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Spatial and Temporal Variability in Zooplankton Distributions and Abundances Across the Gulf Stream

Stuart K. Allison University of Rhode Island

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SPATIAL AND TEMPORAL VARIABILITY IN ZOOPLANKTON DISTRIBUTIONS AND ABUNDANCES

ACROSS THE GULF STREAM

MASTER OF BY ONCE TREETS

STUART K. ALLISON

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

OCEANOGRAPHY

Thesis Committee

UNIVERSITY OF RHODE ISLAND

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succion of the incidinalistic systematic si member piecelhochone and needs ity furnation. **Abstract**

From November, 1981 to November, 1982, zooplankton were sampled bimonthly by oblique net tows in the upper 200 m of the Gulf Stream and nearby regions along a cross-stream 0 0 transect of 9 stations centered at 36 N 73 W, where the Stream turns offshore from Cape Hatteras. In September, 1982 and May, 1983, extensive vertically stratified sampling of zooplankton was conducted at 3 stations along this same transect with a MOCNESS net system in the upper 1000 m of the water column. The zooplankton samples were collected concurrently with measurements of the hydrography and velocity fields of the Stream. This study was initiated in an effort to elucidate relationships between the physical oceanography and biology of the Stream.

An intensive examination was made of the spatial and temporal distribution of selected copepod species across the Gulf Stream during September, 1982. The copepod species distributions grouped together into distinct patterns, which were related to different environmental habitats within the Stream. Biological processes, such as temperature and depth preferences and diel vertical migration, interacted with the physical structure of the Stream to determine whether a species would be found at different cross-stream locations and if so, at what depths in the water column. The community structure of these species groups resembled a modified

ii

version of the individualistic hypothesis of species distributions and community formation.

Zooplankton biomass abundance and distribution was examined for all of the cruises. There was a distinct pattern of seasonal variability in zooplankton biomass with a maximum in the late spring and early summer, and a minimum in the autumn. Zooplankton biomass tended to be highest in the Slope Water, intermediate at the north wall of the Gulf Stream, and lowest in the Gulf Stream proper and Sargasso Sea. The north wall of the Gulf Stream is a frontal region where elevated plankton biomass sometimes occurred.

The association of different copepod species groups with distinct environmental habitats having different velocities and directions of water movement suggests that the species have varying probabilities of downstream and cross-stream transport. Downstream transport of zooplankton species and biomass is probably greatest in the upper 100 m. Cross- C stream transport is probably greatest below the 12 C isotherm, but can also be high in the surface water.

Acknowledgements

I wish to give a special thanks to Karen Wishner who is an extremely generous, able, and understanding major **CONTRACTOR** professor. I'm not sure that she ever really understood where I was coming from (who could?), but she tried hard and taught me a lot along the way. Nelson Hairston, Jr., provided infinite quantities of insight into ecology, and encouragement and inspiration, much more than he is probably aware of. Tom Rossby was incredibly generous in providing ship time, without which this research would not have been possible, and very patient in trying to explain physical oceanography to this biologist. Ted Napora provided dire warnings that I must work diligently for my salvation and a lot of sound advice on more scientific matters.

Elijah Swift generously loaned us his 65 cm plankton net for an extended period of time. John Wormuth loaned us his MOCNESS net system and was a joy to work with at sea. Don Dorson, Jim Fontaine, and Bill Hahn helped set up the MOCNESS to work on the Endeavor. Ed Buskey, Kathi Kelly, Monica Hallisey, and Lynn Beatty all provided valuable assistance at sea, as did the captains and crews of the R/V Endeavor and R/V Cape Hatteras. Wayne Munns, Chris Brown, Richard Chinman, Jeff Rosen, and Arthur Mariano all were very patient in helping me understand statistics and computers. Dan Halkin, John Lillibridge, and Terry Rago were equally patient

iv

in explaining physical oceanography. Craig Gilman helped me get the satellite images I used and Steve Kelly taught me how to use the Turner Fluorometer at MERL. This research was supported by funds from the Graduate School of Oceanography at the University of Rhode Island.

On a more personal note, I must give a great thanks to John Madsen who is the ideal housemate and my friends I can tell you, he is a real hard rocker. Thanks to Chris Brown for keeping the office across the hall open at all hours and always being willing to waste time when both of us should have been working. Thanks to Pete Sampou, Andy Hudson, John Lillibridge, Steve Dickson, Dave Erickson, Dave Gallo, Darryl Keith, Greg Tracey, and all the other members of the GSO surf rats and wild boys who kept me entertained and sane for my time here. Thanks to Celia Chen, Richard Chinman, and Nancy Reichley for demonstrating that it is possible to be a whole person and a graduate student at the same time. Thanks to Carol Meise-Mooselips for sitting in my office and interfering with my work and thanks to Wayne for being Wayne and getting her out of there every now and then. Last, and certainly not least, thanks to Suzanne Bricker and Bonnie Lamb for supplying me with female friendship and always being willing to listen to me complain.

Special thanks to Robert J. Luertsma and Eric Jackson.

v

Pref ace

This thesis is written in manuscript style. It consists of two manuscripts. Both are written in the format of the journal Deep-Sea Research. The introduction to this thesis precedes the two manuscripts. to the physical structure of

biomass across the Gulf Stream....................78

Spatial and temporal variability in sooplankton

Appendix A. Copepod species distributions in September.

gand on said Afrancia compare that the Transmission

Appendix B. Biomass data and sampling information........143

the disks produced briefs in the three and and controlled below

Table of Contents

List of Tables

Application A ... Compact Asserter Historicanociums the Montganizer-

Manuscript I: The distribution and abundance of selected copepod species in relation to the physical structure of the Gulf Stream. The last state in the state of the state of

in the western North Atlantic........................112

viii

Appendix A. Copepod species distributions in September, 1982.

16.

List of Figures

Manuscript I: The distribution and abundance of selected copepod species in relation to the physical structure of the Gulf Stream. Dependentially in Linkers abusing Alarman 118

Manuscript II: Spatial and temporal variability in zooplankton biomass across the Gulf Stream.

Appendix A: Copepod species distributions in September, 1982.

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Introduction to the Thesis

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functions biologically as an evotone, a region in which the local physical oceanography plays a dominant rola in species determining the vertical and horizontal distributions of zooplankton species and hiomass, not in just the Stream oceanography and biology of the Gulf Stream by: these distributions with hydrography, nutrient concentration, distribution of zooplankton biomass in the Stream throughout

Introduction and the contract of the contract

The Gulf Stream current is a region with a complex physical structure (Rossby, 1982; Halkin, 1984) that probably functions biologically as an ecotone, a region in which the local physical oceanography plays a dominant role in species distributions and interactions (McGowan, 1974). The physical structure and dynamics of the Stream may have a large role in determining the vertical and horizontal distributions of zooplankton species and biomass, not in just the Stream itself, but in large areas of the North Atlantic {Cox and Wiebe, 1979). The nature of the interactions between the physics and biology of the Stream, especially downstream of Cape Hatteras, are largely unknown. This study was conducted in order to elucidate relationships between the physical o ceanography and biology of the Gulf Stream by: 1) describing the spatial and temporal distribution of selected copepod species with depth across the Stream, 2) correlating these distributions with hydrography, nutrient concentration, chlorophyll concentration, and the velocity field measured concurrently, 3) describing the spatial and temporal distribution of zooplankton biomass in the Stream throughout a year, and 4) determining qualitatively the amount and direction of zooplankton biomass transport by the Stream at different stations, depths, and times.

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Biological oceanographers have tended to view oceanic

current systems as boundaries between distinct water masses and species (Angel, 1979) or as sources of interesting mesoscale phenomena such as rings and eddies (for example: Ring Group, 1981; Tranter et al., 1983; Haury, 1984), upwelling events (Yoder et al., 1981; Paffenhofer et al., 1984; Diebel, 1985), and as a means of genetic exchange between separated populations (Scheltema, 1971; Backus et al., 1977; Scheltema and Williams, 1983). It is apparent that interactions within the current itself are extremely important in determining the plankton community structure across large areas {Chelton et al., 1982; Wroblewski, 1982; Davis, 1984). The research ingles of the will fire a by I for

The Gulf Stream functions as both a route of faunal dispersal and as a faunal boundary. The Stream transports large amounts of water downstream (Worthington, 1976). As it flows downstream, the Stream entrains increasing amounts of water and also loses water in some areas by processes such as detrainment and eddy formation (Rossby, 1982). Presumably organisms living in the ·water are entrained and detrained with it. The northern edge of the Gulf Stream acts as a boundary between a cool, temperate water mass and a warm, subtropical water mass and forms the northern limit for many warm water species and the southern limit for many cool water species (Angel, 1979). The Gulf Stream has a species composition similar to that of the Sargasso Sea (Grice and Hart, 1962), although the species may have different absolute and relative abundances (Ortner et al., 1979). The Stream is

not an absolute boundary as many species naturally occur on both sides of it (Grice and Hart, 1962). There is direct evidence from in-situ velocity profiles (Halkin, 1984), deep water SOFAR float paths (Shaw and Rossby, 1984), Rafos float trajectories (Rossby et al., 1985), and the distribution of passive tracers along isopycnal surfaces {Bower et al., 1985) which indicates that cross-stream mixing and transport occur along the Stream, especially at depth.

This research on the spatial and temporal variability in zooplankton distributions and abundances across the Gulf Stream was conducted concurrently with in-situ measurement of the velocity and transport fields of the Gulf Stream by H. T. Rossby. This allowed us to correlate biological and physical patterns across the Stream. Emphasis has been placed on determining to what extent zooplankton distributions follow water movements in an effort to estimate the importance of downstream and cross-stream transport to the overall distributional patterns of zooplankton in the western North Atlantic.

The two manuscripts in this thesis are part of a project on the biology of the Gulf Stream directed by K. F. Wishner. During this project, zooplankton samples were collected from the upper 200 m by oblique net tows during bimonthly transects of the Gulf Stream from November, 1981 to November, 1982. In September, 1982 and May, 1983, intensive vertically stratified zooplankton sampling was done along this same transect with a MOCNESS net system. All zooplankton samples were collected in conjunction with the previously mentioned

in-situ measurements of velocity and transport. The first manuscript of this thesis describes the spatial and temporal variability of selected copepod species collected by the MOCNESS in September, 1982. The second manuscript describes the variability in abundance and distribution of zooplankton biomass from all of the samples collected.

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Abstract

The horizontal and vertical distribution of selected copepod species across the Gulf Stream was studied in September, 1982, along a transect located east of Cape Hatteras where the Stream turns offshore. Three Gulf Stream stations, the north wall, the warm core, and the southern edge, were sampled in discrete depth intervals to 1000 m both 2 day and night with a 1 m MOCNESS. Copepod species distributions can be grouped into several distinct patterns related to different environmental habitats within the Stream. Biological processes, such as apparent temperature and depth preferences and diel vertical migration, interact with the complex physical structure of the Stream to determine where in the water column a species is found at different cross-stream locations. The association of different species groups with particular environmental habitats having different velocities- and directions of water movement also suggests that different species have varying probabilities of downstream and cross-stream transport. The community structure of these species groups fits a slightly modified version of the individualistic hypothesis of species distributions and community formation.

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Introduction and the contraction of the contraction

The Gulf Stream, a major feature of the North Atlantic circulation, functions as both a faunal boundary and an important dispersal route. Its biology, however, has not been well studied. In particular, the role that the physical structure and dynamics of the Stream may have in determining the vertical and horizontal distributions and abundances of zooplankton species is unknown.

