

Trends in copepod species abundances across and along a Gulf Stream meander: evidence for entrainment and detrainment of fluid parcels from the Gulf Stream

CARIN J. ASHJIAN*

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Abstract—Abundances of zooplankton populations are hypothesized to change across and along Gulf Stream meanders in response to meander-associated physical processes. Upwelling and northward detrainment of Gulf Stream water occur upstream of the meander crest (trailing flank) while downwelling and entrainment of Slope Water into the Gulf Stream occur downstream of the meander crest (leading flank). Two mesoscale zooplankton surveys of a Gulf Stream meander were conducted in autumn 1988 as part of the BIOSYNOP program to identify cross-stream trends and meander-associated changes in species abundances. The abundances of eight selected copepod species (five Sargasso Sea species, two Slope Water species and one widespread species) were enumerated from samples taken along three transects at different locations along the meander. The integrated abundances (0–1000 m) of seven of the selected species support the hypothesized entrainment and detrainment. Sargasso Sea species were more abundant across the upwelling flank than across the downwelling flank, whereas the opposite was true for Slope Water species. Species abundances on a trailing flank transect (upstream of the upwelling region) demonstrate effective transport of Sargasso Sea/Gulf Stream species out of the current into the Slope Water. The relative proportions of two copepod species (*Pleuromamma borealis* and *P. gracilis*) were sensitive to the processes of entrainment and detrainment in the meander, suggesting that these two species are useful indicator species of their respective water masses. Gulf Stream meanders may be sites of cross-stream exchange of plankton populations between the Sargasso Sea and the Slope Water.

INTRODUCTION

THE Gulf Stream separates the warm, oligotrophic Sargasso Sea to the south from the colder, nutrient-rich Slope Water to the north. Originally, the current was regarded as a distinct biogeographical boundary separating the cold, Slope Water fauna to the north and west from the warm water, Sargasso Sea assemblages to the south and east (GRICE and HART, 1962; HURLBURT, 1964; BACKUS *et al.*, 1970; JAHN and BACKUS, 1976). However, recent studies indicate that considerable cross-stream mixing of plankton may be occurring both by the formation of warm- and cold-core rings (RING GROUP, 1981; JOYCE *et al.*, 1984) and by other physical processes such as the formation of shingles and streamers (GARFIELD and EVANS, 1987), "leakage" from the Stream at depths below the thermocline (BOWER *et al.*, 1985; WISHNER and ALLISON, 1986), and water transfer at meander crests and troughs (SHAW and ROSSBY, 1984; LEVINE *et al.*, 1986; BOWER and ROSSBY, 1989). The

*Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, U.S.A. Present address: Division of Oceanographic and Atmospheric Sciences, Brookhaven National Laboratory, Upton, NY 11973, U.S.A.

Gulf Stream appears to function as a leaky membrane (BOWER *et al.*, 1985), permitting some cross-stream exchange of water and, therefore, plankton populations.

Despite the importance of the Gulf Stream as a biogeographical boundary, there are few studies of the zooplankton within the current itself. ALLISON (1986), WISHNER and ALLISON (1986), ASHJIAN (1991), and ASHJIAN and WISHNER (1993) describe the distribution of 18 copepod species within the Gulf Stream for two sampling times. These studies suggest that certain copepod species are characteristic of particular water types and that the relative abundances of these species may be good indicators of water mass mixing.

Gulf Stream meanders are hypothesized to be features in which enhanced cross-stream transport of water parcels occurs (BOWER and ROSSBY, 1989). Abundances of plankton populations may change across and along a meander as a result of the physical processes (BIOSYNOP, 1987). Detrainment of Gulf Stream water (and plankton populations) into the Slope Water on the north and entrainment of Sargasso Sea water from the south with upwelling in the Gulf Stream may occur on the trailing edge (upstream of the crest), while the reverse pattern (entrainment of Slope Water into the Stream and detrainment of Stream water to the Sargasso Sea with downwelling in the Gulf Stream) is predicted for the leading edge (downstream of the crest) (BIOSYNOP, 1987; BOWER and ROSSBY, 1989) (Fig. 1). In the present study, regions of active upwelling/divergence and downwelling/convergence are called the upwelling (UF) and downwelling flanks (DF), respectively.

Two possible mechanisms have been suggested by which plankton abundances can be changed in the meander: (i) an advective response, where plankton populations act as passive particles and are redistributed in the meander flow field; and (ii) a population response to the upwelling of nutrients in the divergent regions of the meander (BIOSYNOP, 1987; FLIERT and DAVIS, personal communication). All life stages of zooplankton populations would be affected by the first mechanism but only eggs and young stages by the

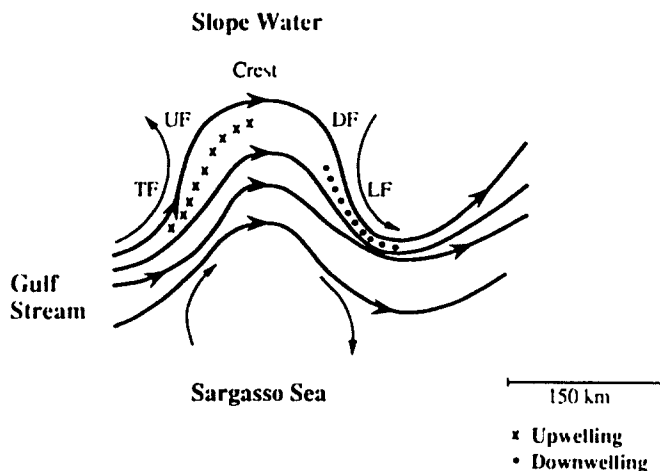


Fig 1 The different regions of a meander and associated physical processes. Upwelling, divergence of flow and detrainment to the north from the current may occur upstream of the meander crest. Downwelling, convergence and entrainment of Slope Water from the north may occur downstream of the crest. Regions of active upwelling and downwelling indicated by symbols. TF = Trailing Flank, UF = Upwelling Flank, DF = Downwelling Flank and LF = Leading Flank (Figure redrawn from BIOSYNOP, 1987)

latter, since the residence time of a population in a meander ($\sim 3\text{--}7$ days) is shorter than the generation time ($\sim 15\text{--}30$ days) (BIOSYNOP, 1987). Only adult stages of these populations were captured adequately by the nets used in this study, so the focus of the analysis is on the first mechanism.

The down- and cross-stream velocity fields of the Gulf Stream are spatially and temporally variable, with average downstream velocities ranging from $4\text{--}188\text{ cm s}^{-1}$ at the surface to $17\text{--}18\text{ cm s}^{-1}$ at 1000 m (HALKIN and ROSSBY, 1985). Average cross-stream velocity fields are an order of magnitude lower than the downstream velocities ($0.3\text{--}10\text{ cm s}^{-1}$), with entrainment into the current occurring from both sides (HALKIN and ROSSBY, 1985). The observed distribution of a copepod species should be the result of both the advective movements of water parcels and the individual behavior of the animal (e.g. vertical migration), which subjects it to different transport regimes. Animals with deeper distributions will experience lower downstream velocities than animals found near the surface, while vertical migrators should experience both high and low downstream velocities during a 24 h period.

This study describes the cross- and along-meander abundance trends of eight "indicator" copepod species to demonstrate: (1) how abundances of adults of selected copepod species change across the Gulf Stream and along the meander; and (2) if changes in the relative abundances of warm- and cold-water species occur in response to physical processes. According to the hypothesized transport processes, loss of water parcels to the north should be indicated by enhanced abundances of Gulf Stream/Sargasso Sea species in the upwelling region, while entrainment of Slope Water should be reflected in enhanced abundances of Slope Water species in the downwelling region of a meander. The species selected for study are characteristic of either the Slope Water or the Sargasso Sea, have distributions strongly associated with specific physical characteristics, and show cross-stream abundance trends that follow the pattern observed by WISHNER and ALLISON (1986), ASHJAN (1991), and ASHJAN and WISHNER (1993). None of the eight species were found exclusively in the Gulf Stream. However, due to the strong fidelity of the species to specific and characteristic physical conditions, it should be possible to use the species as tracers of particular water types.

