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Temporal persistence of copepod species groups in the Gulf Stream

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Abstract—The distributions of 22 copepod types (18 species and the copepodite stage V of four of the species) across a transect of the Gulf Stream near Cape Hatteras, NC, sampled in May 1983 with a MOCNESS, were analyzed and compared with the distributions found on a similar transect sampled in September 1982. Copepod species distributions followed physical characteristics closely and were similar for the two sampling times. Species were found in discrete environments, and species distributions changed across the Stream with changing physical properties. Most of the copepod types (18) were placed into four distributional groups using recurrent group analysis, cluster analysis, and examination of species distributions. The September and May transects were analyzed independently, yet virtually the same groups resulted, implying that these species groups are consistent over time and suggesting that a persistent community structure may be a general feature of the Gulf Stream. The distributions of the species groups were associated with physical properties across the Gulf Stream, with little overlap between group environments. In both September and May cross-stream trends in integrated abundances of two of the species groups followed the patterns expected if continuous cross-stream mixing processes had occurred. Cold-water species had higher abundances at the northern stations, with abundances decreasing across the Stream to the south. Warm-water species abundances followed the opposite pattern (high abundances on the Sargasso Sea side of the Stream and lower abundances on the northern side). Certain species or species groups may be reliable indicators of water type and could be used as tracers of water mass mixing across the Gulf Stream.

INTRODUCTION

THE Gulf Stream is usually regarded as a biogeographical boundary separating the cold-water eutrophic Slope Water faunal assemblages to the north and west from the warm-water oligotrophic Sargasso Sea assemblages to the south and east (GRICE and HART, 1962; HURLBURT, 1964; BACKUS *et al.*, 1970; JAHN and BACKUS, 1976; CHENEY, 1985). However, studies of zooplankton populations in the northwest Atlantic have noted the presence of non-endemic species in both the Slope Water and the Sargasso Sea. Their transport across the Gulf Stream has been attributed either to an unspecified large-scale lateral mixing or to the formation of Gulf Stream rings (e.g. GRICE and HART, 1962; BOWMAN, 1971; DEEVEY, 1971; WIEBE *et al.*, 1976b; DEEVEY and BROOKS, 1977; COX and WIEBE, 1979; JOYCE *et al.*, 1984). Smaller-scale physical processes, also identified as agents

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of cross-stream water transport, include shingle formation (Slope Water entrainment) and decay (e.g. LILLIBRIDGE and ROSSBY, 1986; HITCHCOCK *et al.*, 1986; GARFIELD and EVANS, 1987), formation of streamers associated with ring–Stream interactions (NOF, 1988), "leakage" from the Stream at depths below the thermocline (SHAW and ROSSBY, 1984), and water transfer at meander crests and troughs (BOWER *et al.*, 1985; BOWER and ROSSBY, 1989; HOGG, 1986). Therefore the Gulf Stream functions as a leaky membrane (BOWER *et al.*, 1985), permitting some cross-stream exchange of water and plankton populations.

Despite the importance of the Gulf Stream as a biogeographical boundary, there are few in-depth studies of the zooplankton within the current itself. Most studies of Gulf Stream zooplankton populations have been done near the Straits of Florida, where the current is still discrete (e.g. MOORE and O'BERRY, 1957; ROEHR and MOORE, 1965; WORTHINGTON, 1976). Earlier studies in areas north of Cape Hatteras have usually been limited to a few samples, taken either on a transect of the area or in conjunction with investigations of Gulf Stream rings, and have concentrated on species assemblages in the Slope Water and Sargasso Sea (GRICE and HART, 1962; DEEVEY, 1971; DEEVEY and BROOKS, 1971, 1977; COX and WIEBE, 1979).

Strong associations between species distributions and physical characteristics and a consistent community structure (species groups) were found across the Gulf Stream on a September 1982 transect (ALLISON, 1986; WISHNER and ALLISON, 1986) Despite the changing environment, copepod species distributions could be grouped into a few distinct patterns at all points along the transect using recurrent group analysis (FAGER, 1957), suggesting a stable community structure (WISHNER and ALLISON, 1986). Furthermore, the abundance trends of some copepod species groups across the Gulf Stream followed the patterns expected if continuous cross-stream mixing processes were operating (WISHNER and ALLISON, 1986). Cold-water species were in higher abundances at the northern stations, with abundances decreasing across the Stream to the south. In contrast, warm-water species abundances followed the opposite pattern, with highest abundances on the Sargasso side of the Stream. However, this study was limited to a single transect of the Gulf Stream.

The present study analyzed copepod species distributions and community structure from a spring (May 1983) transect of the Gulf Stream near Cape Hatteras, in comparison with the fall transect (September 1982) at the same location (73°W), previously described by WISHNER and ALLISON (1986) and ALLISON (1986). This paper describes the May results, includes further analyses of September data, and presents comparisons between the two times. Specific questions include: (1) Is there a consistent community structure in the copepod assemblages across the Gulf Stream, and was this structure the same at the two times? (2) Do copepod species' groups abundances follow changing environmental characteristics across the Gulf Stream, and are these associations observed consistently over time? (3) Which copepod species are most useful over time as water mass indicators? (4) Are there patterns in total abundance of copepod species groups across the Gulf Stream, and what are the implications of these patterns for cross-stream transport of plankton?

METHODS

Sampling

Samples were collected from two transects of the Gulf Stream, done in September 1982 (WISHNER and ALLISON, 1986; ALLISON, 1986) and in May 1983, off Cape Hatteras, NC

Table 1. Sampling data for the three stations conducted in May 1983 See Wishner *and* Allison (1986) *for September 1982 sampling information*

Region	Operation	Start latitude (°N)	Start longitude (°W)	Date (1983)	Local time Start	Local time End	Max. depth (dbar)
Northern edge	MOCNESS 15	36 07 11	73 17 79	19 May	11 07	12 11	200
	MOCNESS 16	36 06 04	73 21 86	19 May	13 53	16 21	1000
	MOCNESS 17	36 05 80	73 23 88	19 May	21 42	22 44	200
	MOCNESS 18	36 03 78	73 22 56	20 May	0 11	2 54	930
	Hydrocast	36 08 04	73 16 91	19 May	18 42		591
Central Stream	MOCNESS 19	35 56 49	73 12 10	20 May	10 46	10 46	1000
	MOCNESS 20	35 56 53	73 11 70	20 May	15 09	15 09	200
	MOCNESS 21	35 56 95	73 13 00	20 May	21 29	21·29	193
	MOCNESS 22	35 56 93	73 12 93	20 May	23 42	23 42	1000
	Hydrocast	35 57 12	73 09 95	20 May	16 39		773
South edge	MOCNESS 10	35 43 72	73 01 96	12 May	23 40	1 28	200
	MOCNESS 11	35 44 05	73 03 32	13 May	1 18	4 06	1000
	MOCNESS 12	35 44 20	73 01 38	13 May	9 34	12 02	1000
	MOCNESS 13	35 42 33	73 05 24	13 May	13 23	14 12	200
	Hydrocast	35 44 45	73 01 18	13 May	7 07		928

(Table 1). These 2 months were chosen to provide the maximum contrast in temperature gradient across the North Wall (between the Gulf Stream and the Slope Water), which might affect plankton dispersion and distributions. The transects consisted of three stations, located 20–40 km apart, and oriented such that the transect was perpendicular to the mean direction of the Gulf Stream. The stations were sampled intensively, from 0 to 1000 m, at three locations: a North Wall station (located where the 15°C isotherm was at 200 m), a Central Stream station, and a station at the Sargasso Sea edge of the Stream. The transect was located across a fairly straight, non-meandering segment of the Gulf Stream at both sampling times (Fig. 1; Wishner and Allison, 1986).

At each station, four MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System; Wiebe *et al.*, 1976a) plankton tows, using 335 μm mesh, were conducted, two during the day and two at night. The MOCNESS was equipped with temperature and pressure sensors and a flow meter. For each time period (day and night) both a shallow, fine-scale tow, from 0 to 200 m at 25 m intervals, and a deep, coarse-scale tow, from 0 to 1000 m at 100 or 150 m intervals, were done (1000–850, 850–700, 700–550, 550–400, 400–300, 300–200, 200–100, 100–0), resulting in eight discrete net samples from each tow. Zooplankton samples were preserved in 4% buffered formalin immediately following collection. Hydrocasts were done at each of the three stations to obtain temperature, salinity, density (sigma-*t*), oxygen, and nutrient information. Downstream and cross-stream velocities for all stations were available from the Pegasus program (Halkin *et al.*, 1985).

Sample analysis

Samples were analyzed for the abundances of 22 copepod types, 18 species and the copepodite stage V of four of these species. The same copepod types were enumerated from each transect to maintain consistency between the two sampling times (ALLISON, 1986; WISHNER and ALLISON, 1986). The species selected were common in the samples, had different depth distributions, and represented 13–95% of the adult copepods in a sample, at least for the September 1982 samples (ALLISON, 1986). Copepod species were identified according to the keys of STEUR (1932), ROSE (1933), HULSEMANN (1966), and OWRE and FOYO (1967). Analysis was done by first splitting the sample down to a fraction where at least 200 of the target copepod types were present. The counts were then extrapolated to No. animals/1000 m^3 according to the number of splits and the volume of water filtered during that particular tow. Ninety-six samples were counted from the September transect and 83 samples from the May transect. For the upper 200 m, only the data from the fine-scale sampling were used.

Total integrated abundances (animals m^{-2}) over the 1000 m sampled were calculated for each species at the three cross-stream locations from both day and night for both data sets. The fine-scale samples (25 m intervals) were used for the top 200 m, and the coarse-scale samples (100 and 150 m intervals) were used for the rest of the water column.

Statistical analyses

Species abundances (animals/1000 m^3) from all samples (84 for September and 83 for May) were compared for each species between September and May using the Mann-Whitney U test (SOKAL and ROHLF, 1981; ZAR, 1984). Multivariate statistics were employed to determine grouping of copepod types. In these analyses, all abundances $< 20\%$ of the median abundance of that species were counted as "0" for statistical simplification and to emphasize the major distributions (MCGOWAN and WALKER, 1979, ALLISON, 1986; WISHNER and ALLISON, 1986).

Recurrent group analysis (FAGER, 1957; FAGER and MCGOWAN, 1963) was used to place species into groups on the basis of co-occurrence using presence/absence data. An index of affinity, I, was calculated for each species pair according to the formula in FAGER and MCGOWAN (1963). The minimum value of I below which the species were not considered to have strong affinity was 0.5 (WISHNER and ALLISON, 1986). Groups were formed between those species that had indices of affinity (I) >0.5 for all pairwise combinations. The degree of association between species groups or between groups and individual species was determined from the percentage of pairwise combinations of species from that particular group that had significant indices of affinity with another group or species. Recurrent group analysis for the September data was presented in ALLISON (1986) and WISHNER and ALLISON (1986).

Copepod species groups also were identified using cluster analysis. A hierarchical agglomerative, polythetic cluster analysis was done separately for each transect using the cluster procedure of the Statistical Analysis System (SAS) (PIELOU, 1977; SAS INSTITUTE INC., 1985; KREBS, 1989). Copepod species were clustered using Spearman's Rho between species pairs, rather than differences of abundance. The TREE procedure was used to draw dendrograms of the clusters, based on the distance coefficient between species calculated by the cluster procedure (SAS INSTITUTE INC., 1985). The dendrograms were then visually examined to identify the groups of species.