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The Gulf Stream current can be viewed as both a river in the ocean and a boundary between two distinct water masses. As a river, it is seen as a core of warm, fast-flowing water about 100 km wide (Stommel, 1965). It flows to the northeast from the Florida Straits in a course parallel to the coastline. At Cape Hatteras it turns offshore and moves into deeper water where its geographic position is highly variable as it forms large meanders which may pinch off into eddies and rings (Fofonoff, 1981). As it flows downstream from the Florida Straits, the Gulf Stream picks up and transports increasing amounts of water (Worthington, 1976). At first, most of the entrained water comes from the Sargasso Sea, but once it turns offshore, Slope, and possibly even Shelf, water is also entrained (Rossby, 1982). Entrainment and detrainment may occur on both sides of the Stream for much of its length (Halkin, 1984). The Gulf Stream has a low oxygen

signature at several hundred meters depth which is derived from the Gulf of Mexico and is readily observable well downstream of Cape Hatteras (Rossby, 1982). This indicates that the original source water of the Stream remains intact as a discrete entity for a long period of time and distance.

As a boundary, the Gulf Stream separates colder, seasonally variable, nutrient rich Slope and Shelf water from the warmer less variable, nutrient poor subtropical water of the Sargasso Sea. However it is not an absolute boundary. Lateral shifts in position and lateral mixing processes across the Stream may transport large amounts of water and heat energy cross-stream (Parker, 1976; Lambert, 1982}. SOFAR float data have shown that floats at 700 m react to the Gulf Stream as if it were a boundary, while floats set at 1300 m cross the Stream readily (Shaw and Rossby, 1984). Rafos float studies have also shown that water parcels in the main thermocline will tend to be carried downstream for long distances unless disturbed by unstable meanders, or rings and eddies near the Stream (Rossby et al., 1985). Distributions of physical parameters and oxygen concentrations along isopycnal surfaces, which slope downward from the Slope Water to the Sargasso Sea, have also indicated that, at shallower levels, the Stream is a distinct boundary to cross-stream transport, but that below the oxygen minimum layer (σ_{α} =27.0) cross-stream exchanges occur along with considerable downstream water flow (Bower et al., 1985). Presumably, when water is entrained or detrained from the Stream, or Pinches off to form cold core or warm core rings, the

organisms in that water are carried along with it, at least initially. See the search times of the same space precisions of

The Gulf Stream is a highly dynamic system in which processes occurring at any one time and place are the result of events which happened at some point earlier in time. These events are occurring continuously and in the entire northwestern Atlantic region. Thus any pattern of distribution of properties across the Stream represents an image of the state of the Stream at that particular place and time resulting from these events and processes and is unique to that time and place (Rossby, 1982).

Ecologically the Gulf Stream region functions as an ecotone, a transition region in which local physical oceanography plays a dominant role in species distributions and interactions (McGowan, 1974). The physical oceanography of this region is exceedingly complex, and it follows that the ecology is complex too. Zoogeographic studies of the North Atlantic reveal that the Stream can act as a barrier for some species, as a region of dispersal and distributional extension for others, and as a region of subtle changes in abundance and distribution for still others (McIntyre and Be, 1967; Backus et al., 1977; Nafpaktitus et al., 1977; Angel, 1979; Colebrook, 1982; Pierrot-Bults, 1982). There is some evidence that the Stream may separate populations of a single species which have subtle differences in genotype (Brand, 1982). wicker the shalf edge south or taps Antesnas (Flanten

The northern edge of the Gulf Stream, a sharp frontal

region, is an important biogeographic boundary marking the northern distributional limit of many warm water species and the southern distributional limit of many cold water species (Angel, 1979). The southern edge is a zone of gradual transition from the Gulf Stream to the Sargasso Sea. The surface of the Stream tends to have a species composition and seasonal variability similar to that of the Sargasso Sea {Grice and Hart, 1962), although the absolute and relative species abundances can differ (Ortner et al., 1979). Deeper water of the Gulf Stream shows faunal affinities with both the Slope Water and Sargasso Sea {Jahn and Backus, 1976). The Stream is not an absolute boundary, and the Slope Water, Gulf Stream, and Sargasso Sea have species in common {Grice and Hart, 1962; Ortner et al., 1979).

Numerous studies have been done on aspects of the biology of the Gulf Stream, but its ecological role has remained elusive. Extensive work, mostly in the Florida Straits region and south of Cape Hatteras, records species . distributions (Lewis, 1954; Bsharah, 1957; Moore and O'Berry, 1957; Owre, 1960; Grice and Hart, 1962; Pierce and Wass, 1962; Wormelle, 1962; Roehr and Moore, 1965; Owre and Foyo, 1967; Park, 1970; Bowman, 1971; Jahn and Backus, 1976; Michel et al., 1976; Stepien, 1980; Ortner et al., 1981). Enhanced biomass and productivity associated with the Stream have also been documented. For example, intrusions and upwelling events along the shelf edge south of Cape Hatteras (Blanton et al., 1981; Hoffman et al., 1981; Lee et al., 1981) result in patches of high primary production, chlorophyll, and

zooplankton (Atkinson et al., 1978; Paffenhofer, 1980; 1983; paffenhofer et al. 1980; 1984; Yoder et al., 1981; Deibel, 1985). Offshore, east of Cape Hatteras, biomass peaks of zooplankton (Allison and Wishner, in review) and phytoplankton (Lessard, 1984) are associated with the north wall front. Some species of phytoplankton are able to grow faster in the Stream than in the Sargasso Sea {Voytek, 1984).

The zooplankton in Gulf Stream cold core and warm core rings have also been intensively studied (Wiebe et al., 1976a; 1985; Boyd et al., 1978; Ortner et al., 1978; 1979; 1980; Wiebe and Boyd, 1978; Ring Group, 1981; Backus and Craddock, 1982; Haury and Wiebe, 1982; Wiebe and Flierl, 1983; Wroblewski and Cheney, 1984), and the fact that rings can transport organisms between water masses in the North Atlantic is well documented. However, these studies have discussed only briefly the biology of the "ring fringe" (the Gulf Stream remnant encircling a ring) and have rarely considered the question of direct cross-stream exchange of organisms. The The Frition and Decimal at the Series

This paper describes the spatial and temporal distributions of selected copepod species with depth across the Stream and correlates these distributions with various biological and physical parameters. This study is part of a Project directed by Dr. K. Wishner, and many of the ideas were discussed in Wishner (1983). This paper will examine in detail: Friedrick Sandy Schulzon, auch (1997) Sandywd fo 750 Sandy

1) Can copepod species distributions be grouped into

distinct patterns?

2) If such patterns are found, can they be related to distinct oceanic habitats within the Gulf Stream?

3) Are there regions of the Gulf Stream in which downstream and cross-stream dispersal are more likely to occur than in others?

4) What processes are the major mechanisms causing cross-stream and down stre am transport of zooplankton?

5) What types of community structure exist within the Gulf Stream copepod community?

Stream copepod community?

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Methods **William The Tened South Chamber of the Times of the United States of the United States**

Sampling and a deep oblique for transition and what

The data were collected during September 5-17, 1982, on cruise 89 of the R/V Endeavor in the Gulf Stream region just east of Cape Hatteras. Samples were collected at three stations positioned 20 to 40 km apart perpendicular to the mean direction of the Stream along a .transect centered at 0 0 36 N 73 W (Fig. 1). The· stations were located at the north \circ wall of the Stream (15 C isotherm at 200m and surface -1 velocity > 100 cm s), the warm high velocity central core -1 0 (surface velocity > 100 cm s and temperature > 27.5 C), and the southern edge of the Stream, a region of downstream movement, but slower than the warm core (surface velocity 40 -1 to 100 cm s). The position of the Stream was determined from expendable bathythermographs (XBT) deployed to 750 m, infrared satellite imagery of sea surface temperatures, and

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results from a three-day temperature and velocity profiling program by Dr. H. T. Rossby immediately preceeding biological sampling along the same transect.

At each station vertically stratified zooplankton 2 sampling was done with a MOCNESS net (1 m mouth opening, 333 um mesh) (Wiebe et al., 1976b). This opening-closing net system allows one to collect 9 sequential samples along with in-situ environmental information {depth and temperature} and sampling data (volume filtered and net angle). Data from the MOCNESS was processed and stored at sea on a Hewlett-Packard 85 computer. The net was towed into the flow of the Stream to maintain a constant cross-stream location. MOCNESS tow series consisted of a deep oblique tow from 1000 m to the surface {in intervals of 1000-850 m, 850-700 m, 700-550 m, 550-400 m, 400-300 m, 300-200 m, 200-100 m, and 100-0 m) and a shallow oblique tow from 200 m to the surface in 25 m intervals. The maximum depth of sampling (1000 m) was close to the bottom of the permanent thermqcline and a depth at which SOFAR floats sometimes cross the Stream. A day and night tow series, centered at noon and midnight, was $\overline{\mathbf{3}}$ conducted at each station. Each net filtered 300 to 1000 m of water. Samples were preserved in 4% buffered Formalin. Sampling information is given in Table 1.

At each station, in-situ water velocity and transport direction to a depth of 2000 m was measured with a cast of a free vehicle Pegasus velocity profiler (Spain et al., 1981) undertaken by Dr. H. T. Rossby {of the University of Rhode Island) and his group, who also analyzed the data.

Hydrocasts with 5 1 Niskin bottles at 25 m intervals from the surface to 200 m and 100 m intervals from 200 m to 1000 m at each station provided data on temperature, salinity, and concentrations of oxygen, total nutrients (NO and NO , PO , 2 **3 4** siO), chlorophyll a, and phaeophytin. Oxygen was measured 2 by the Winkler titration method on board ship immediately after being collected (Strickland and Parsons, 1968). seawater for the nutrient analysis was drawn through a 0.45 um type A/E glass fiber filter to remove organisms and large particles. Nutrient samples were then poured into 50 ml plastic bottles that had been acid washed. Samples for NO 2 and NO were preserved with 100 <u>u</u>l of concentrated H SO 3 refrigerated. Samples for PO and SiO were preserved by 2 4 4 4 2 and freezing. NO 2 and NO , PO , and SiO were measured with an 3×4 2 auto-analyzer (Strickland and Parsons, 1968}. Chlorophyll samples were collected on 0.45 um type A/E glass fiber filters. The filters were wrapped in aluminum foil, frozen, and stored in a desiccator. Chlorophyll a and phaeophytin were measured fluorometrically on shore within 6 weeks of their collection (Strickland and Parsons, 1968). Satellite infrared imagery was obtained from the Remote Sensing Center at the Graduate School of Oceanography of the University of Rhode Island.

assessment of the bealing objectively defined groups of species ant are doned upon presence and suspens, sales: There ... and the scondenne, the use of personnel and special data

Analysis and Siler of the common no membership

zooplankton samples were analyzed for selected copepod species composition and abundances. Copepods were chosen for analysis because of their numerical dominance in the area (Grice and Hart, 1962), laboratory expertise in their identification, and the fact that different species have been shown to react differently to the changing conditions in cold core rings (Ring Group, 1981}. Twenty-two taxonomic units, which included adults of 18 species and the fifth stage copepodites of the 4 species of the family Calanidae examined, were selected for detailed analysis because they were common in the samples, exhibited differing distribution patterns, and were relatively easy to identify. Aliquots, obtained with a Folsom plankton splitter, were used so that approximately 500 adult copepods of all species present were counted per sample. The selected species represented 13 to 95% of all adult copepods in a sample. The percentage similarity index (Whittaker, 1975) between a set of paired aliquots was 96% and species abundances between the aliquots varied by 0 to 50% of the mean for the two samples. From 1/4 to 1/32 of the original sample was counted.

