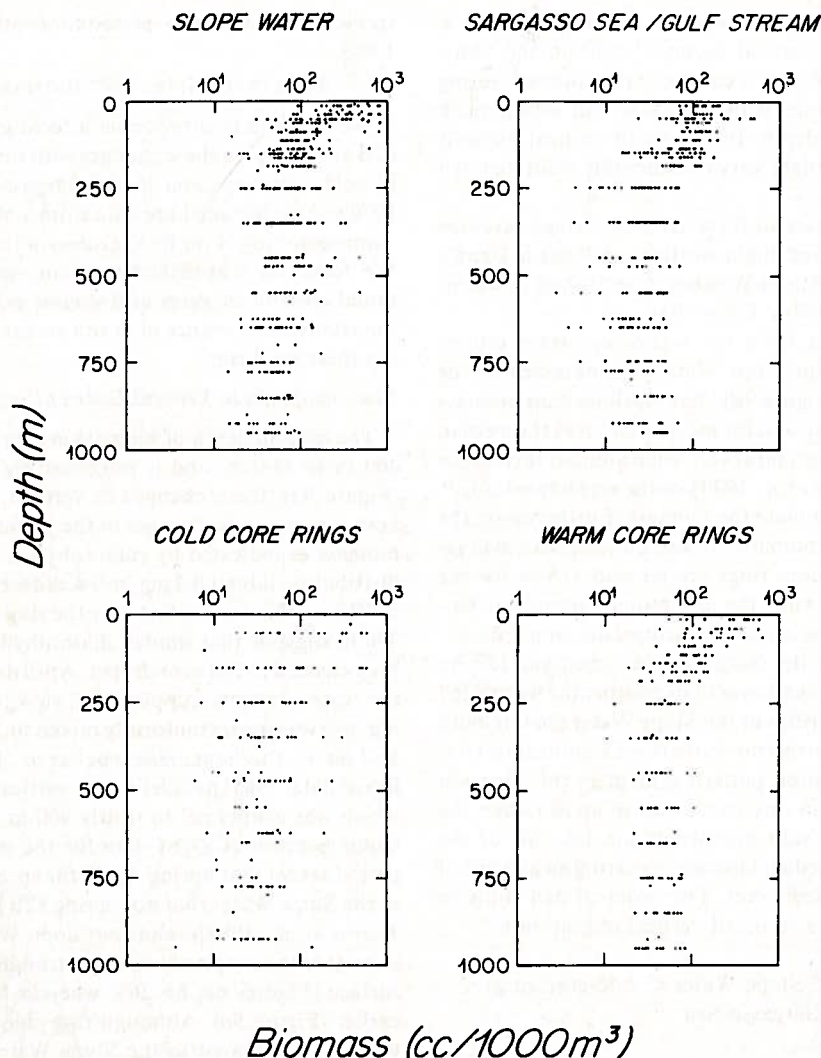


Fig. 9. Regional envelopes of zooplankton biomass versus depth based upon 0–1000 m oblique MOCNESS tows made on warm- and cold-core rings cruises. Each point represents the midpoint of a stratified oblique sample from a tow. The number of tows used to make the plots is 44, Slope Water; 13, warm-core ring center; 26, cold-core ring center; 33, Gulf Stream/Sargasso Sea; (see Figure 10 legend for additional information).

water, which form a ring, may have higher zooplankton biomass than water farther south of the Gulf Stream [Wiebe *et al.*, 1976a; Ortnner *et al.*, 1978].

Warm-core ring evolution leads to a decrease in zooplankton biomass gradients between the ring core and the Slope Water at a faster rate than the decrease observed for the gradient between cold-core rings and the Sargasso Sea (Figure 10a, b). Cold-core rings with known or estimated ages of less than a year, without exception, have an integrated biomass that is greater than the adjacent Sargasso Sea region. Only a single ring, Emerson, with an estimated age of 12 months or greater, had a biomass approximately equal to that of the Sargasso Sea. In sharp contrast, zooplankton biomass in warm-core rings can exceed that in the adjacent Slope Water within 3 months after ring formation, a rate of change 4 times faster than that observed with cold-core rings (Figure 10a, b). Physical evolution of warm-core rings also appears to proceed at a more rapid rate than in cold-core rings [Joyce *et al.*, 1984], apparently because of the more frequent interaction of warm-core rings with the Gulf Stream, the continental shelf, and the New England seamounts. It may also be related to the fact that warm-core rings are, on average, smaller at the time of formation and thus