METHODS

Sample collection

Plankton samples were collected during two mesoscale surveys of a Gulf Stream meander located due east of Delaware Bay (Table 1, Fig. 2). The surveys were conducted approximately 2 weeks apart in autumn 1989 from the R.V. *Cape Hatteras* as part of the BIOSYNOP program (BIOSYNOP, 1987; OLSON, in preparation). A second ship (the R.V. *Endeavor*) conducted physical surveys of the meander during the first 2 weeks. During each survey on the *Cape Hatteras*, zooplankton were collected on four or five transects across the different sections of the meander [Trailing Flank (TF), Upwelling/Divergent Flank (UF), Crest, Downwelling/Convergent Flank (DF), Leading Flank (LF)] (Fig. 1) according to the BIOSYNOP Zooplankton Group plan. Zooplankton samples were collected using a 1 m^2 , $150\text{ }\mu\text{m}$ mesh MOCNESS plankton net system (WIEBE *et al.*, 1976a), equipped with temperature and salinity sensors, from eight discrete depth intervals (0–50, 50–100, 100–150, 150–200, 200–400, 400–600, 600–800, 800–1000 dbars).

Table 1 Sampling data for the stations. "Mean eta" refers to the mean of the start and end cross-meander position and "mean tau" refers to the mean of the start and end along-meander position for each tow. Eta and tau were computed by A. Mariano

| MOCNESS No | Region of meander | Date (1988) | Time (GMT) | Latitude (°N) | Longitude (°W) | Mean eta (km) | Mean tau (km) | Depth range (dbars) |
|------------|-------------------|--------------|------------|---------------|----------------|---------------|---------------|---------------------|
| 1 | Trailing flank | 21 September | 16.35 | 37° 34 25 | 73° 14 76 | 101.61 | -149 15 | 0-990 |
| 2 | Trailing flank | 21 September | 21 52 | 37° 32 31 | 72° 54 38 | 71 23 | -141 98 | 0-990 |
| 4 | Trailing flank | 21 September | 7 14 | 37° 28 90 | 72° 21 10 | 25 57 | -143 35 | 0-1000 |
| 5 | Trailing flank | 22 September | 12.42 | 37° 27 45 | 71° 55 99 | -7 80 | -130 92 | 0-1000 |
| 8 | Upwelling flank | 23 September | 5.32 | 38° 09.35 | 72° 00 48 | 52 59 | -91 00 | 0-1000 |
| 9 | Upwelling flank | 23 September | 11:36 | 37° 02 73 | 71° 35 90 | 20 76 | -76.99 | 0-1000 |
| 10 | Upwelling flank | 23 September | 22 26 | 37° 42 83 | 71° 28 06 | -13 89 | -94 53 | 0-1000 |
| 11 | Upwelling flank | 24 September | 4 58 | 37° 32 20 | 71° 18 70 | -37 09 | -99 56 | 0-1000 |
| 13 | Downwelling flank | 24 September | 21 11 | 37° 50 54 | 70° 31 35 | -32 52 | 40 73 | 0-1000 |
| 14 | Downwelling flank | 25 September | 4 32 | 37° 58 10 | 70° 14 10 | -8 92 | 34 85 | 0-1000 |
| 15 | Downwelling flank | 25 September | 12 23 | 38° 12.90 | 70° 40.23 | 20 59 | 35.08 | 0-1000 |
| 16 | Downwelling flank | 25 September | 17 21 | 38° 18.25 | 69° 52 30 | 37 06 | 130 04 | 0-1000 |
| 17 | Leading flank | 26 September | 12 57 | 37° 38 98 | 68° 52 03 | 54 56 | 115 12 | 0-1000 |
| 18 | Leading flank | 26 September | 20 56 | 37° 34 20 | 69° 15 10 | 18 96 | 73 09 | 0-1000 |
| 19 | Leading flank | 27 September | 6 10 | 37° 42 80 | 69° 50 50 | -15 17 | 48 16 | 0-1000 |
| 40 | Crest | 14 October | 18 49 | 38° 07 37 | 68° 27 14 | 41 82 | 9 46 | 0-1000 |
| 41 | Crest | 14 October | 0 25 | 37° 55.73 | 68° 29 90 | 17 95 | 7.37 | 0-1005 |
| 42 | Crest | 15 October | 9 10 | 37° 48 29 | 68° 38 69 | 2 08 | 0 00 | 0-1000 |

Three to five MOCNESS tows were done along each transect. A single tow was done at each station regardless of the time of day. Samples were preserved in 4% buffered formalin immediately following collection.

Five MOCNESS transects across different regions of the meander were used in this study: at the western/upstream end of the Trailing Flank (M1-M5), the Upwelling or Divergent Flank (M8-M11), the Crest (M40-M42), the Downwelling Flank (M13-M16), and at the eastern/downstream end of the Leading Flank (M17-M19). All were conducted during the first leg of the cruise except the crest transect, which was conducted during the second leg (Table 1)

Sample analysis

Samples from three transects (trailing flank, upwelling flank, downwelling flank) from the first survey of the meander were analysed for the adult abundances of eight copepod species. Of the eight species, two are considered Slope Water species (*Pleuromamma borealis*, *Metridia lucens*), five Sargasso Sea/Gulf Stream species (*Calanus tenuicornis*, *P. abdominalis*, *P. gracilis*, *P. piseki*, *P. xiphias*) and one occurs in both regions (*Nannocalanus minor*) (GRICE and HART, 1962; DEEVEY and BROOKS, 1977; COX and WIEBE, 1979). Six of the species are vertical migrators (*M. lucens*, *Pleuromamma* spp.), and two are characteristically found in the upper 200 m in the Gulf Stream (*C. tenuicornis*, *N. minor*) (WISHNER and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993). Previous work has shown that the distributions of these species in the Gulf Stream are closely associated with specific physical characteristics such as temperature and density (WISHNER