Recurrent group analysis (Fager, 1957; Fager and McGowan, 1963; McGowan and Walker, 1979) was used to examine the copepod distribution data. This method was chosen because it produces objectively defined groups of species that are based upon presence and absence, rather than absolute abundances. The use of presence and absence data

reduces the possibility of errors caused by patchiness and variable abundance estimates. The groups are formed using an index of affinity between all species in which: $-1/2$ $-1/2$ $\alpha = J$ (n n) $-1/2$ $-1/2$ ab a b where: in the part of the power boundary of the season J is the number of joint occurrences of species a and ab species but all data with the second state of the second state n is the number of occurrences of species a a n is the number of occurrences of species b b the where n > n all self-dree support supports, and , all b a $-1/2$ and $-1/2$ and 0 is 1 and $1/2$. The $1/2$ and $1/2$ and $1/2$ and $1/2$ 2(n) is a correction for unequal sample sizes. **b** Groups of species are formed so that all species pairs in a group have an α value greater than or equal to a preassigned value. Selection of an appropriate affinity level is subjective and is done to maximize the interpretetability of results. Once an α value is chosen, group formation is objective. In this study, an α value of 0.50 was used. Other studies have used values of α from 0.30 to 0.80 (Fager and McGowan, 1963; Brinton, 1979; McGowan and Walker, 1979; Venrick, 1982; Loeb et al., 1983). The probability of obtaining any particular α value is dependent upon the frequencies of occurrence of the species pair under consideration. In this study the probability of an α value being 0.5 or greater by chance alone ranged from 0.005 to 0.30, from a possible range of 0 to 1.

After the analysis had divided the species into distinct groups, percentage affinities were calculated between all

groups. The percentage affinity between groups, or the amount of connection, is the proportion of all species pairs, between two groups, that have an affinity index greater than 0.5. Jalinity 1969. Ami is high and failure un form in the

Principal component analysis (PCA) {Pielou, 1977) was used as a descriptive tool to determine relationships among the environmental data. The variables used in the PCA were -3 total zooplankton biomass [ml (1000)] depth, median temperature in the sampling interval, temperature range of the sampling interval, salinity, sigma-t, oxygen, SiO , PO , 2 4 chlorophyll a, and velocity. Before performing the PCA, all data were log transformed [ln(x+l)] and standardized to a mean of 0 and standard deviation of 1. The PCA was done using SAS statistical programs. The number of axes to retain for further analysis was determined by a graphical procedure for deciding which eigenvalues are significant (Preisendorfer, 1981). Sample scores were graphed along these axes and grouped by eye into environmental groups.

Results Results

Environment Maria in the present that

The distributions of environmental parameters with depth are contoured in Fig. 2. Near the surface, temperature (Fig. 2a) is high, and isotherms are horizontal across the Stream. The mixed layer is 50 to 60 m deep across the Stream. Below \circ 20 C, the isotherms slope downward from the north wall to the \circ southern edge. The 15 C isotherm (used to define the

northern edge of the Gulf Stream) is at 220 m at the north wall, 440 m at the warm core, and 530 m at the southern edge stations.

salinity (Fig. 2b) is high and fairly uniform in the surface waters. A salinity maximum occurs from about 100 to 150 m at the north wall and from about 50 to 350 m at the 0 southern edge. This region includes the 18 C water, characteristic of the Sargasso Sea (Worthington, 1976). Isohalines below 200 m slope downward from the north wall to the southern edge. Issue I have the southern edge. Issue I have been

The density surfaces, σ isopycnals, (Fig. 2c) are t uniform in depth across the Stream in the surface waters. Below σ =26.0, the isopycnals slope downward across the t Stream from the north wall to the southern edge. $\sigma = 27.0$ is o t about equal to the 12 C isotherm and corresponds to the depth of the oxygen minimum zone.

The distribution of total PO (Fig. 2d) is typical of 4 all the nutrients in the Gulf Stream region. The amount of PO is extremely low in the surface waters and increases with 4 increasing depth. Below 200 m the depth of the nutricline slopes downward cross-stream in the same manner that σ t does. That all the and olide, and the the sa

Dissolved oxygen also tends to slope downward across the Stream along isopycnal surfaces (Fig. 2e). This has been observed to occur on a large scale all along the Gulf Stream (Bower et al., 1985). The oxygen minimum zone occurs at 200 to 400 m at the north wall and slopes down to a depth range

Witleity of the stake on. The Minson be in a commonly found

of 600 to 750 m at the southern edge. σ =27.0 occurs in the t middle of this zone. The distribution of oxygen in the upper waters is complex. The same state of the state of the

The distribution of chlorophyll a cross-stream is also complex (Fig. 2f). The chlorophyll a concentration is low in all the samples. There is an indication of a peak in chlorophyll concentration from 50 to 160 m at the north wall and 60 m at the southern edge. Chlorophyll a tends to be highest at the north wall.

Downstream velocity {Fig. 3a) is greatest in the surface waters to a depth of 150 m near the north wall. Fairly high -1 velocity (> 100 cm s) extends to about 400 m depth at the warm core. In general, velocity tends to decrease with depth. Velocities below about 800 m at the north wall are low -1 { < 20 cm s) . At the southern edge velocities do not fall -1 below 20 cm s until a depth of about 1000 m.

At the north wall and warm core, cross-stream transport is in a southeasterly direction, i.e. towards the Sargasso Sea {Fig. 3b). At the southern edge, cross-stream transport is toward the northwest resulting in an area of convergence between the warm core and southern edge stations. This implies that, at this time and place, entrainment is occurring on both sides of the Stream.

The satellite infrared imagery of the Gulf Stream region just east of Cape Hatteras on September 14, 1982 (Fig. 1) reveals a normal Stream. There are no obvious rings impinging on the Stream or large meanders in the immediate vicinity of the transect. The Stream is in a commonly found

position for this area, occurring in the middle of the 0 0 transect centered at 36 N 73 W (Halkin, 1984). The north wall is not at the north edge of the Gulf Stream in the satellilite thermal image because a thin layer of warm water extended beyond the Stream into the Slope Water.

Copepod Distributions

Copepod species distribution and abundance data are summarized in Table 2. A detailed list of abundances in each sample and vertical distributions of each species is given in Appendix A. The species exhibit a wide variety of distribution patterns with some having shallow water distributions (such as Calanus minor), some intermediate depth distributions (Lucicutia clausi), and others deep distributions (Calanus finmarchicus). Some have very high maximum abundances (Lucicutia flavicornis), while others have fairly low maximum abundances (Metridia venusta).

Recurrent group analysis, at the 0.50 level of affinity, resulted in the formation of three species groups (a group has > 2 taxonomic units), two species pairs, and four species which were not associated with any groups. These groupings, and the relationships among them, are diagrammed in Fig. 4. Species in these groupings are considered to have a high likelihood of influencing each other biologically. Pair 1 and Pleuromamma borealis had no interconnections with any of the other groups or species. Because the analysis was Performed on a limited set of species, instead of all species

present, it is not surprising that some groups and species would have no associations with any other, even if all were fairly common in the total sample set.

Group 1, consisting of 4 species and the fifth stage copepodite of an adult in the group, occurs as a group (100% of the species present) between 50 m and 100 m across the entire transect (Fig. 5). 80% of the species are consistently present from 50 m to the surface. This group appears to be a shallow water group, probably with an affinity for warmer water. The species in this group tend to be fairly abundant. The deep distributional tail is due to the presence over a broad depth range of Lucicutia flavicornis. This group is strongly connected with Pair 2 e, and in destayed widde tos (60%) and with Group 3 (40%).

Group 2, consisting of 4 species and the fifth stage copepodite of an adult in the group, occurs as a full group at depth with an upper boundary that follows the sloping σ =27.0 isopycnal across the Stream (Fig. 6). The full group t occurs from 300 m to 1000 m at the north wall and from 850 m to 1000 m at the southern edge during the night. This is the deepest group and is composed of what are usually considered to be Slope Water species (Grice and Hart, 1962). These species tend to be fairly abundant. Occurrences in the upper waters by this group are primarily due to Rhincalanus cornutus. This group is slightly connected {5%) with Group 3.

Group 3, consisting of 4 species, occurs in only one sample as a full group during the daytime (Fig. 7). However,
at night, the full group occupies a broad intermediate depth range (50 m to 200 m at the north wall, 50 m to 650 m at the southern edge) with the lower boundary following the sloping σ =27.0 isopycnal. This group is made up of species which are t
strong diel vertical migrators. The diffuse distribution pattern of the group as a whole during the day is due to the fact that each of the species has a slightly different depth distribution (see Appendix A). The group is most strongly connected (40%) with Group 1.

Pair 1 is made up of two less abundant species which occur deep in the water column over a narrow depth range (Fig. 8). The distribution pattern slopes downward from the north wall to the southern edge, and is centered along the σ =27.25 isopycnal. The species in this pair are probably not t diel vertical migrators although each occurs in a single sample in the upper waters of the warm core at night. This pair has no connections or associations with other species.

Pair 2 consists of the Mesocalanus tenuicornis adult and fifth stage copepodite. They are fairly abundant and occur primarily in the upper water column (Fig. 9). The pair occurs together between 75 m and 200 m, and both are absent from the upper 50 m at night. This pair is strongly connected (60%) to Group 1.

Of the four ungrouped species, two have especially interesting distributions. Pleuromamma borealis was found only at the north wall (Fig. 10). It is fairly abundant at night. It is considered to be a Slope Water species (Grice

and Hart, 1962). It is not associated with any of the recurrent groups. Lucicutia clausi occurs almost exclusively from 100 m to 550 m at the warm core and southern edge of the stream (Fig. 11). Its center of abundance is the warm high velocity region of the Stream. It is partially associated (40%) with Group 3. dryirermayal group 3 (poster-staly)

Principal Components Analysis

The 11 environmental variables were reduced to 2 significant axes, which are the first two eigenvectors. The eigenvalues are listed in Table 3. The first eigenvector (Axis 1) accounts for 58% of the variability and is dominated by the large scale physical parameters of median temperature, salinity, velocity, σ , and depth. The second eigenvector t (Axis 2) accounts for 17% of the variability and is dominated by parameters showing large gradients, i.e. temperature range and oxygen. The remaining eigenvectors are insignificant. The third eigenvector, although in the range of expected noise, still accounts for 11% of the variability and is dominated by parameters closely tied to the biology of the Stream, i.e. zooplankton biomass, chlorophyll a, and SiO . 2 The 96 samples used in the analysis were plotted on a Projection of Axis 1 by Axis 2 and clustered into environmental groups by eye (Fig. 12). Samples from the coarse and fine scaled sampling were clustered separately. The distribution of these environmental groups in the water column is shown in Fig. 13.

Environmental group A, from the deep coarse-scaled

sampling (0-1000 m), encompasses the subsurface core of the Gulf stream and southern edge from 100 to 550 m. This is a region of relatively warm water, high salinity, and high downstream velocity. Group A, which is below the mixed layer, extends down to the upper part of the oxygen minimum zone and nutricline. Environmental group B (coarse-scaled sampling) consists of surface water samples across the stream. This is a region of high water temperatures, fairly high salinity, high downstream velocity, low nutrients, and relatively high chlorophyll. Environmental group C (coarsescaled sampling) consists of the deep water samples and north wall samples from below 100 m. These samples come from a region which includes the oxygen minimum zone and is characterized by cold water, higher nutrients, lower downstream velocities, and lower salinity.

Environmental group D {from the shallow fine-scaled sampling, 0-200 m), consists of samples at the north wall from 150 to 200 m. These are slightly colder for their depth than the other fine-scaled samples and occur at the upper part of the oxygen minimum zone and nutricline. Environmental group E (fine-scaled sampling) includes surface water samples, similar to the coarse scale environmental group B. These samples are from a region of high water temperatures, fairly high salinity, high downstream velocity, low nutrients, and relatively high chlorophyll a. Environmental group F (fine-scaled sampling) is from the upper part of the core of the Stream, a region of high

salinity, warm water, and higher downstream velocity. Environmental group G (fine-scaled sampling) is composed of samples from a region of transition between surface water and deeper Gulf Stream core water and occurs near the base of the mixed layer. necetes that the water column dan re histori

The recurrent groups of copepods and the environmental groups from the PCA appear to be strongly related to each other. The percentage of samples in a particular environmental group in which a full species group occurs {100% of species present) are listed in Table 4. The distributions of the recurrent groups (100% level) are outlined on the plot of environmental samples from the PCA in Fig. 12. It should be noted that species group 3, which consists of strong diel vertical migrators, is hard to characterize in terms of relationships to environmental groups when both day and night samples are used. Therefore the environmental groups were split into day and night samples when examining species group 3. In the daytime, it only occurs in one environmental group as a full species group, but in the nighttime it is highly associated with 4 environmental groups.
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Copepod species distributions in the Gulf Stream during September, 1982 can be grouped into several distinct Patterns. The fact that most of the selected species could be put into groups and that these groupings have

interconnections, indicates that the chosen species are a frequent component of each other's biological environment. These groupings also indicate that copepod species may be interacting with the Gulf Stream in a few distinct ways in response to the Stream environment. The distribution of species groups indicates that the water column can be divided into distinct oceanic habitats, which may change in depth across the Stream. Species distribution patterns suggest a variety of physical and biological processes that may be regulating the species structure of the copepod community.