exchange processes or decay through Rossby wave generation [McWilliams and Flierl, 1979] occur more rapidly. Significantly more rapid change is evident in a plot of age versus the depth of the 10°C isotherm in warm- and cold-core rings and the anomaly in this depth with respect to that in the adjacent water mass (Figure 10c, d, e). For a given ring age, significant differences exist between warm- and cold-core rings in this anomaly, with warm-core ring 10°C isotherm depth approaching the background water mass value at a rate faster by a factor of 2 (10°C rate of rise, 2 m/d in warm-core rings; 10°C rate of sinking, 1 m/d in cold-core rings). This interpretation must, however, be qualified because there is evidence that, at the time of formation, some warm-core rings, such as 82B, may not have a 10°C isotherm depth as deep as that found in the Sargasso Sea. Smaller initial anomalies than expected would give rise to overestimates of the rate of ring evolution. Although the rate at which the zooplankton biomass gradients decrease must be in part be a function of the starting conditions, this by itself cannot explain differences in rates of evolution in warm- and cold-core rings. Cold-core rings should be equally likely to form with lower-than-expected biomass contrast and with similar effects on estimates of rates of change.



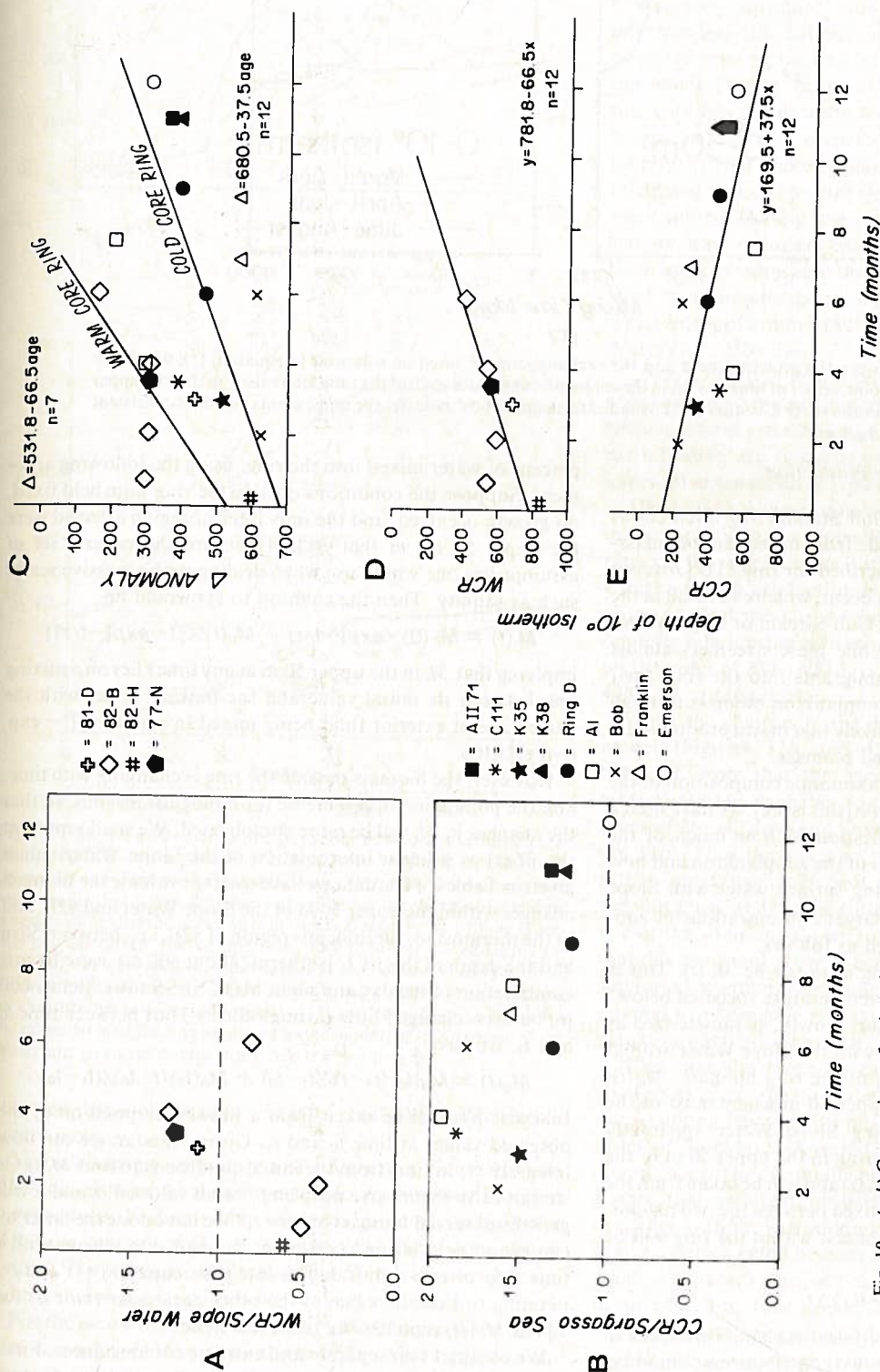


Fig. 10. (a,b) Comparison of ratios of warm-core (WCR) and cold-core (CCR) ring zooplankton biomass divided by surrounding water biomass versus ring age. Warm-core rings 81D, 82B, and 82H were sampled during the 1981–1982 rings cruises; ring 77N was sampled in 1977 on return from an August cold-core ring cruise aboard R/V *Endeavor*. The cold-core rings were sampled between 1972 and 1977. Ring Bob, which was formed in February 1977, was sampled at two time points: 2 months