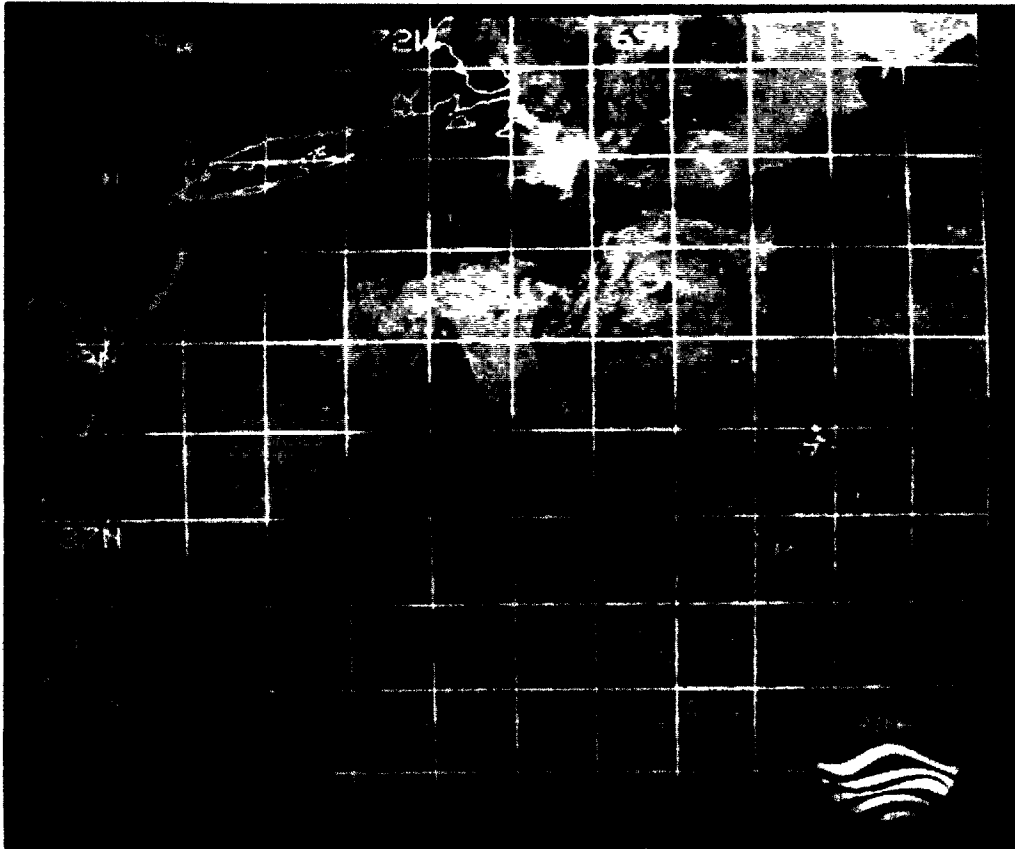


Fig. 2. Satellite image showing sea surface temperature of the meander on 23–24 September 1988. Dark areas indicate warmer water (Gulf Stream) and light areas indicate colder water. A strong meander–ring interaction was occurring near the crest of the meander on this date, however POGIO velocity vectors indicated that sampling of the trailing, upwelling, and downwelling flanks had been completed before detrainment of Gulf Stream water into the ring occurred (I. ROSSBY, personal communication).

and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993). Copepod species were identified according to the keys of STEUR (1932), ROSE (1933), HULSEMAN (1966), and OWRE and FOYO (1969).

The sample was first split to a fraction where at least 200 of the target copepod types were present, using a Folsom plankton splitter. The counts were then extrapolated to numbers 1000 m^{-3} . Integrated total abundances for the copepod species were calculated over the depth interval of 0–1000 dbars for each sample to examine cross- and along-meander trends in abundance. Integrating over the water column has the advantage that diel samples can be directly compared since day/night differences in species distribution are not considered. Populations of these species across the Gulf Stream occur almost entirely in the top 1000 m of the water column (WISHNER and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993).

Abundances were compared for each species across each of the three transects of the meander (trailing, upwelling, and downwelling flanks) to analyse cross-stream trends. Kendall's coefficient of concordance (W) was calculated, using integrated species abundances, between tows along each transect to indicate any significant agreement between species in abundance trends across the transect (ZAR, 1984). Concordance in abundance trends was calculated separately for Sargasso Sea and Slope Water species across the upwelling and downwelling flank transects but was calculated with all seven species across the trailing flank (*N. minor*, the species from both regions, was not included). Abundance differences at similar cross-stream locations were compared between transects for each species to define along-meander trends. Because of the low number (4) of samples along the transects, statistical comparison of the sample pairs (samples at similar cross-stream locations on different transects) can give a level of significance no smaller than $P = 0.20$ (Wilcoxon test, SOKAL and ROHLF, 1981).

The abundances of the females of two *Pleuromamma* species (*P. borealis* and *P. gracilis*) were enumerated from samples collected on two transects: on the leading flank and at the crest of the meander (Table 1). Since no samples were taken in the crest region of the meander during the first leg, stations taken near the crest during the second leg were included to determine the abundances of the two species for this region of the meander.

The *Pleuromamma* proportion was calculated to indicate whether Gulf Stream water and plankton populations were mixing with the Slope Water. Since *P. borealis* (Slope type) and *P. gracilis* (Sargasso type) are very similar in size and behavior (both are vertical migrators and co-occur at the same depths) (WISHNER and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993), their abundances at a particular location may be affected by similar physical mixing mechanisms. Furthermore, *P. borealis* is a strong indicator of Slope Water and is usually not found beyond the North Wall (WISHNER and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993). The proportion of adult females (F) of each species out of the total of the two was calculated for each tow.

Sample locations

Relative positions (along meander and cross-stream) of the MOCNESS tows were computed by A. Mariano. In this analysis, all XBT and CTD data collected during the program (over 500 measurements) from both ships was used to construct daily maps of the depth of the 12°C isotherm using objective analysis (MARIANO, 1990). A local curvilinear coordinate system was developed from the maps in which locations were translated from

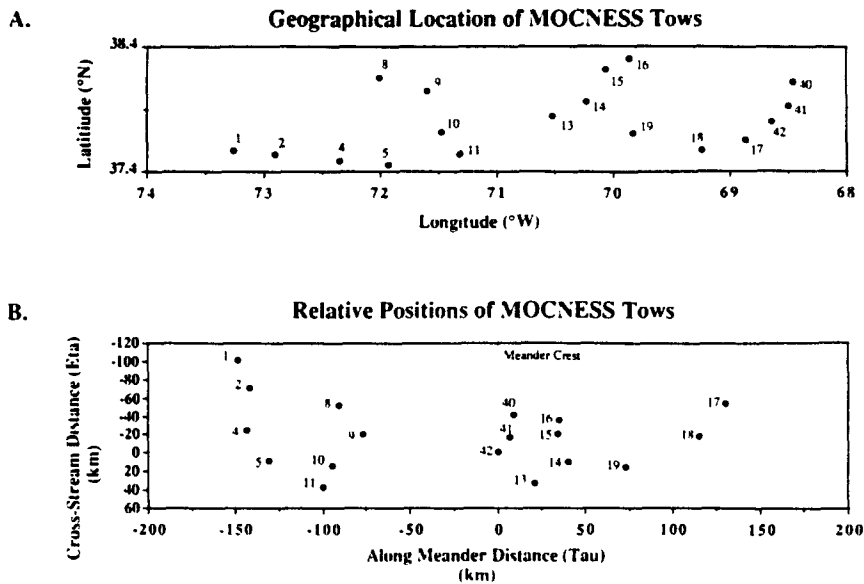


Fig. 3 (A) Geographic positions of the zooplankton (MOCNESS) tows used in this study (B) Positions of the zooplankton (MOCNESS) tows used in this study relative to meander features. Relative positions were calculated by A. Mariano (MARIANO, 1990). The meander crest is located at $\tau = 0$ (along meander distance) and the cross-stream location where the depth of the 12°C isotherm was at 400 m is indicated by $\eta = 0$ (cross-stream position). In this figure, the sign of the η (cross-stream location) is reversed from that reported by A. Mariano (Table 1) so that locations to the north of the Gulf Stream axis are indicated by "negative η ." The meander extends straight across the figure in the relative coordinate system.

geographic positions into positions relative to meander features (MARIANO, 1990). The location of each station relative to the meander features was identified using this analysis. Cross-stream position of each station (η) was expressed as the distance in kilometers from where the depth of the 12°C isotherm equaled 400 m. This placed the origin of the coordinate system in the core of the current rather than at the North Wall. [The isoline for the 12°C at 300 m deviated from the Gulf Stream around a warm core ring outside the mapping region and therefore was not used (MARIANO, 1990).] Along-meander position (τ) of each station was expressed as the distance in kilometers from the crest of the meander.

Since zooplankton distributions in the Gulf Stream correspond with hydrographic features, the relative positions of the MOCNESS stations rather than geographic ones were used in this study to compare copepod abundances across the different transects. The positions of the stations relative to each other and to meander features were quite different in geographic space compared to relative coordinates (Fig. 3A and B).

RESULTS

The abundances of the copepod species indicate that the hypothesized entrainment and detrainment was occurring in this Gulf Stream meander. Two copepod species (*P. borealis*, a Slope Water species, and *P. gracilis*, a Sargasso Sea species) were useful indicator species of their respective water masses.