The species groups described by the cluster analysis and the recurrent group analysis were compared independently for the two data sets to describe one set of groups for each sampling time. If different group compositions were defined by the two statistical analyses,

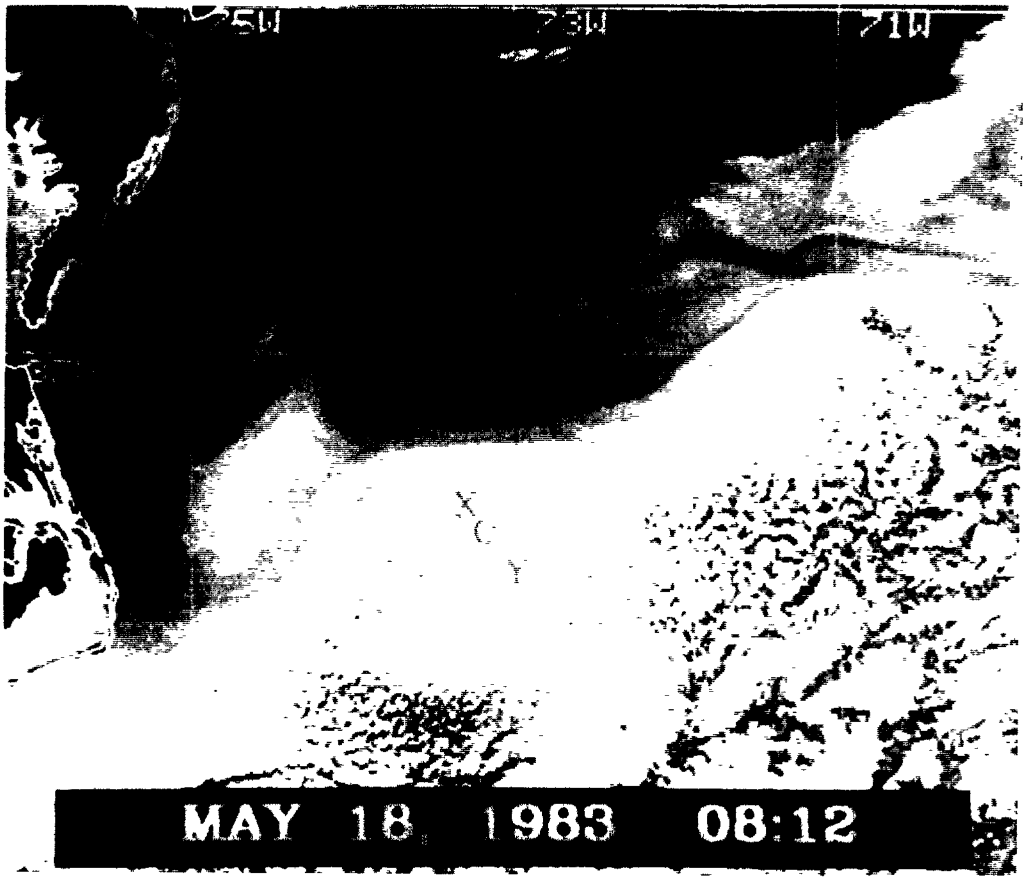


Fig. 1. Satellite infrared image of the sampling area from May 1983. Cape Hatteras, NC, is located in the lower left and the Gulf Stream is the lighter colored area extending across the figure. The three stations are marked by the X, O and Y (X = North Wall, O = Central Stream, Y = Sargasso Sea side).

then the distributions of the individual component species across the Gulf Stream were compared to insure that species grouped together had common distribution patterns. Copepod species groups for the September transect were redefined [from the groups of ALLISON (1986) and WISHNER and ALLISON (1986)] based on the new statistical analysis. The species groups from each sampling time were then compared with each other.

Total integrated group abundances (animals m^{-2}) were summed for each group at the three cross-stream locations from both day and night for both data sets. Maximum group abundances (animals/1000 m^3) and integrated group abundances (animals/m^2) were compared for each species group between (1) September and May and (2) day and night for each cross-stream location using Wilcoxon's signed-rank test (abundances of the group members were used as variables, SOKAL and ROHLF, 1981; ZAR, 1984). For tests of day versus night abundances, both September and May data were used in each category (day and night), with pairings between the same species and the same month, resulting in a sample size of eight for Groups 1–3 (four species, each with 2 months) and of six for Group 4 (three species). Similar calculations were employed for the September versus May comparisons, with both day and night abundances used. Integrated and maximum abundances were compared separately for September and May between cross-stream locations using Wilcoxon's signed-rank test and appropriately paired abundances of the component species (SOKAL and ROHLF, 1981; ZAR, 1984).

Kendall's coefficient of concordance (W; ZAR, 1984) was calculated, using integrated abundances for each species, to indicate if there was significant agreement between the species in a group in abundance trends with cross-stream location. Day and night data were both used in the same test for groups with no differences in day–night integrated abundance. Correlation in cross-stream trends in group integrated abundance between September and May was calculated using the Spearman rank order coefficient (ZAR, 1984)

RESULTS

Environmental data

The physical structure across the two transects was similar at both times, and typical of the Gulf Stream (FUGLISTER, 1960; STOMMEL, 1966). Temperature, salinity and density isopleths in the top 200 m approximately paralleled the surface, while isopleths below 200 m sloped downwards across the stream from the North Wall to the Sargasso Sea [Fig. 2; for September sections, see WISHNER and ALLISON (1986)]. The top of the main thermocline sloped down from 200 m at the North Wall station to 550 m at the Sargasso Sea station. Characteristic "Eighteen Degree Water" (SCHROEDER *et al.*, 1959; WORTHINGTON, 1959, 1976) was found in a lens at the Sargasso Sea station and, with reduced range, at the Central Stream station. Density (sigma-t) in the surface layers of the September transect was lower (< 24.1; WISHNER and ALLISON, 1986) than in the May transect (24.1–24.5). The 27.0 isopycnal was located slightly deeper in the water column during the May transect than in September, especially in the core of the Gulf Stream and on the Sargasso Sea side.

The surface temperature gradient between the North Wall station and the Slope Water to the north was greater in May than in September. The mean Slope Water surface temperature 55 km to the north of the North Wall station was 23.65°C during the September cruise and 15.25°C during the May cruise (HALKIN *et al.*, 1985). The surface

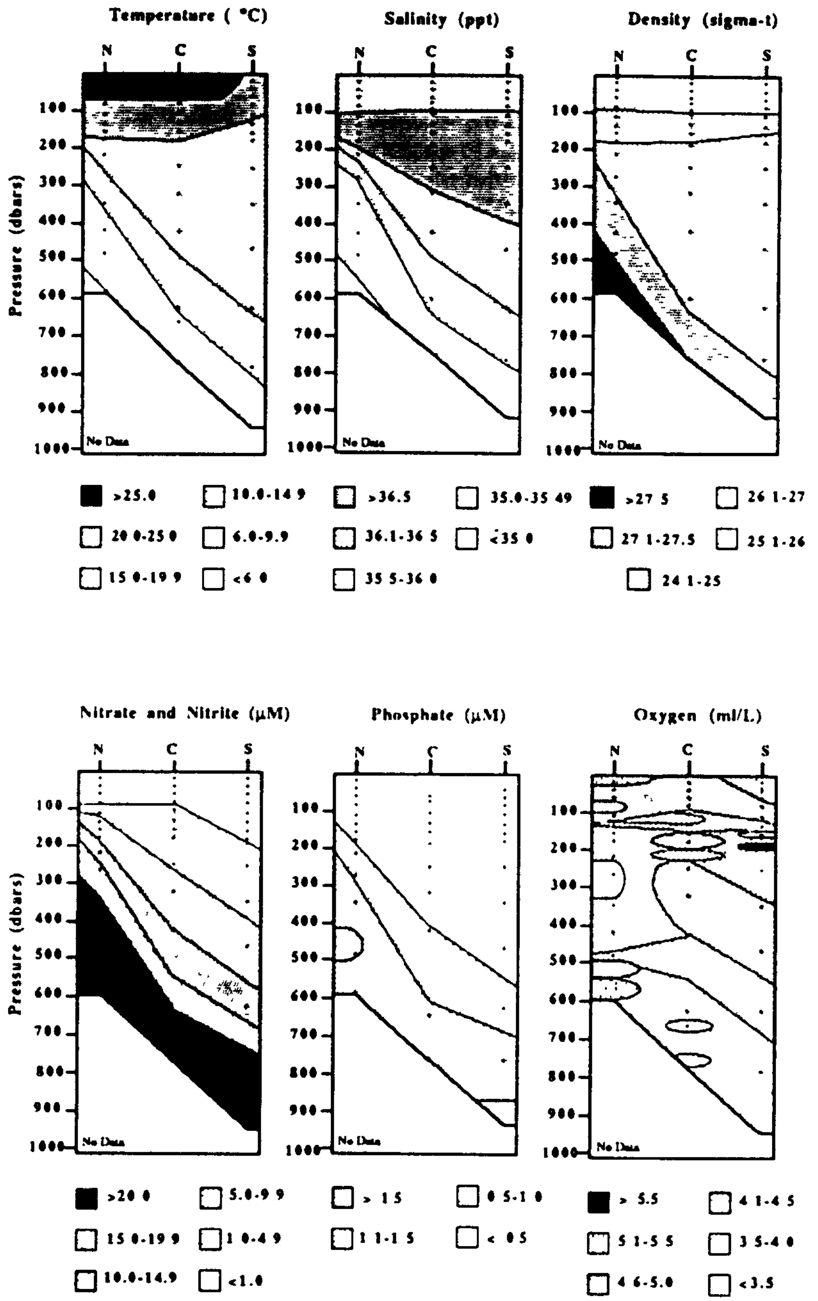


Fig 2. Cross-stream sections of environmental data collected with hydrocasts in May 1983 The three station locations are designated N (North Wall), C (Central Stream) and S (Sargasso Sea side) Note that the data do not extend down to 1000 m at all three locations. See Wishner and Allison (1986) for September sections

temperatures at the North Wall stations, located 20 km from the Stream axis, were 28.0 and 25.5°C for September and May, respectively. This resulted in a mean temperature difference between these two locations of 10°C (0.18°C km^{-1}) in May but only 4.35°C (0.08°C km^{-1}) in September (HALKIN *et al.*, 1985). In contrast, there was little difference in the surface temperature gradient between the North Wall and Central Stream stations at the two times. Very warm (>25°C) surface water extended across the top 50 m of the September 1982 temperature section (WISHNER and ALLISON, 1986), while in the May 1983 temperature section the surface water was cooler (24.88°C) at the Sargasso Sea side station (Fig. 2).

Nutrient sections from May were similar to the September sections (WISHNER and ALLISON, 1986) with nutrient distributions following the sloping isotherms across the Stream (Fig. 2). Lowest concentrations were found near the surface with increasing concentrations at depth. Lowest oxygen concentrations were found in the deep core (225–325 m at North Wall) and along the main thermocline across the Stream, with high concentrations found at depth in and below the main thermocline and in the Eighteen Degree Water.

The downstream velocity field in May was "typical" for the Gulf Stream (HALKIN and ROSSBY, 1985) [Fig. 3; see WISHNER and ALLISON (1986) for September sections].