The association between different groups of species and environmental habitats results in species having varying probabilities of downstream and cross-stream transport. A diagram of hypothesized zooplankton dispersal paths, based on velocity profiles and direction (Halkin, 1984), is shown in Fig. 14. Cross-stream mixing is most probable near the surface and at depth. Near the surface, mixing is most likely to occur on the southern side of the Stream, since the Stream and Sargasso Sea have many similar physical characteristics and much Sargasso Sea water is entrained into the Stream. Cross-stream mixing at depth probably happens below the oxygen minimum zone (σ =27.0) where water may cross t the Stream on isopycnal surfaces (Bower et al., 1985). Long distance downstream transport is most probable in the warm high velocity core of the Stream, a few hundred meters below the surface, and at the surface near the north wall.

There are three possible types of processes which may be affecting dispersal in this region: purely biological

processes, purely physical processes, and a combination of biological and physical processes. The likelihood of purely biological processes, such as horizontal swimming by the zooplankters, accounting for cross-stream movement is probably small. Using as a rule of thumb that an organism can swim 10 body lengths per second (Barkley, 1972), a 2 mm long copepod swimming non-stop horizontally in a cross-stream direction would take almost 59 days to cross a 100 km wide stream. Foraging, predator avoidance, resting, and the fact that some species will expend swimming energy in vertical migration, are all forces that will prevent constant , unidirectional swimming. Thus it seems unlikely that swimming alone would allow cross-stream mixing to occur.

If physical processes alone are causing the dispersal, the zooplankton should act as passive particles and be distributed like other passive tracers such as oxygen. The distribution of oxygen cross-stream in this study and in a much more extensive study {Bower et al., 1985) indicates that oxygen is transported cross-stream along isopycnal surfaces, especially at depths below σ =27.0. -1 t Cross-stream velocities as high as 10 cm s were measured in the depth range of species group 2 during September, 1982. At this rate a drifting particle could cross the Stream in approximately 10 days. Although in a strict sense, copepods are not passive Particles, since they do swim, advection by water movements could result in long range transport if their swimming is random with respect to the current.

some of the copepod group distributions resemble those of passive tracers whereas others do not. For example pleuromamma borealis (Fig. 10) occurs over a depth range at the north wall similar to that of species group 2, yet, unlike Group 2, it does not appear to be dispersed crossstream. Vertical migration to depths with different velocity $vectors$ is not an adequate explanation, since both P . borealis as well as three members of species group 2 vertically migrate at the north wall. Furthermore, at the north wall, the cross-stream transport at all depths during this cruise is southerly {Fig. 3b) {albeit at different velocities), so it is not likely that inhabiting different depth strata would prevent cross-stream dispersal. Thus there are probably both physical and biological interactions occurring which result in some species being dispersed crossstream and others avoiding it. we have also that the same of the s

Diel vertical migration is the main biological phenomenon which influences the transport regime which a zooplankton species experiences. Not all zooplankton vertically migrate, and those that do not should experience a fairly constant transport regime. Those that do migrate, however, may be subject to different degrees of cross-stream and downstream transport during their migration. For example, members of species group 3 are found mainly in the warm core of the Gulf Stream during the day. They experience considerable downstream transport, but relatively little cross-stream transport while in this region. At night, the members of species group 3 migrate up into the top 100 m. In

the surface water (during our sampling period) they experience considerable cross-stream and downstream transport. Thus in one daily period these species are being transported for long distances both downstream and cross-A group I are prohably being dispersed stream.

The cross-stream and downstream transport observed during September, 1982, are representative of what is considered to be an average Gulf Stream {Halkin, 1984). Halkin (1984) found that the mean cross-stream velocity field indicated an inflow toward the center of the Stream from the north and south sides above 2000 m. This inflow was not observed in all individual transects, although it was observed in September, 1982. The mean downstream velocity field tended to have steeply sloping isotachs representative of a large amount of current shear at the north wall and more gently sloping isotachs on the southern edge (Halkin, 1984). In general the downstream profile in September {Fig. 3) is aiss und im the reqion of 18 C typical of the mean Stream.

Species group 1 (Fig. 5} and species pair 2 {Fig. 9) appear to be transported cross-stream in the surface mixed layer. The direction of this surface mixing is not readily discernible. Examination of the individual species abundance patterns (Appendix A) reveals no clear trends in changes in abundance cross-stream.

The distribution of species group 2 (Fig. 6) indicates that cold water zooplankton are being dispersed cross-stream along isopycnals at the base of the oxygen minimum zone.

This zone slopes down across the Stream from 300 m at the north wall to 700 m at the southern edge. Examination of the individual species abundance patterns (Appendix A) and the direction of cross-stream velocity, indicates that the members of species group 2 are probably being dispersed cross-stream from the north wall to the southern edge. The species in this group have their maximum abundances at the north wall and the abundances decrease as the southern edge 在的复数形式的过去分词 的复数化学 医神经性 医神经性 医中心性 医中心性贫血 医中心性的 is approached.

The core of the Gulf Stream appears to be a region in which it is unlikely for cross-stream zooplankton dispersal to occur. Lucicutia clausi (Fig. 11), which underwent only a small amount of vertical migration, occupies a region of 100 to 550 m in the main core of the Stream. It has one occurrence at the north wall at 550 m, but for the most part it seems to be restricted to the main body of the Stream. This core region of the Stream, which contains the low oxygen \circ signature from the Gulf of Mexico and is the region of 18 C water, is a coherent feature of the Stream for a long distance out into the Atlantic (Rossby, 1982). Cross-stream mixing appears to be at a minimum here, while downstream transport is high. L. clausi has fairly even abundances in the Stream core with no indication of input or output from the Stream.

Wiebe and Flierl (1983) extensively examined euphausiid dispersal into and out of cold core rings. They found that euphausiids tended to be dispersed out of cold core rings across the surface waters, as the ring warmed up, and at

depths of 400-1000 m. At depths below the mixed layer and above 400 m, they felt it was unlikely for euphausiids to be advected into or out of a ring. The depths at which dispersal is most likely to occur out of a cold core ring are similar to the depths at which dispersal occurs across the Stream. It may be that similar processes govern crossboundary transport in both systems. The Stream may be simpler in terms of transport processes than are rings, since -1 the high cross-stream velocities (1 to 10 cm s) are great enough to account for the dispersal of zooplankton crossstream. Wiebe and Flierl (1983) constructed complex models to explain the dispersal and retention of zooplankton by a cold core ring, because the observed inward and outward flow -1 rates (0.02 cm s) were too small, by themselves, to account for the dispersal which occurred. Wiebe et al. (1985) determined that changes in the biomass structure of a warm core ring were due to in-situ processes because the ring center was relatively isolated from the surrounding water.

Copepod species crossing the Gulf Stream may be changing their depth in the water column and their vertical migration patterns to remain in an optimal or preferred temperature regime. For example, the members of species group 2 increase their depth of occurrence from the north wall to the southern edge of the Stream so that their upper limit is defined by 0 the 12 C isotherm cross-stream. At the north wall, the species in group 2 perform a limited range of diel vertical migration, but almost no migration occurs at the southern

edge. The only vertical migration occurring at the southern edge in this group is attributable to Rhincalanus cornutus. species group 3, which is scattered throughout the water column during the day, is brought together by vertical migration at night {Fig. 7). The lowest limit at which all the species of group 3 co-occur is 200 m at the north wall and 600 m at the southern edge. This lower limit is roughly 0 the depth of the 12 C isotherm cross-stream. Temperature is considered to be a major factor influencing the range of vertical migrations of oceanic zooplankton (McLaren, 1963), and it may be that both groups of species determine the range over which they migrate by temperature cues. Members of species group 2 will not migrate up at night into water that \circ is warmer than 12 C, and members of species group 3 migrate \circ up at night into water that is 12 C or warmer. This would explain the inhibition of vertical migration as species group 2 crosses the Stream from the north wall to the southern edge and the shoaling of the maximum depth of nighttime distribution observed as· species group 3 approaches the north wall. An examination of the individual species distributions for species group 3 (Appendix A) reveals that these species are most abundant at the southern edge and are probably being transported north from the Sargasso Sea. This dispersal may be aided by migration up into the mixed layer at night where wind driven mixing could carry them cross-stream.

Changes in the depth range and vertical migration Patterns over time have also been observed in zooplankton and fish species trapped in warm and cold core rings (Wiebe et

al., 1976a; Ortner et al., 1978; 1979; Wiebe and Boyd, 1978; Brandt, 1981; Ring Group, 1981; Backus and Craddock, 1982; Griffiths and Brandt, 1983a; 1983b; Tranter et al. 1983; Wiebe and Flierl, 1983). The copepod Pareuchaeta norvegica gradually moved deeper in the water column with the aging of a cold core ring and with distance from the ring center. This change in depth occupied presumably occurred to remain in a preferred temperature regime (Ring Group, 1981). copepods at the shelf-slope front off Nova Scotia do not migrate through the sharp physical gradient of the front (Herman and Denman, 1979; Herman et al., 1981; Sameoto, 1984), which is a pattern similar to that of species group 2 which did not migrate up through a region of sharp physical gradients during this study. Copepod species in the upwelling region off the Oregon coast demonstrate a variety of horizontal, vertical, and ontogenetic distribution patterns, which interact with the complex current regime and result in the maintenance of endemic populations (Peterson et al., 1979; Wroblewski, 1982). Similar mechanisms could be maintaining zooplankton populations in the Gulf Stream, but this study was not extensive enough to make that determination.

At any one depth across the Gulf Stream, the physical gradients may be large. However the magnitude of change may be no more than an organism would experience in daily or seasonal vertical migrations, or a population would experience through wide vertical, horizontal, or seasonal witch of individuals of them upsoles by the Stream may

distributions {Wiebe ·and Boyd, 1978). The physical properties of the regions that copepods would be transported to by cross-stream mixing along isopycnals are also of ten within that experienced in their daily ambit. The likelihood of an organism surviving cross-stream transport may be more dependent on the availability of food than on the ability to withstand physical changes, as was hypothesized for a euphausiid species transported from the Slope Water to the Sargasso Sea in a cold core ring {Boyd et al., 1978). On a population level, a slight environmental change which causes birth rates to be lower than death rates would be enough to insure that a species could not survive in the new environment. For example, warm water chaetognaths transported by an intrusion of the Gulf Stream into cool Shelf Water near Chesapeake Bay have been found dead or dying in the water column (Bushing and Fiegenbaum, 1984).