The temperature–salinity characteristics of the MOCNESS stations were used to identify the water types present at each sampling location. Three water types have been identified for this region: Gulf Stream/Sargasso Sea ($>14^{\circ}\text{C}$, >36 ppt), Slope Water (14 – 22°C , 35.5 – 36.0 ppt), and Ford Water (14 – 22°C , <35.5 ppt) (LILLIBRIDGE *et al.*, 1990). MOCNESS stations on the Sargasso Sea side of the Stream axis were characteristic of the Gulf Stream/Sargasso Sea (Tows 4, 5, 10, 11, 13, 14, 19, 41), while tows on the Slope Water end of the transects had fresher, colder water characteristic of Slope Water or of Ford Water (Tows, 1, 2, 8, 9, 40, 15, 16, 17, 18) (Figs 3 and 4)

Abundance trends across the upwelling and downwelling flanks were similar for the Sargasso Sea species (*C. tenuicornis*, *P. abdominalis*, *P. gracilis*, *P. piseki*, *P. xiphias*) and were the same for both the vertical migrators (*Pleuromamma* spp.) and the non-migrating species (*C. tenuicornis*) (Fig. 5, Table 2). Abundances of the Sargasso Sea species decreased across the Stream from the Sargasso Sea side towards the Slope side across both flanks of the meander. The very low abundances of all species observed on the Sargasso Sea end of the upwelling flank transect (M11) may have been due to: (1) actual low abundances of zooplankton in the Sargasso Sea (GRICE and HART, 1962; ALLISON, 1986) or (2) underestimates caused by partial destruction of the sample during collection. With the exception of *P. xiphias*, abundances of the Sargasso Sea species were lower along the downwelling transect than along the upwelling transect (Fig. 6). Highest abundances were observed on the south (Sargasso Sea) side of the upwelling flank transect (excepting abundances from M11 at the Sargasso Sea terminus of the transect) with lower abundances observed at the Slope Water end of the downwelling flank transect. The rank order of tows by species abundances for the five species (Table 2) was significantly concordant across both flanks (Kendall's W , $P < 0.001$ for upwelling flank, $P < 0.05$ for downwelling flank).

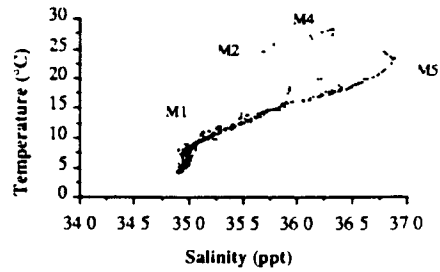
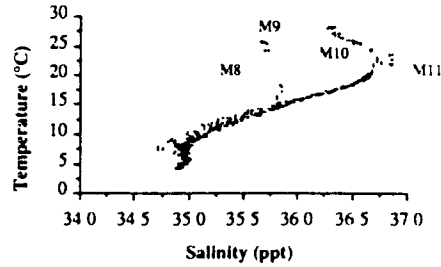
Abundance trends for the two Slope Water species across these two flanks were also similar and showed patterns opposite to those observed for the Sargasso Sea species (Fig. 5). Both *M. lucens* and *P. borealis* abundances decreased across the Stream from the Slope side to the Sargasso Sea side, although *P. borealis* was not found as far across the Gulf Stream as *M. lucens*. Abundances were greater on the convergent/downwelling flank transect than on the upwelling flank, and highest abundances were observed on the Slope Water side of the downwelling flank transect (Fig. 6). The rank order of tows by abundance for the two species (Table 2) was not significantly concordant, probably because of small sample size (Kendall's W , $P < 0.20$).

In contrast to the upwelling and downwelling flanks, abundance trends across the trailing flank (Fig. 1) were virtually the same for both Sargasso Sea and Slope Water species (Fig. 5, Table 2). Sargasso Sea species had patterns opposite to those observed across the upwelling and downwelling flanks, with highest abundances on the Slope Water side of the trailing flank transect and declining abundances across the transect into the Gulf Stream. Abundance trends of the Slope Water species resembled patterns observed on the upwelling and downwelling flanks. The rank orders of tows by abundance of the seven species across the transect were significantly concordant (Kendall's W , $P < 0.01$).

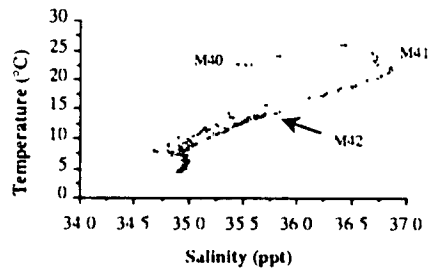
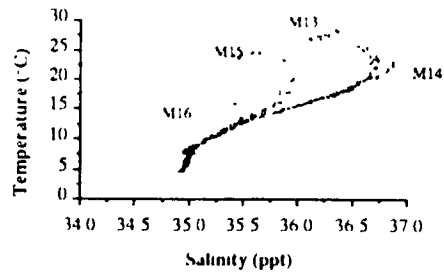
Nannocalanus minor, the widespread species, had abundance trends similar to the two Slope Water species across all transects of the meander, with abundances dropping off across the transect from the Slope Water into the Gulf Stream (Fig. 5). However, unlike the two Slope Water species, the abundance of *N. minor* was not greater in the downwelling flank of the meander (Fig. 6).

Cross-stream trends in abundance for females of *P. borealis* and *P. gracilis* across the

Trailing Flank

Upwelling /
Divergent Flank

Crest

Downwelling /
Convergent Flank

Leading Flank

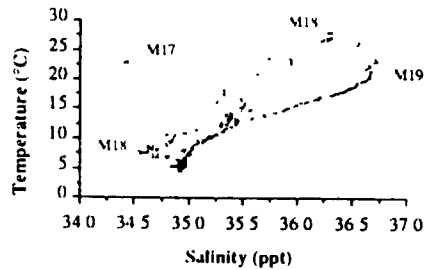


Fig. 4 Temperature vs salinity ($T-S$) plots for the MOCNESS stations (shown in Fig. 3) from each of the five transects conducted across the different regions of the meander (MOCNESS data processed and supplied by S. R. Cummings, NOAA/AOML.)