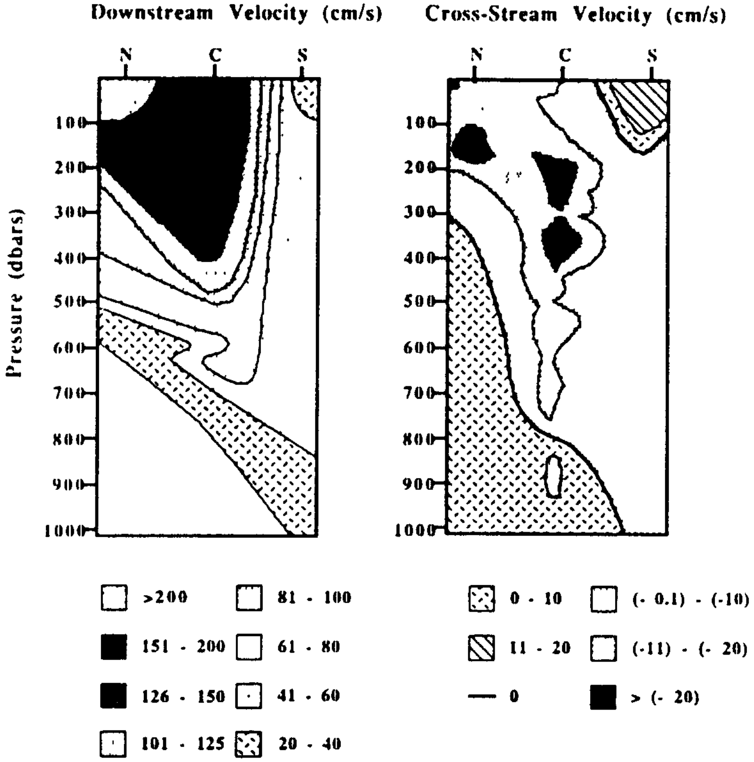


Fig. 3. Cross-stream sections showing the downstream and cross-stream velocity fields for May 1983. Stations designations (N, C and S) are as described for Fig. 2. Sections are composites of the May 1983(A) and May 1983(B) velocity fields (Redrawn from HALKIN *et al.*, 1985).

Maximum downstream velocities (150–200 cm s^{-1}) were found from 0–150 m at the North Wall station of the Gulf Stream. Downstream velocity in the core of the Gulf Stream ranged from 100–150 cm s^{-1} and decreased with depth. Velocities were greatest at the North Wall station and least at the Sargasso Sea side of the Gulf Stream. The cross-stream velocity field was similar to the mean Gulf Stream cross-stream velocity section derived by Halkin *et al.* (1985), except that the magnitude of the cross-stream velocity toward the north in the core of the Gulf Stream was greater in the May section (~10–20 cm s^{-1}) than in the mean velocity section (~0–5 cm s^{-1}).

Copepod species groups

Cluster analysis and recurrent group analysis produced similar groupings. Species characteristic of Slope Water (*Calanus finmarchicus*, *C. finmarchicus C5*, *Pleuromamma borealis*, *Rhincalanus nasutus*, and *Metridia lucens*; Deevey and Brooks, 1977; Grice and Hart, 1962) were clearly separated from other species. The vertically migrating *Pleuromamma* species, with the exception of *P. borealis*, were also well separated from the non-migrating species. Species grouped together were generally at the same depth ranges and exhibited similar behavior (i.e. diel vertical migration; Table 2).

Groups defined using recurrent group analysis from the two transects had some differences. Twelve copepod types were grouped similarly from the two sampling times; however, eight types were grouped differently in the two analyses (Fig. 4), and two species were consistently not placed in species groups (*Neocalanus gracilis* and *P. borealis*) The groups defined for the May analysis were more biologically meaningful in that associations of species with similar behaviors were identified. For example, *Pleuromamma piseki*, a vertical migrator, was associated with other vertically-migrating *Pleuromamma* species (Group 3) in the analysis of the May data but was unassociated with those species in the September analysis *Lucicutia flavicornis*, a vertical migrator, was associated with shallow-living, non-migrating species in the September analysis, but more logically grouped with *N. gracilis* and *Rhincalanus cornutus* as an association of "ubiquitous" species in the May analysis.

The recurrent species groups were more distinct in the May data than in the September data, as indicated by the lower levels of association between all groups. For example, in September, Group 3 was associated at the 38% level with Species Pair 2 (Group 4 in the May data), at the 40% level with Group 1, and at the 5% level with Group 2. However, in the May analysis, Group 3 was associated only at the 16.6% level with Group 4, at the 6.25% level with Group 1, and not at all with Group 2.

Similar species groups occurred at the two sampling times according to the cluster analysis (Fig. 5), in contrast to the results of the recurrent group analysis. Nineteen out of 22 copepod types clustered into the same groups in both September and May. Certain species were more closely associated than others, and these associations were consistent between both data sets.

Summary groups for 15 of the 22 copepod types were defined based on the two grouping analyses and the species' distributions (Fig. 6). In compiling the final groups, the results from the two data sets (May and September) were compared and species' distributions and behavior were considered. Species not consistently associated with a specific group between the two data sets were not placed in the final groups (*Lucicutia clausi*, *L. flavicornis*, *Metridia brevicauda*, *Metridia venusta*, *N. gracilis*, *P. borealis* and *R cornu-*

Table 2 *Distributions of the 22 copepod types in May 1983 September 1982 distributions are presented in* ALLISON *(1986) and as graphs in* WISHNER *and* ALLISON *(1986) Locations and times for which there were no overlap in a particular species distribution with the September distribution are designated with an asterisk Median abundances (No animals/1000 m^3) for the September data are presented for comparison (*ALLISON*, 1986) Significantly greater median abundances are designated by a dagger (P ≤ 0 05, Mann-Whitney U test for abundances for the species between the two times)*

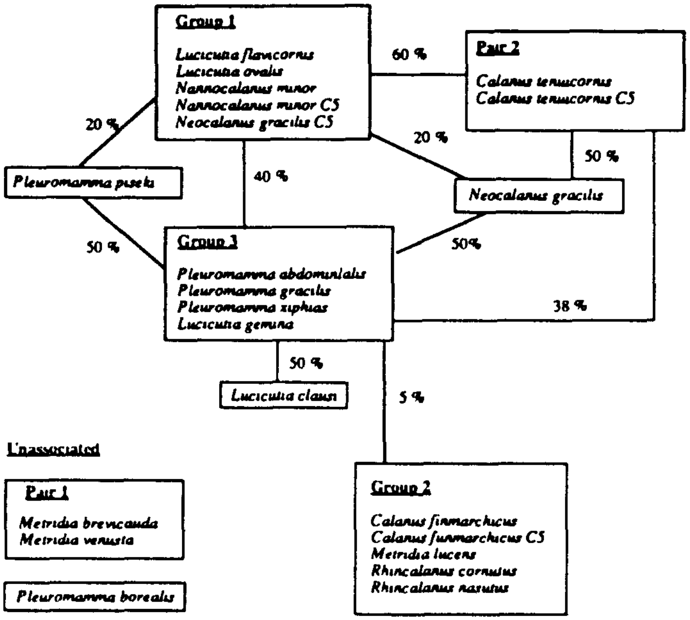
		Depth range			Depth of maximum abundance			Maximum	Median	Sept median	
Species	Time	North Wall	Central Stream	Sargasso Sea	North Wall	Central Stream	Sargasso Sea	abundance (No /1000 m^3)	abundance (No /1000 m^3)	abundance (No /1000 m^3)	Species group
Calanus finmarchicus	Day	200–1000	—*	300–1000	550–700	—	400–550	820	27	11	2
	Night	100–200 300–930	200–300 550–850	100–125 700–850	175–200	550–700	100–125				
Calanus finmarchicus C5	Day	200–1000	400–550	550–1000	550–700	—	850–1000	1451	77	54	2
	Night	125–200 550–930	400–850	0–50 550–750	550–700	700–850	25–50				
Calanus tenuicornis	Day	50–175 200–300	75–200 700–850	150–200	100–125	125–150	175	1763	92	152	4
	Night	75–175 200–300	74–400	75–200	75–100	75–100	100–125				
Calanus tenuicornis C5	Day	75–175	75–200	50–100 150–175	75–100	100–125	50–75	648	86	70	4
	Night	75–175	75–125 150–175	75–200	75–100	75–100	125–150				
Lucicutia clausi	Day	125–150* 200–300	75–50 175–550	75–100*	200–300	300–400	75–100	227	17	24†	—
	Night	100–300* 550–850	100–850	150–550 700–1000	200–300	120–150	200–300				
Lucicutia flavicornis	Day	0–25 50–175 200–550	75–700 850–1000	25–50 75–700	125–150	100–120	150–175	18,527	89	266†	—
	Night	0–200 400–700	0–300 400–850	0–1000	25–50	25–50	0–25				
Lucicutia gemina	Day	100–175 200–300	50–700 850–100	150–700	125–150	125–150	175–200	902	47	86	4
	Night	75–400	25–700	125–1000	75–100	75–100	150–175				

Continued

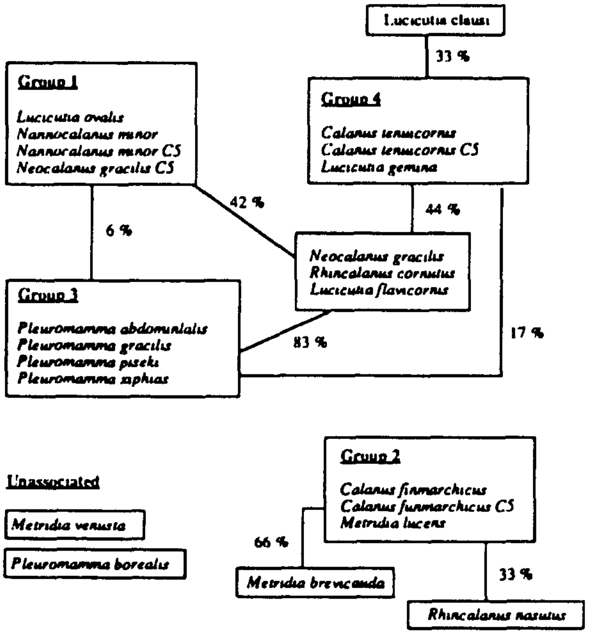
Table 2 *Continued*

Species	Time	Depth range			Depth of maximum abundance			Maximum	Median	Sept median	Species group
		North Wall	Central Stream	Sargasso Sea	North Wall	Central Stream	Sargasso Sea	abundance (No./1000 m^3)	abundance (No./1000 m^3)	abundance (No./1000 m^3)	
Lucicutia ovalis	Day	50–100 125–150	0–200	100–150*	75–100	50–75	100–125	1498	53	68	1
	Night	0–175 550–700	0–175	0–75 150–175	25–50	75–100	25–50				
Metridia brevicauda	Day	400–1000	550–1000	700–1000	850–1000	850–1000	850–1000	122	15	16	—
	Night	550–930	550–1000	300–400 700–850	700–850	850–1000	700–850				
Metridia lucens	Day	400–1000	300–400*	700–850	700–850	300–400	700–850	345	19	80†	2
	Night	150–200 300–830	550–1000	700–850	175–200	700–850	700–850				
Metridia venusta	Day	550–700*	400–550	550–1000	550–700	400–550	550–700	29	10	13	—
	Night	550–700*	400–700	400–850	550–700	550–700	700–850				
Nannocalanus minor	Day	0–25 50–175	0–75 100–175 200–300 400–550	0–200	50–75	25–50	75–100	14,964	321	194	1
	Night	0–150 175–200	0–100 125–150	0–200	25–50	0–25	75–100				
Nannocalanus minor C5	Day	0–25 50–150	0–50	0–200	50–75	25–50	50–75	3840	402	218	1
	Night	0–100	0–125 400–550	0–200	50–75	0–25	125–150				
Neocalanus gracilis	Day	50–100 200–400	25–75 175–200 400–700	50–125 400–850	50–75	25–50	75–100	326	18	31	—
	Night	0–75 100–400	0–200 400–550	50–100 175–200 700–850	50–75	0–25	75–100				
Neocalanus gracilis C5	Day	50–100 200–300	25–150	0–125	50–75	25–50	75–100	694	44	281	1
	Night	0–75 150–300	0–175 400–550	50–175	50–75	25–50	75–100				