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The copepod species examined in this study tend to have fairly widespread distributions in the Atlantic {Table 5) although some species are restricted to either warm or cold water. Many of the species which occur on both sides of the Gulf Stream {such as Calanus minor) have distinctly deeper distributions in the water column in the southern subtropical region than in the northern temperate region. As has been shown, species distributions tend to increase in depth across the Stream from the north wall to the southern edge. This change in depth cross-stream appears to connect the different habitats the species occupy on either side of the Stream. Advection of individuals of these species by the Stream may

represent a loss from a source population or a connection and means of genetic exchange between populations (Scheltema, 1971; Backus et al., 1977; Fleminger and Hulsemann, 1977; Scheltema and Williams, 1983).

some species of warm water zooplankton occur in the slope water in the summer and early fall (Cox and Wiebe, 1979). These species are absent for the remainder of the year and apparently are reintroduced to the Slope Water from the Sargasso Sea each year. These species may reproduce successfully in the Slope Water during the warm months and thus are referred to as forming expatriate populations (Cox and Wiebe, 1979). Direct cross-stream mixing is a likely mechanism by which reintroduction occurs. Our findings indicate that warm water species can be transported directly across the Gulf Stream in the surface water. This transport probably occurs throughout the year, and becomes an important input source for these species in midsummer when surface temperatures in the Slope Water warm up enough to allow them to survive there. There is a net non-tidal surface drift to the north in the Slope Water in the late spring and summer (Bumpus, 1973), which could carry these warm water species, transported cross-stream, into Slope and Shelf areas during the summer and early fall. Cox and Wiebe (1979) account for the presence of such expatriates by a complex cycling of organisms through the Shelf and Slope waters in the summer and early fall, winter transport in the Gulf Stream, and summer seeding by a warm core ring. This mechanism may be

possible, but may not be reliable. There is no seasonality to the production of warm core rings {Bisagni, 1976; Cerrone, 1984) and there have been periods of time as long as eight months in which no warm core rings were produced {Cerrone, l984). Direct cross-stream surface mixing is a more predictable event that would occur at approximately the same time each year and could provide a reliable mechanism for the import of warm water species to the Slope and Shelf waters. These warm water species are present in the Sargasso Sea throughout the year {Grice and Hart, 1962) and would potentially provide a constant source of species for crossstream mixing. Seasonal input of zooplankton by currents as a regular event has been shown to occur on a smaller scale with copepod species on Georges Bank {Davis, 1984).

Grice and Hart (1962) also examined the zooplankton of the Gulf Stream. They collected samples at one Gulf Stream station three times in the course of a year with oblique net tows from 0-200 m. They found the Stream and Sargasso Sea to be similar in terms of species composition and abundances. The Slope Water was distinct from these two regions, although Gulf Stream and Sargasso Sea species were found there, especially in their July and September collections. Table 6 compares the distribution and abundance patterns of the species we examined with the distribution and abundance Patterns observed by Grice and Hart. Especially interesting is a comparison of the distribution of Rhincalanus cornutus. In September Grice and Hart (1962) found R. cornutus in the Slope Water. They characterized it as a warm water species

and its presence along with other warm water species gave their September Slope Water collections a "decidedly warm water appearance". We found R. cornutus to be abundant in species group 2 at the north wall and at depth across the stream. However, its cross-stream abundance pattern (Appendix 1) suggests that it is being transported from the north wall to the southern edge although it did migrate up into warmer water at night more than did any other members of species group 2.

It is interesting to examine the species groups which were determined in this paper, in light of two distinct views of community structure, the community-unit hypothesis and the individualistic hypothesis {as defined in Whittaker, 1975). The community-unit hypothesis states that species co-occur in distinct well defined groupings of associated species. The individualistic hypothesis states that each species has its own unique distribution and that species do not form well defined groupings or associations. The species examined in this study did form well defined groups, which tends to fit in with the community-unit hypothesis. However these groupings were not absolutely distinct. The species within each group had different distribution ranges, although they had maximum occurrences together in a central region of the group distribution. Species from different groups had distribution patterns which overlapped to varying degrees. These findings tend to fit the individualistic hypothesis. The distribution patterns are grouped in a way which

resembles that of the third type of species and community grouping listed in Whittaker (1975, page 113), a slightly. modified version of the individualistic hypothesis, in which "groups characterize different kinds of communities, but the communities intergrade continuously". This is a rather surprising finding. The Gulf Stream is characterized by strong horizontal and vertical gradients. In such a region with sharp physical boundaries, abrupt discontinuities in species groups would also be expected. The fact that species groups intergrade continuously, despite sharp physical boundaries, indicates that biological factors are very important in shaping species distribution patterns, even in areas such as the Gulf Stream.

Similar distribution patterns of community groups which intergrade have been found before in marine zooplankton (Angel and Fasham, 1973; 1974; Marlowe and Miller, 1975; McGowan and Walker, 1979; Tranter et al., 1983) and marine phytoplankton (Venrick, 1982). With .the exception of Tranter et al. (1983), these studies all examined communities in the middle of gyres where physical properties have small gradients and do not vary spatially or temporally to a large extent. Tranter et al. (1983}, studied a warm core ring off the coast of Australia, an environment that would be expected to have large variability temporally and spatially. They found that the copepod species formed intergrading community groups over time. Lane (1975; 1978) found similar patterns in lake zooplankton communities over time, but Makarewicz and Likens (1975; 1978) found no such groupings in lake

zooplankton. Marine zooplankton communities seem to have species distributions which intergrade spatially and temporally in areas of both large and small physical gradients. Recent evidence suggests that marine zooplankton communities may be arranged in slightly different ways than are terrestrial communities (Dayton, 1984; McGowan and walker, 1985). It may be that species distributions arranged into intergrading groups is a general feature of marine zooplankton community structure.

Hayward and McGowan (1979) and McGowan and Walker (1979) have examined species distribution patterns and their relation to community structure in marine zooplankton. Hayward and McGowan (1979), in a theorectical study of the copepod species of the north Pacific central gyre, inferred that competition must be occurring because of the high diversity of the zooplankton community, the limited availability of food, and apparent lack of specialization in feeding or distribution of copepods. McGowan and Walker (1979) stated three main hypotheses to account for the cooccurrence of large numbers of copepod species in the central Pacific gyre. These hypotheses were: 1) the copepod species used qualitatively different food resources, 2) the copepod species avoided competition for the same food items by eating at different times and/or places, and 3) selective predation on individual species allowed co-existence. They were unable to find support for any of these hypotheses in their data and concluded that the copepod species may be co-existing without

41 niche separation. In light of the apparent lack of niche separation, Hayward and McGowan (1979) posited predation as a likely regulator of community structure. Upon further examination, they decided that the consistent occurrence of rare species which are probably of little importance to predators and hard for predators to select, rules out predation as regulating community structure. However the occurrence of rare species is not enough to rule out predation as an important regulatory agent. Dayton (1984) has clearly shown how a rare predator keeps its prey rare and thus regulates the community structure of the Antarctic benthos. Such a relationship would be difficult to detect in the plankton.

Both McGowan and Walker (1979), and Hayward and McGowan (1979) concluded that the lack of apparent niche separation was not a sampling artifact. McGowan and Walker's sampling scheme (and the sampling scheme of this study) is best suited for the examination of meso-scale {100-1000 km) and coarse scale (1-10 km) phenomena (scales as defined in Haury et al., 1978). Recent papers (Omori and Hamner, 1982; Alldredge et al., 1984} have emphasized the need to examine zooplankton species on the fine $(10-100 \text{ m})$ and micro $($ $($ 1 $\text{m})$ scales in order to understand their interaction. Haury and Wiebe (1982) found multi-species zooplankton groups occurring on scales of 10-100 m. This finding plus the facts that zooplankton vertically migrate over hundreds of meters, that Water in the ocean is constantly moving, and that zooplankters occur in everchanging associations, further

emphasizes the point that each species and group of species must be carefully studied on a variety of scales with different methods in order to understand its population dynamics (Omori and Hamner, 1982). While changing the scales at which a population is studied may provide new insights into processes causing the patterns exhibited by that population (Dayton and Tegner, 1984), it is doubtful that a study which relies solely on sampling will be able to resolve such complex problems as niche separation. Connell (1961) demonstrated that species that do not overlap in spatial distribution may in fact be competing with each other, and the lack of spatial overlap is a result of that competition. Studies such as the present one and others previously mentioned, which investigated community structure in the marine plankton, reveal many intriguing patterns of species distribution. Reasonable processes to account for these patterns can be hypothesized, but sampling alone is not likely to resolve which hypotheses are most nearly correct. Careful experimentation, technologically difficult at present with open ocean plankton, could resolve these questions, and it is hoped that such experimentation will become possible in the future.

Conclusions

Examination of selected copepod species distributions and abundances in the Gulf Stream region during September, 1982 has revealed:

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1) Copepod species distributions can be grouped into several distinct patterns.

2) These patterns are related to distinct oceanic habitats within the Gulf Stream.

3) As a result of the association between different species groups and environmental habitats, it is apparent that different species have quite different probabilities of downstream and cross-stream transport.

4) cross-stream dispersal of copepod species is most likely to occur in the surface mixed layer and below the oxygen minimum zone. Species in the central core area of the Stream are not likely to be dispersed cross-stream but are likely to be carried downstream for long distances.

5) The interaction of biological processes, especially vertical migration, with physical features and processes of the Gulf Stream determines the degree of downstream and cross-stream transport of zooplankton.

6) The community structure of copepod species forming community groups which continuously intergrade supports a modified version of the individualistic hypothesis of species distributions and community formation. This type of pattern has been observed before in marine zooplankton communities and it may be a general feature of such communities.

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Fig. 1. Satellite infrared image of the Gulf Stream region near Cape Hatteras on Sept. 14, 1982. Lighter colors represent warmer temperatures, and the Gulf Stream is the light colored band running diagonally through the picture. The sampling stations are marked by letters such that X is the north wall station, 0 is the central core station, and Y is the southern edge station. Cape Hatteras and the mouth of the Cheasapeake Bay are the white land masses on the left edge of the picture.
The state of the state strain of the state of

Fig. 2. Contour plots of environmental data across the Gulf Stream. a is temperature, b is salinity, *c* is density, d is POP, e is oxygen, and f is chlorophyll \underline{a} . P6 is the north 4 wall station, PS is the central core station, and P4 is the southern edge station.
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Fig. 3. Contour plots of downstream and cross-stream velocity, a is downstream velocity and b is cross-stream velocity. Stations are as in Fig. 2. Downstream velocity values represented measurements that have been rotated to a C direction 57 true. Positive cross-stream values indicate motion to the southeast, and negative values indicate motion to the northwest. Figure was redrawn with permission of Rossby and Halkin.
All the Contract blots of the Messachusetts distribution and

Fig. 4. Copepod species groupings as determined by recurrent group analysis. Groups are arranged vertically as they tend to occur in the water column with surface water groups higher in the figure and deep water groups low in the figure. Group connections are shown by lines between groups. Percentages show the amount of connection between groups.

Fig. s. Contour plots of the cross-stream distribution and abundance of Species Group 1. Stations are as in Fig. 2.

Fig. 6. Contour plots of the cross-stream distribution and abundance of Species Group 2. Stations are as in Fig. 2. Fig. 13. The distribution of principle components

Fig. 7. Contour plots of the cross-stream distribution and abundance of Species Group 3. Stations are as in Fig. 2. Mistions are as to Fig. G.

Fig. 8. Contour plots of the cross-stream distribution and abundance of Species Pair 1. Stations are as in Fig. 2.

Fig. 9. Contour plots of the cross-stream distribution and abundance of Species Pair 2. Stations are as in Fig. 2.

TABLE I. Summary of campling information

Fig. 10. Contour plots of the cross-stream distribution and abundance of <u>Pleuromamma</u> borealis. Stations are as in Fig. 2.

Fig. 11. Contour plots of the cross-stream distribution and

abundance of Lucicutia clausi. Stations are as in Fig. 2.

Fig. 12. Zooplankton samples plotted on a projection of principle component Axis 1 by Axis 2. Axis were determined by principle components analysis on physical and biological data collected for each sample. The samples were grouped by eye into environmental groups, labelled $A - G$, indicated by different symbols. The samples in which each species group is present at the 100 % level are shown by tone. Coarse (0 - 1000 m and fine $(0 - 200 \text{ m})$ scaled samples are plotted and grouped separately. RG = recurrent group.
 Example 20

Fig. 13. The distribution of principle components environmental groups cross-stream in the water column. Coarse and fine scale sampling groups are shown separately. Stations are as in Fig. 2.
Stations are comparison of the distribution and short are

Fig. 14. Diagram of hypothesized zooplankton dispersal paths based on velocity profiles and directions. See text for explanation. Figure redrawn from Wishner, 1983.