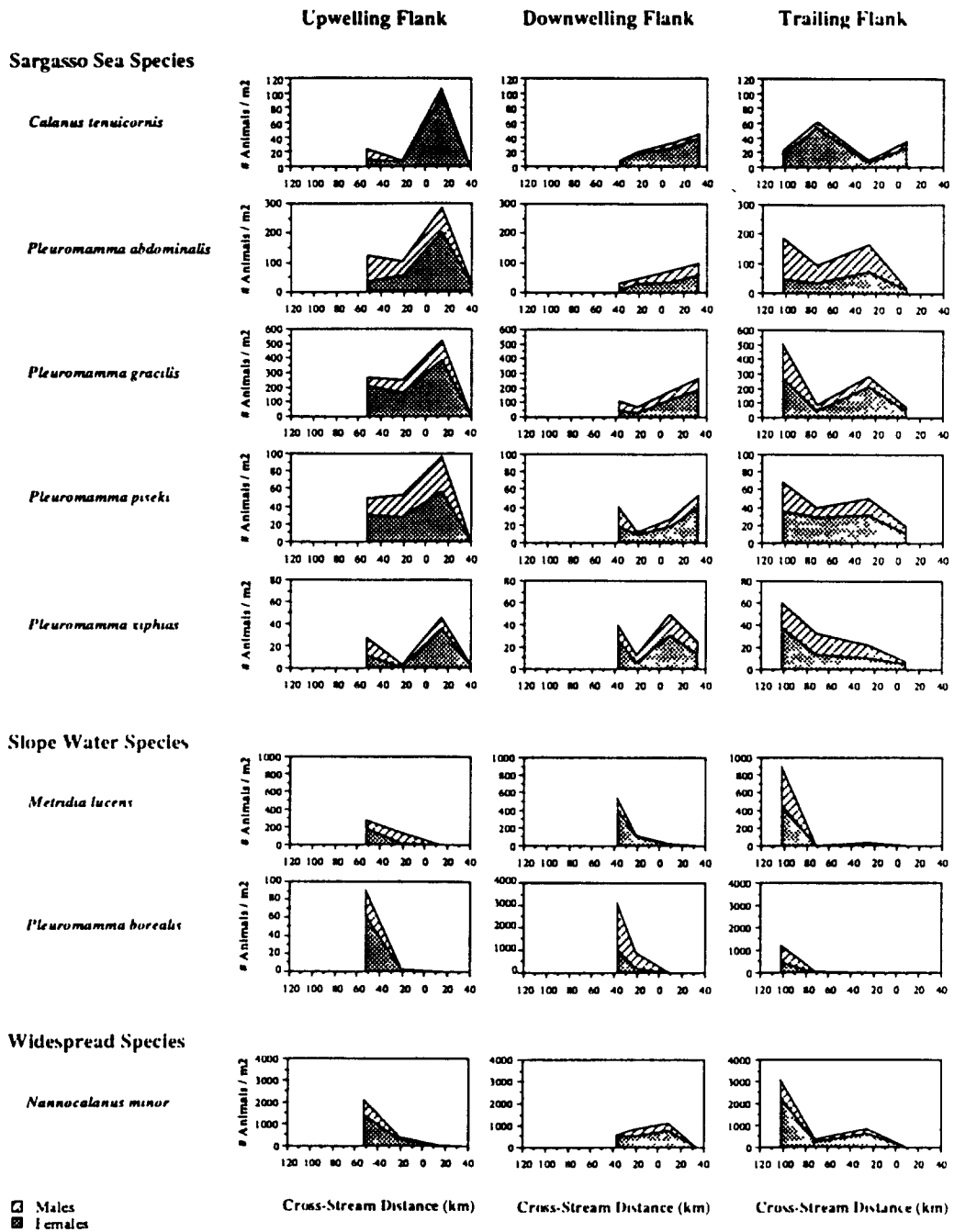


Fig. 5. Abundances of the eight copepod species across the Trailing, Upwelling and Downwelling Flanks of the meander. Integrated abundance ($\text{No. animals m}^{-2}$) is plotted vs relative cross-stream distance in kilometers for each species. The cross-stream position where depth of the 12°C isotherm is at 400 m is located at the origin (0 km), with locations to the Slope Water side of the Stream axis indicated by negative cross-stream distances and locations to the Sargasso Sea side indicated by positive cross-stream distances. Cross-stream distances were computed by A. Mariano.

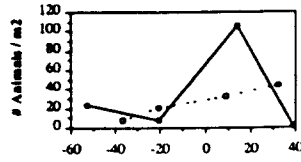
Table 2. Results of Kendall Concordance tests. The ranks of the tows by integrated abundance for each species across each of the transects and the coefficient of concordance (Kendall's W) for each transect is shown for: (A) Sargasso Sea species and (B) Slope Water species across the upwelling and downwelling flanks and (C) combined Sargasso Sea and Slope Water species across the trailing flank "Tow" refers to the MOCNESS tow with Slope Water tows to the left and Sargasso Sea tows on the right. Abundances were ranked with "1" being the least abundant and "4" being the most abundant (SOKAL and ROHLF, 1981)

| (A) Sargasso Sea species | Upwelling flank | Species | 8 | 9 | Tow | | Kendall's W | Significance | |
|--|--------------------|-----------------------|-----------------------|-----|-----|-------|---------------|--------------|------------|
| | | | | | 10 | 11 | | | |
| | | <i>C. tenuicornis</i> | 3 | 2 | 4 | 1 | | | |
| | | <i>P. abdominalis</i> | 3 | 2 | 4 | 1 | | | |
| | | <i>P. gracilis</i> | 3 | 2 | 4 | 1 | | | |
| | | <i>P. piseki</i> | 3 | 2 | 4 | 1 | | | |
| | | <i>P. xiphius</i> | 3 | 1 | 4 | 2 | 0.936 | $P < 0.001$ | |
| | Downwelling flank | Species | 16 | 15 | Tow | | | | |
| | | | | | 14 | 13 | | | |
| | | | <i>C. tenuicornis</i> | 1 | 2 | 3 | 4 | | |
| | | | <i>P. abdominalis</i> | 1 | 2 | 3 | 4 | | |
| | | | <i>P. gracilis</i> | 2 | 1 | 3 | 4 | | |
| | | | <i>P. xiphius</i> | 3 | 1 | 4 | 2 | 0.584 | $P < 0.05$ |
| (B) Slope Water species | Upwelling flank | Species | 8 | 9 | Tow | | | | |
| | | | | | 10 | 11 | | | |
| | | <i>M. lucens</i> | 4 | 3 | 1.5 | 1.5 | | | |
| | | <i>P. borealis</i> | 4 | 3 | 2 | 1 | 0.925 | $P < .20$ | |
| | Downwelling flank | Species | 16 | 15 | Tow | | | | |
| | | | | | 14 | 13 | | | |
| <i>M. lucens</i> | | 4 | 3 | 1.5 | 1.5 | | | | |
| | <i>P. borealis</i> | 4 | 3 | 2 | 1 | 0.925 | $P < .20$ | | |
| (C) Sargasso Sea and Slope Water species | Leading flank | Species | 1 | 2 | Tow | | | | |
| | | | | | 4 | 5 | | | |
| | | <i>C. tenuicornis</i> | 2 | 4 | 1 | 3 | | | |
| | | <i>P. abdominalis</i> | 4 | 2 | 3 | 1 | | | |
| | | <i>P. gracilis</i> | 4 | 2 | 3 | 1 | | | |
| | | <i>P. piseki</i> | 4 | 2 | 3 | 1 | | | |
| | | <i>P. xiphius</i> | 4 | 3 | 2 | 1 | | | |
| | | <i>M. lucens</i> | 4 | 3 | 2 | 1 | | | |
| | | <i>P. borealis</i> | 4 | 1.5 | 3 | 1.5 | 0.557 | $P < .01$ | |

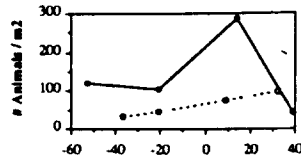
leading flank of the meander (Fig. 7) were the same as those observed along the downwelling flank. Abundances of *P. gracilis* (Sargasso Sea species) decreased and abundances of *P. borealis* (Slope Water species) increased across the Gulf Stream from the Sargasso Sea to the Slope Water. The integrated abundances of females were of the same order of magnitude at similar cross-stream locations between the leading flank and downwelling flank transects for both species (Figs 5 and 7). For seven of the eight species there was little cross-stream pattern in the proportion of females out of the total adults in

Sargasso Sea Species

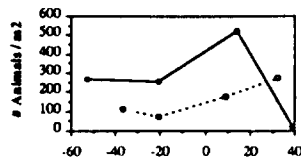
Calanus tenuicornis



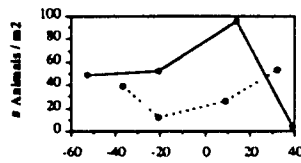
Pleuromamma abdominalis



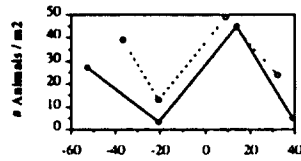
Pleuromamma gracilis



Pleuromamma piseki

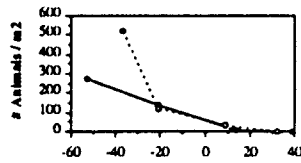


Pleuromamma xiphias

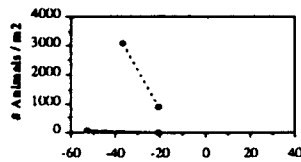


Slope Water Species

Metridia lucens

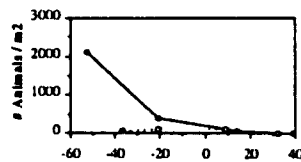


Pleuromamma borealis



Widespread Species

Nannocalanus minor



—●— Upwelling Flank
○..... Downwelling Flank

Cross-stream Distance (km)

Fig 6 Comparison of the integrated abundances of the eight copepod species across the upwelling and downwelling flanks of the meander. Axes are as in Fig 5.

