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The influence of a Gulf Stream meander on the distribution of zooplankton biomass in the Slope Water, the Gulf Stream, and the Sargasso Sea, described using a shipboard acoustic Doppler current profiler

CARIN J. ASHJIAN,* SHARON L. SMITH,*‡ CHARLES N. FLAGG,* ARTHUR J. MARIANO,† WILLIAM J. BEHRENS* and PETER V. Z. LANE*‡

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Abstract—Patterns in zooplankton biomass distribution in a Gulf Stream meander were documented using a ship-mounted acoustic Doppler current profiler (ADCP) in fall 1988 as part of the BIOSYNOP program. The dominant signal in biomass was the regional variation between water masses, with greatest biomass recorded in the Slope Water, intermediate biomass at the Slope Water–Gulf Stream front, and lowest biomass in the Gulf Stream/Sargasso Sea. Biomass was more variable in the Slope Water than in the Sargasso Sea. Diel variation, a consequence of diel vertical migration, was also observed. Comprehensive maps of the surveyed region documented meander associated enhancement of zooplankton biomass. Elevated biomass was documented in the region downstream of the meander crest, where entrainment of Slope Water and convergence of flow are hypothesized to occur. The ADCP was demonstrated to be an effective means of documenting patterns in zooplankton biomass, including estimates of the variability (patchiness).

INTRODUCTION

SUBSTANTIAL variation in the magnitude and distribution of zooplankton biomass exists within and between oceanic regions. Quantification of zooplankton biomass traditionally has been accomplished using invasive techniques such as net tows and towed recorders, resulting in limited information integrated over a great horizontal distance. The advent of generally accessible acoustic techniques for estimating zooplankton biomass has greatly increased both the efficiency of collecting and analysing data as well as the sample size used in the estimation of zooplankton biomass. Furthermore, the use of non-invasive techniques circumvents the potential response of the zooplankton to the sampling instrument (net avoidance) and eliminates behavior-based biases in the data (SMITH *et al.*, 1992).

Most previous studies of zooplankton using acoustic techniques have relied on instruments that are typically towed behind a ship in the region of interest, using single or multiple frequency acoustics (SMITH *et al.*, 1992). The potential of the acoustic Doppler

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*Oceanographic and Atmospheric Sciences Division, Department of Applied Sciences, Brookhaven National Laboratory, Upton, NY 11973, U.S.A.

†Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, U.S.A.

‡Present address: Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, U.S.A.

current profiler (ADCP) as a means to measure zooplankton biomass only recently has been realized. Initially, the use of the ADCP was demonstrated using a bottom mounted unit on the continental shelf (Flagg and Smith, 1989; Flagg *et al.*, in press). Recently, the feasibility of using a hull mounted ADCP to collect acoustic backscatter data and, therefore, to measure zooplankton biomass has been explored (Flagg and Smith, 1989; Heywood *et al.*, 1991; Roe and Griffiths, 1993). In the present study, we utilize a hull mounted ADCP to describe zooplankton biomass in the Gulf Stream region.

The BIOSYNOP program was a multi-investigator study designed to investigate the effects of the dynamics of Gulf Stream meandering on the biology of the Gulf Stream and surrounding water masses. Extensive fluid exchange between the Gulf Stream and the neighboring Slope Water and Sargasso Sea has been demonstrated to occur in conjunction with meander development, particularly at the northern edge of the current (Bower *et al.*, 1985; Bower and Rossby, 1989; Bower, 1991). These processes are associated with both northward meanders (crests) and those that protrude to the south (troughs). In particular, loss of water from the Gulf Stream to the Slope Water is expected to occur upstream of meander crests on the northern side of the Stream, because of flow divergence and shoaling of isopycnals, while the opposite process, entrainment of water from the north and submergence of isopycnals, is predicted to occur following the crest. Various effects on the regional biology have been predicted, including enhancement of primary productivity and standing stock in response to elevated nutrients in upwelling areas, a concomitant increase in zooplankton biomass in the region following the crest as a result of increased secondary production and/or the concentration of animals by convergence in that region, and a change in the species composition of the plankton (BIOSYNOP, 1987; Hitchcock, 1988; Olson, 1990).

The primary goal of our study was to produce comprehensive maps of the surveyed region that would demonstrate the hypothesized meander-associated enhancement of zooplankton biomass. Since the ADCP measures total zooplankton biomass without any size structure information, data collected using this instrument could be expected to document elevation of zooplankton biomass but could not identify species/size specific mechanisms for observed patterns.

The BIOSYNOP biomass data are influenced by three major factors, each of which must be accounted for separately during the analyses. The first factor is the geographic variation in water masses, each of which contain differing zooplankton biomasses and species (e.g. Slope Water, Gulf Stream, Sargasso Sea). A second factor is the temporal variation resulting from the diel vertical migration of the zooplankton. Superimposed on these fluctuations are the potential effects of meander-associated physical processes on distributions of zooplankton communities containing different species.

METHODS

Data were collected over 4 m depth bins and averaged for 1 or 5 min averages using a hull mounted 150 kHz acoustic Doppler current profiler (ADCP) on the R.V. *Cape Hatteras* in fall 1988. The cruise consisted of two legs, each approximately 2 weeks in length, (21 September–5 October 1988 and 11–21 October 1988), surveying a northward (crest) Gulf Stream meander located in the NW Atlantic Ocean east of Delaware, U.S.A. (Fig. 1).

Temporal changes in the shape and amplitude of the meander were observed using satellite images of sea surface temperature.

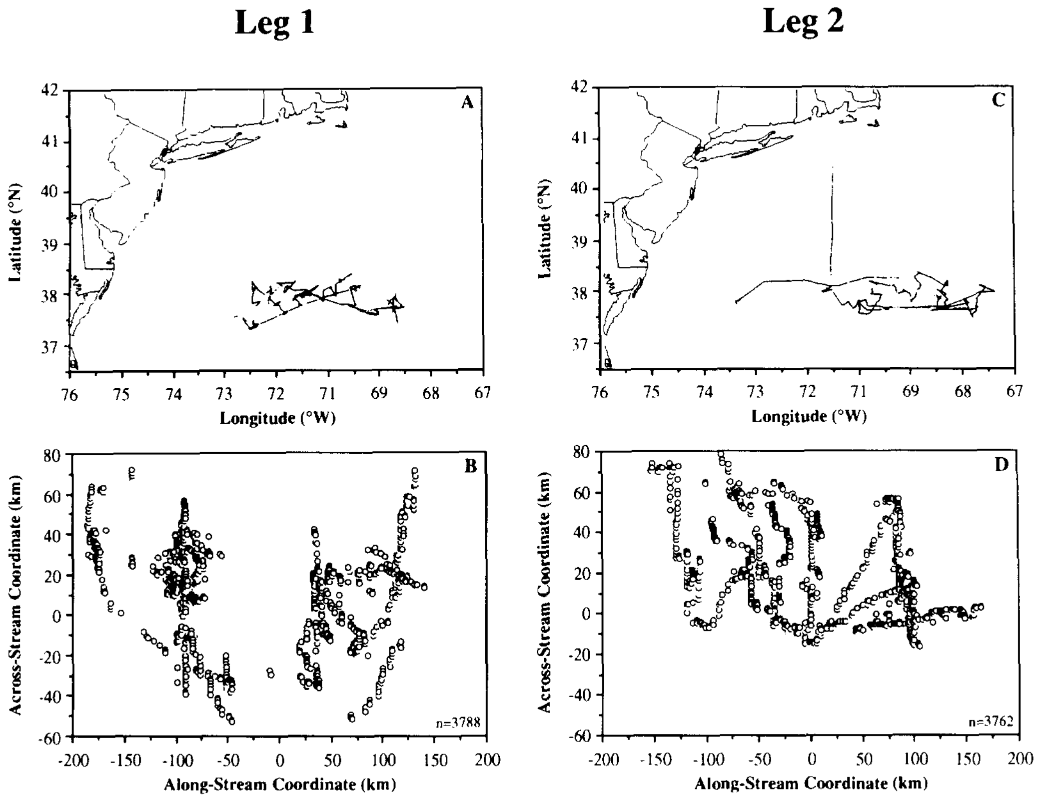

Fig. 1. (A,C) Cruise track of the R.V. *Cape Hatteras* during the two legs of the Fall 1988 BIOSYNOP cruises plotted in geographic coordinates. (B,D) Cruise tracks for the two legs plotted in the meander coordinate system. The crest of the meander is located at 0 km on the along-meander (horizontal) axis while the Gulf Stream axis (12°C at 400 m) is located at 0 km on the across-meander (vertical) axis. Locations in the Slope Water are designated as positive cross-stream distances while those to the south of the axis (Sargasso Sea) are designated as negative cross-stream distances. Only those locations where ADCP profiles were successfully collected have been plotted.

Calibration net tows using a 1 m^2 MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System (Wiebe *et al.*, 1976)), equipped with 150 μm mesh nets, were conducted to collect samples with which to establish a displacement volume to dry weight conversion for this region. Displacement volumes from 39 samples were measured following the general method of Ahlstrom and Thrailkill (1963). The samples were allowed to stabilize for at least 6 weeks prior to processing. After measuring the total volume of each sample in a graduated cylinder, the sample was poured through a cone-shaped sieve (150 μm mesh), allowed to drain for approximately 5 min, and the volume of the filtrate measured. The difference between the two volumes was the biomass as displacement volume. Specimens larger than *ca* 5 cc were removed prior to the sample biomass determination and their volumes were measured separately.

The total dry weight of each of the 39 samples was determined following the method described by Flagg and Smith (1989). Each sample was analysed for the abundance of the various species and taxonomic categories. Representatives of these categories were sorted

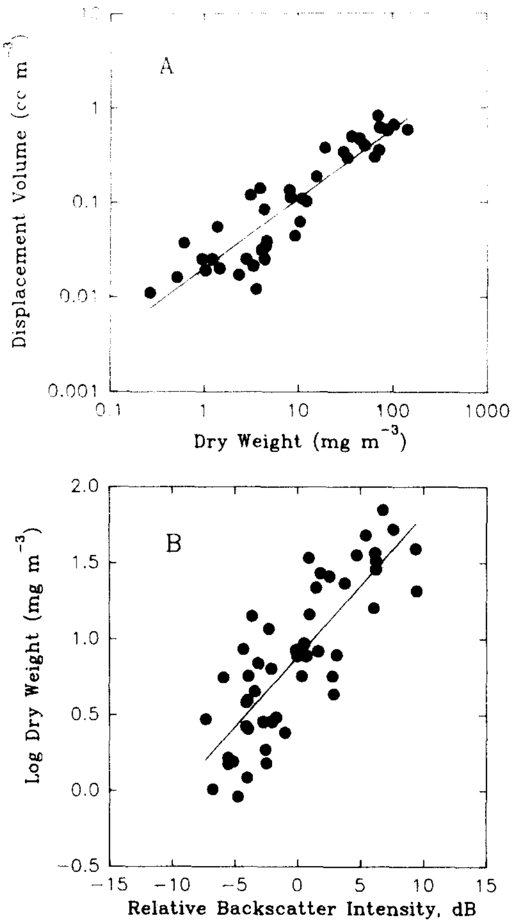

Fig. 2. (A) Relationship between dry weight and displacement volume for the calibration MOCNESS tows. The linear regression line is shown. The functional regression equation is derived from the linear regression. (B) Relationship between relative backscatter intensity and dry weight for the calibration MOCNESS tows. The linear regression is shown. The linear regression equation was used to calculate zooplankton biomass from the backscatter data.

and dry weight was measured on a Cahn electrobalance. The abundance of each category was multiplied by its mean dry weight to obtain total dry weight, and the categories were then summed to yield the total dry weight for each sample.