and 6 months [The Ring Group, 1981]. Ring Franklin was estimated to be 6–8 months of age when sampled in October–November 1977, which would give a springtime birth. Ring "D" was formed in February of 1975 and was 6 months old at first sampling and 9 months old when sampled again. Only rings AI and Emerson may have been formed at other times of the year. Based on satellite imagery, ring AI was thought to have been 2–3 months old when first sampled in December 1976, but even then it appeared to have been older, based on its physical structure, and it is possible that it was an older ring that had become reattached to the Gulf Stream when first observed. The second sampling of AI took place 4 months after the first, but in the intervening time it underwent a major interaction with the Gulf Stream and possibly the Slope Water. Ring Emerson (also sampled in October–November 1977) appeared physically older than any other ring sampled during the cold-core rings time series cruises except AI (depth of 15°C isotherm, 545–560 m) and was estimated to be 12+ months old. (c) Difference in ring center depth of the 10°C isotherm and the average depth of this isotherm in the surrounding water mass (850 m for Sargasso Sea and 250 m for the Slope Water) versus ring age (months). (d, e) Relationship between the depth of the 10°C isotherm and the age of warm- and cold-core rings.



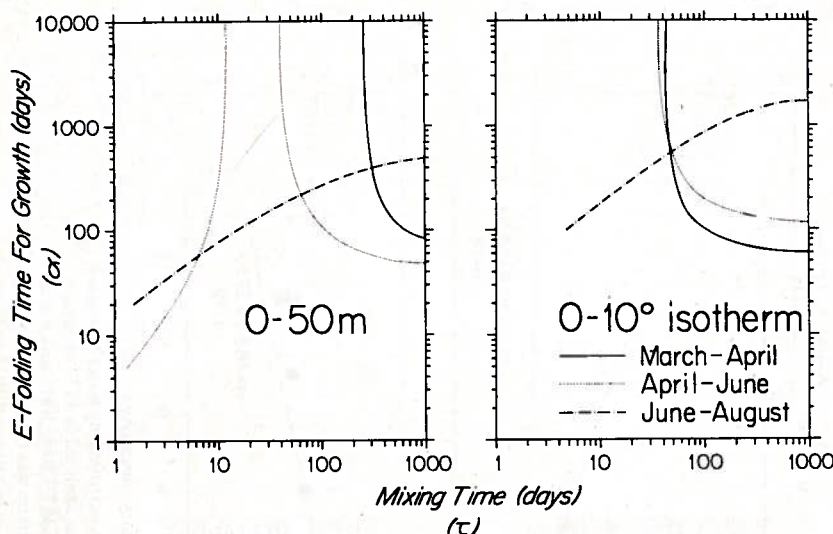


Fig. 11. Relationship between the growth time  $\alpha$  and the exchange time  $\tau$  based on solutions to equation (1), which are required to match the endpoint values of biomass  $M_i$  in the center of ring 82B for each of the time intervals: (a) for the upper 50 m only; (b) for the column above  $10^\circ\text{C}$  isotherm. The shaded rectangular box indicates the range of mixing times consistent with the 0–50 m salinity changes.