Table 1. Summary of sampling information.

Table 2. Copepod species distribution and abundance data for this study.

Table 3. Eigenvalues from the principle components analysis.

Table 4. Percentage of samples in a particular environmental group in which a species group occurs at a 100% level (all species present). Changeval an era constant composition

Table 5. Summary of the North Atlantic distributions for the copepod species considered in this study. The temperate Atlantic is north of the Gulf Stream and the subtropical Atlantic is south of the Stream. Depth ranges are in meters. NR = not recorded in these sources. Sources are: 1. Steuer (1932) 2. Rose (1933) 3. Moore and O'Berry {1957) 4. Grice (1963) 5. Grice and Hulsemann (1965) 6. Hulsemann (1966) 7. Owre and Foyo (1967) 8. Park (1970} 9. Bowman (1971) 10. Roe (1972) 11. Michel et al. (1976) 12. Fleminger and Hulsemann (1977) 13. Roe (1984).

Table 6. A comparison of the distribution and abundance patterns of the species examined in this study with the distribution and abundance patterns for these species observed by Grice and Hart (1962).

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Table 1 Summary of data collected during Endeavor cruise ♦ 1962, and used in this study.

Note: MGCNESS = zooplankton sampling, Pegasus = in-situ velocity profile, XBT = expendable bathythermagraph, Hydrocast start time and position is when the messenger was deployed to close the bottles.

Table 2 Summary of copepod species distribution and abundance data.

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S6 = Species Group
SF = Species Pair
--- = Unassociated

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Table 4a Percentage of samples of an environmental group in which all members of a species group co-occur.

Table 4b Percentage of a full species group occurring in an environmental group.

Note: EG = Environmental Group, SG = Species Group, SP = Species Pair

Table 5 Summary of the North Atlantic distributions of copepod

species enumerated in this study. The temperate Atlantic is the area north of the Gulf Stream and the subtropical Atlantic is the area south of the Gulf Stream. Depth ranges for each species in each area are given in meters. 26.9

		Area of the Atlantic Temperate Subtropical Gulf of		Florida	Migration Fattern	Source
Species	Atlantic	Atlantic	Mexico and Caribbean	Straits		
C. finmarchicus	$0 - 1400$	N. R.	N. R.		N. R. ontogenetic	3, 4, 10
C. gracilis	shailow	$0 - 950$	$0 - 950$	N. R.	diel	1, 3, 6, 8
C. minor	$0 - 150$	$0 - 620$	$0 - 500$	$0 - 70$	none	1, 2, 3, 6, 7, 8
C. tenuicornis	N. R.	$0 - 300$	$0 - 500$	$0 - 195$	none	1, 4, 5, 6, 7, 8
L. clausi	N. R.	190-850	$100 - 950$	$100 - 440$	none	4, 5, 6, 8, 12
L. flavicornis	$0 - 1700$	$0 - 2000$	$0 - 3200$	$0 - 550$	diel	3, 4, 5, 6, 7, 8, 9, 12
L. gemina	present	$0 - 960$	100-200	N. R.	N. R.	1,4,6,12
L. ovalis	$0 - 200$	$0 - 3000$	500-2800	N. R.	N. R.	1, 3, 4, 6, 8, 12
M. brevicauda	600-1000	190-1900	500-1900	N. R.	N. R.	1, 3, 4, 5, 6, 8
M. lucens	100-1400	200-1150	N. R.	N. R.	diel	1,3,4,8
M. venusta	620-700	450-1900	200-1000	N. R.	N. R.	1, 3, 5, 6, 8
P. abdominalis	$0 - 900$	$0 - 2000$	$0 - 1900$	$0 - 900$	diel	1, 2, 3, 4, 5, 6, 7, 8, 11
P. borealis	$0 - 1200$	$0 - 2500$	N. R.	N. R.	diel	1, 3, 4, 8, 11
F. gracilis	$0 - 500$	$0 - 1500$	$0 - 1900$	$0 - 500$	diel	1, 2, 3, 4, 5, 6, 7, 8, 11
P. piseki	present	$0 - 1500$	N. R.	$0 - 500$	diel	1, 3, 4, 5, 7, 8, 11
P. xiphias	$0 - 1300$	50-2000	200-950	$0 - 820$	diel	1, 2, 3, 4, 5, 6, 7, 8, 11
R. cornutus	$0 - 270$	$0 - 1000$	200-1900	$0 - 1500$	diel	1, 2, 3, 4, 5, 6, 7, 8, 9
R. nasutus	$0 - 1400$	$0 - 1150$	present	150-880	diel	1, 3, 4, 5, 8

Sources:

1 = Rose, 1933; 2 = Moore and D'Berry, 1957; 3 = Brice, 1963; 4 = Brice and Hulsemann, 1965; 5 = Owre and Foyo, 1967; 6 = Park, 1970; 7 = Bowaan, 1971; B = Roe, 1972; 9 = Michel et al., 1976; 10 = Fleminger
and Hulsemann, 1977; 11 = Steuer, 1932; 12 = Hulsemann, 1966.

 $N. R. = not recorded in these sources$

Note: Very Abundant > 1000 copepods (1000 m)-3
Abundant 101-1000 copepods (1000 m)-3
Common 51-100 copepods (1000 m)-3
Rare 1-50 copepods (1000 m)-3

Shallow = 0-200 a depth, Deep = Below 400 a depth N. R. = not recorded

Fig. 2

d. Phosphate

f. Chlorophyll a

SIMILI $\sqrt{2}(-0.1) - (-10)$ $\sqrt{2}(-11) - (-20)$ P4 Cross-stream PS $\boxed{}$ 11 – 20 $\boxed{10}$ 0 - 10 Velocity P6 $\frac{1}{100}$ L e $100₇$ τ $800 500 000$ 600 . 900 1000 200 400 $\boxed{21 - 50}$ $101 - 150$ 11 - 20 $P₄$ \Box 1 - 10 Downstream PS $\frac{1}{2}$ 51 - 100 Velocity $\overline{150}$ P6 $100 1000 600 -$ - 008 - 006 $500 -001$ 200 400 300

Fig. 4

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Species Group Two

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Fig. 8

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 $Fig. 9$

Day $P₄$ **P6 P5** 100 $200 -$ 300 400 \bullet 500 600 ٠ 700 800 900 $1000 -$ **Both members** 1 member

Species Pair Two

Fig. 10

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Fig. 11

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Fig. 13

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Spatial and Temperal Verisbility in Cooplankton Bicmann

Spatial and Temporal Variability in Zooplankton Biomass Across the Gulf Stream

biamas in the support 1000 m at 3 stations screen the Gulf

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enhanced over that of the control Stream and Sergenso Sum. Toopismeton biomnes is high it the upper 100 m of the water

Abstract

From November, 1981 to November, 1982, zooplankton biomass was sampled bimonthly by oblique net tows in the upper 200 m along a 9 station transect of the Gulf Stream region east of Cape Hatteras. In September, 1982 and May, 1983, extensive vertically stratified sampling of zooplankton biomass in the upper 1000 m at 3 stations across the Gulf stream was done with a MOCNESS net system. Concurrent insitu water velocity, transport, and hydrographic measurements were also made.

Zooplankton biomass tends to be highest in the Slope Water, intermediate at the north wall of the Gulf Stream. and lowest in the Gulf Stream proper and Sargasso Sea. The north wall of the Gulf Stream is a frontal region in which zooplankton and phytoplankton biomass can be considerably enhanced over that of the central Stream and Sargasso Sea. Zooplankton biomass is high in the upper 100 m of the water column across the Stream both day and night, and there is a deep biomass maximum below 400 m during the day. As much as 40% of the zooplankton biomass in the upper 1000 m migrates into the top 200 m at night. Zooplankton biomass in the upper 200 m shows a distinct seasonal pattern with maximum abundances in late spring and early summer and a minimum in the autumn.

Introduction alle alle daily weat to be hand allege and

The northwestern Atlantic Ocean is one of the most extensively studied open ocean regions of the world. However, the biology of the Gulf Stream itself, a major feature of the region, is not well known, especially downstream of Cape Hatteras, where it turns offshore. Biologically, the Gulf stream functions as a means of downstream transport, as a boundary between cool water temperate communities and warm water sub-tropical communities, and as a region of crossstream mixing between these communities (Wishner and Allison, in press}. The local physical oceanography plays a dominant role in the ecology of the Stream, and complex interactions between biological and physical processes affect the distribution of individual zooplankton species inhabiting this region (Stepien, 1980; Wishner and Allison, in press).

Total zooplankton biomass measurements can provide a broad view of spatial and temporal patterns of abundance and distribution across the Stream. Although numerous studies have examined the zooplankton biomass of the northwestern Atlantic (Moore, 1949; Fish, 1954; Bsharah, 1957; Menzel and Ryther, 1961; Grice and Hart, 1962; Be et al., 1971; Deevey, 1971; Deevey and Brooks, 1971; Ortner et al., 1978), most have concentrated on the Slope Water and Sargasso Sea. Grice and Hart (1962) and Be et al. (1971) reported a few biomasses of Gulf Stream zooplankton, while Bsharah (1957) looked at the zooplankton biomass in the Florida Straits region. Since

all of these studies used different nets, mesh sizes, and sampling strategies, it is difficult to compare absolute biomass values between studies. However, it is possible to compare biomass patterns. For example, all of these workers observed a seasonal pattern in zooplankton abundances in the slope Water. Some also found evidence of seasonal zooplankton variations in the Sargasso Sea (Moore, 1949; Fish, 1954; Menzel and Ryther, 1961; Deevey, 1971; Deevey and Brooks, 1971; Ortner et al., 1978), although Grice and Hart (1962) did not observe a seasonal cycle of zooplankton abundance there. Bsharah (1957) found seasonality in zooplankton abundance in the Florida Straits region. Most of this information is based on oblique tows in the upper several hundred meters. The manufacturer is a several hundred meters.

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Vertical sampling of discrete depth intervals in the Sargasso Sea (Deevey and Brooks, 1971) and in the Slope Water, Sargasso Sea, and cold core Guif Stream rings (Ortner et al., 1978), found a maximum in zooplankton biomass near the surface water during both the day and night, often around 50-100 m depth, and a subsurface biomass peak during the day at 400-600 m. Diel vertical migration of a major portion of the zooplankton biomass in the Slope Water and Sargasso Sea is evident from these studies.

The northern boundary {north wall) of the Gulf Stream downstream and offshore from Cape Hatteras is a sharp frontal region (Stammel, 1965). Zooplankton often show increased concentrations at fronts (Herman and Denman, 1979; Herman et

al., 1981; Parrish et al., 1981; Mackas and Sefton, 1982; zeldis and Jillet, 1982; Haury, 1984; Boucher, 1984). several studies have reported biomass peaks and aggregations of organisms related to frontal upwelling and eddies along the western edge of the Gulf Stream off the southeastern coast of the United States south of Cape Hatteras (Atkinson et al., 1978; Paffenhofer, 1983; Paffenhofer et al., 1984; Deibel, 1985), but this region is quite different from the north wall of the Gulf Stream further offshore, because the stream along the coast is topographically constrained by the continental shelf. Whether such aggregations occur at the north wall of the Gulf Stream has not previously been examined, although Lessard (1984) has observed peaks of phytoplankton at the north wall.

The potential downstream and cross-stream transport of copepod species in the Gulf Stream (Wishner and Allison, in press) varies with the horizontal and vertical location of the species within the Stream. Downstream transport is greatest in the central core region of the Stream and in the high velocity surface water. Cross-stream transport is most likely below the oxygen minimum zone, at approximately the \circ depth of the 12 C isotherm, which changes from 250 m at the northern edge to 700 m at the southern portion of the Stream. Cross-stream mixing is also probable in the surface water. Because zooplankton biomass is distributed unevenly horizontally and vertically, it is likely that the transport of zooplankton biomass also varies in the different regions of the Stream. The warm wallowsed as a web of mine atations

This paper describes the spatial and temporal variability of zooplankton biomass distribution over a yearlong period along a transect from the Slope Water across the Gulf stream into the Sargasso Sea. This study is part of a project on Gulf Stream biology directed by Dr. K. Wishner. This paper will examine in detail:

1) Aspects of the spatial and temporal variability of zooplankton biomass with depth across the Stream.