The relationship between displacement volume and total dry weight for each sample was then established using a geometric mean functional regression (Fig. 2A) (RICKER, 1973; WIEBE *et al.*, 1975). The dry weight:displacement volume functional relationship was:

$$\log(\mathrm{DV}) = 0.81 * \log(\mathrm{DW}) - 1.77, \tag{1}$$

where DW and DV refer to dry weight (mg m^{-3}), and displacement volume (ml m^{-3}), respectively ($r^2 = 0.75$ and $n = 39$).

The relation between zooplankton biomass and acoustic intensity was established by comparing biomass obtained from net tows with coincident ADCP ensembles. Dry weights were derived from displacement volume from 51 samples using the geometric mean functional regression (equation (1)). The average relative backscatter intensity from the ADCP (FLAGG and SMITH, 1989) corresponding to each sample was determined using the start and stop times and depth ranges of each MOCNESS net opening and closing. The relationship between dry weight and relative backscatter intensity for each tow was described using a linear regression between log(Dry Weight) and intensity (Fig. 2B). The biomass–intensity relationship is given by:

$$\log(\mathrm{DW}) = 0.0930 * I + 0.885, \tag{2}$$

where dry weight, DW, is in mg m^{-3} and relative backscatter intensity, I, is in dB (r^2 value $= 0.67$, $n = 51$).

Several characteristics of this particular data set complicated our interpretation, specifically the convoluted nature of the cruise track (Fig. 1) and the variation in the vertical range of the data. The ADCP measures the magnitude of the acoustic return from particles suspended in the water column. To a very large extent the particles consist of zooplankton small enough so that the return echo is produced by Rayleigh scattering. Rayleigh scattering is strongly size dependent so that larger particles produce a larger return than small particles but there is no size cut off below which there is no return echo. Nevertheless, in practice the return is weighted toward the larger zooplankton. Therefore biomass estimates based on acoustic backscatter are not size-specific. Since the instrument is mounted on the ship's hull and operates continuously, the spatial and temporal coverage is extensive. Conventional biomass vs distance contour plots can be generated, however these types of plots were not useful because of the convoluted cruise track. Where typically an investigator may obtain fewer than 10 vertical profiles from a particular region using a MOCNESS (e.g. ORTNER *et al.*, 1978, 1980; ROMAN *et al.*, 1985; WIEBE *et al.*, 1985; ALLISON and WISHNER, 1986), we collected over several thousand individual profiles with the ADCP in both the Slope Water and Sargasso Sea. Additionally, the depth over which the acoustic signal-to-noise ratio was acceptable varied between profiles, resulting in substantial variation in depth penetration. These special characteristics of ADCP data mandated a non-conventional approach to the analysis.

We chose to reduce the vertical distributions for each profile to two statistics that represented the magnitude and distribution of the biomass in the water column and allowed comparison of profiles despite variations in vertical coverage. Biomass measurements were not obtained for the top of the water column (usually the top 20 m). Only those profiles where the maximum depth of the data was at least 100 m were used. Two descriptors (mean biomass and mean depth, which represents the center of "mass" of the zooplankton biomass) were then calculated over the 20–100 m depth interval of these selected profiles. Initially, several statistics were calculated (e.g. maximum biomass, integrated biomass (Σbin biomass concentration × bin depth range), depth of maximum biomass). After comparison of the spatial dependence of these statistics mean biomass and mean depth appeared to be the most useful. Mean depth was defined as:

$$\text{Mean depth} = \left(\int_{20}^{100} \mathrm{DW} * z * \mathrm{d}z \middle/ \int_{20}^{100} \mathrm{DW} * \mathrm{d}z \right), \tag{3}$$

where z is depth, and represents the vertical center of biomass within the specified portion of the water column.

Sea surface temperature data were collected every 5 min underway using the Serial

ASCII Instrumentation Loop (SAIL) shipboard data communication system on the *Cape Hatteras*. Although the ADCP records sea temperature, the temperature probe on the *Cape Hatteras* ADCP was mounted behind a Lexan covering, which insulated the probe and resulted in a delayed response time to temperature change in the water. The SAIL temperature data and the ADCP data were merged, with interpolation of temperatures for missing values.

The biomass data were categorized as either day or night to segregate the effects of diel vertical migration for some comparisons. Day was considered to be all the hours of daylight except the 30 min following sunrise and the 30 min preceding sunset. Night was considered to be all the hours between sunset and sunrise except the 30 min following sunset and the 30 min preceding sunrise. Examination of plots of biomass vs time of day suggested that a 60 min interval was sufficient to complete the change in biomass distribution associated with diel vertical migration at sunrise and sunset over the 20–100 m depth interval. According to this scheme, all data available from 22 h of each day have been used in the regional and temporal comparisons.

Data interpretation was greatly simplified through the use of a local stream-based curvilinear coordinate system defined by the position of the Gulf Stream core relative to the apex of the meander crest. The along-stream and cross-stream coordinate values were calculated from objective analysis maps of the depth of the 12° isotherm, Z_{12}. Daily maps of Z_{12} were constructed using the parameter matrix algorithm (Mariano and Brown, 1992) and over 500 CTD, XBT, and AXBT measurements. For each daily map, the $Z_{12}=400$ m contour corresponding to the Gulf Stream core was identified using a pattern recognition algorithm similar to the algorithm used in Mariano (1990). This particular contour was picked since (i) it is the only contour from the Gulf Stream core that was not affected by stream–ring interactions in both the fall and spring experiments, and (ii) it is the approximate location of the greatest cyclonic shear. Each of the daily $Z_{12}=400$ m contours serve as a basis for the along-stream coordinate, τ, and are stored as daily files containing longitude, latitude, and along-stream coordinate distance, τ, respectively. For each file, the origin of the along-stream coordinate, τ, is set at the apex of the meander crest. Each daily apex is defined as the maximum latitude of the corresponding daily $Z_{12}=400$ m contour. The τ values, in km, are calculated relative to the apex using a Mercator projection and the differences in longitude and latitude between the apex and the set of $Z_{12}=400$ m contour positions. Negative τ values are downstream of the apex, e.g. west of the meander crest, while positive τ values are upstream of the apex. The origin of the cross-stream coordinate, $\eta=0$ km, is defined at $Z_{12}=400$ m. Negative η values correspond to Gulf Stream core and Sargasso Sea locations, while positive η values correspond to North Wall and Slope Water locations.

Mean biomass and mean depth were analysed as a function of cross-stream distance for all the data (24 h), night data only, and day data only. The data were grouped into three categories based on cross-stream distance to describe temporal changes in the magnitude of biomass or in the mean depth as a result of diel vertical migration within each region. All data collected to the south of the Gulf Stream axis (cross-stream distance = 0) were considered to be of Gulf Stream–Sargasso Sea origin. Data collected within the region 30 km to the north of the Gulf Stream axis were considered to have originated in a "frontal region" containing the boundary between the Gulf Stream and the Slope Water, including the traditional North Wall. Data collected at locations farther than 30 km to the north of the Gulf Stream axis were considered to be Slope Water. The selection of these cross-stream distances was accomplished through consideration of: (i) plots of mean biomass versus cross-stream distance across the entire region, and (ii) examination of the average Gulf Stream cross-stream sections in stream coordinates of temperature and velocity from HALKIN and ROSSBY (1985). Both the magnitude and variability of the mean biomass increased noticeably to the north of the Gulf Stream axis (cross-stream distance = 0) and then reached a relatively consistent level of magnitude and variability by 30 km to the north of the axis, suggesting that the 30 km wide region was a transitional zone between two regions of different and characteristic biomass distributions. The average sections of HALKIN and ROSSBY (1985) indicated that surface downstream velocities dropped off rapidly within this 30 km zone and that, furthermore, this transition zone encompassed both the traditional "North Wall" (15°C at 200 m) and the region in which many isotherms surfaced (surface front). It should be noted that the "Slope Water" and "Sargasso Sea" regions designated in this study include the fringe regions of those water masses associated with the Gulf Stream as well as regions farther away from the current.

Mesoscale or regional patterns in biomass and mean depth potentially influenced by meander-associated physical processes were identified by averaging the data into 10 by 10 km bins in the across and along meander directions. Day and night data were binned separately. Because of the irregular coverage by the cruise track, there is a wide range in the data density in different regions of the meander.

All comparisons of biomass and mean depth within each region (day versus night), and between regions were made using the general linear models procedure of the Statistical Analysis System (SAS) (SAS Institute Inc., 1985). Where appropriate, multiple comparison of means was done using the Student–Newman–Keuls test option of the general linear models procedure. Calculation of means and coefficients of variation:

$$\text{Coeff.var.} = (\text{standard deviation}/\text{mean}) \times 100,$$

and verification of normality for various subsets of the data were done using the univariate procedure of SAS. Comparisons of regional means were made using all data points, rather than the binned averages.

RESULTS

The total biomass data set collected on the R.V. *Cape Hatteras* includes 8487 ADCP profiles with a mean biomass of 14.5 mg dry weight m^{-3} and a maximum of 736.3 mg m^{-3}. Values of over 500 mg m^{-3} occurred rarely, but values of 100–200 mg m^{-3} were common.

The maximum ADCP penetration depth for biomass varied considerably over the cruise track. The mean depths of maximum penetration for the profiles from the two legs were 155 and 153 m for Legs 1 and 2, respectively. For both legs, 75% of the profiles extended to depths deeper than 127 m. Of the 8487 profiles, 7550 extended to at least 100 m and were used in this analysis (3788 from Leg 1 and 3762 from Leg 2, representing approximately 89% of the available data).

When the ADCP is profiling below the ship in deep water, there necessarily will be a range limitation on the data when the backscatter decreases to the point where noise, from whatever source, becomes a significant fraction of the total signal. After examination of a large number of backscatter profiles and consideration of a number of methods to reduce the effect of noise, we determined that the sampling range of the backscatter data should be defined by the ADCP's per cent good parameter. While velocity data are generally useful down to the 25% good level, the acoustic backscatter data were only deemed acceptable on the *Cape Hatteras* when greater than 92% good. The 92% good criterion is based upon the observation that for the instrument used in this study ship–flow–instrument noise limited the minimum backscatter intensity below this level. We did not subtract ship–instrument–flow noise from the backscatter estimates. Attempts to date have not been particularly successful at removing noise. This is an issue that merits further study.