#### Lateral Exchange Versus In Situ Production

But what is the link between Gulf Stream/ring interactions and changes in ring biomass? Aside from infrequent but massive interactions, such as those described for ring 81D [Joyce *et al.*, 1984], less intense interactions occur, which can result in the production of streamers of either Gulf Stream or Slope Water that spiral into the ring core. While these streamers almost certainly carry zooplanktonic immigrants into the ring, their contributions to the increase in zooplankton biomass through time appears to be small, and it is likely that in situ production is the major contributor to increased biomass.

In addition to evidence in the taxonomic composition of the plankton given in Davis and Wiebe [this issue], we have used a simple model to explore the question of how much of the increase was due to in situ growth of the zooplankton and how much was due to exchange of ring surface water with Slope Water, which usually contained larger concentrations of zooplankton. The model is developed as follows.

Let the biomass within the ring at time  $t$  be  $M_i(t)$ . This is biomass integrated to a depth or temperature specified below.  $M_i(t)$  changes through population growth, parameterized as  $1/\alpha \times M_i$ , and through exchange with the Slope Water around the ring. Let  $f(t)$  be the fraction of the ring biomass,  $M_i(t)$ , which is contained within the upper 50 m where most of the interchange with the surrounding Slope Water apparently occurs. The biomass outside the ring in the upper 50 m of the Slope Water will be denoted by  $M_o(t)$  and will be taken from the Slope Water stations. If water is mixed between the two regions, with an exchange time  $\tau$ , the biomass within the ring will be changed by an amount:

$$(M_o/\tau - M_i/\tau)\Delta t$$

in a time  $\Delta t$  resulting from the physical exchange processes in the upper 50 m. Combining these two contributions to biomass change leads to the equation for the temporal changes in the total zooplankton biomass in the ring:

$$\frac{dM_i(t)}{dt} = \frac{1}{\tau} [M_o(t) - f(t)M_i(t)] + \frac{1}{\alpha} M_i(t) \quad (1)$$

We shall discuss below methods for estimating the value of  $\tau$ ; its interpretation, however, can be clarified by relating it to the

percent of water mixed into the ring, using the following argument. Suppose the conditions outside the ring were held fixed, no growth occurred, and the only interior region affected were the upper 50 m, so that  $f=1$ . These are the natural set of assumptions one would use when dealing with a passive scalar such as salinity. Then the solution to (1) would be

$$M_i(t) = M_i(0) \exp(-t/\tau) + M_o(t) \times (1 - \exp(-t/\tau))$$

implying that  $M_i$  in the upper 50 m at any time  $t$  lies on a mixing line between its initial value and the outside value, with the percentage of exterior fluid being mixed in equal to  $[1 - \exp(-t/\tau)] \times 100$ .

However, the biomass outside the ring is changing with time, and the population may increase for biological reasons, so that the changes in  $M_i$  will be more complicated. We shall represent the  $M_o(t)$  as a linear interpolation of the Slope Water values given in Table 2. (The data we have used to evaluate the biomass changes within the upper 50 m of the Slope Water and 82B, and in the thermocline/thermocline region of 82B, i.e., between 50 m and the depth of the  $10^\circ\text{C}$  isotherm (about 600 m), were from a combination of the day and night MOCNESS tows. Below 600 m, biomass changed little through time.) Thus between time  $t_0$  and  $t_1$ , we have

$$M_o(t) = M_o(t_0)(t-t_0)/(t_1-t_0) + M_o(t_1)(t-t_1)/(t_1-t_0)$$

Likewise  $f(t)$  will be taken from a linear interpolation of the observed values at time  $t_0$  and  $t_1$ . Given  $\tau$  and  $\alpha$ , we can now integrate (1) in time from the initial conditions to find  $M_i(t)$ . Or we can solve the inverse problem: what values of  $\tau$  and  $\alpha$  will give the observed biomass at time  $t_1$ ? We have done the latter by choosing  $\tau$  or  $\alpha$ , using a two-point Runge Kutta scheme with a time step of one-eighth day to integrate equation (1) and by iterating to find the value of the other parameter ( $\tau$  or  $\alpha$ ) for which  $M_i(t_1)$  matches the observed value.