Pleuromamma abdominalis	Day	75–100 200–700	400–700	75–100 125–150 400–1000	400–550	400–550	400–550	4189	48	70	3
	Night	0–550 830–930	0–175 200–1000	0–1000	25–50	75–100	75–100				
Pleuromamma borealis	Day	400–1000	—	—	550–700	—	—	379	23	27	—
	Night	75–200	—	—	150–175	—	—				
Pleuromamma gracilis	Day	200–550 850–1000	175–850	25–100 125–150 200–850	200–300	300–400	200–300	5184	91	123	3
	Night	0–400 850–1000	0–700 850–1000	0–700 850–1000	25–50	75–100	50–75				
Pleuromamma piseki	Day	200–550	200–1000	25–50 200–850	200–300	300–400	200–300	4474	48	34	3
	Night	0–125 150–200	0–200 400–700	0–125 175–700 850–1000	50–75	25–50	75–100				
Pleuromamma xiphias	Day	200–700	125–150 200–300 400–700	400–1000	400–550	550–700	400–550	1428	19	30†	3
	Night	75–300 400–850	75–850	0–1000	100–125	120–150	75–100				
Rhincalanus cornutus	Day	75–125 150–175 200–1000	0–1000	25–50 100–150 200–1000	200–300	300–400	125–150	935	39	78†	—
	Night	0–930	0–75 120–1000	0–25 50–75 100–1000	300–400	550–700	100–125				
Rhincalanus nasutus	Day	200–1000	50–75*	75–100 550–700 850–1000	700–850	50–75	75–100	264	14	22	2
	Night	125–150 400–930	550–1000	100–175 700–1000	830–930	700–850	100–125				



September 1982



May 1983

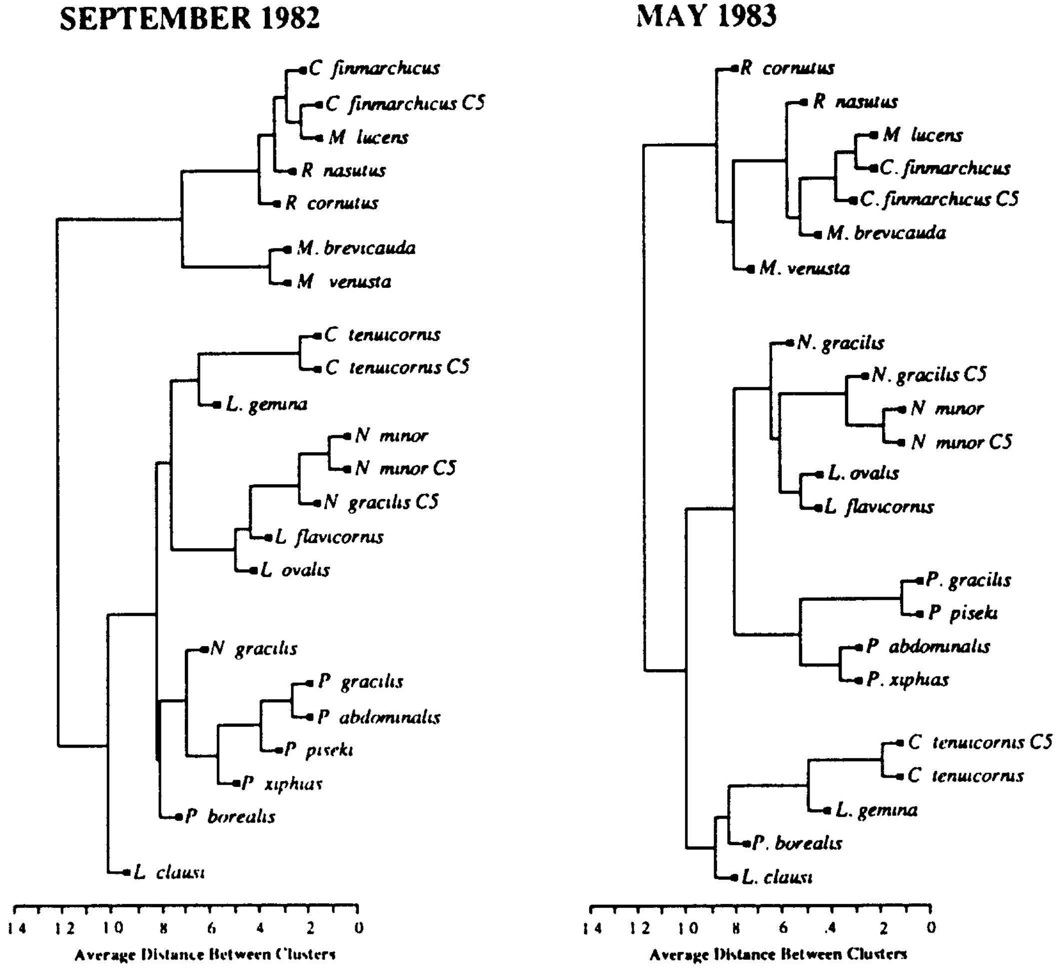


Fig. 5. Results of the two cluster analyses of copepod species for September 1982 and May 1983. Dendrogram not drawn exactly to scale.

tus) For example, *L flavicornis* was eliminated from Group I because the distribution of the species was markedly different from those of other group members. *L. flavicornis* had both a deeper distribution and a different behavioral pattern (diel vertical migration) than other Group I members.

Species and species group distributions

In general, copepod distributions (Table 2) followed the same trends in May as in September (ALLISON, 1986). Species distributions followed physical characteristics across the Gulf Stream, with some distribution patterns paralleling the surface and others following sloping isopleths across the Stream with changes in depth range from station to

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Fig. 4. Copepod species groups determined by recurrent group analysis. The numbers linking boxes refer to the per cent association of species between groups (the per cent association within a group is 100%). (September 1982 analysis redrawn from WISHNER and ALLISON, 1986.)

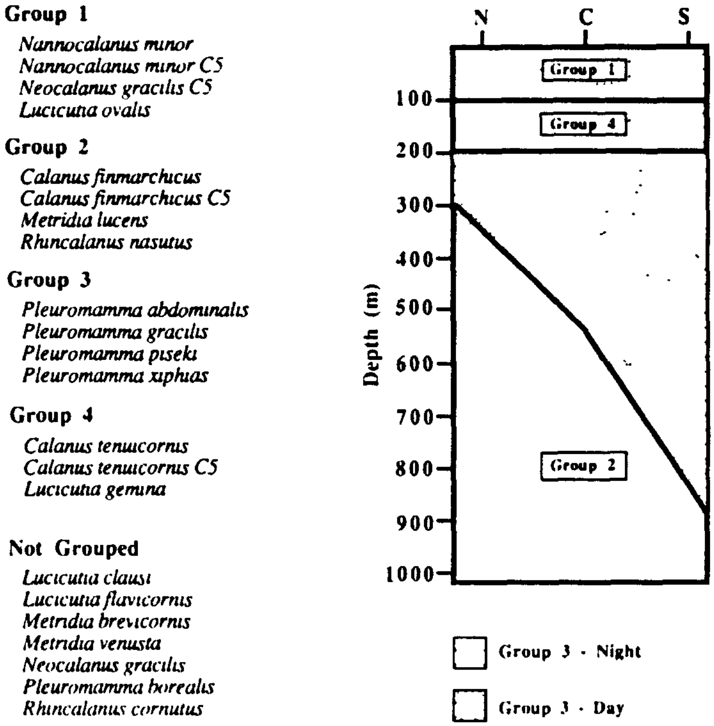


Fig 6 Summary group compositions and approximate group distributions across the Gulf Stream

station. Of the 22 copepod types, seven were found primarily in the upper 200 m (*Nannocalanus minor*, *N. minor* C5, *Calanus tenuicornis*, *C. tenuicornis* C5, *N. gracilis* C5, *Lucicutia gemina*, *Lucicutia ovalis*), six were strong vertical migrators (*Pleuromamma abdominalis*, *P. borealis*, *P. gracilis*, *P. piseki*, *P. xiphias* and *L. flavicornis*), and nine (*C. finmarchicus*, *C. finmarchicus* C5, *L. clausi*, *N. gracilis*, *R. cornutus*, *R. nasutus*, *M. brevicauda*, *M. lucens* and *M. venusta*) inhabited mid-depths (>200 m) of the Gulf Stream.

Members of Group 1 were found in the top 100 m across the Stream (Table 2, Fig. 7) and remained at approximately the same depth ranges at all three locations across the transect. Members of this group (*N. minor*, *N. minor* C5, *N. gracilis* C5 and *L. ovalis*) are shallow-living species from warm, high salinity water in the Gulf Stream (approximately 19–25°C, 36.1–36.5 ppt) and are not diel vertical migrators (Farran, 1947; Roe, 1972, 1984; Wishner and Allison, 1986, Ambler and Miller, 1987). The species did not co-occur as frequently in May as in September (in 46 and 28% of all samples in September and May, respectively); however, three out of the four group members were found together frequently. At most locations, there was a single peak in group abundance (Fig. 8), usually located in water of 25°C or greater (Fig. 2; Wishner and Allison, 1986).

Group 2, composed mainly of Slope Water species (*C. finmarchicus*, *C. finmarchicus* C5, *M. lucens* and *R. nasutus*; Grice and Hart, 1962; Roe, 1972), was found in and below the thermocline (10–15°C, approximated by the sigma-t = 27.0 isopycnal) across the Gulf Stream, following the sloping isotherms and isopycnals (Fig. 7). The distributions of these species had broad depth ranges at the North Wall station (~200–1000 m) which narrowed across the Stream to the Sargasso Sea side (Table 2). Co-occurrence of all group members was more frequent in September (in 48 and 35% of all samples in September and May, respectively). Although some of these species may be vertical migrators (e.g. *C. finmarchicus*), the diel migration pattern was inconsistent between the two times, with no migration in September but limited migration in May at the North Wall and Sargasso Sea (Figs 7 and 8). Night group abundance peaks were progressively deeper in the water column across the Stream from north to south (this was also true for the day group abundance peaks in September because little diel migration occurred; Fig. 8).

Group 3, composed of four congeneric Sargasso Sea–Gulf Stream species (*P. abdominalis*, *P. gracilis*, *P. piseki* and *P. xiphias*; GRICE and HART, 1962; DEEVEY and BROOKS, 1977), showed strong diel vertical migration. Day distributions extended from just above the thermocline to approximately 200 m (Table 2; Fig. 7) and were constrained to narrower depth ranges at the North Wall side compared with the Sargasso Sea side, so that the maximum depths of the vertical migrators were considerably shallower at the North Wall station than at the Sargasso Sea station. This resulted in a decreasing vertical migration range for deeper-living members of the population across the Gulf Stream from south to north as the thermocline shoaled (night abundance maxima were located at similar depths at all three locations). *P. abdominalis* and *P. xiphias* had slightly deeper ranges than the other two species, so that all four species did not always co-occur. For example, only three out of four members were ever together in the Central Stream during the day in May (Fig. 7; all four species were found in 30 and 50% of all samples in September and May, respectively). At night, Group 3 species were mainly in the upper 200 m (Fig. 8) and night distribution ranges were similar across the Gulf Stream There was evidence of reverse or no migration of some individuals from all four species, resulting in the nighttime occurrence of Group 3 species at depth (Table 2). The peak nighttime abundance for the group was always located in the top 125 m (Fig. 8). Day distributions were less sharply defined than the night distributions (Table 2), being spread over a greater depth range, but peak group abundances for day and night were well separated in the water column (Fig. 8).