The range of ship mounted ADCPs depends on a number of factors, including ship speed, sea state, heading relative to the swell (New, 1992), biomass concentration, and details of the installation. Range limitation in this data set was particularly noticeable when a section consisted of both periods of low speed such as during a MOCNESS two or CTD cast, and periods of higher speed in transit between stations. Generally, deeper penetration was achieved during periods of low speed.

Development and collapse of the meander

The meander propagated to the east and was transformed from a sharp arc to a straight stream during the period of the cruise (21 September 1988–21 October 1988). During Leg 1 (21 September–5 October) the meander had a large amplitude and a length to amplitude ratio, a rough indicator of the degree of curvature, of 2.0–3.0 (Fig. 3A). A strong meander–ring interaction occurred to the north at the crest of the meander (23 September–29 September) during the first half of the leg (Fig. 3B). This interaction was evident in both the satellite i.r. imagery and in velocity vectors measured in the meander during this period (Hummon *et al.*, 1991). Since most of the ADCP biomass data were collected in the flanks of the meander, the biomass data do not include the region of strongest interaction. The meander became asymmetrical following the meander–ring interaction, developing a deep trough to the east at the end of Leg 1 (2 October).

The meander flattened out and essentially disappeared during Leg 2 (11–21 October 1988) of the cruise (Fig. 3C, D). The deep trough that had formed at the end of Leg 1 was apparent at the beginning of Leg 2 (11–13 October), but the crest of the meander was almost imperceptible during this period. The trough had pinched off as a cold core ring and all surface manifestations of the meander had disappeared by 15 October 1988. The data collected during Leg 2 of the cruise may be considered a survey of the Gulf Stream and Gulf Stream front, but should not be regarded as a survey of a meander. Because of the collapse of this meander, and because the data from the two legs of the cruise demonstrated the same regional patterns, we have chosen to present only the data from Leg 1 (21 September–5 October) of the cruise in most of the following analyses. Where appropriate, reference is made to the data collected on Leg 2 (11–21 October).

Effectiveness of the mean depth and mean biomass statistics

The mean depth and mean biomass statistics were effective in describing trends in the magnitude and distribution of the zooplankton biomass (Fig. 4). These data were collected along a north–south transect while the ship was steaming south from Woods Hole at the start of the Leg 2 (Fig. 1). The cruise track was relatively straight, consisted mainly of data collected at night, and passed across the continental shelf and slope through water masses of varying origin.

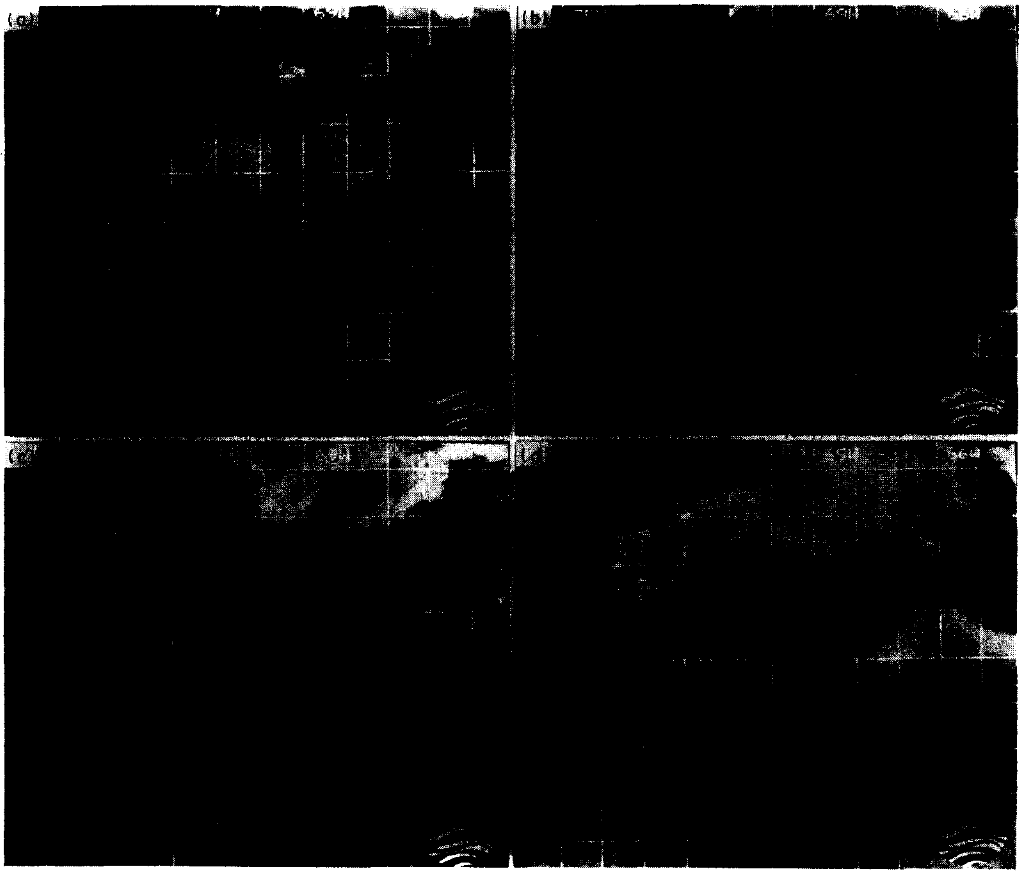

Fig. 3. Sea surface infrared temperature images demonstrating the evolution of the meander from an arc to an essentially straight stream during the period of the cruise.

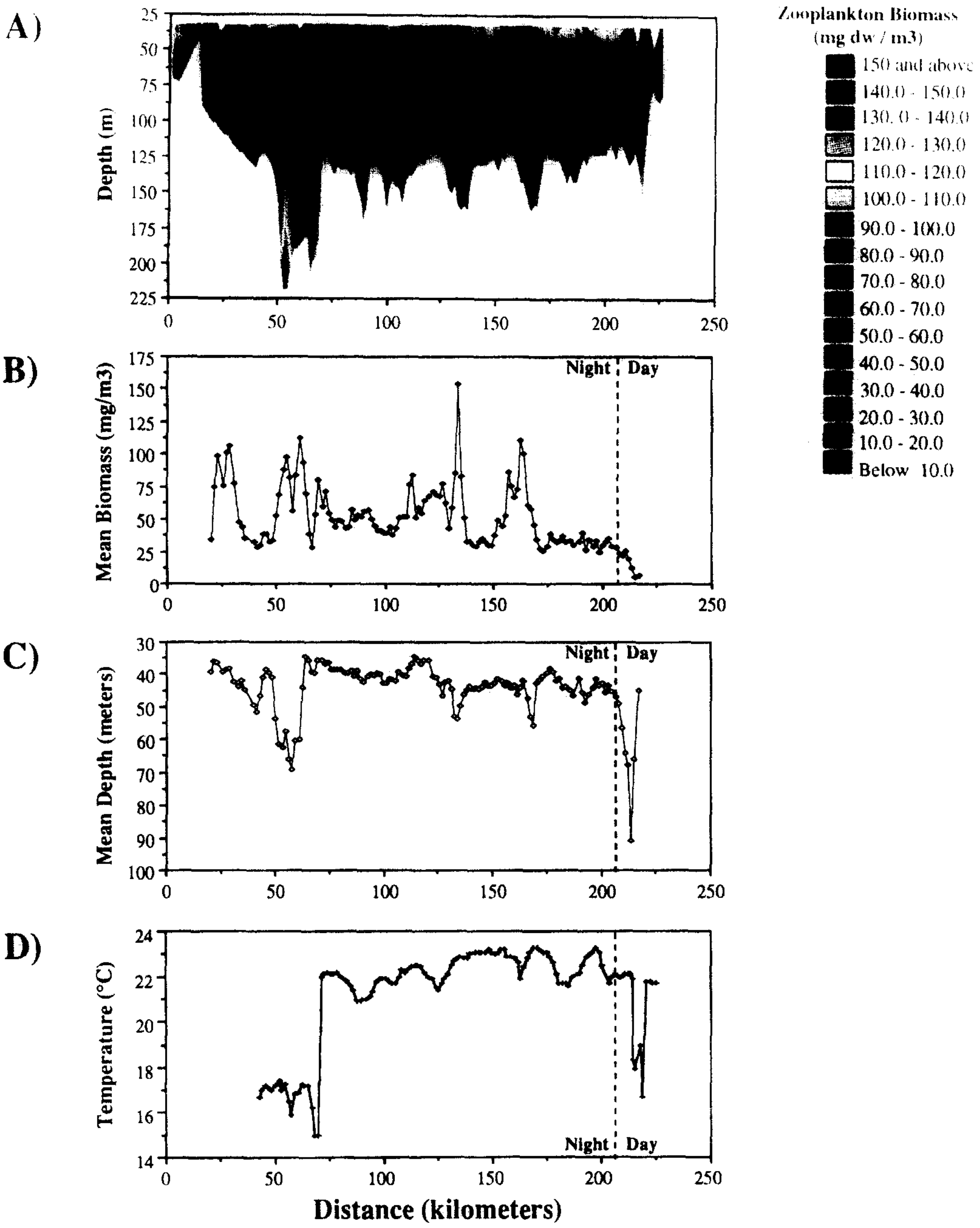

Fig. 4. (A) Biomass measured by the ADCP along a N–S transect during Leg 2 of the cruise (10–11 October 1988). Highest biomass (150 mg dw m^{-3}) is indicated by red shading and lowest biomass (below 10 mg dw m^{-3}) is indicated by blue shading. The biomass variations reflect passage through water masses of varying origin. (B) Mean biomass over the 20–100 m depth interval for the N–S transect. Mean biomass was calculated only for those profiles where data extended to at least 100 m. (C) Mean depth over the same 20–100 m interval for the N–S transect. (D) Sea surface temperature measured by the SAIL system for the N–S transect.