We consider two separate and extreme circumstances. First, suppose that the deep population is isolated from the surface, so that the upper 50 m evolves independently through growth and mixing. In this case,  $f(t)=1$  and  $M_i$  represents only the population in the upper 50 m (Table 2). Second, we shall regard the ring as a large "mixing bowl" so that  $M_i(t)$  represents the total zooplankton biomass beneath a square meter, integrated to  $10^\circ\text{C}$  isotherm depth, and the  $f(t)$ 's are computed from the

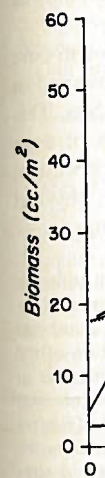
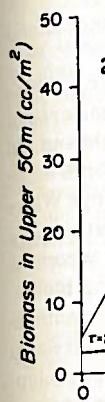


Fig. 12. Biomass  $M_i(t)$  in ring 82B (50 days). Equation (1) shows biomass changes as a function of time, satisfying the  $10^\circ\text{C}$  isotherm depth for the diff. the upper 50 m Slope Water are

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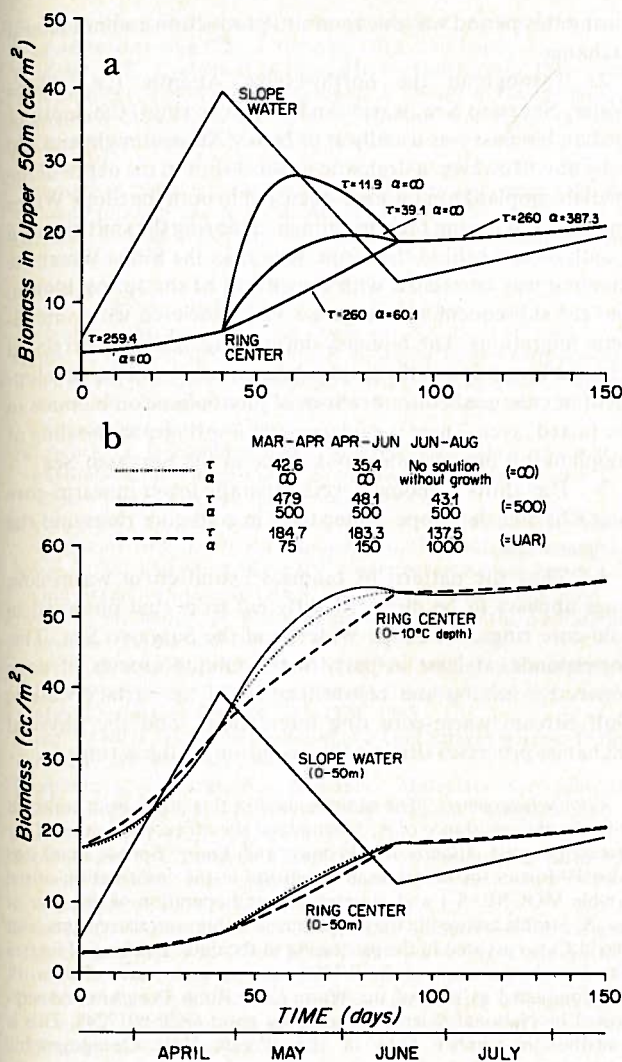


Fig. 12. Model prediction of the trajectory of biomass evolution [ $M_i(t)$ ] in ring 82B for the periods March to April (40 days), April to June (50 days), and June to August (60 days), 1982: (a) solutions to text equation (1) that satisfy the observed values for the starting and ending biomass values for the upper 50 m at ring center ( $f(t) = 1$ )—Slope Water changes are given for comparison; (b) solutions to equation (1) satisfying the observed biomass values in the column above the 10°C isotherm depth in the ring. The values of  $\tau$  and  $\alpha$  used in the model runs for the different time periods appear at the top of the figure. Changes in the upper 50 m of the ring predicted by the model ( $M_i(t) \times f(t)$ ) and Slope Water are given for comparison. See text for details.

observed ratios of the upper 50 m to total biomass beneath a square meter.