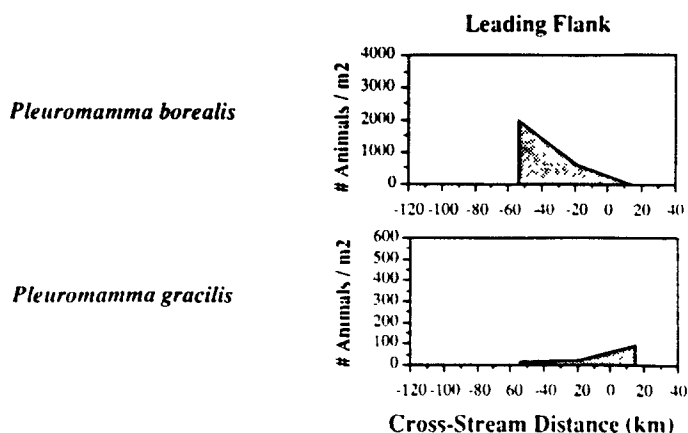


Fig. 7 Abundances for females of *P. borealis* and *P. gracilis* across the Leading Flank of the meander. Axes are as in Fig. 5

the population, suggesting little differential cross-stream effect on the two sexes (ASHJIAN, 1991). The cross-stream trends in abundance of the females may accurately represent those seen in the total adult population.

The cross-stream distance on the five transects at which numerical dominance in a tow changes from *P. borealis* to *P. gracilis* (and vice versa) shifted progressively towards the Sargasso Sea along the meander from the trailing flank to the leading flank (Fig. 8). The relative proportions of the two species for all five transects followed three distinct patterns. The trailing and upwelling flank showed one type of pattern (*P. gracilis* dominant far into Slope Water from Stream axis), the downwelling and leading flanks showed another type of pattern (*P. borealis* dominant through the Slope Water into the Stream), and the crest showed a third intermediate pattern.

Five of the MOCNESS stations from the transects were located approximately 15–22 km towards the Slope Water from where the 12°C isotherm was at 400 m (Table 1). The *Pleuromamma* proportions from these Slope Water stations were compared along the meander to determine if there was a shift in numerical dominance from one species to the other through the meander (Fig. 9). *Pleuromamma gracilis* was the dominant species at locations before the meander crest ($\eta = 0$) in the trailing/upwelling flank, while *P. borealis* was dominant at locations beyond the crest in the leading/downwelling flank.

The *Pleuromamma* proportion for *P. gracilis* was plotted vs the depth of the 10°C isotherm (Fig. 10) for all stations to illustrate the changes in this proportion with meander location. Previous studies indicated that the 10°C isotherm was usually located deeper than the abundance maxima for these species (WISHNER and ALISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993). The depth of the 10°C isotherm was similar for like cross-stream distances along all transects (Fig. 10a). However, there was no consistent correlation between the depth of the isotherm and the proportion of *P. gracilis* along the various transects (Fig. 10b). For locations with the 10°C isotherms at similar depths, such as 300 dbars, the proportions of *P. gracilis* were dramatically different at the two flanks (<0.1 at the downwelling/leading flank and 1.0 at the upwelling flank). All locations to the south of the Stream axis had only *P. gracilis* present.

DISCUSSION

Abundance trends across the "active" flanks (upwelling and downwelling) for six of the eight copepod species are consistent with a circulation dominated by entrainment and detrainment of water parcels. Trends along transects for species from the same region (ex. Sargasso Sea species) were significantly correlated (Kendall's W, Table 2), suggesting that species from a particular habitat were similarly influenced by the physical mechanisms.

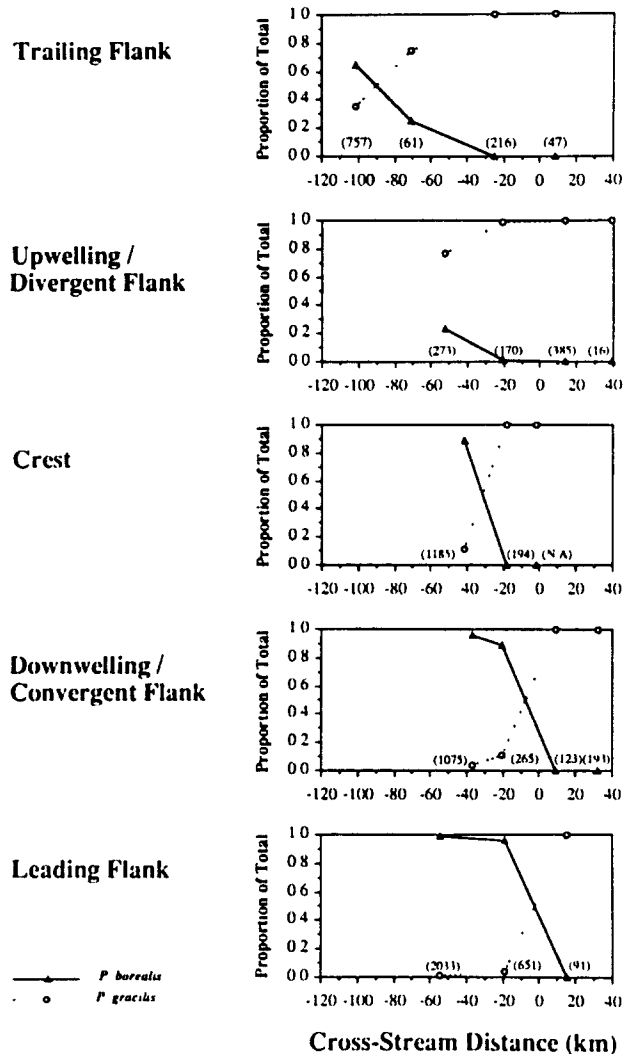


Fig. 8. *Pleuromamma* proportion for *P. borealis* and *P. gracilis* from the five transects of the meander. Proportions were calculated from integrated abundances at each location according to the formulas (1) proportion *P. gracilis* $F = \frac{[No. P. gracilis F]}{[No. P. gracilis F + No. P. borealis F]}$, (2) proportion *P. borealis* $F = \frac{[No. P. borealis F]}{[No. P. gracilis F + No. P. borealis F]}$. The proportion of the total for each species is plotted on the vertical axis. Horizontal axes are as in Fig. 5. The numbers in parentheses are the total of the integrated abundances of both species at each location.

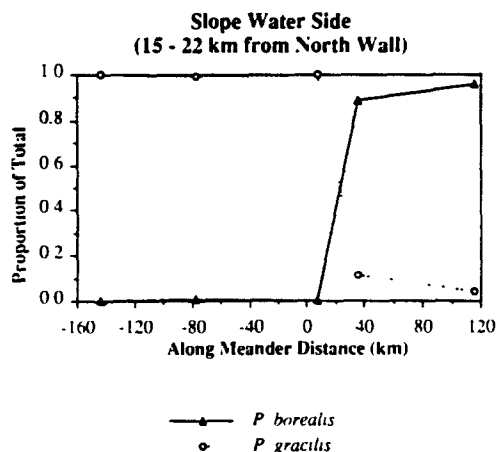


Fig. 9 "Pleuromamma" proportion for *P. borealis* and *P. gracilis* along the meander. Relative along meander distance (tau) is plotted in kilometers on the horizontal axis with "0" indicating the position of the meander crest. Positions on the trailing flank are denoted by negative values and positions on the leading flank are denoted by positive values. Along-stream distances were computed by A. Martiano.