Zooplankton biomass along this N–S transect (Fig. 4A) showed substantial variation in both magnitude and distribution. These variations were associated with changing water types surveyed along the section (Fig. 4D). For example, the section crossed the outer continental shelf–slope (100–2000 m) within approximately the first 50 km of the transect, and showed maximum biomass near the surface which was apparently related to a slope water intrusion onto the shelf (seen in the satellite image for this date, not presented here). Slightly farther offshore, between 50 and 65 km, the biomass shows a deep maximum and greater vertical structure coinciding with the position of the shelf–slope front. The next 120 km (between 60 and 180 km) are characteristic of slope water zooplankton distributions. The deeper penetrations of zooplankton at 135 and 170 km coincide with a slightly cooler water mass containing either water of shelf origin or water upwelled from within the Slope Water, both of which should have elevated zooplankton concentrations. Near the end of the transect at ~205 km there was a sudden decrease in and deepening of biomass coinciding with dawn, a time at which zooplankton normally start their downward diel migration. The cold water observed at ~215–225 km was probably a filament of shelf water associated with the northern edge of the Gulf Stream. The calculated descriptors (mean biomass and mean depth) reflect the above changes. Mean biomass increased where the biomass contours indicate both higher levels of biomass and a deeper distribution (Fig. 4B). The mean depth descriptor showed the changes in depth distribution, with deeper mean depths found at the frontal locations (Fig. 4C).

Distribution of biomass in the water column in the Slope Water and Sargasso Sea

The biomass data collected using the ADCP are similar to conventionally collected data in that estimates of biomass at specific depths in the water column can be obtained using both methods. As discussed above, we have chosen to represent the depth distribution of biomass through the use of the mean depth statistic and to reduce much of the data to regional means. However, to demonstrate the effectiveness of the ADCP in describing regional biomass distributions, we present average biomass profiles for the Sargasso Sea and the Slope water from Leg 1 (21 September–5 October) (Fig. 5). Biomass values estimated by the ADCP were averaged over 20 m depth intervals separately for day and night. Between 773 (minimum) and 3458 (maximum) observations were used in calculating each mean. Both diel and regional patterns in the vertical distribution and concentration of biomass were observed. In the Sargasso Sea, biomass increased with depth, during both day and night, while in the Slope Water the biomass maximum was at 60–80 m during the day but in the 20–40 m depth range at night. Biomass more than doubled in the 20–100 m layer at night in the Sargasso Sea, while the contrast between day and night biomass levels was not as dramatic in Slope Water. The Slope Water biomass concentrations were at least double those of the Sargasso Sea for all depth intervals (Fig. 5). The frequency distributions for different levels of biomass at specific depth intervals during day and night for the Sargasso Sea and the Slope Water during Leg 1 (21 September–5 October) showed similar patterns (Fig. 6A,B). Low biomass was observed in the Sargasso Sea at all depths in the 20–100 m range during the day, with highest biomass found at 50–100 m. During the night, maximum biomass remained at depth, however there were occurrences of higher biomass levels in the upper part of the water column and the frequency distributions were more diffuse. Biomass levels in the Slope Water were more variable than in the Sargasso Sea. During the day in the Slope Water, high biomass levels

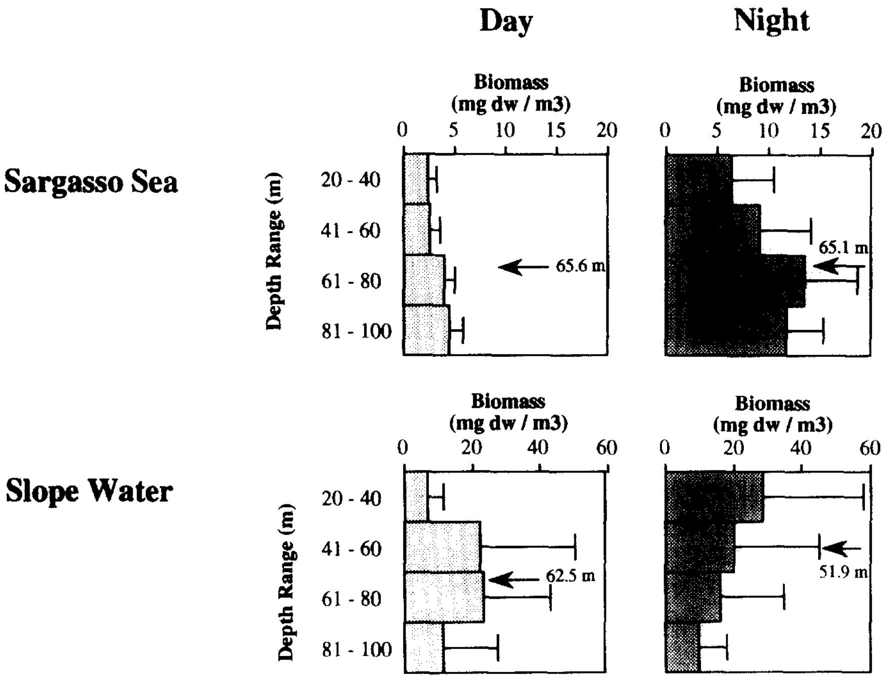

Fig. 5. Distribution of biomass with depth for Leg 1 in the Sargasso Sea and Slope Water. Day and night data are presented separately. Mean biomass for each depth interval is shown with error bars representing standard deviations. The mean depth for each profile has been calculated and is noted on the graphs with the arrow and text.

were generally at mid-depths (60–80 m), while at night high biomass was in the upper layers (20–60 m).

Zooplankton biomass estimates measured by other investigators (Ortner *et al.*, 1980; Roman *et al.*, 1985; Allison, 1986), using the MOCNESS plankton net system and displacement volume techniques, were compared with our results. Biomass observations measured from individual net samples for the Slope Water and Sargasso Sea were compared to the 20 m averages of ADCP measured biomass values, with day and night analysed separately (Fig. 7) (ADCP biomass was converted from dry weight to displacement volume using equation (1)). The biomass levels obtained using the ADCP were usually of similar orders of magnitude to those observed previously (Ortner *et al.*, 1980; Roman *et al.*, 1985; Allison, 1986). The observed differences were not consistently associated with a particular region or time. For example, ADCP measured biomass estimates were approximately double the net measured biomass estimates in both the Slope Water during the day and the Sargasso Sea at night. The distribution of biomass with depth was similar in the Slope Water for both time periods, however the depth distribution measured using the ADCP in the Sargasso Sea at night was dissimilar to the distributions obtained from the net tows (there was no consistent shape to the biomass distribution during the day in the Sargasso Sea between any of the studies). Some of these discrepancies may be attributed to seasonality, since the month of sampling in these studies varied through the year. Most previous studies measured only the >333 μm biomass, while the present ADCP estimates were calculated from a calibration fit using samples collected with 150 μm nets. This may account for the greater magnitude of biomass observed in some plots. Furthermore, the number of observations used in the present study vastly exceed the numbers obtained in earlier studies (usually a single net tow).

Cross-stream/regional trends

The Sargasso Sea region was characterized by consistently low biomass concentrations; the Slope Water region was associated with higher concentrations and greater variability; and the Frontal Region was intermediate or transitional between the two. Mean biomass between 20 and 100 m decreased across the Gulf Stream from north (Slope Water) to south (Sargasso Sea) during both day and night (Fig. 8A–C). The mean biomass estimates in the three regions (Slope Water, Frontal Region, Sargasso Sea) were significantly different during both day and night (analysis of variance, $P < 0.0001$, Student–Newman–Keuls test, $P < 0.05$), with the exception of daytime when biomass levels in the Sargasso Sea and Frontal regions were not statistically different (Table 1A). Biomass in the Slope Water was usually at least double that observed in the Sargasso Sea (Slope Water:Sargasso Sea ratio of average mean biomass = 4.7 and 1.9 for day and night, respectively), with the Frontal Region being intermediate (Frontal Region:Sargasso Sea ratio of average mean biomass = 1.3 and 1.1 for day and night).

Variability in biomass within each region (day and night considered separately) also decreased across the Gulf Stream from north to south, with concentrations in the Sargasso Sea region being the most consistent (least patchy) and those in the Slope Water being the most variable (Fig. 8A–C, Table 1A). The coefficients of variation in the Slope Water were approximately 2.5 times greater than those observed in the Sargasso Sea. Within each region, biomass levels were more variable during the night than during the day.

The mean depth statistic was an indicator of the depth at which the zooplankton biomass was found within the vertical range considered by the analysis. Regional and cross-stream differences in the mean depth were found, with zooplankton biomass usually being deeper in the Sargasso Sea than in the Slope Water and at intermediate depths in the Frontal Region ($P < 0.0001$) (Fig. 8D–F, Table 1B). An exception was observed during daytime when the Slope Water and the Frontal Region had similar average mean depths (Student–Newman–Keuls test, $P < 0.05$; Table 1B). In both the Slope Water and the Frontal Region, the average mean depth was greater during the day than during the night (Table 1B; $P < 0.0001$). In contrast, the average mean depth in the Sargasso Sea was the same (~67 m) during both day and night.

If biomass were vertically homogeneous, then the mean depth would be the center of the depth range under consideration, in this case 60 m. Accordingly, the average mean depths from the three regions, for both day and night (Table 1), were compared statistically to 60 m. The average mean depth was significantly different from 60 m for all three regions during both day and night ($P < 0.01$, t-test; ZAR, 1984).

The mean depth was more variable in the Slope Water than in the Sargasso Sea, with the coefficients of variation in the Slope Water being three to four times greater than those found in the Sargasso Sea (Table 1B). The Frontal Region was intermediate between the Slope Water and the Sargasso Sea in the magnitude of variation (3.3 and 1.94 times greater than in Sargasso Sea). No consistent day versus night pattern in the magnitude of variation was observed.