The distribution of Group 4, composed of warm-water species (*C. tenuicornis*, *C. tenuicornis* C5 and *L. gemina*; ROL, 1972; WISHNER and ALLISON, 1986), was usually centered at 100–200 m in water of 20–25°C across the Stream (Fig. 7) and did not vary across the transect. Group coherence across the Stream was good in both data sets (in 57 and 60% of all samples in September and May, respectively). A subtle diel pattern in the location of the abundance maximum existed such that at five out of six of the locations, the day group abundance maximum was 25–50 m deeper than the night abundance maximum (Fig. 8).

With the exception of Group 3 (vertical migrators), distributional overlap between groups was minimal, suggesting habitat partitioning. Groups 1 and 4 had little overlap in the top 200 m and Group 2 was found primarily below the main thermocline. The distribution of Group 3 (vertical migrators) overlapped completely with Groups 1 and 4 at night in the top 200 m, but during the day Group 3 did not overlap significantly with other groups.

Seven copepod types were not placed into copepod groups because their distributions or behavior were dissimilar to those of other types. Of these, one species, *P. borealis*, was notable in that it occurred only at the North Wall station at both times. *P. borealis*, a Slope Water species, has not been found in the Gulf Stream and the Sargasso Sea (e.g. GRICE and HART, 1962; WISHNER and ALLISON, 1986). The Gulf Stream functions as a sharp boundary to the distribution of this species, in contrast to the other 21 copepod types examined in this study.

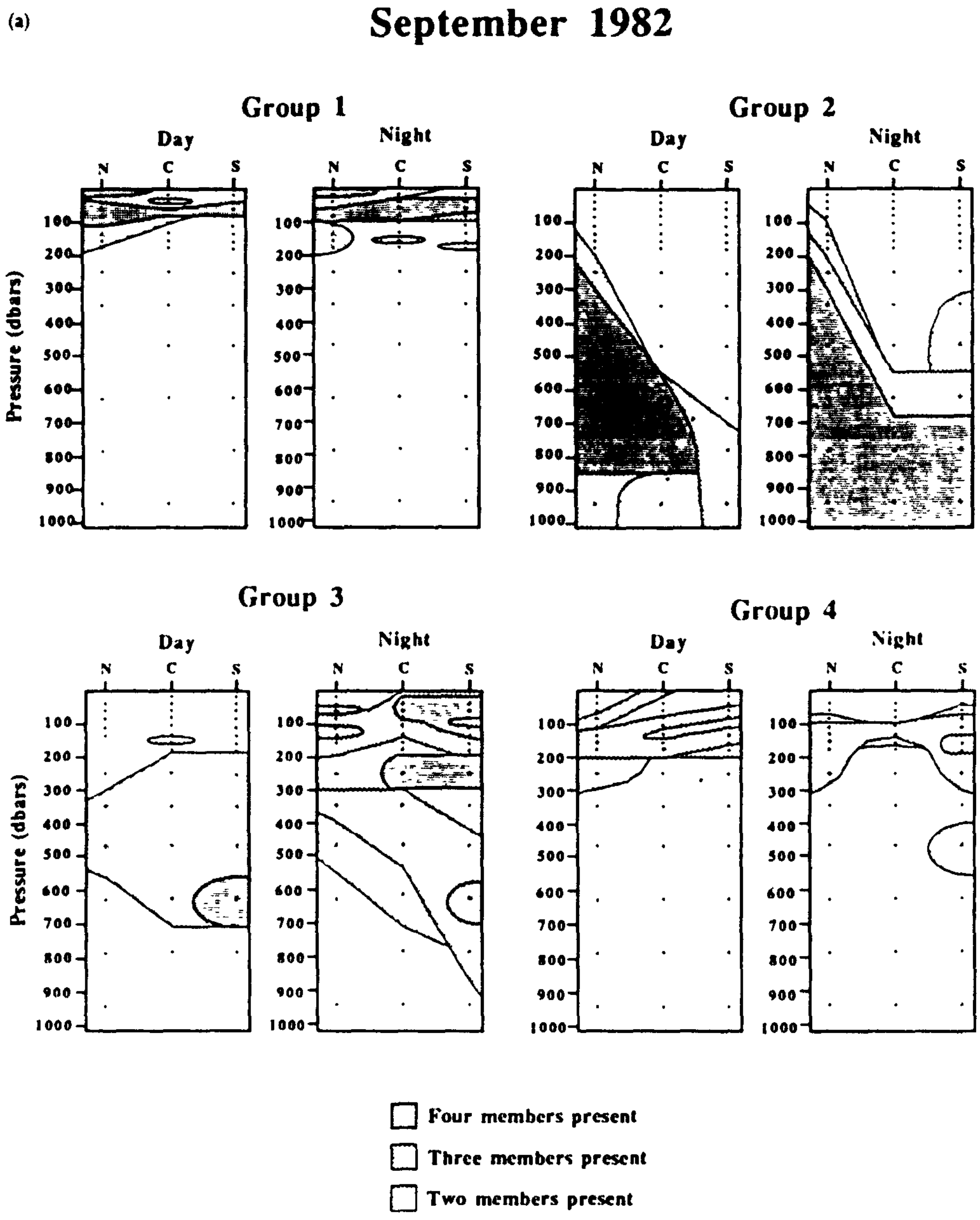
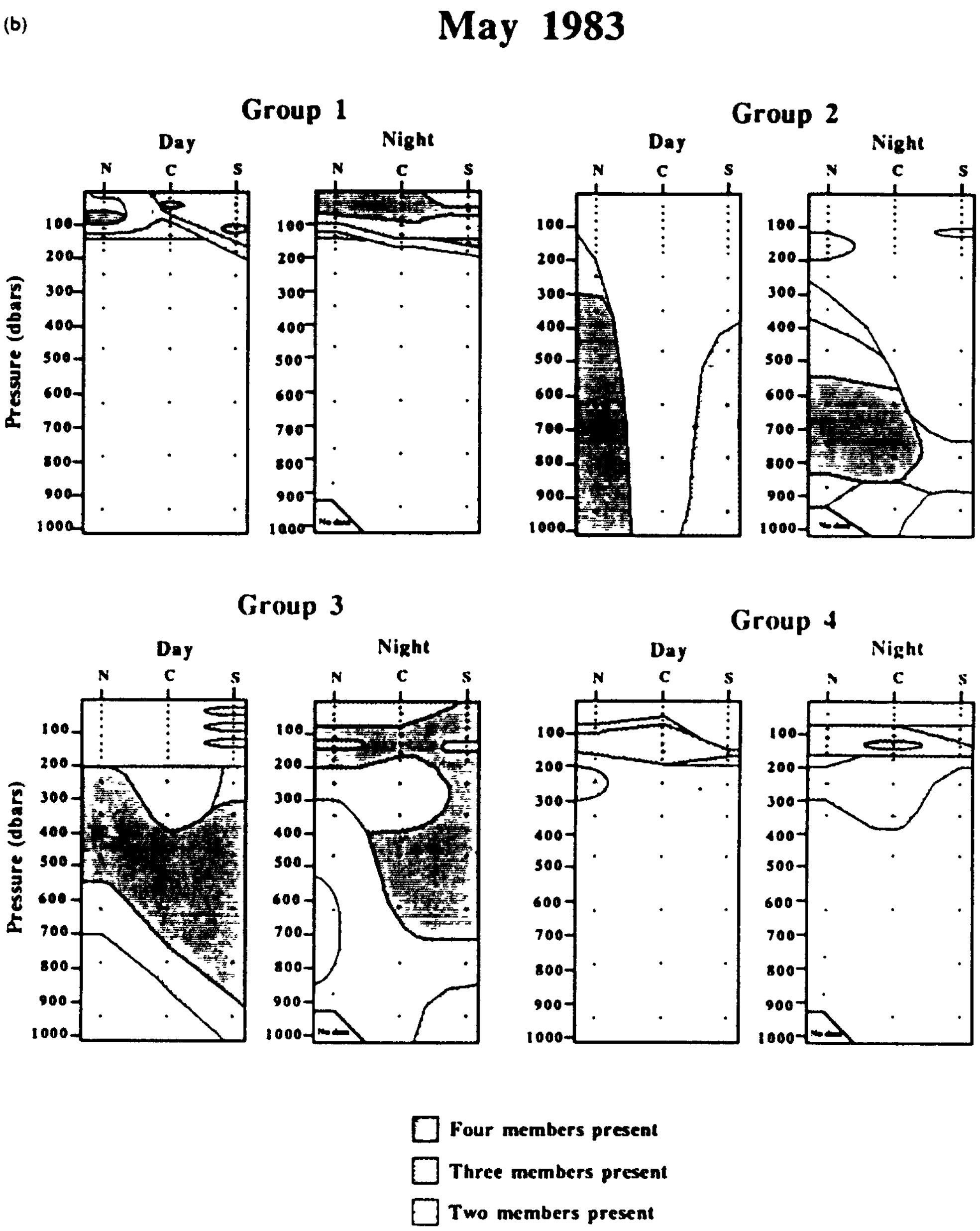


Fig. 7. Day and night summary copepod species groups distribution across the Gulf Stream for (a) September 1982 and (b) May 1983. Stations designations (N, C and S) are as in Fig. 2. Locations of the full group (all members present) are indicated by the darkest shading, with lighter tones representing depths where some group members were absent. Note: September group distributions are different than those presented in WISHNER and ALLISON (1986), because of the redefinition of group members in this study.