2) The northern boundary {north wall region) of the Gulf stream as a front and location of increased biomass concentrations.

3) Seasonal variations in zooplankton biomass distributions and abundances along the transect.

4) The potential cross-stream and downstream transport of zooplankton biomass in different regions of the Gulf Stream.
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The data were collected on seven cruises aboard the R/V Endeavor and R/V Cape Hatteras in the Gulf Stream region just east of Cape Hatteras. The cruises occurred bimonthly from November, 1981 to November, 1982 as part of an intensive study of the physical oceanography of the Stream by H. T. Rossby, of the University of Rhode Island. Biological sampling was interspersed with the physical measurements. Cruise dates and other sampling information are summarized in Table 1. Samples were collected at a set of nine stations

positioned 20 km apart perpendicular to the mean direction of the flow of the Stream along a transect centered at 36 N \circ 73 W. The stations are located such that if the Gulf Stream is in an average position, the northern stations will be in the slope Water, the central stations in the Stream, and the southern stations in the Sargasso Sea (Halkin, 1984).

At each station, in-situ velocity and transport direction to a depth of 2000 m or greater was measured with a cast of a free vehicle Pegasus velocity profiler (Spain et al., 1981) by H. T. Rossby and his group at the University of Rhode Island, who analyzed the data. Expendable bathythermographs (XBTs) deployed to 750 m and infrared satellite imagery of sea surface temperature were also used to determine the position and structure of the Stream. Satellite infrared imagery was obtained from the Remote Sensing Center at the Graduate School of Oceanography of the University of Rhode Island.

Replicate zooplankton samples were collected at these stations using a 202 um mesh, 0.65 m diameter net towed obliquely through the upper 200 m of the water column. Each 3 tow filtered 100 to 260 m of water. Samples were preserved in 4% buffered Formalin. Because of the necessity of coordinating the sampling with the physical oceanography, the time of day of sampling at each station varied. Day and night samples were analyzed separately. Dawn and dusk samples were eliminated from the analysis. Dawn was considered to be the period of time from 2 hours before until ²hours after sunrise, and dusk was the period of time from 2 hours before until 2 hours after sunset. The times of sunrise and sunset for a paticular date and geographic position were obtained from The Nautical Almanac (1981; 1982; 1983) .

During September, 1982 and May, 1983, vertically stratified zooplankton sampling was done with a MOCNESS net 2 $(1 \text{ m}$ mouth opening, 333 $\underline{\text{ u}}$ m mesh) (Wiebe et al., 1976). This opening-closing net system allows one to collect 9 sequential samples along with in-situ environmental information (depth, temperature) and sampling data (volume filtered, net angle). Data from the MOCNESS was processed and stored at sea on a Hewlett-Packard 85 computer. A transect of the Gulf Stream was done using the MOCNESS at all 9 stations to collect zooplankton from 400 m to the surface in 50 m intervals. In addition, 3 stations, 20-40 km apart located at the north wall of the Stream, the warm high velocity core, and the southern edge of the Stream, were sampled intensively. At each of these stations, MOCNESS tow series were centered at noon and midnight, with each series consisting of a deep and shallow sample set. The deep tow collected samples from 1000 m to the surface, in intervals of 150 m from 1000 to 400 m and in intervals of 100 m from 400 m to the surface. The shallow samples were collected from 200 m to the surface, in intervals of 25 m. Each net in a MOCNESS tow filtered from 3 300 to 1000 m of water. Samples were preserved in 4% buffered Formalin. For more information on the three intensive MOCNESS stations in September, 1982, see Wishner

and Allison (in press).

The biomass of the zooplankton samples was measured using the displacement volume method (Beers, 1976), after first removing large gelatinous zooplankton and fish. The displacement volume method was used because it is a simple, widely used measure which allows the estimation of biomass without destroying the sample for future analysis. Displacement volumes of the samples were measured 8 to 10 weeks after collection.

All station data were analyzed relative to natural Gulf stream co-ordinates, with axes parallel to and perpendicular to the mean direction of flow. The angle is determined at which the mean direction of Stream flow intersects the transect line on each cruise, and the relative Stream positions of each station are then rotated into a Stream coordinate system (Halkin, 1984}. Therefore, samples collected at the same cross-stream position on different cruises are comparable, even though their geographic positions may differ (Fig. 1).

For each cruise, the zooplankton biomasses were divided into four cross-stream regions: the Slope Water, the north wall of the Gulf Stream, the Gulf Stream proper, and the Sargasso Sea. Slope Water stations were those northwest of 0 the location at which the 15 C isotherm was 200 m deep. Surface downstream velocity was low in the Slope Water, less than 30 cm s . The north wall was the station where the \circ 15 C isotherm was about 200 m deep. Surface downstream

velocity was high at this station, usually greater than 100 -1 cm s The Gulf Stream proper was the region in which the o
15 C isotherm continued to deepen from north to south. surface downstream velocities in the Gulf Stream ranged from -1 40 to 200 cm s . The Sargasso Sea was the region in which 0 the 15 c isotherm levelled out at about 650 m depth and where -1 surface downstream velocities were less than 30 cm s

Results The Johnson Kremer a spot plant and of minimum

Horizontal Patterns and Communications of the Manual Patterns and Communications and Comm

All of the zooplankton biomasses collected in the 200 m oblique tows from November, 1981 to November, 1982 are graphed together in Fig. 2. The position of the north wall is used as the reference point, and the stations at which zooplankton were collected are arrayed relative to the north \circ wall. This is done by aligning the 15 C isotherm for each cruise so that the geographic location where this isotherm is at 200 m depth (which is defined as the north wall of the Gulf Stream) intersects for all cruises. The seasonal pattern of biomass, separated by region, is diagrammed in hedian biemseses for the Gulf Stroom and the Fig. 3.

The zooplankton samples collected from November, 1981 to November, 1982 with the 200 m oblique tows were tested to determine if tnere were differences in total zooplankton **ATAC ERAN** biomass between the regions. The biomasses were standardized by dividing each measurement by the median Sargasso Sea biomass value for that cruise (Table 2). Day

and night samples were standardized separately. This procedure was done to highlight the overall relationships between the four areas by reducing the effects of seasonal changes in absolute abundance. The relative biomasses for the four regions were compared using the Kruskal-Wallis Test (Sokal and Rohlf, 1981). Night biomasses, but not day biomasses, were significantly different among the regions (P (0.05) . The Tukey-Kramer a posteriori test of minimum significant difference {Sokal and Rohlf, 1981) was used to determine which regions differed significantly among the night samples. The Slope Water was significantly different from both the Gulf Stream and the Sargasso Sea {P < 0.05). The north wall was intermediate between the Slope Water and the Gulf Stream, but was not significantly different from either of them or the Sargasso Sea. The Gulf Stream and Sargasso Sea were not significantly different.

The Slope Water tended to have the highest biomasses of the four regions {Table 2). The median biomass for the Slope Water was greater than the median biomass for the north wall. The median biomass for the north wall, however, was greater than the median biomasses for the Gulf Stream and the Sargasso Sea. **Executive Sargasso** Sea.

These same general trends were found in the MOCNESS samples (Table 2). The integrated water column (0-400 m) -2 biomass (ml m) of the Slope Water was 2 times greater than the north wall, 3 times greater than the Gulf Stream, and 1.5 times greater than the Sargasso Sea biomass.

Although not significantly different overall from the Gulf stream and Sargasso Sea, the north wall region frequently had increased zooplankton concentrations relative to the Gulf Stream and Sargasso Sea (Fig. 2). For example, during March 1982, the highest zooplankton biomasses across the whole transect occurred at the north wall. This biomass peak was accompanied by high concentrations of the diatom Thalassiosira partheneia. In July, September, and November, 1982, and May, 1983, biomass at the north wall was 1.5 to 3.5 times greater than in the Gulf Stream and Sargasso Sea. During May, 1983, there were large concentrations of the salp, Salpa fusiformis, and the ctenophore, Pleurobrachia pileus, at the north wall and Slope Water stations.

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Biomass in the upper 200 m was 1.3 to 3.5 times higher in night than day with all sampling methods in all regions. This difference was probably caused by a combination of vertical migration of zooplankton into the upper 200 m at night and decreased net avoidance at night. The intensive MOCNESS series revealed that the total biomass of the 0-1000 m depth range was similar both day and night, which indicates that there was little upward vertical migration of zooplankton from below 1000 m and that diel differences in net avoidance were not a problem.

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Biomass concentrations from the 200 m oblique tow series Were tested to determine if there were significant

differences between day and night biomasses within each region. Biomass concentrations were compared using the wilcoxen Two Sample Test (Sokal and Rohlf, 1981). The day and night biomasses were significantly different in the Gulf stream and Sargasso Sea (P < 0.05). Day and night biomasses were not significantly different in the Slope Water and at the north wall. We have a series of the series of the

Vertical Patterns

panin, good is on high in those on the upper

The distribution of biomass with depth in the MOCNESS samples is contoured in Fig. 4. We also calculuated the cumulative percentages of water column biomass from the surface to 1000 m for each station, and the depth of the 50% level is shown in Fig. 4. The 50% level of biomass from the intensive MOCNESS series was at 50 to 150 m during the day in all regions, and was at 50 to 100 m for all regions in the night. Nineteen to 66% of the integrated water column biomass (0-1000 m) was in the upper 100 m during the day and 50 to 78% of the integrated water column biomass was in the upper 100 m at night. This implies that the 200 m oblique tow series observed a large proportion of the total water column biomass and variations in biomass occurring there reflect variations occurring to most of the biomass. Fifteen to 44% of the integrated water column biomass {0-1000 m) appeared to be migrating into the upper 200 m at night.

The intensive MOCNESS sampling revealed that the highest -3 biomass concentrations (ml m) tended to occur in the upper

. 100 m of the water column {0-1000 m), especially at night. During the night biomass concentrations in the upper 100 m typically were at least 1.5 times those in any other depth range, and .could be as much as 25 times greater than the lowest values measured. During the day the upper 100 m biomass concentrations were still high, but there was often an additional biomass peak at depth. These deeper biomass peaks, could be as high as those in the upper 100 m.

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Seasonal Patterns Seasonal Patterns

The 200 m oblique tow series were examined within each region {Fig. 3) to determine whether apparent seasonal changes occurred during the course of the study. Since the study extended for only one year, it is not possible to establish the limits of variability in seasonal patterns, which would require many complete yearly cycles. Biomass anomalies, the difference between a sample and the median value for that region, were calculated for each sample. Anomalies for day and night samples were calculated separately to reduce the effects of possible diel differences between samples. Day and night samples were then examined together so that all samples for one area were compared. Kruskal-Wallis tests {Sokal and Rohlf, 1981) indicated that the Slope Water, north wall, and Gulf Stream proper all had significant variability between cruises {P < 0.05). The Sargasso Sea biomasses did not exhibit significant temporal variability.

The highest biomasses occured in the spring months of March and May, with the highest of all in May. The lowest biomasses occurred in the autumn months of September and November, with September having the lowest values. In the slope water, the median of May, the month with the highest biomass, was 5 -times the median of September. At the north wall, the median of March, the month with the highest biomass here, was 10 times that of September, the month with the lowest biomass. In the Gulf Stream proper, the median of January, the month with the highest biomass here, was 6 times that of September, the month with the lowest biomass. The spring maximum occurs earliest in the most southern region, the Gulf Stream, and then moves north to the next regions. It may be that conditions necessary for a spring increase are met at earlier times in the more southerly and warmer regions.