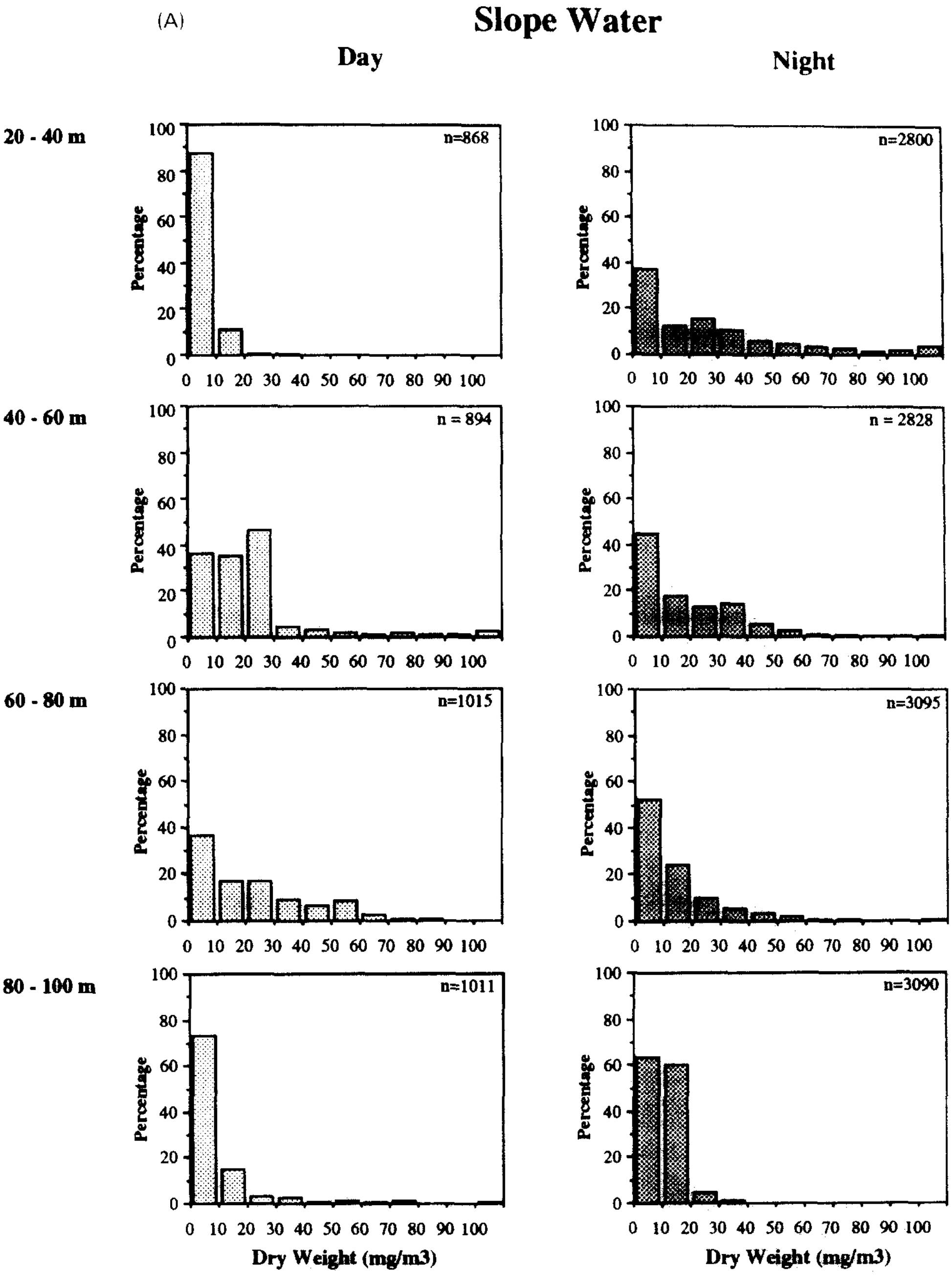

Fig. 6. Frequency distribution of biomass categories in four depth ranges for (A) the Slope Water, and (B) Sargasso Sea. Day and night data presented separately.

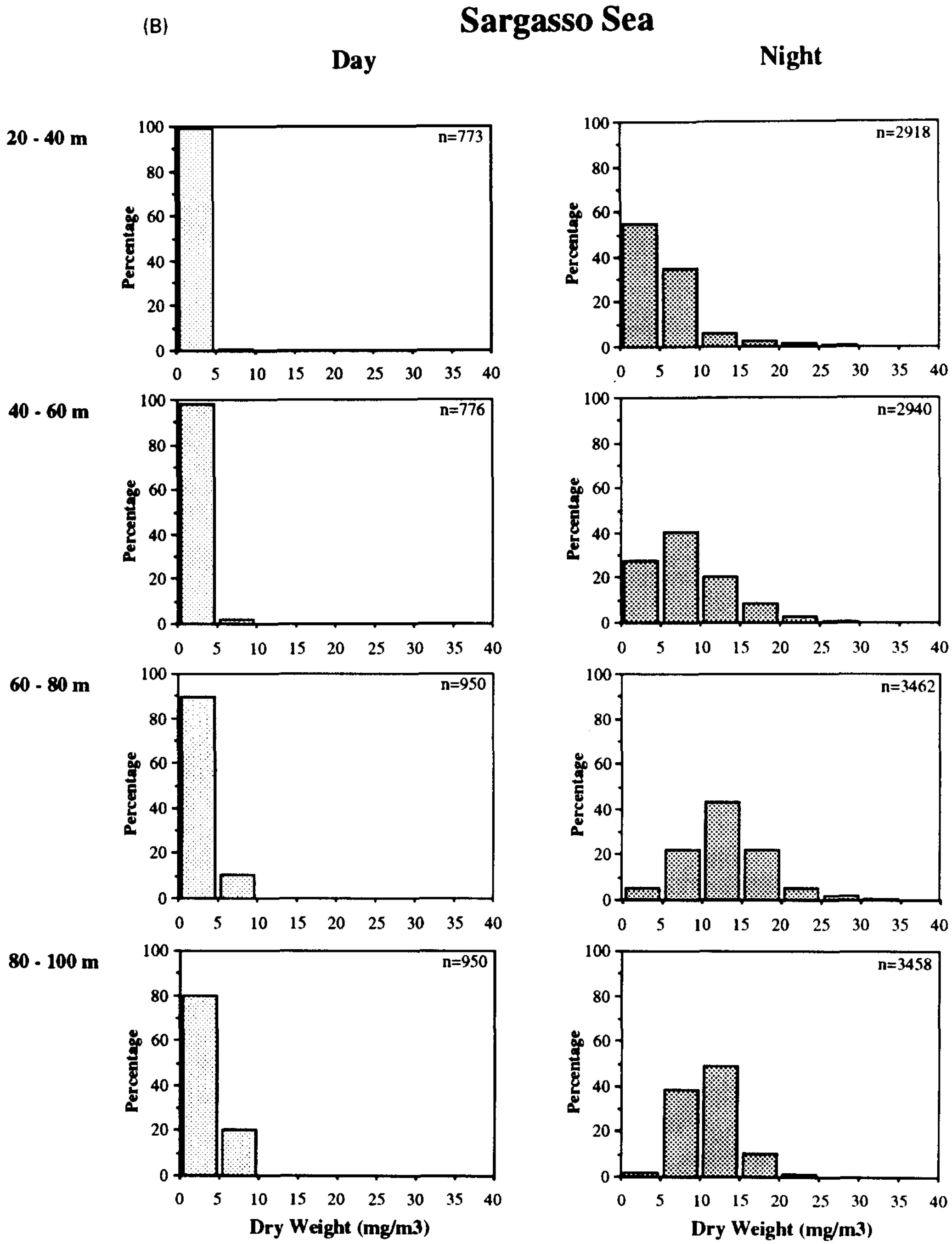

Fig. 6. *Continued*

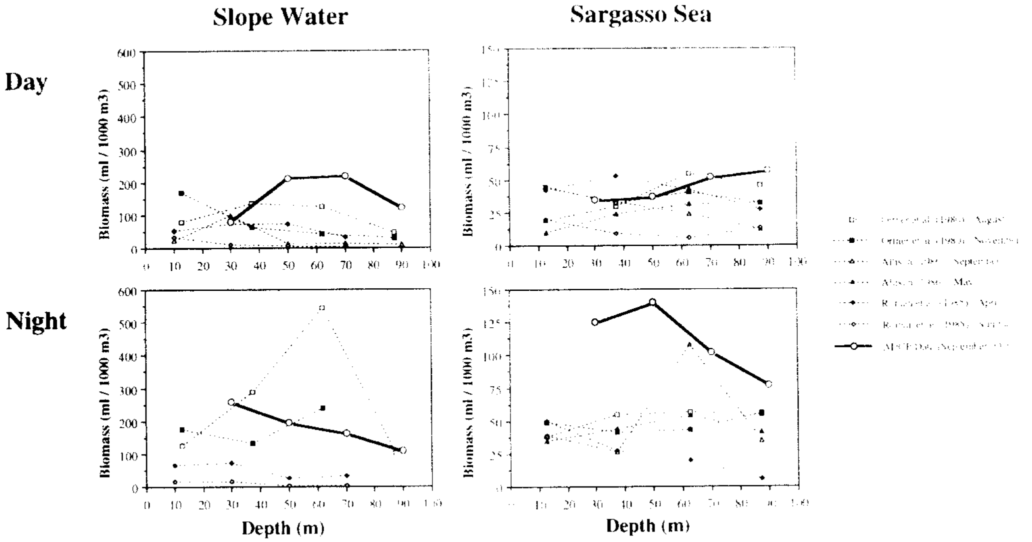

Fig. 7. Comparison of magnitude and depth distribution of mean ADCP biomass with observations from previous studies for the Slope Water and Sargasso Sea. The number of observations used in estimating each value for the previous studies range from one to three while the number of observations used in calculating the means for the ADCP data range from 868 to 3095 for the Slope Water and 773 to 3463 for the Sargasso Sea.

Sea surface temperature variation

Although sea surface temperature differences between the three regions are not typically large during September and October, comparison of the sea surface temperature with cross-stream position during Leg 1 demonstrates the change associated with the three different regions (Sargasso Sea, Frontal Region and Slope Water), the variation in cross-stream location at which the sea surface temperature front is located (dependent on along meander location), and small scale, local variability (Fig. 9A). Sea surface temperatures were usually high within the Gulf Stream and Sargasso Sea, although temperatures of as low as 18°C were observed in this region. Lower temperatures (~23°C) were found in the Slope Water, with the cross-stream location of the sea surface temperature front being associated with the along-meander position of the transect. In the upwelling–divergent region of the meander (preceding the crest), the temperature front was farther away from the Gulf Stream axis (cross-stream position = 0 km) than in the downwelling–convergent region of the meander (following the crest). Anomalously low temperatures (~20°C) were recorded at some locations in the Gulf Stream (cross-stream distance ~10–20 km), which may be a consequence of filaments or eddies of colder water.

Biomass was expected to increase with decreasing temperature, since lower temperatures characteristic of Slope Water should be associated with higher biomass. Overall, higher biomass was found in the temperature range between 22 and 25°C, associated with the frontal zone and the Slope Water (Fig. 9B and C). Lower biomass was found at higher temperatures (26–28°C), associated with waters from the Sargasso Sea. The anomalously low temperatures (18–20°C) recorded at some locations in the Gulf Stream (Fig. 9A) were associated with biomass levels characteristic of the Sargasso Sea–Gulf Stream (Fig. 9C).