The relationship between  $\tau$  and  $\alpha$  shown in Figure 11a and 11b allows us to assess the amount of mixing or growth required to reproduce the final value of  $M_i(t_1)$  given the initial value  $M_i(t_0)$  for each interval, i.e., March-April, April-June, June-August. The left figure is for the upper 50 m scenario, while the right includes the modifications of the deep biomass.

For the case when only the zooplankton biomass in the upper 50 m is considered we see that the March to April transition can be explained by invoking either rather slow mixing (exchange times, 259 days) without growth or modest population growth ( $e$ -folding times, 62 days) without mixing. These rates seem reasonable. For the April to June changes, however, we find that there are two possible solutions; with no net growth, both require extremely rapid exchange (70% and 99% of the water replaced over this period). Since the Slope Water biomass is

decreasing with time, these cases both show the interior biomass increasing rapidly and overshooting its final value, with mixing serving to reduce the interior biomass during early June (Figure 12a). Even with growth considered, one of these solutions still requires extremely rapid interchange of water (Figure 11a).

We can estimate mixing rates from independent information—the salinity data. Streamers of water were observed entering the ring between April and June [Evans *et al.*, this issue]. During this period, salinity in the upper 50 m of the ring core was significantly reduced, whereas in the thermostad below, little change occurred. To account for the changes in salinity in ring center, Schmitt and Olson [this issue] have calculated that an exchange of about 10% of the surface water was required, leading to a  $\tau$  on the order of 390 days. Streamer activity also occurred between March and April, bringing lower-salinity water into the ring, and Schmitt and Olson calculated that the change in salinity in the ring was caused by replacement of around 15% of the ring surface water with Slope Water ( $\tau = 250$  days).

These estimates rule out the rapid mixing solutions described above for the April to June transition. If we accept the 390-day exchange time, population growth times on the order of 60 days per  $e$ -folding are required to account for the changes in the upper 50 m (modeled as isolated from the thermostad region).

The June to August transition is rather different in character in the upper 50 m; the Slope Water has a lower biomass than the ring, yet the ring biomass is still increasing with time (Table 2). Clearly, in situ production is essential to explain the changes observed, and the  $\tau - \alpha$  relationship in Figure 11a shows an opposite relationship between these variables. For mixing times on the order of 200–400 days, growth  $e$ -folding times of about 400 days are required.

When the changes in the deep biomass are included in the model (Figures 11b and 12b), rather similar results are obtained. Note that the curves for this case show a rather remarkable but probably fortuitous coincidence at exchange times of 38–42 days and growth times of 550–650 days (Figure 11b). Thus there is a single combination of parameters—rather rapid exchange and rather slow growth—that can account fairly well for the entire set of biomass changes. This is one of the solutions shown in Figure 12b; however, it is clear that this “constant growth, constant mixing” hypothesis is not supported by either the salinity data (indicating much less rapid mixing) or reasonable estimates of the potential rates of zooplankton population growth.

If we take the exchange rates estimated from the salinity changes as given, the estimated  $e$ -folding times for the population resulting from in situ processes are required to be on the order of 70 (March–April), 130 (April–June), or 1500 (June–August) days. The essentially negligible growth in the last case is simply that required to balance out the losses caused by exchange with the surroundings. The zooplankton assemblage in our samples could be increasing with these net growth time scales. For these values of  $\tau$  and  $\alpha$ , most of the biomass change in the March to June period is produced by in situ processes.

These model analyses lead us to conclude, then, that in situ growth produces a large fraction of the biomass change; that during the March to June period, the ring core waters were relatively isolated from adjacent water bodies; and, not surprisingly, that the growth rate for the population is variable over the lifetime of this ring. In addition to the physical and biological evidence cited above, there is independent biological evidence that supports this view. Nelson *et al.* [1985] have summarized a suite of measurements (chlorophyll *a*, phaeopigment, ATP,