The higher abundances of four of the Sargasso species and the low abundances of the two Slope Water species across the upwelling flank transect indicate that entrainment of Sargasso water from the south and its detrainment to the north was occurring. On the downwelling flank, low abundances of Sargasso species but high abundances of Slope Water species at the northern (Slope Water) end of the transect suggest that Slope Water was being entrained and mixed across the Stream.

The predicted patterns of entrainment and detrainment of water along the meander were supported by the T - S characteristics of the water column at the MOCNESS stations. In interpreting the degree of Slope Water penetration into the Gulf Stream, stations were compared with reference to their cross-stream distance (Fig. 2). The most dramatic comparison was between the upwelling and downwelling flanks. The Slope Water end of the upwelling flank transect (M8) was located farther (52.59 km) into the Slope Water from the Gulf Stream axis than the Slope Water terminus (M16) of the downwelling transect (37.06 km). However, the physical characteristics of the water at the end of the upwelling flank transect (35.5–36.0 ppt, 15–20°C) were less characteristic of Slope Water than were the conditions (34.5–35.5 ppt, 15–18°C) at the end of the downwelling flank transect. The northern end of the crest transect (M40) had T - S characteristics intermediate between those observed on the two flanks, suggesting that some entrainment of Slope Water had occurred at that location. This station was located a comparable cross-stream distance from the Gulf Stream axis as the station at the end of the downwelling flank transect (M16). Apparently there was more Slope Water in the meander at the convergent/downwelling flank (downstream of the crest) than at the divergent/upwelling flank (upstream of the crest) and more Sargasso Sea/Gulf Stream type water in the upwelling flank than at the downwelling flank.

Two of the copepod species [*P. borealis* (Slope Water), *P. gracilis* (Sargasso Sea/Gulf Stream)] were useful indicators of their respective water types, with both species

abundances and species proportions demonstrating that the predicted physical mechanisms were occurring in the meander. The progressive shift along the meander of the cross-stream distance at which numerical dominance shifted from one species to the other reflected ongoing physical transport processes in the meander. At the trailing and upwelling flanks, where Gulf Stream water was predicted to be upwelled and to spill over into the Slope Water (detrainment), samples were dominated by *P. gracilis* quite far from the Stream axis (>80 km). (For this transect, *P. borealis* probably would have become

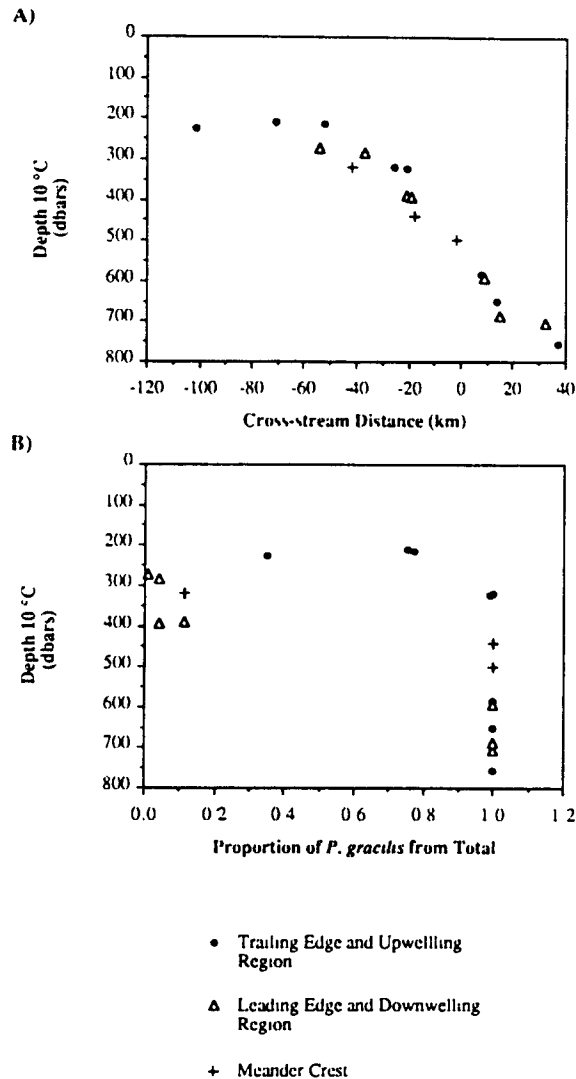


Fig. 10. (A) Relationship between the depth of the 10°C isotherm and cross-stream distance (km). Depth (dbars) is plotted on the vertical axis vs cross-stream distance (km). Cross-stream distances were computed by A. Mariano. (B) Relationship between the depth of the 10°C isotherm and the "Pleuromamma proportion" for *P. gracilis*. Depth (dbars) is plotted on the vertical axis vs the proportion of *P. gracilis*.

dominant at some point farther into the Slope Water beyond that sampled.) Abundances of *P. gracilis* were high relative to those of *P. borealis*, which were especially low. However, in the downwelling flank sections, a switch in the dominant *Pleuromamma* species occurred approximately 10 km to the north of the Gulf Stream axis ($\eta = 0$) for both transects, with *P. borealis* dominant (>90%) to the Slope Water side and *P. gracilis* dominant ($\approx 100\%$) to the Sargasso Sea side of this point. The abundances of *P. borealis* on the Slope Water side of the downwelling flank were dramatically greater relative to abundances on the upwelling flank (Figs 5, 6 and 7), indicating that entrainment of Slope Water parcels and their resident copepod populations had occurred on the downwelling flank. The distance into the Gulf Stream to which *P. borealis* was found was associated with the degree of entrainment of Slope Water, with animals of this species occurring farther into the Stream at the downwelling/convergent flank than on the upwelling/divergent flank. Furthermore, the lack of a strong correlation between the depth of the 10°C isotherm and the "Pleuromamma proportion" for *P. gracilis* (Fig. 10) suggests that the observed patterns of species abundances and the relative proportion of warm- vs cold-water species was due to the replacement of water parcels, and their plankton populations, in the meander.

The shift in dominance from *P. gracilis* to *P. borealis* with distance along the meander (Fig. 9) on the Slope Water side of the Stream axis also demonstrates the effects of the detrainment and entrainment of water parcels. These stations were located 15–22 km to the north from where the 12°C isotherm was at 400 m, in a region probably strongly affected by the physical exchange. In regions of the meander upstream of the crest, upwelling and detrainment of Gulf Stream water (and plankton) into the Slope Water occurred, while in the region downstream of the crest downwelling and entrainment of Slope Water transported Slope Water plankton populations into the Gulf Stream. The proportion of these two copepod species may be an accurate indicator of water parcel exchange both along and across a meander.

Abundances of Sargasso Sea species along the trailing flank transect, especially at the northern end, were surprisingly high, especially since this probably was not a region of the meander with active upwelling. The *T-S* signatures for these stations indicated that the terminus of the transect was in Slope Water, yet four out of five of the Sargasso Sea species (the four *Pleuromamma* spp.) had maximum abundances for the transect at the northern end. Furthermore, abundance trends across this flank of the five Sargasso Sea species and the two Slope Water species were similar and were significantly correlated (Table 2). The high abundances of Sargasso Sea species at that location may reflect a past history of cross-stream water exchange. Animals may have been transported out of the Gulf Stream into the Slope Water at the upwelling region of the meander. The subsequent shift of the meander downstream to the east would then leave the transported populations behind in the Slope Water at the northern end of the trailing flank transect.