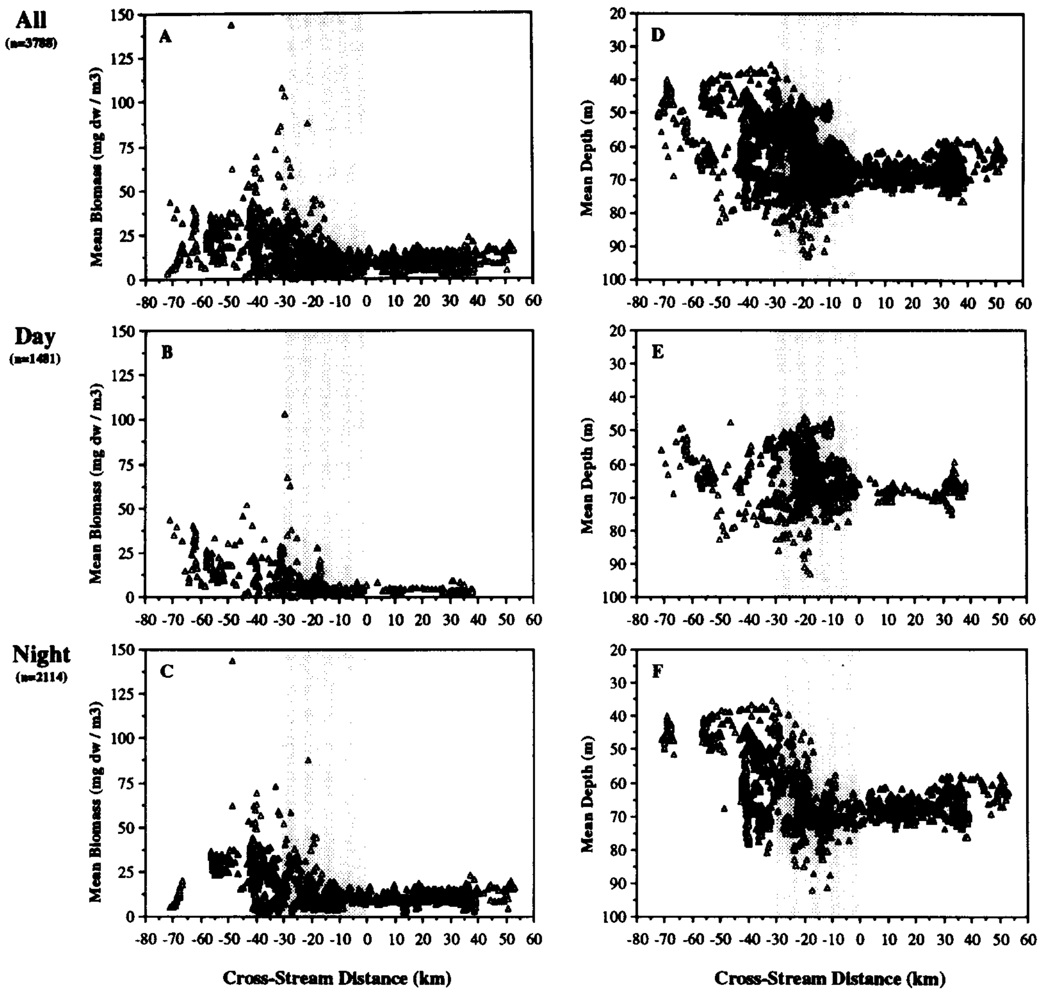

Fig. 8. Mean biomass and mean depth plotted as a function of cross-stream distance from data collected during Leg. 1. All data are plotted in the upper panel and day and night data are plotted separately in the lower two panels. The cross-stream location of the Frontal Region is indicated by the shading with the Slope Water to the left (negative cross-stream positions) and the Sargasso Sea to the right (positive cross-stream positions).

However, examination of the satellite images suggested no obvious feature associated with the low temperatures.

Temporal trends—diel vertical migration

Temporal variations in zooplankton biomass within each region resulted in part from diel vertical migration (Fig. 10A–C). Higher biomass was observed during the night period while significantly lower biomass was observed during the day. The pattern was especially striking in data collected in the Sargasso Sea where biomass at night was three times higher than that of the day (Fig. 10, Table 1A). The elevated variability in the zooplankton biomass found in both the Slope Water and the Frontal Region obscured the pattern somewhat in these regions, however the diel signature is still present. A secondary signal observed in these plots is a temporary enhancement of biomass at approximately or slightly preceding 09:00 GMT, corresponding to sunrise. This feature may be a result of the passage of zooplankton through the depth interval used in this analysis (20–100 m) from above (0–20 m) during downward migration, resulting in an enhanced biomass. A similar peak occurs in some of the plots just following sunset (21:00 GMT), perhaps because of elevated numbers of zooplankton migrating up through the 20–100 m depth range at that time.

There is no consistent diel pattern in mean depth (Fig. 10D–F). Although the mean depth within each region usually was different between day and night for each leg of the cruise (see above, Table 1B), the differences are not apparent in these plots (Fig. 10). A subtle change in mean depth may be found near sunrise and/or sunset in some plots, perhaps resulting from a sudden influx of migrating animals into the 20–100 m depth interval, however this pattern is not regular. Variation in mean depth is more obvious on the regional–spatial scale than on the temporal scale.

Meander-associated variation in zooplankton biomass

The biomass maps generated from 10 × 10 km binned data reveal both regional variability, especially a north–south biomass gradient, and meander induced variability in zooplankton biomass (Fig. 11). Higher biomasses were observed to the north, in the Slope Water and the Frontal Regions, relative to those in the Sargasso Sea, as discussed previously. Following the crest, enhanced biomass is observed in both the Frontal and Slope Water regions relative to the biomass observed at locations preceding the crest for both day and night data (analysis of variance, $P < 0.027$–0.0001; Fig. 8). These observations are consistent with the predicted convergence and entrainment of high

Table 1. Regional averages and coefficients of variation of (A) mean biomass and (B) mean depth. The number of observations included in each regional average is indicated in parentheses below the mean depth average. Notice that, because values from dawn and dusk are excluded from these averages, the total observations are lower than the total of the available profiles for each leg. Those regions having similar average mean biomass or average mean depths are indicated by symbols (, †, ‡). All other comparisons between regions were significantly different. All data sets distributed normally unless otherwise indicated by (§)*

			Day	Night
(A) Biomass (mg m^{-3})	Regional mean	Slope Water	15.9 ($n = 203$)	19.3 ($n = 620$)
		Frontal Region	4.4* ($n = 1012$)	11.3 ($n = 773$)
		Sargasso Sea	3.4* ($n = 190$)	10.1 ($n = 694$)
	Coefficient of variation	Slope Water	57.95	70.53
		Frontal Region	58.49	61.83
		Sargasso Sea	19.91	29.77
(B) Mean depth (m)	Regional mean	Slope Water	62.11‡	56.7
		Frontal Region	62.60‡	68.67
		Sargasso Sea	67.59†	67.49†§
	Coefficient of variation	Slope Water	11.24	20.82
		Frontal Region	12.28	9.17
		Sargasso Sea	3.74	4.72

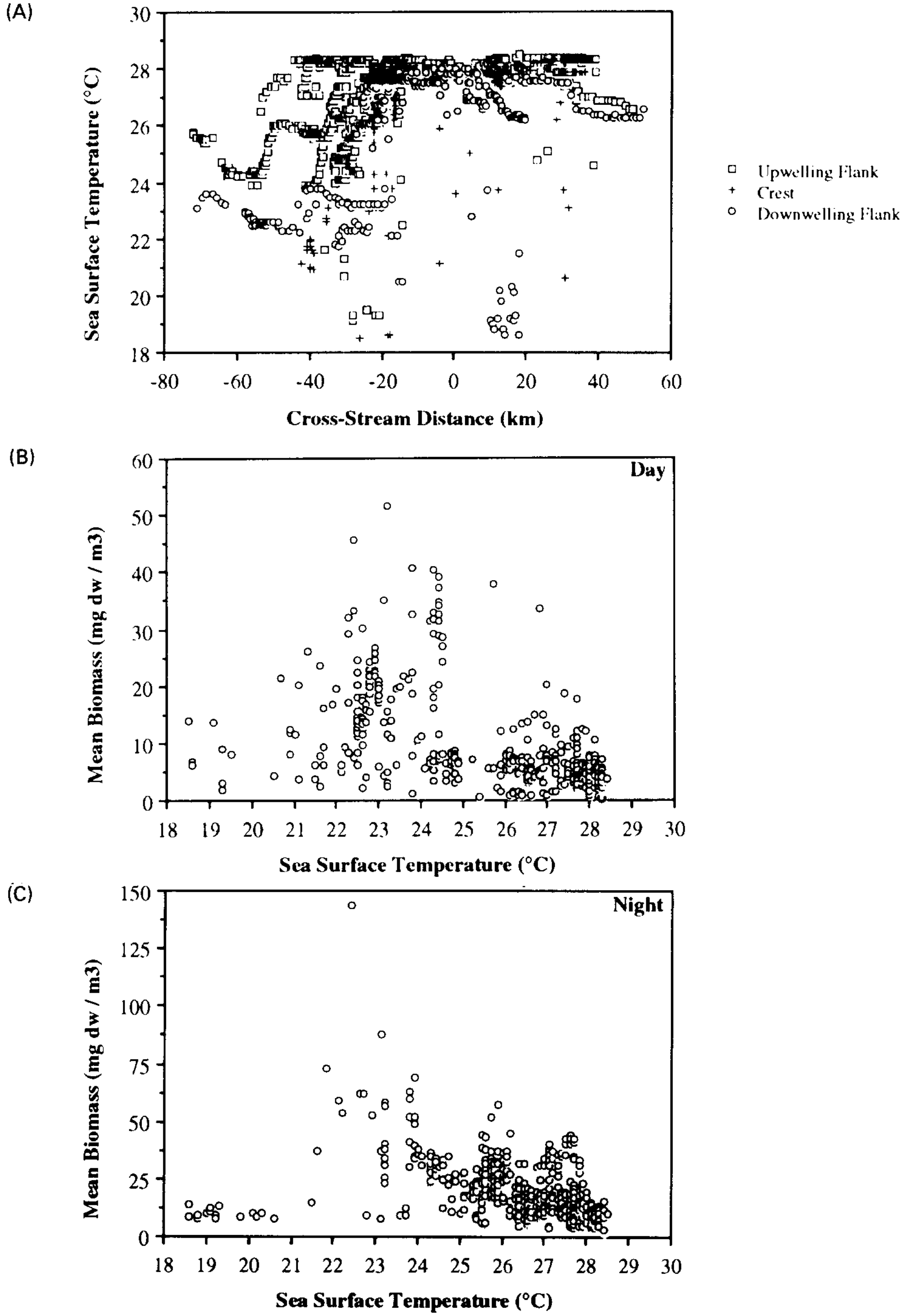

Fig. 9. (A) Sea surface temperature plotted as a function of cross-stream distance for Leg 1. Data collected in the upwelling flank, downwelling flank, and near the meander crest are differentiated with the symbols. The horizontal axis is as in Fig. 8. (B) Mean biomass plotted as a function of sea surface temperature for Leg 1 during the day. (C) Mean biomass plotted as a function of sea surface temperature for Leg 1 during the night.