(b)


May 1983
Group 1
Group 2
Group 3
Group 4
Day
Night
N
C
S
Pressure (dbars)
100
200
300
400
500
600
700
800
900
1000
No data
Four members present
Three members present
Two members present

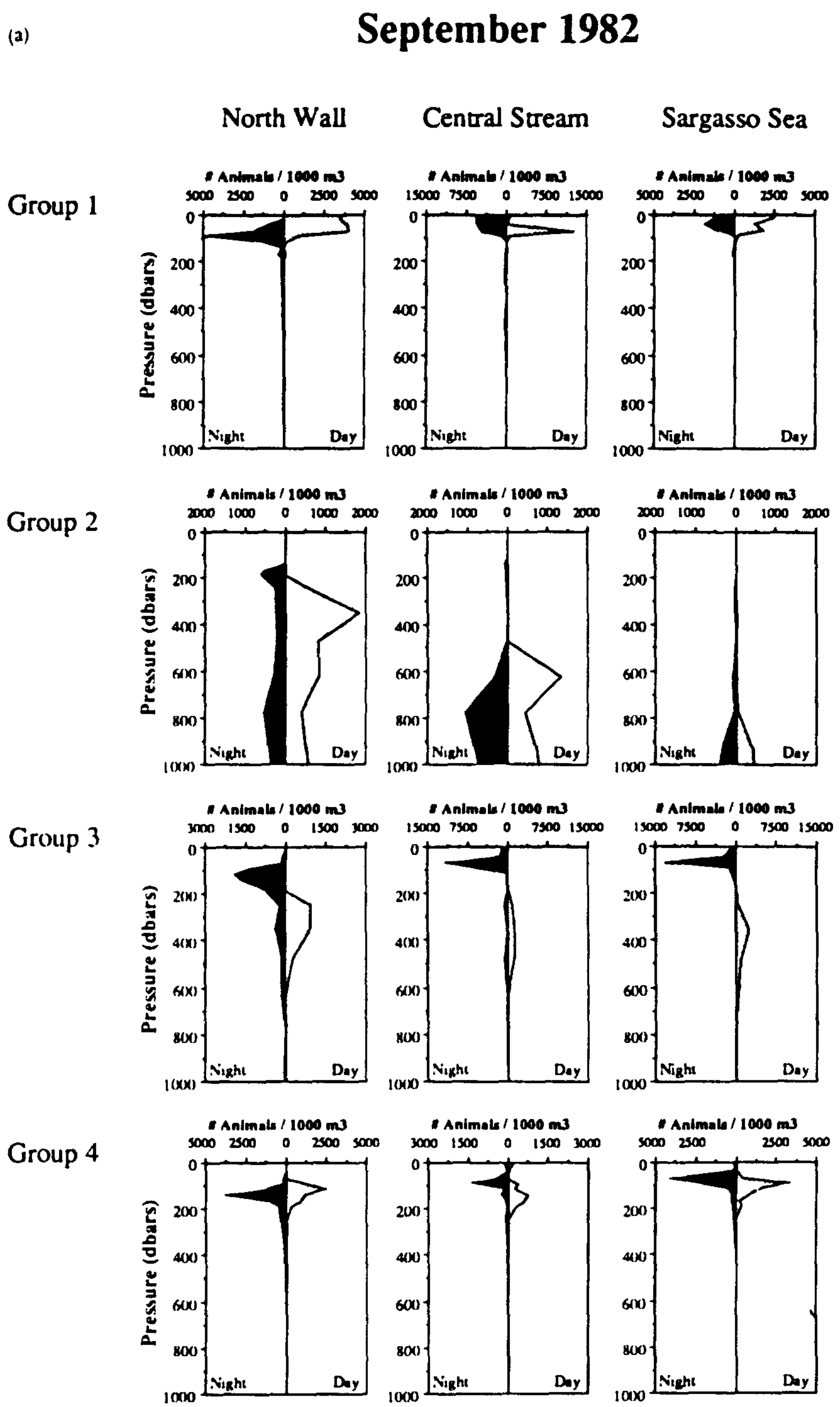
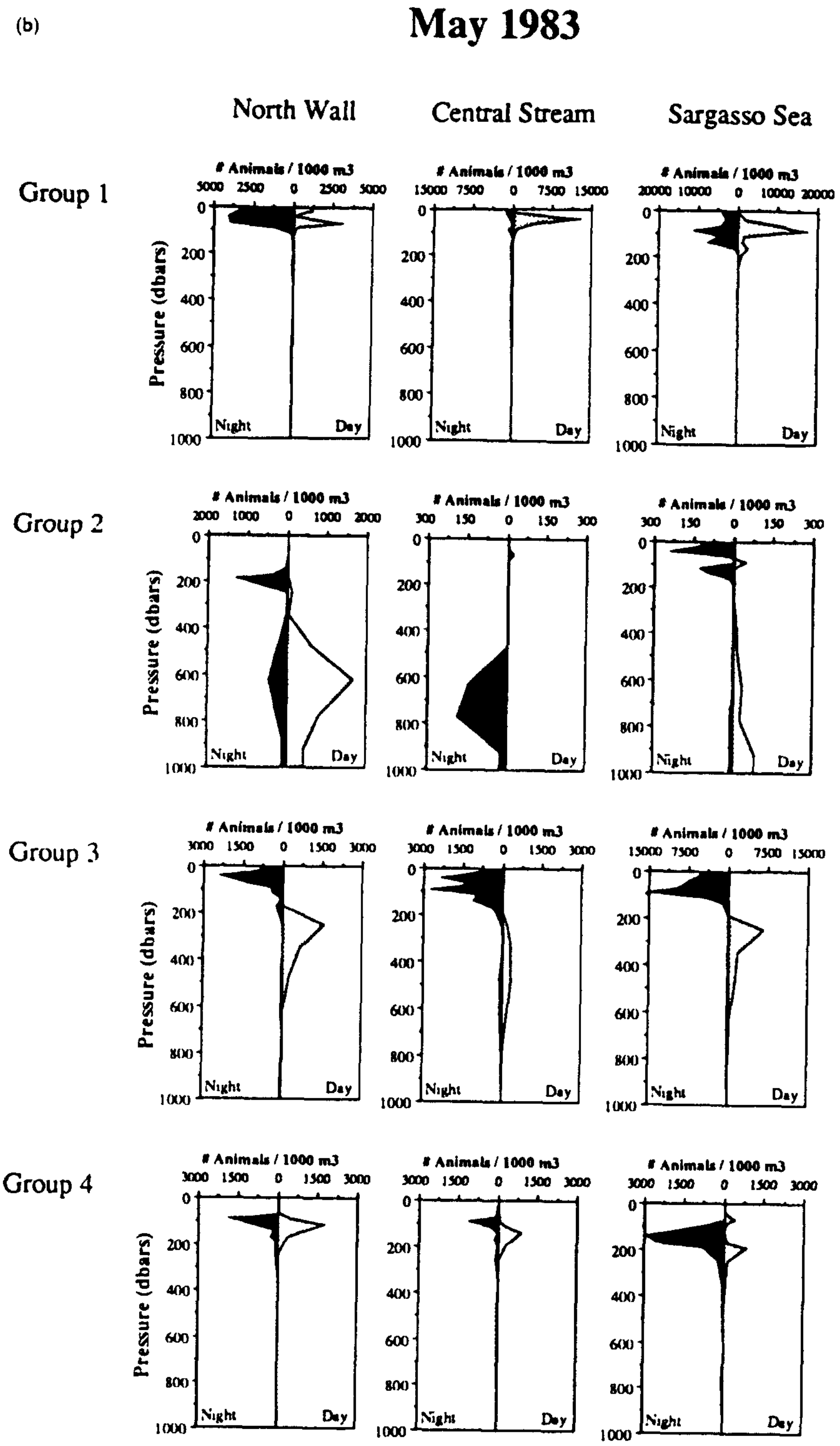


Fig. 8. Total day and night abundances with depth of the summary copepod species groups for (a) September 1982 and (b) May 1983. Night abundances (dark shade) are to the left side of each panel and day abundances (light shade) are on the right. Note different abundance axes.


(b)
May 1983
North Wall
Central Stream
Sargasso Sea
Group 1
Group 2
Group 3
Group 4
Animals / 1000 m3
5000 2500 0 2500 5000
15000 7500 0 7500 15000
20000 10000 0 10000 20000
2000 1000 0 1000 2000
300 150 0 150 300
3000 1500 0 1500 3000
15000 7500 0 7500 15000
Pressure (dbars)
0
200
400
600
800
1000
Night
Day

Day–night and between-cruise differences

Overall, both species and summary group abundances (integrated and maximum) were similar in September and May, and few differences were observed between day and night. Only five copepod species had significantly different median abundances between the 2 months (Mann-Whitney U test, $P \leq 0.05$; Table 2). Maximum and integrated group abundances at the three cross-stream locations were usually not significantly different between day and night or between September or May (only 3/24 and 5/24 comparisons for day versus night and September versus May, respectively, were significantly different: Wilcoxon's paired-sign test; Table 3a; Figs 8 and 9)

Cross-stream trends in abundance

Species group abundance (integrated and maximum) differences between cross-stream locations were confined to Groups 2 and 3, the deeper-living species groups. Integrated and maximum abundances of Group 2 were greatest at the North Wall station in both September and May ($P = 0.02$–0.05, Wilcoxon's signed-rank test; Figs 8 and 9; Table 3b) and abundances decreased across the Stream from the North Wall to the Sargasso Sea. Cross-stream trends in integrated abundance between the two times were positively correlated (Spearman's Rho = 0.60). In contrast, integrated and maximum abundances of Group 3 were greater at the Sargasso Sea than at the North Wall for both September and May (P = 0.02, Wilcoxon's signed-rank test; Figs 8 and 9; Table 3b). Central Stream abundances resembled the Sargasso Sea in September and the North Wall in May. Cross-stream trends in integrated group abundance were positively correlated between the two times (Spearman's Rho = 0.575).

Most cross-stream comparisons of integrated and maximum group abundances for the shallow-living groups (Groups 1 and 4) revealed similar abundances across the current (Table 3b). Only two exceptions were noted for Group 1: the September integrated and the May maximum abundances were different between the North Wall and the Sargasso Sea (Figs 8 and 9; Table 3b). Exceptions for Group 4 were confined to the Central Stream and Sargasso Sea comparison: both integrated and maximum abundances for September but only integrated abundances for May were different between the two locations (Figs 8 and 9; Table 3b). Cross-stream changes in integrated abundance were negatively correlated for Group 1 between September and May (Spearman's rho = −0.771), probably due to the higher abundances of the group at the Sargasso Sea in May, but were positively correlated for Group 4 for the two sampling dates (Spearman's rho = 0.829).

Within-group species abundance trends across the Stream showed significant agreement for two of four groups from May and for one of four groups from September (Kendall concordance test, Table 4). Only Group 2, composed of Slope Water species, showed significant concordance at both times. The abundances of these species decreased dramatically across the Gulf Stream from north to south (Figs 8 and 9).

DISCUSSION

The distributions of plankton species result from biological and physical processes acting in conjunction. Biological characteristics of the organisms (e.g. behavior, food requirements, tolerance to physical environment and reproductive success) respond to