Vertically migrating species (*Pleuromamma* spp.) and the non-migrating species (*C. tenuicornis*) had similar abundance trends across three of the transects. The diel migrations of the *Pleuromamma* species should subject these animals to variable conditions of cross- and downstream transport, resulting in different abundance trends for the migrating vs non-migrating species. The apparent lack of a significant difference in their abundance trends suggested that: (1) the advective processes determining relative abundances of the species were operating throughout the water column; or (2) the advective processes in the top 200 m may be the dominant transport mechanisms determining the

distributions of these species. However, the second possibility would be inconsistent with the present understanding of cross-stream exchange in meanders, as most transfer of water parcels occurs in the main thermocline (BOWER, 1991). Analysis of the abundance trends of other shallow water, Sargasso Sea species should indicate if the trends observed for *C. tenuicornis* are consistent for all species found at that depth range.

The abundance trends observed in this study may represent "average" abundances in the current. At the scale of this study (1–2 km/tow) small scale (<1 km) patchiness in zooplankton abundance would be obscured (HAURY, 1982). Since the advective processes in meanders are continuous, animals advected away from a particular position will be replaced immediately. The correlation between species abundance trends observed across transects is encouraging, since it suggests that the observed patterns may be more widely characteristic of meanders. However, more intense sampling involving repetitive stations in the Gulf Stream is necessary to resolve the temporal and spatial variability of species distributions in the Gulf Stream.

Meander-associated cross-stream transport may be an effective mechanism promoting cross-stream exchange for Gulf Stream/Sargasso Sea zooplankton populations (Fig. 11). These species would be detrained (No. 2 in Fig. 11A) from the Stream on the northern side of the upwelling flank (Fig. 11A), although downstream transport of populations in the high velocity core of the current would also occur (No. 3). The detrained populations would remain in the Slope Water following downstream propagation of the meander (No.

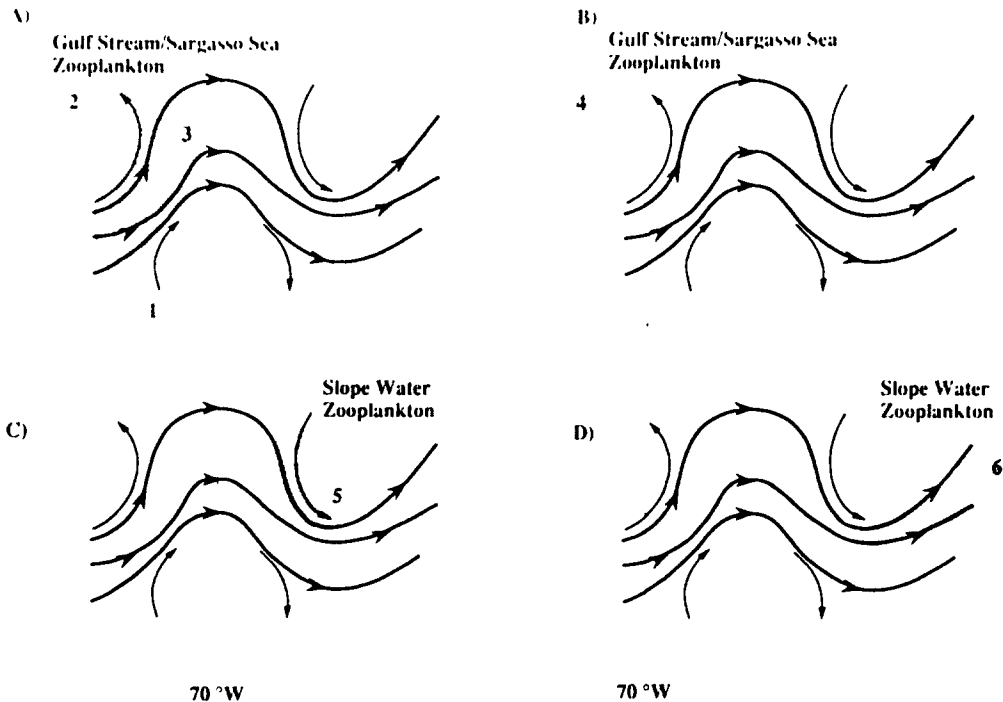


Fig. 11 Cross-stream exchange mechanisms in Gulf Stream meanders. Sargasso Sea/Gulf Stream species may be transported across the Gulf Stream to the Slope Water (A and B), and Slope Water species will be predominantly transported downstream rather than across the Gulf Stream to the Sargasso Sea (C and D). The numbers in the figures refer to processes described in the text.

4 in Fig. 11B), especially if entrainment into the downwelling flank of a subsequent meander did not occur. Entrainment of Sargasso Sea populations into the Gulf Stream from the south would also occur (No. 1 in Fig. 11A); however, differentiating between Sargasso Sea and Gulf Stream populations would be difficult since the same copepod species occur in both water types.

This mechanism for the transport of Sargasso Sea/Gulf Stream species out of the Gulf Stream into the Slope Water has been predicted by a kinematic model in which meander phase speed (downstream propagation), amplitude, and current velocity interact to determine the volume of water transported out of the current (BOWER, 1991). For a meander of 50 km amplitude with a phase speed of 10 km day^{-1} [typical for meanders east of 73°W (GILMAN, 1988)], only 42% of the fluid in the lower thermocline is predicted to remain in the jet, while 87% of the fluid in the near-surface waters will remain (BOWER, 1991). This type of cross-stream mixing will be most effective for copepod species found in the thermocline of the Gulf Stream, such as *P. gracilis* which has daytime abundance maxima located in the thermocline (WISHNER and ALLISON, 1986; ASHJIAN, 1991; ASHJIAN and WISHNER, 1993).

In contrast, effective cross-stream transport of Slope Water populations across the Gulf Stream into the Sargasso Sea is not likely to occur by these processes. Although Slope Water populations may be entrained into the Gulf Stream in the downwelling flank of a meander (No. 5 in Fig. 11C), these animals can be advected downstream (No. 6 in Fig. 11D) by the high velocities of the current, perhaps even into the upwelling zone of the next meander where detrainment from the Stream back into the Slope Water may occur. Maximum downstream velocities occur at the northern edge of the current and exceed cross-stream velocities by several orders of magnitude. Slope Water populations may not be transported across the current before being advected downstream.

Meander-associated cross-stream flow has the potential to transport significant numbers of Sargasso Sea zooplankton across the Gulf Stream. Cold- and warm-core rings are also known to transport Slope Water and Sargasso Sea populations across the Gulf Stream (WILBE *et al.*, 1976b; WILBE and BOYD, 1978; RING GROUP, 1981; WIEBE and FLILRI, 1983; DAVIS and WILBE, 1985; WILBE *et al.*, 1985; WIEBE and McDOUGALL, 1986). Cross-stream transport associated with water parcel transfer along isopycnals, especially in meanders, may be of at least the same magnitude as that associated with cold- and warm-core ring formation (RICHARDSON, 1983; BOWER and ROSSBY, 1989; T. ROSSBY, personal communication). However, the effectiveness of these processes as seeding mechanisms for these species in the new regions will depend on the ability of the transplanted populations to survive and reproduce.

Differences between the divergent (upwelling) and convergent (downwelling) regions of meanders have been observed for other organisms as well as for zooplankton species. Highest primary production was measured in the upwelling region of the meander (KENNEDY and LOHREINZ, 1990), and the distribution of chlorophyll with depth through the meander indicate that upwelling occurs on the leading edge and that convergence was occurring on the trailing edge of the meander (FITCHCOCK and OLSON, 1990). Acoustic detection of nekton indicate that biomass was more diffuse and extended farther along isotherms in the upwelling region than in the downwelling region (ARNONE *et al.*, 1990; NERO *et al.*, 1990). Therefore Gulf Stream meanders are dynamic zones in the ocean, where cross-stream mixing processes are enhanced.

The consequences of the cross-stream mixing include greater dispersal of species.

enhanced opportunity for speciation, increased competition and predation between species endemic to the Slope Water and Sargasso Sea expatriates, and increased genetic exchange among populations. The results of this study suggest that meander-associated cross-stream mixing, at least of Sargasso Sea species, may be a significant process in promoting regional dispersal of zooplankton species.

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