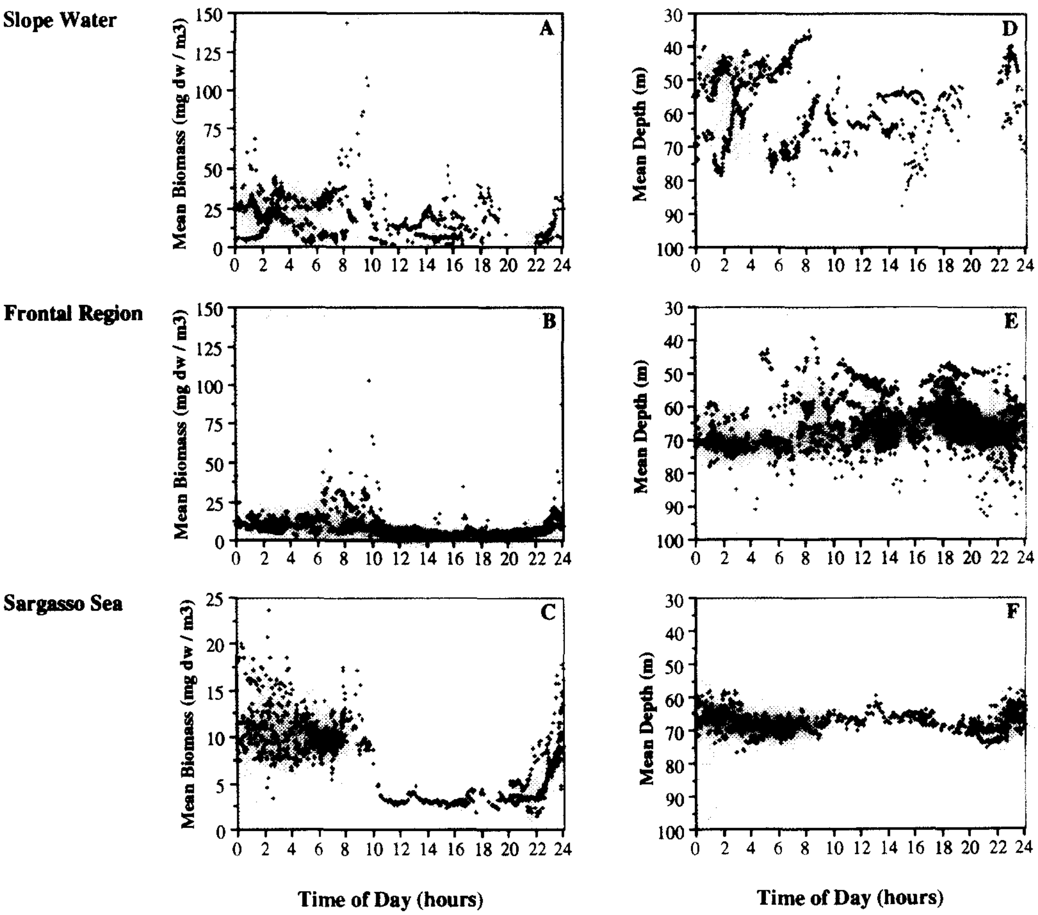

Fig. 10. Mean biomass and mean depth plotted as a function of time of day for the three cross-stream regions during Leg 1. Time is in Greenwich Mean Time (GMT). Local night is indicated by the shading.

biomass Slope Water into the meander in the region following the crest. In contrast, these differences were not observed during Leg 2, following the collapse of the meander.

Meander associated changes in the mean zooplankton depth also were observed (Table 2). For both day and night, the mean depth in the Slope Water was deeper in the region following the crest than in the region preceding the crest ($P < 0.0001$ (day), $P < 0.04$ (night)). If the predicted physical processes are present in the meander, the region following the crest should be characterized by downwelling and hence, depression of isotherms. Since some zooplankton species have preferred physical environments within the Gulf Stream and would tend to follow changes of the environment (Ashjian and Wishner, 1993), a deeper mean biomass depth is consistent with these predictions. However, this hypothesis was only true during the day within the Frontal and Sargasso Sea regions ($P < 0.0004$ and $P < 0.0001$, respectively). The mean depths before and after the meander crest during the night were similar for those regions.

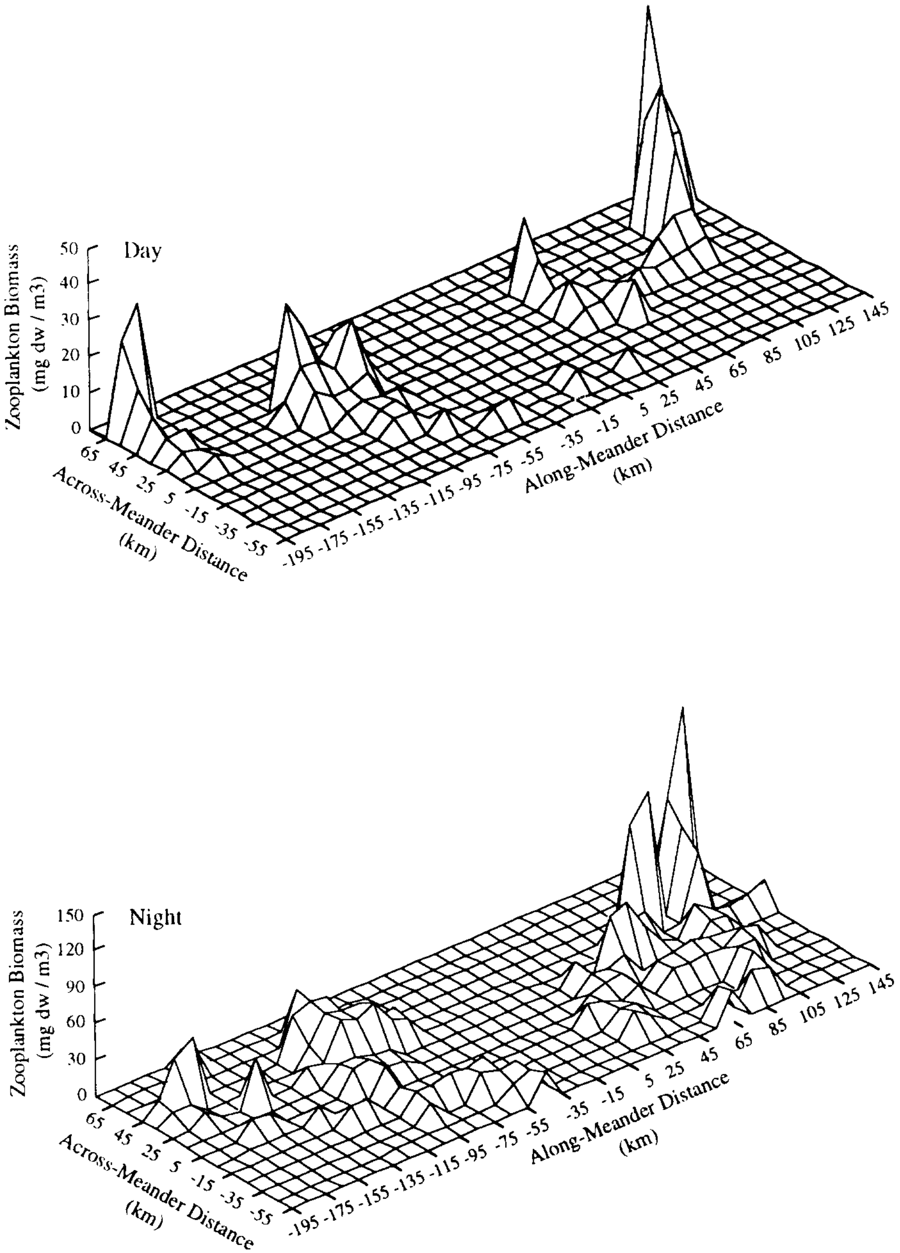

Fig. 11. Mean biomass (10 × 10 km bins) plotted as a function of along-meander and across-meander location for Leg 1 (day and night data plotted separately).

DISCUSSION

The Gulf Stream is a particularly complex, and therefore appealing, region in which to demonstrate the feasibility of the ADCP as a zooplankton sampling instrument, since cross-stream location, diel vertical migration, and advection (both that associated with the normal Gulf Stream and that associated with meander or eddy formation, for example) all interact to produce the local zooplankton biomass field. It has been difficult or impossible to adequately describe this zooplankton biomass field previously with conventional instrumentation or sampling techniques, however the spatially and temporally broad coverage of the ADCP permits us to approach a more complete description. Reduction of the data to regional or mesoscale averages has allowed us to identify regional, diel and meander associated patterns in the distribution of zooplankton biomass consistent with previous results and with hypotheses based upon meander-associated advection.

The dominant signal in the zooplankton biomass was the regional variation in the magnitude of biomass among the Slope Water, the Frontal Region, and the Sargasso Sea. Previous investigators have identified a similar gradient in biomass between the regions (CLARKE, 1940; GRICE and HART, 1962; BÉ *et al.*, 1971; ORTNER *et al.*, 1978, 1980; ROMAN *et al.*, 1985; ALLISON and WISHNER, 1986). Although methods and temporal scales differed between these studies, comparison of results can be accomplished through reduction of the biomass values to ratios relative to those found in the Sargasso Sea. Accordingly, Slope Water biomass was approximately four times greater than Sargasso Sea biomass in most studies (mean = 3.97, range: 0.25–15.0). A similar pattern was observed in the present study where the average Slope Water biomass was 3.49 times greater than that observed in the Sargasso Sea (both day and night considered). Few previous studies differentiated between the Gulf Stream and the Sargasso Sea but those that did reported equivalent (BÉ *et al.*, 1971) or somewhat enhanced biomass (1.25) in the Gulf Stream, especially near the North Wall (1.90) (ALLISON and WISHNER, 1986). In the present study, biomass in the Frontal Region was approximately twice that in the Sargasso Sea, however the Frontal Region included the North Wall and, potentially, Slope Water so that the relatively higher biomass found in that region was not surprising. The data collected using the ADCP, therefore, corresponds well with previous studies of variations in biomass associated with water masses. However, none of the previous studies have documented this regional pattern with as many observations nor with the spatial and temporal resolution possible in this study.

One of the great advantages of continuous, acoustic sampling methods, such as the ADCP, is that a measure of the variability or patchiness of zooplankton biomass is

Table 2. Mean depths for the three cross-stream regions before and after the crest of the meander. Mean depth is in meters. Numbers in parentheses refer to the sample size. The significance level (P) *for the before and after crest comparisons (analysis of variance) are indicated*

		Mean depth (m)		
		Before crest	After crest	*P*
Slope Water	Day	57.7(84)	65.2(119)	0.0001
	Night	56.6(611)	64.9(9)	0.0400
Frontal Region	Day	61.9(624)	63.7(388)	0.0004
	Night	68.9(516)	68.1(257)	0.0860
Sargasso Sea	Day	67.2(176)	72 (14)	0.0001
	Night	67.4(565)	67.5(219)	0.6160

obtained. We have not attempted detailed analysis of this variability in the present study. However, the coefficients of variation demonstrated that the distribution of zooplankton biomass is more variable, or patchy, in the Slope Water, than in the Sargasso Sea. Few studies have documented the variability of zooplankton biomass in these regions or have demonstrated that the patchiness of zooplankton biomass varies between the regions, as in the present study. Previous investigators have quantified the patchiness of 70 kHz acoustic scattering (nekton) (Nero and Magnuson, 1989; Nero *et al.*, 1990), and it should be possible to describe patchiness in the zooplankton biomass using ADCP data. Furthermore, because ADCPs have been installed on many oceanographic vessels, measures of this type may be obtained from many regions without the procurement of specialized equipment.