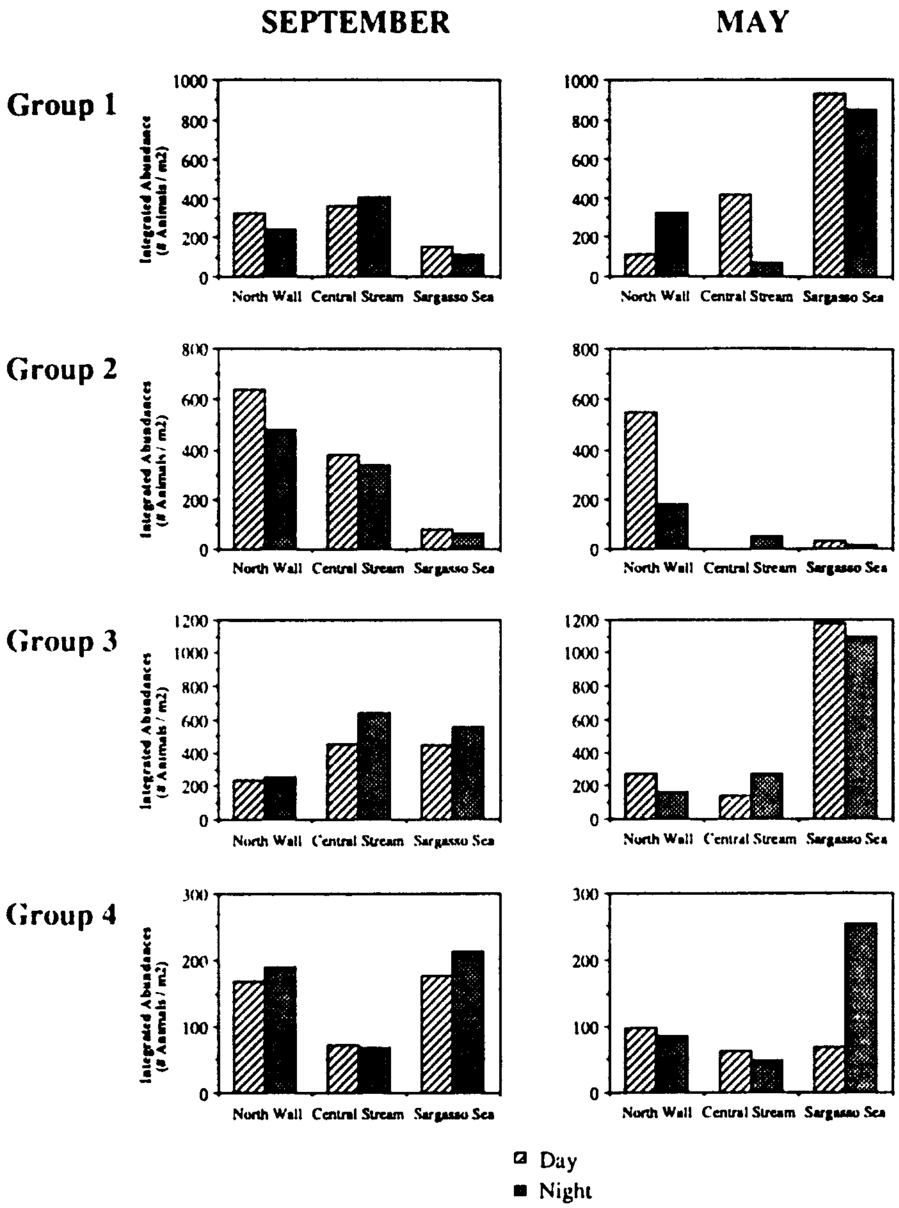


Fig 9 Total day and night integrated abundances (0–1000 m) for the four summary copepod species groups for September and May. Night (dark shade) and day (light shade) integrated abundances (No. animals m^{-2}) are plotted for each cross-stream location for each species group

physical characteristics of the water column (e.g. temperature, salinity or oxygen) and affect the depth and horizontal distribution. Diel vertical migration may result in a species being subjected to two different physical and advective regimes within a single 24 h period. Advection may act to concentrate or dilute species abundances. The consistent association

Table 3. Results of Wilcoxon's paired sample tests for copepod group abundances. (A) Differences between September 1982 (S) and May 1983 (M) and between day (D) and night (N) integrated (No./m^2) and maximum (No./1000 m^3) abundances were tested at each cross-stream location for each group using the abundances of the component species. (B) Pairwise comparison of the integrated and maximum abundances at the three cross-stream locations for each group for each sampling time, using the abundances of the component species. Both day and night abundances were used for the sampling time comparisons and both September and May abundances were used for the day–night comparisons. (N = North Wall Sta., C = Central Stream Sta., S = Sargasso Sea Sta., "n.s." = not significant)

		(A)				(B)											
		Integrated abundance (No./m^2)		Maximum abundance (No./1000 m^3)		Integrated abundance (No./m^2)						Maximum abundance (No./1000 m^3)					
						September			May			September			May		
		S vs M	D vs N	S vs M	D vs N	N	C	S	N	C	S	N	C	S	N	C	S
Group 1																	
	N	n.s.	n.s.	n.s.	n.s.	—	n.s.	0.02	—	n.s.	n.s.	—	n.s.	n.s.	—	n.s.	0.05
	C	n.s.	n.s.	n.s.	0.05 (D > N)		—	n.s.		—	n.s.		—	n.s.		—	n.s.
	S	n.s.	n.s.	n.s.	n.s.			—			—			—			—
Group 2																	
	N	n.s.	n.s.	n.s.	n.s.	—	0.05	0.02	—	0.02	0.02	—	n.s.	0.02	—	0.02	0.05
	C	0.02 (S > M)	n.s.	0.05 (S > M)	n.s.		—	n.s.		—	n.s.		—	0.05		—	n.s.
	S	0.05 (S > M)	n.s.	n.s.	n.s.			—			—			—			—
Group 3																	
	N	n.s.	n.s.	n.s.	0.05 (N > D)	—	0.02	0.02	—	n.s.	0.02	—	n.s.	0.05	—	n.s.	0.02
	C	n.s.	n.s.	n.s.	0.02 (N > D)		—	n.s.		—	0.02		—	n.s.		—	0.02
	S	0.02 (M > S)	n.s.	n.s.	n.s.			—			—			—			—
Group 4																	
	N	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	—	n.s.	n.s.	—	n.s.	n.s.	—	n.s.	n.s.
	C	n.s.	n.s.	n.s.	n.s.		—	0.05		—	0.05		—	0.05		—	n.s.
	S	n.s.	n.s.	0.05 (S > M)	n.s.			—			—			—			—

*Table 4 Results of the Kendall Concordance tests. Kendall's coefficient of concordance (W) was used to establish agreement between species in a group in abundance trends with cross-stream location. Columns contain sums of the cross-stream ranks of abundances of the component species for each group. Kendall's W and the significance level. Abundances were ranked with "1" being the least abundant (*Sokal *and* Rohlf*, 1981). All six "samples" (three locations, day and night) were used in each concordance test*

		_ ranks							
	Species group	North Wall Day	North Wall Night	Central Stream Day	Central Stream Night	Sargasso Sea Day	Sargasso Sea Night	W	Significance
September									
	1	18	17	16	14	12	7	0.293	>0.2
	2	23	18	14	14	7.5	7.5	0.648	0.01
	3	6.5	10.5	14	18	15	20	0.434	0.20
	4	11	14	8	4	12	14	0.479	>0.20
May									
	1	6.5	15	19	8.5	19.5	14.5	0.411	0.20
	2	22	22	5	14	11	10	0.836	0.01
	3	12.5	6	8	13.5	22	22	0.823	0.01
	4	10	11	8	7	9	18	0.492	0.20

of a species with particular environmental conditions results in a predictable distribution of that species in the Gulf Stream.

Biological-physical associations

During both September 1982 and May 1983, the Gulf Stream could be divided into two environmental zones: (1) The surface down through the main thermocline, typical of the upper Sargasso Sea. The lower boundary of this region was constricted as the thermocline shoaled from south to north, but the top 200 m of the Gulf Stream showed little change in environment across the sections. (2) A Slope Water environment extending into the Stream from the north below the main thermocline, becoming constricted from the upper boundary as the thermocline deepened from north to south. These regions were important for the distribution of different plankton types and copepod species groups.

The distributions of the copepod species groups were strongly associated with characteristic environmental conditions across the Gulf Stream. Groups 1 and 4 were associated with the top 200 m of the upper zone of the Gulf Stream, where isopleths extended parallel across the section. Group 3, the vertically migrating group, was associated with the whole upper zone. Group 2 was associated with the lower, Slope Water zone of the current. Associations between hydrographic features and distributions of zooplankton have been identified in the northwest Atlantic for water masses (e.g. Grice and Hart, 1962; Cox and Wiebe, 1979; Davis, 1984) and Gulf Stream rings (e.g. Wiebe *et al.* 1976b; Ring Group, 1981; Joyce *et al.*, 1984; Davis and Wiebe, 1985). The distributions of copepod species and species groups are also associated with the vertical structure of the environment in other regions of the ocean (e.g. McGowan and Walker, 1979; Cummings, 1983; Longhurst, 1985). This study and the work of Wishner and Allison (1986) are the first to identify these associations in different zones of the Gulf Stream and suggest that consistent associations between plankton species and the environment may be characteristic of zooplankton communities in the current.

Temporal similarities and differences: physical environment

Most differences in the physical environment between the two sampling times may be attributed to seasonal changes. The physical structure of the Gulf Stream itself was similar in September 1982 and May 1983, although the temperature difference between the Slope Water and the Gulf Stream was much larger in the spring. The cooler surface water (<25°C) at the Sargasso Sea side station in the May hydrocast section (Fig. 2) may be due to winter cooling (Schroeder *et al.*, 1959; Worthington, 1959; Menzel and Ryther, 1960, 1961a), but an alternative explanation may be the occurrence of a recently described Gulf Stream phenomenon, the "warm surge" (Gilman and Rothstein, submitted). The May Sargasso Sea station was sampled 6–8 days earlier than the Central Stream and North Wall stations (Table 1) so that the Sargasso Sea station was sampled during the "cold phase" while the Central Stream and North Wall stations were sampled during the "warm phase" of a warm surge event (Gilman and Rothstein, submitted). However, the potential effect of this event on copepod species distribution and abundances is unclear. The lower density in the surface layers of the September transect, relative to May, is indicative of stratification of the upper layers during summer and early fall (Siegel *et al.*, 1990)

The cross-stream velocity field indicated that bi-directional cross-stream transport of water parcels, and potentially plankton populations, was present during both sampling times. In the September transect, convergence of cross-stream velocities from the edges of the Gulf Stream to the center indicated that entrainment of water parcels from both sides of the current was occurring (Wishner and Allison, 1986). However, in May three types of cross-stream transport were occurring simultaneously (Fig. 2): (1) cross-stream flow from the northwest to southeast (Slope Water to Sargasso Sea) below the thermocline and 27.00 isopycnal, suggesting entrainment of Slope Water into the Gulf Stream at depth, (2) cross-stream flow from southeast to northwest in the core of the Gulf Stream and above the thermocline (except on the Sargasso Sea side), suggesting entrainment and cross-stream transport of Sargasso Sea water, and (3) flow out of the Gulf Stream from northwest to southeast in the top 150 m at the Sargasso Sea side station, indicating detrainment of Gulf Stream surface water to the Sargasso Sea.

Temporal similarities and differences: copepod species and community structure

Copepod species responded in a similar manner to the changing environmental conditions across the Gulf Stream during both sampling times so that species distributions generally followed the same trends across the Gulf Stream in September and May, although some depth ranges differed (Table 2; Allison, 1986; Wishner and Allison, 1986). Vertical distributions in the North Atlantic have been described for many of these species (Wishner and Allison, 1986 and references therein) and species distributions at the Sargasso Sea side of the Gulf Stream were in general agreement with these previous reports. However, a consistent pattern of environmentally associated change in species' vertical distribution across the Gulf Stream was not described previous to this study and that of Allison (1986) and Wishner and Allison (1986).

Although total zooplankton biomass from the samples was greater in September than in May (Allison and Wishner, 1986), this difference was not seen in the abundances of most of the selected copepod species (Table 2). Maximum and integrated group abundances at similar cross-stream locations were similar for the two sampling times for most species groups. The absence of differences in abundance between the two times suggests that, for these species, there may be little seasonal change in abundance. Differences and similarities between September and May species abundances in this study cannot be conclusively attributed to seasonality, however, since only one cycle was sampled.

In two previous year-long studies in the Northern Sargasso Sea, which included data on 14 of the 18 species in the present study, total copepod numbers reached a spring maximum (following the spring phytoplankton bloom), with a second maximum in fall and minima in early summer and late fall (Deevey, 1971, Deevey and Brooks, 1977). Most species followed this same seasonal cycle. Abundances in 1961 (Deevey, 1971) were greater in May than September for 11 species, approximately equal for two species, and greater in September than May for only one species. The discrepancy between the present study (with no apparent change in abundance between September and May for these species) and the earlier ones could be due to sampling differences or differences between the 2 years in the timing of the spring bloom and the spring copepod maximum.