biogenic silica, POC, PCN, nutrients, particle volume and size spectrum, bacterial abundance and cell volume, and phytoplankton abundance and major taxa) made in 82B and the Slope Water during April and June 1982 that complement our zooplankton measurements in both time and space. Biogenic particulate matter increased dramatically between April and June and was distinctly different from waters outside the ring. A comparison of data collected on two transects across the ring in June showed that many of these biological properties had significant axial symmetry with high biomass at ring center, a low in the high-velocity region, and a high in an entrainment field of shelf and Slope Water to the east of the ring. The biogenic silica fraction of the biomass was an order-of-magnitude larger in the ring center than in the entrainment streamers during this period, while bacterial biomass and coccolithophore abundance was low in the ring but high in the entrainment field. Nelson et al. concluded that the transformations of the microplankton in the ring from April through June were largely due to dynamical processes within the ring rather than to horizontal advective processes. *Tranter et al.* [1980] also argued that a fivefold increase in phytoplankton concentration at the center of a Tasman Sea eddy over a 3-month period was due to in situ processes and not advection. *Angel and Fasham* [1983, p. 499] showed how growth, coupled with diffusion ( $k = 10^4 \text{ cm}^2 \text{ s}^{-1}$ ), could lead to movement into a ring of a population of fast-growing organisms (doubling every 3–10 days). However, the front of organisms moves in at  $0.2\text{--}0.4 \text{ cm/s}$ , so that it would take 200 to 400 days just to reach ring center (150-km-diameter eddy). If  $k$  were as large as  $10^6 \text{ cm}^2 \text{ s}^{-1}$  and zooplankton could double in 20 days, the time to reach ring center could be as short as 60 days. These relatively slow times support the idea that in situ growth is a major contributor to the changes in ring zooplankton biomass.

At different times, Gulf Stream rings and also other meso-scale eddies can exhibit a different balance between in situ production and lateral exchange. We have observed periods of strong interaction with the Gulf Stream when physical, chemical, and biological properties can change rapidly because of lateral exchange [*Joyce et al.*, 1984]. *Haury* [1984] suggests that on the basis of his biological data and complementary physical and chemical data of *Simpson et al.* [1984] and *Simpson* [1984] that biological structure in a quasi-permanent and semistationary offshore eddy of the California Current system (CCS) is controlled largely by lateral advection and mixing. *Simpson* further concludes that continuous interaction between coastal and offshore waters of the CCS with offshore eddies of the type studies makes them fundamentally different from Gulf Stream cold-core rings but more similar to warm-core eddies like those of the East Australia Current.

#### CONCLUSIONS

1. Zooplankton biomass concentrations in warm-core ring 82B were significantly lower than in the adjacent Slope Water during the first 2 months after formation. In addition the vertical distribution of zooplankton biomass was substantially deeper in the core of ring 82B than in the adjacent Slope Water during this period. Net growth of ring biomass was relatively rapid, and within 3–4 months the ring-standing crop reached levels equal to those in the surrounding Slope Water, a rate 3–4 times faster than cold-core rings appear to reach equivalent levels with the Sargasso Sea. Model analysis of these data lead to the conclusion that most of the ring 82B biomass increase

during this period was due to in situ production and not lateral exchange.

2. Throughout the northwestern Atlantic (i.e., Slope Water, Sargasso Sea, warm- and cold-core rings) the depth of median biomass was usually at or below 200 m at night and 300 m by day. However, a dramatic upward shift in the depth of the median zooplankton biomass occurred in both the Slope Water and ring 82B during the springtime; in the ring the shift lagged a month or two behind the Slope Water. In the Slope Water the shoaling was correlated with the advent of the spring bloom, and the subsequent submergence was associated with ontogenetic migrations. The biomass shift in ring 82B was correlated with the formation of the seasonal thermocline and the development of enhanced concentrations of phytoplankton biomass in the mixed layer. There is evidence that a springtime shoaling of zooplankton biomass also took place in the Sargasso Sea.

3. Diel shifts in biomass were generally lower in warm-core ring 82B and the Slope Water than in cold-core rings and the Sargasso Sea.

4. Thus the pattern of biomass evolution in warm-core rings appears to be distinctly different from that observed in cold-core rings, the Slope Water, and the Sargasso Sea. This corresponds, at least in part, to the unique aspects of deep convective mixing and restratification of the surface waters, Gulf Stream/warm-core ring interactions, and the physical exchange processes driving the evolution of these rings.

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