Vertical distribution of zooplankton

Although not specifically addressed in this study, our limited analysis demonstrates the utility of the ADCP in documenting the distribution of zooplankton biomass with depth. Both the contour plot (Fig. 4) and the mean biomass vs depth plots (Fig. 5) demonstrate that conventional measures of zooplankton biomass are feasible using the instrument. The biomass measurements obtained with the ADCP, furthermore, are comparable in magnitude and depth distribution to those documented in similar regions by previous investigators (Fig. 7) (Ortner *et al.*, 1978, 1980; Roman *et al.*, 1985; Wiebe *et al.*, 1985; Allison, 1986). The advantage of the ADCP is the relative ease with which large numbers of observations can be collected, allowing a more reliable estimate of the temporal–spatial variability of zooplankton biomass distributions.

One potential disadvantage to using the ADCP in documenting zooplankton biomass is the inability of the ship-mounted instrument to produce data within the top portion (20 m in the present study) of the water column. The contribution of this depth range to overall biomass is variable. Previous studies have documented that from 10 to 39% in the Sargasso Sea and 12–55% in the Slope Water of total biomass in the 0–100 m depth range was actually in the 0–25 m depth range (day and night combined) (Ortner *et al.*, 1980; Roman *et al.*, 1985; Allison, 1986). Measurements of biomass (11 stations) in top 20 m from the BIOSYNOP study are available only from locations in the Slope Water and Frontal Region. The proportion of biomass in this depth range varied (6–48%), however for some locations a substantial proportion (>40%) of the total biomass in the 0–100 m depth range was in the 0–20 m interval (Napp and Ortner, personal communication). Although the inability to measure biomass from this depth range is unfortunate, many features were clearly observed and the utility of the ADCP in documenting mesoscale and regional biomass distributions has been demonstrated.

The similarity in results between the previous studies and our study was encouraging, particularly since the ADCP biomass data utilized in this analysis extends only over a small portion of the total water column. Most previous studies measured biomass over the 0–200 m depth range and our limitation to the 20–100 m range potentially could have resulted in a different regional pattern. However, previous studies have also demonstrated that a substantial portion (19–47.1%) of the 0–1000 m water column biomass in the Gulf Stream, Sargasso Sea, and Slope Water is found in the top 200 m, suggesting that biomass measured in that depth range accurately reflects water column trends (Ortner *et al.*, 1978; Allison and Wishner, 1986). The patterns in the regional distribution of biomass described in our investigation were similar to those observed in studies in which biomass was measured over a greater portion of the water column.

The use of the mean depth statistic, or vertical center of biomass, was an effective means by which to express the distribution of biomass in the water column. The mean depth was well below the upper limit to our depth range (20 m) for all three regions and documented a subsurface zooplankton biomass peak. A persistent subsurface biomass peak in the 20–100 m range has been observed previously for the Slope Water, Gulf Stream, and Sargasso Sea (ORTNER *et al.*, 1978, 1980; ALLISON and WISHNER, 1986). Although our operational depth range was limited, we were successful in identifying a similar peak.

Diel migration patterns

The diel vertical migration of zooplankton was a distinct feature of the biomass data. The signal was clearest in the Sargasso Sea and less clear in the Slope Water, perhaps because spatial variability (i.e. patchiness) was greater in the Slope Water. The night:day ratio of zooplankton biomass at a particular location both reflects the intensity of the vertical migration (ORTNER *et al.*, 1978) and allows comparison of the migration intensity between different studies. In the present study, the magnitude of change (night:day ratio) between day and night mean biomass was similar in the Sargasso Sea and Frontal Regions (3.0 and 2.6, respectively) and lower in the Slope Water (1.2) (Table 1). Differences in the magnitude of change between the regions may be a consequence of a greater proportion of the total water column biomass being found in the 20–100 m depth range in the Slope Water than in the Sargasso Sea and Gulf Stream (see above; ALLISON, 1986). The magnitude of the night:day ratio (and hence diel biomass change) has been observed previously to be greatest in the Sargasso Sea and lowest in the Slope Water in some investigations (e.g. WIEBE *et al.*, 1985; ALLISON and WISHNER, 1986) while the reverse was observed during other studies (e.g. ORTNER *et al.*, 1980; ROMAN *et al.*, 1985). Differences in the ratio between regions have been suggested to be artifacts in the data because of increased or more effective net avoidance during the day, with the effect being more pronounced in some regions, and probably dependent on the type of sampling gear utilized (WIEBE *et al.*, 1985). However, net avoidance is not a factor in the data collected with the ADCP. The differences observed in the intensity of diel vertical migration between the three regions in the present study may thus be attributed to differences in the distribution and natural behavior of the zooplankton populations from each region.

Meander-associated patterns

The distribution of zooplankton biomass documented in the Gulf Stream meander during Leg 1 (21 September–5 October) was consistent with enhancement of biomass predicted for Gulf Stream meanders (BIOSYNOP, 1987; HITCHCOCK, 1988; OLSON, 1990). According to the BIOSYNOP hypothesis (*op. cit.*), entrainment of Slope Water, and higher abundances of plankton, should occur in the region of the meander following the crest. The region preceding the crest, in contrast, should be characterized by upwelling and detrainment of Gulf Stream water to the north, diluting zooplankton abundances in that region with Gulf Stream–Sargasso Sea water characterized by low levels of biomass. The maps of zooplankton biomass generated from the ADCP measurements support the hypothesized entrainment and detrainment processes in Gulf Stream meanders. For both day and night, higher biomass was observed to the north of the Stream axis in the flank of the meander following the crest, where Slope Water entrainment should occur, relative to biomass levels in the region preceding the crest.

In some instances, the mean depths of the zooplankton biomass on the two flanks of the meander suggested that meander-induced upwelling and downwelling may have influenced the distribution of biomass. Mean depths during the day were shallower on the western (upwelling) flank in all three cross-stream regions relative to the mean depths observed on the eastern (downwelling) flank. The signal was only observed during the day, however, perhaps because of day–night differences in the species composition of the plankton and their preferred environments. Copepod species in the Gulf Stream have been demonstrated to have strong fidelity to particular environmental conditions such that their distributions change as the depth of the preferred environment changes (WISHNER and ALLISON, 1986; ASHJIAN and WISHNER, 1993). This observed elevation of the mean depth of the zooplankton biomass may correspond to a shoaling of the preferred environment of the zooplankton because of upwelling of isopycnals on the eastern flank.

Similar changes in the depth distribution of both chlorophyll and nekton and in the depth of σ_θ surfaces along the meander also were observed. The biomass of nekton measured with downward-directed, three frequency (38, 70 and 200 kHz) towed sonar was found to be more diffuse across the Gulf Stream front in the upwelling–divergent region of the meander, with a distribution of scatterers near the surface (20–40 m), compared to the downwelling–convergent region where biological scatterers were more concentrated and were located deeper in the water column at 80 m (ARNONE *et al.*, 1990). Maximum chlorophyll concentrations were deeper on the eastern (downwelling) flank (75–100 m), than on the western (upwelling) flank (0–50 m) and coincided with the deepening of the 24.4–25.7 σ_θ surfaces from west to east (HITCHCOCK *et al.*, 1993).

Analysis of the relative abundances of some Slope Water and Sargasso Sea copepod species during the BIOSYNOP study supported the meander-associated transfer of water parcels (ASHJIAN, 1993). The upwelling flank of the meander and regions in the Slope Water to the north of the front along that flank were characterized by a relatively, and surprisingly, high proportion of Sargasso Sea species, especially relative to the proportions observed on the downwelling flank, where Slope Water species dominated at all locations to the north of the Gulf Stream axis (ASHJIAN, 1993). These results suggested that upwelling and detrainment of water parcels, and intrinsic plankton species, was occurring in the upstream flank of the meander while the opposite process (entrainment of Slope Water) was occurring in the downstream flank of the meander. These observations converge in a common hypothesis of meander-induced upwelling and downwelling.

In contrast to the ADCP zooplankton biomass data, biomass measured during the BIOSYNOP cruise with the more conventional method of net tows and displacement volume did not indicate a meander effect, although a similar north–south gradient in biomass was documented (J. NAPP, personal communication). The difference between the two conclusions may be a consequence of the low number of observations obtained with the conventional methods. The high variability of the biomass measured with the ACDP suggests a patchy distribution. Measurements collected using the MOCNESS may not have resolved the zooplankton distributions because the relatively low number of samples obtained and the (relatively) small area sampled may result in net tows missing the regions of higher biomass. Comparison of the ADCP data collected both during and between the MOCNESS tows within a particular region indicates that the segments sampled with the nets were, in fact, characterized by lower biomass than other segments of the cruise track. (Because biomass values measured during the MOCNESS tows were used to derive the calibration equation for the ADCP, the biomass estimates from the two methods for the periods during the tows are virtually the same.) This comparison emphasizes the advantages of using the ADCP in measuring zooplankton biomass.

Enhancement of phytoplankton and zooplankton biomass associated with Gulf Stream meanders was originally hypothesized to result from one of two processes: advection and concentration of plankton by physical processes or a production (primary and secondary) response to elevated nutrients that would occur in the upwelling region (BIOSYNOP, 1987; Hitchcock, 1988; Olson, 1990). However, studies measuring production in the meander did not detect a meander-associated enhancement of rates so it is unlikely that the observed higher biomass levels were a response to elevated primary and secondary production (Lohrenz *et al.*, 1993). Furthermore, the time period during which a zooplankter would transit a meander (~7 days) is too short to stimulate a reproductive response. Therefore, the mechanism producing the observed biomass enhancement and change in species composition was probably advection of high biomass Slope Water into the Gulf Stream region on the downwelling flank. These observations suggest that, at least for this meander, changes in biomass and species composition were primarily influenced by meander-associated advection.

In conclusion, Gulf Stream meanders are regions where localized enhancement of zooplankton biomass should occur as a consequence of the physical exchange of fluid associated with the meandering of the current. Elevated biomass was documented in the downwelling flank of the meander which was consistent with the entrainment of Slope Water and fluid convergence hypothesized to occur at that location. The use of the ADCP to measure zooplankton biomass afforded us the opportunity to successfully document this biomass enhancement because of the broad spatial and temporal range of the data collected using the instrument. In contrast, conventional methods of measuring biomass (net tows) were not successful in identifying a similar pattern in the meander, perhaps because of the spatial patchiness of the biomass distributions. Furthermore, biomass measurements obtained using the ADCP were based on much greater sample sizes than those obtained in previous studies, allowing reliable estimates of the variability of the biomass. The ADCP has been demonstrated to be an effective and valuable method of describing the distribution of zooplankton biomass.

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