It was somewhat unexpected to find community structure in the plankton within the Gulf Stream, since physical characteristics change over a relatively short distance and advection is strong. Community structures for phytoplankton, zooplankton and mesopelagic fish have been identified using descriptive statistical techniques in "conservative environments" (Venrick, 1971) such as gyre systems (e.g. Jahn and Backus, 1976; McGowan, 1977, Venrick, 1982; McGowan and Walker, 1979) and young warm-core rings (Gould *et al.*, 1986), while less distinct species groups were identified in environments such as the North Pacific Transition Zone (Venrick, 1971), the California Current (McGowan, 1977), and the Gulf Stream (Jahn and Backus, 1976) [although recent work in the California Current has shown associations of plankton with physical features such as jets (Haury, 1984; Mackas *et al.*, 1991)]. Community structure might be less likely in a "physically disturbed" region, such as the Gulf Stream, than in a more stable, "biologically accommodated" area because physical conditions fluctuate unpredictably, presumably preventing the establishment of a structured biological community (Sanders, 1968, 1969). However, the cross-stream vertical structure of the Gulf Stream is itself a persistent feature (Stommel, 1966; Halkin *et al.*, 1985) and also may be considered predictable (Williams, 1988).

Community structure in the oceanic zooplankton has been described, however the mechanisms regulating this structure are poorly understood (Hayward and McGowan, 1979; McGowan and Walker, 1979; Longhurst, 1985; Williams, 1988) and the coexistence of multiple species at similar depths is still paradoxical (e.g. Hutchinson, 1964; Ghilarov, 1984). The vertical structure of the environment appears to influence community structure, as evidenced by associations observed consistently between copepod species (and species groups) distributions and particular depth intervals (e.g. Pipe and Coombs, 1980, Hopkins, 1982; Cummings, 1983, Sameoto, 1984, Longhurst, 1985; Sameoto, 1986, Williams, 1988). Competition and niche partitioning, the spatial diversity of the physical environment, and predation have all been suggested as mechanisms regulating the observed community structures, however, unlike freshwater and terrestrial environments, a particular mechanism has yet to be confirmed for an oceanic community (e.g. Longhurst, 1985, Williams, 1988).

In the Gulf Stream, species groups were consistent at the two sampling times and were biologically meaningful, with species grouped together having similar distributions and behavior. However, because this study consisted of only two sampling times, caution is required when concluding that the similarities in community structure are evidence for longer term consistent or persistent community structure (Connell and Sousa, 1983). May and September are physical extremes in the Gulf Stream environment and would be the most likely times to reveal differences in copepod species distributions and community structure, if these differences exist. The consistency in species groups across the Gulf Stream and between these two sampling times suggests that a stable zooplankton community structure persists over time and space even in the highly advective Gulf Stream.

In summary, both the physical environment and biological distributions in the Gulf Stream were remarkably similar in September 1982 and May 1983, despite the strong temperature gradient between the current and the Slope Water during May. Few differences were observed between the two times in individual species distribution, species abundances, community structure, and environmentally associated patterns of species (groups) vertical distributions. The structure of the physical environment in the Gulf Stream system strongly affects the distributions and abundances of these species, and their distributions in the current may be predictable.

Species groups as indicators

The consistent association of species groups with physical characteristics of environment suggested that certain copepod species or groups may be used as indicators of specific regions of the Gulf Stream. In a related study, the strong associations between these copepod species, species groups, and environmental characteristics were demonstrated by the successful development of linear discriminant models that differentiated between samples collected in different regions of the Gulf Stream on the basis of the copepod species or species assemblages alone (Ashjian, 1991). Other researchers have previously classified some of these copepod species studied as indicators of water type (Grice and Hart, 1962; Bowman, 1971; Deevey and Brooks, 1977; Cox and Wiebe, 1979). On a smaller scale, Haury (1984) and Haury *et al.* (1986) utilized changes in abundance of plankton species characteristic of specific water masses as evidence of water mass mixing in eddies in the California Current System.

Indicator copepod species may be useful in identifying water mass exchange across the Gulf Stream, especially on the northern edge of the current between Gulf Stream–Sargasso type water and Slope Water (Ashjian, 1991, 1993). For example, *P. borealis*, a Slope Water species, was found in the Gulf Stream only at the North Wall station (Table 2, Grice and Hart, 1962). Its congener, *P. gracilis*, is similar in size and behavior (diel migration) and is considered to be a Sargasso Sea–Gulf Stream species (Grice and Hart, 1962; Deevey and Brooks, 1977). These two closely related species can be utilized as reliable indicators of water mass type and mixing (Ashjian, 1991, 1993). Certain species are characteristic of only the top 200 m of the Gulf Stream (Group 4) while others are characteristic of middle–deep regions (Groups 2 and 3). Trends in cross-stream abundance of indicator species or groups can be indicative of continuous cross-stream mixing processes occurring at different depths in the Gulf Stream.

Role of the Gulf Stream in cross-stream transport of plankton populations

A hypothesis describing possible zooplankton transport routes by small-scale continuous processes across the Gulf Stream, based on cross-stream and downstream velocity sections, was proposed by WISHNER and ALLISON (1986). In this hypothesis, cross-stream mixing of water and populations is most likely in the surface layers of the current (streamers and filaments) and in and below the main thermocline, where loss of water parcels from the Gulf Stream along isopycnals, especially in meanders, has been demonstrated (BOWER *et al.*, 1985; BOWER and ROSSBY, 1989). Recent modeling of Gulf Stream meanders suggested that considerable cross-stream exchange of water parcels occurs in the main thermocline (only 42% of the water is retained in the jet in a "typical" meander), while greater retention of water parcels is found in the surface layers (87% retained; BOWER, 1991).

The vertical distributions of the zooplankton across the Gulf Stream would determine the transport regimes the animals would experience. Species from Groups 1 and 4 would be subjected to cross-stream transport and mixing in the top 200 m of the current. This type of mixing might include water transfer through the formation of small-scale eddies or shingles as well as diffusion. Species from Group 2 would experience cross-stream mixing along isopycnals in and below the main thermocline. Species from Group 3 would be subjected to three types of transport during a 24 h period: (1) cross-stream mixing in the surface layers at night, (2) downstream transport in the core of the Gulf Stream during the day, and (3) isopycnal cross-stream transport in the main thermocline (deeper-living individuals).

If continuous cross-stream mixing processes are occurring, then abundances of indicator species would be highest near their source and decrease across the Stream. Cold-water species would be found in highest abundances at the northern stations and warm-water species would have highest abundances on the Sargasso Sea side. Two of the four copepod species groups demonstrated these patterns. Group 2, composed of vertically migrating Slope Water species, had highest abundances on the northern side of the Gulf Stream, and a reduced depth range from north to south (Figs 7–9). These patterns are consistent with the hypothesis that these species are of Slope Water origin and have been entrained into the Gulf Stream system in Slope Water which is being mixed below the thermocline. Group 3, composed of vertically migrating Sargasso Sea species, had highest abundances in the Sargasso Sea in May and in both the Sargasso Sea and the Central Stream in September but lowest abundances at the North Wall for both times (Figs 8 and 9). These trends are consistent with a Sargasso Sea source for Group 3 (and an endemic Gulf Stream population). The decrease in abundance of both copepod groups across the Stream may reflect an inability to survive where changes in the physical environment result in a decline in the quality or quantity of food or alter behavior, such as restricting depth range or reducing migration (e.g. BOYD *et al.*, 1978).

The abundances of Groups 2 and 3 were also consistent with the observed cross-stream velocity fields, especially in May (Fig. 3). At that time, cross-stream transport occurred above the thermocline from east (Sargasso Sea) to west. High abundances of Group 3 animals were observed at the Sargasso Sea station both day and night, reflecting possible entrainment of Sargasso Sea water into the Stream. Cross-stream transport from west (North Wall) to east occurred below the main thermocline, and high abundances of Group 2 animals at the North Wall of the Stream may be due to entrainment of Slope Water into the Stream. These results suggest that the September sampling was conducted during a period of enhanced entrainment of Slope Water (and Slope Water species), while the May sampling was conducted during enhanced entrainment of Sargasso Sea water (and species). Both Groups 2 and 3 showed concordance of component species' abundance trends (Kendall's *W*, Table 4), supporting the idea that these trends are due to physical transport, which would act equally on all species within a group. Since these differences were confined to species found below the mixed layer, the cross-stream mixing probably occurred along isopycnals of the main thermocline (BOWER *et al.*, 1985; BOWER and ROSSBY, 1989).

The two groups found in the upper 200 m of the Gulf Stream (Groups 1 and 4) showed little consistent pattern of increase or decrease across the Stream. Differences in the integrated abundances of Group 1 between the two sampling times may be due to seasonal differences or cross-stream transport. During May, abundances of shallow-living copepod species at the Sargasso Sea station may have been elevated in response to enhanced food conditions following the spring bloom in the Northern Sargasso Sea (MENZEL and RYTHER, 1961a,b; DEEVEY, 1971). The higher abundances observed in September at the Central Stream and North Wall stations may be due to convergence of flow at that location (WISHNER and ALLISON, 1986).

The existence of cross-stream exchange of plankton populations has important implications for regional biogeography. The consequences of cross-stream mixing include greater dispersal of species with enhanced opportunity for speciation, increased competition and predation between Slope Water and Sargasso Sea species, and the possibility of genetic exchange between populations. Estimates of the cross-stream transport associated with continuous mixing processes suggest that the contribution of these processes to the mixing of plankton populations, especially when enhanced in dynamic features of the Gulf Stream such as meanders, may be significant and of the same or greater magnitude as the transport associated with ring formation (BOWER and ROSSBY, 1989; T. ROSSBY, personal communication). Based on RAFOS float data, BOWER and ROSSBY (1989) suggested that up to 60% of the water in the core of the current at main thermocline depths between 65 and 75°W may be exchanged with water from outside the Gulf Stream. If the average Gulf Stream transport at 73°W is $87.8 \times 10^6\ m^3\ s^{-1}$ (HALKIN and ROSSBY, 1985), then $1.66 \times 10^{15}\ m^3\ y^{-1}$ of Gulf Stream core water may be lost through this process. In contrast, cross-stream transport associated with cold-core ring formation has been estimated to be $9.0 \times 10^{13}\ m^3\ y^{-1}$ (FUGLISTER, 1972; RICHARDSON, 1983). (This term does not include effects of subsequent resorption of the ring into the Gulf Stream.) A similar calculation for warm-core rings is not available; however, transport is probably less for warm-core rings, because of their smaller diameter and shallower depth (WIEBE, 1982; RICHARDSON, 1983; JOYCE *et al.*, 1984). Therefore, transport of water parcels and zooplankton populations by continuous cross-stream mixing processes may be a significant source of expatriate zooplankton populations in the northwestern Atlantic.

CONCLUSIONS

(1) Although the temperature gradient between the Gulf Stream and the Slope Water was greater in May 1983 than in September 1982, the physical environment of the Gulf Stream itself was similar at the two times. Differences that were observed can be attributed to seasonality or to a warm-surge event during the May study. The downstream velocity field was also similar at both times, but the cross-stream velocity field showed differences in magnitude and directionality.

(2) Adult copepod species distribution patterns were similar for the two sampling times.

(3) The same copepod species groups were derived independently for the two sampling

times, suggesting that a persistent copepod community structure may be a general feature of the Gulf Stream.

(4) Copepod species group distributions were associated with specific environmental conditions and regions of the Gulf Stream. Group distributions changed across the Gulf Stream in conjunction with the changing distributions of physical characteristics.

(5) Copepod species groups may be reliable indicators of regions of the Gulf Stream and could be used as tracers of water mass mixing.

(6) The integrated abundances of two of the four copepod species groups supported the hypothesis that cross-stream mixing of water parcels and zooplankton populations by continuous small-scale processes is operating in the Gulf Stream.

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