The two MOCNESS tow series were separated by about 8 months. Consequently it is not possible to consider seasonality in the MOCNESS tows, but one can fit them into the pattern observed in the year long 200 m oblique tow series. In September, 1982, zooplankton biomass -3 concentration {ml m) from the MOCNESS series {0-400 m) had a similar cross-stream pattern to that obtained during the same cruise with the 200 m oblique tows. Although the MOCNESS and small open net are different systems with different mesh sizes and may not be comparable for absolute Values, they do show similar patterns across the Stream.

The September, 1982 MOCNESS total water column -2 zooplankton biomasses (ml m) were 2 to 5 times higher than the May, 1983 ones except on the southern edge of the Stream where they were similar in both months (Fig. 4). Yet during the year-long 200 m oblique tow series, the September, 1982 biomasses were among the lowest observed, while the May, 1982 biomasses were the highest observed. No 200 m oblique tows were taken in May, 1983. In May, 1983 (but not in 1982), dense aggregations of the salp, Salpa fusiformis, and the ctenophore, Pleurobrachia pileus, were encountered in the upper 100 m in the Slope Water and north wall regions. These large gelatinous animals were not included in the measurements of displacement volume, which considered only smaller zooplankton. The contract of the contr

Discussion

Horizontal Patterns

Zooplankton biomass varied horizontally among regions from the Slope Water to the Sargasso Sea. The regions were significantly different in the night biomass samples. Our results tend to agree with those of other studies of the northwestern Atlantic {summarized in Table 3), which have found zooplankton biomass 4 to 11 times greater in the Slope Water than the Gulf Stream and Sargasso Sea. No previous studies have differentiated between the various regions of the Gulf Stream, especially the north wall.

Enhanced concentrations of zooplankton biomass were often found at the north wall front of the Gulf Stream. In March, 1982, the highest zooplankton biomasses of the cruise occurred at the north wall, and during several other cruises (July, September, and November, 1982, and May, 1983) zooplankton biomass, although lower than the Slope Water, was 2 to 5 times higher at the north wall than in the Gulf Stream and Sargasso Sea. These increases in biomass were observed in the upper 200 m, where the water at the north wall and stream is similar in temperature and other physical properties (Wishner and Allison, in press).

An increase in zooplankton biomass at frontal regions is a common occurrence in marine environments (Herman and Denman, 1979; Herman et al., 1981; Parrish et al., 1981; Mackas and Sefton, 1982; Zeldis and Jillet, 1982; Boucher, 1984). Frontal regions are areas of enhanced biological activity in general (Pingree et al., 1974) and many types of organisms are concentrated in such regions. Increased primary productivity and phytoplankton biomass are often observed at fronts (Pingree et al., 1975; Fournier et al., 1977). Fish (Atkinson and Targett, 1981; Mishima, 1981; Olson and Backus, 1985) and seabirds (Schneider, 1982) also may be concentrated at fronts. The increased biological activity at fronts may be attributed to two main causes, Which may act singly or in concert. Fronts may experience an input of nutrients which enhances primary production and Provides food that allows for increases in the numbers of all organisms in the community. Alternatively, the water
movement and structure at the front may interact with the behavior of zooplankton being advected to the frontal region and result in their concentration. This concentration could then attract more active organisms such as fish and birds. our sampling was not extensive enough to determine whether there were increased nutrients at the north wall. During some cruises, cross-stream transport converged at the north wall, but it did not converge in all of the cruises in which increased zooplankton biomasses were observed at the north wall (Halkin, 1984). The contract of the contr

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In March, 1982, there was a large concentration of the diatom Thalassiosira partheneia at the north wall which apparently extended for a considerable distance along the frontal edge. We did not measure its actual concentration, but detected it because it clogged our zooplankton nets. The diatoms were encountered at 3 stations, two in the Slope Water (PS and P7) and one at the north wall (P6) over a width of 60 km on March 13 at the start of a north-south transect and again at the same stations on March 19 at the end of a south-north Stream transect. Downstream velocity was -1 -1 -1 approximately 10 cm s at PS, 20 cm s at P7, and SO cm s at P6. Cross-stream transport was toward the south at PS, toward the north at P7, and toward the south at P6 (Halkin, 1984). Based on the probable occurrence of this patch at P6 -1 over 6 days, a station where the current was moving 80 cm s downstream, this diatom patch could have been 415 km long. It is possible, however, that some kind of re-circulation

kept this patch localized. During this cruise, the direction of cross-stream transport indicated a divergence at P6, which implies that upwelling was also occurring. Increased continuous nutrient input may have been sustaining the bloom of the diatom along the north wall. There was no evidence of an eddy or ring in the area at this time (Halkin, 1984). Zooplankton biomass was also elevated at the north wall during this cruise. T. partheneia forms large colonies, which are commonly found in the Northwest African upwelling region (Elbrachter and Boje, 1978). These colonies often disintegrate into single cells, which can be a good food source for copepods {Schnack, 1983). If the diatom bloom had persisted along the north wall for several weeks, it may have directly led to the increase in zooplankton. Copepods along the Georgia coast respond to upwelling events in 3 weeks (Paffenhofer, 1980) and doliolids respond in 7 to 9 days (Deibel, 1985), so such a direct increase is possible. Alternatively, it is possible that advection concentrated the zooplankton independently in the same area.

A large aggregation of salps and ctenophores was observed at the north wall and the adjacent Slope Water station, 20 km away, during May, 1983, when the abundance of smaller zooplankton was unusually low. In our 1000 m deep MOCNESS tows, these gelatinous zooplankters were abundant in the top 100 m of the water column on May 10 and 11, but had disappeared from the upper 1000 m of the water column by May 19 when we returned to these stations. Dense patches of gelatinous zooplankton are fairly common in the world's

oceans and can occur over huge areas (Omori and Hamner, 1982). Large aggregations of ctenophores or other carnivorous gelatinous zooplankton can consume a high percentage of smaller zooplankton present (Swanberg, 1974; omori and Hamner, 1982; Purcell, 1983). Predation by the ctenophore Pleurobrachia pileus may have reduced the standing stock of smaller zooplankton during May, 1983. Salp blooms have been observed in the Slope Water on several occasions (Grice and Hart, 1962; Wiebe, et al., 1979). Salps are voracious herbivores (Alldredge and Madin, 1982) and the S . fusiformis present in May, 1983, may have consumed so much food that other herbivorous zooplankters were not able to survive. Rockeds analient word similar by these abrained by

Vertical Patterns

The vertical structure in the zooplankton biomass distributions observed in the MOCNESS collections revealed that there was a biomass peak in the upper 100 m both day and night. During the day there was a second biomass peak below 400 m depth. The surface biomass peak usually was located in the mixed layer and the deep biomass peak was below the 15 \circ ^Cisotherm. The increase in biomass in the upper 200 m at night was probably due to zooplankton migrating vertically into the surface water, rather than decreased net avoidance.

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Ortner et al., (1978) found that zooplankton biomass tended to have a maximum near 50 m depth in both the Slope Water and Sargasso Sea. They found a deep daytime maximum in

zooplankton biomass at 400-600 m depth, but only in the Slope water. They found that the percent of the 0-800 m biomass present in the upper 200 m was 45 to 51 % for the Sargasso sea and 32 to 34 % for the Slope Water. Ortner et al., found 24 to 30 % of the zooplankton biomass to be migrating into the upper 200 m at night. Deevey and Brooks {1971} felt that there were indications of different seasonal patterns at depth in the Sargasso Sea than in the upper water column. our sampling was not extensive enough to determine deep water seasonality.

The total water column (0-1000 m) integrated zooplankton -2 biomass {ml m) and the depth distribution pattern for the intensive MOCNESS stations were similar to those obtained by 1000 m MOCNESS tows by Wiebe et al. (1985} in the Gulf Stream and Sargasso Sea. Wiebe et al. {1985} observed a significantly stronger diel vertical migration pattern in the Sargasso Sea than in the Slope Water and warm-core and coldcore Gulf Stream rings. This pattern may explain why there were significant day and night biomass differences in our Sargasso Sea and Gulf Stream samples, but not in our Slope Water and north wall samples.

Seasonal Patterns Seasonal Patterns

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Significant seasonal variation was detected in the Slope Water, the north wall, and Gulf Stream, but not in the Sargasso Sea. The seasonal variability observed in this study is similar to that observed in other studies

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(summarized in Table 3). These studies found a seasonal maximum in zooplankton biomass in the spring, March to May, and a minimum in the fall, September to December. Grice and Hart (1962) found the biomass to be at a maximum in July in the Slope Water. Many studies (Moore, 1949; Menzel and Ryther, 1961; Be et al., 1971; Deevey, 1971; Deevey and Brooks, 1971) found evidence of a seasonal cycle in the Sargasso Sea, although this variation was small compared to the Slope Water (Be et al., 1971). Fish (1954) observed irregular fluctuations in biomass in the Sargasso Sea, and Grice and Hart (1962) found no evidence of seasonality in the Gulf Stream or Sargasso Sea. Bsharah (1957) examined the Gulf Stream in the Florida Straits region and observed that in the top 100 m the biomass was 4 times higher in the spring than in the rest of the year, and in the upper 600 m it was 2 to 3 times higher in the spring.

The MOCNESS samples and Pegasus velocity profiles (Halkin, 19 84) from September, 1982 and May, 1983 can be used to examine the transport of zooplankton biomass and species in the Gulf Stream. For copepods in September (Wishner and Allison, in press), long distance downstream transport was most likely in the central core of the Stream and in the high velocity surface water. Cross-stream transport was most likely at depth below the oxygen minimum zone and in the surface mixed layer.

During both September and May, there was a peak in the Upper 100 m across the Stream during both day and night,

which accounted for 44.7 to 81.9 % of the total 0-1000 m zooplankton biomass. Within the central Stream, the upper 100 m is a region of high downstream velocity. Therefore it is likely that much zooplankton biomass is transported downstream in the surface water. In May, 1983, the surface \overline{a} temperatures were 10 C different between the Slope Water and stream (Halkin, 1984) so it is unlikely that surface crossstream transport of biomass was occurring. However, in September, 1982, the surface temperatures were similar \circ (within 2 C) (Halkin, 1984) in the Slope Water and Stream, and some cross-stream mixing along with downstream transport may have been occurring at the surface.

During both of these cruises there was also a biomass $\overline{}$ peak at depth below the 15 C isotherm during the day across the Stream. This biomass peak, which usually accounted for 20 to 40% of the total 1000 m biomass, extended to depths \circ below the 12 C isotherm and oxygen minimum zone (Fig. 4). In this depth region, cross-stream transpprt along isopycnals occurs (Bower et al., 1985) and it is likely that zooplankton were being transported cross-stream when they migrated to these depths during the day. At night, much of the zooplankton biomass migrated to shallower depths with less chance of cross-stream mixing.

In the central core of the Gulf Stream, at 100 m to 400 m depth, downstream transport is large and cross-stream transport small. Although zooplankton biomass at any one time was low in this region, typically 5 to 15 % of the 0-1000 m total biomass, many zooplankton travel through this

region in diel migrations between 400 to 500 m and the surface. For these brief periods of time, they are subject to extensive downstream transport. Therefore the amount of zooplankton biomass advected downstream in the central core probably varies strongly with a diel cycle.

conclusions

1) Zooplankton biomass is highest in the Slope Water, intermediate, although more variable at the north wall of the Gulf Stream, and lowest in the Stream and Sargasso Sea.

2) The north wall front of the Gulf Stream is a region in which zooplankton and phytoplankton biomass can be enhanced considerably over that of the central Stream despite similarities in the physical properties of the surface water in the two regions.

3) There is a distinct seasonal pattern in the abundance of zooplankton biomass in the Slope Water, north wall of the Gulf Stream, and central Stream regions, with a maximum in late spring and early summer and a minimum in the autumn.

4) The amount and direction of zooplankton biomass transported varies with position in the Stream. The vertical distribution of zooplankton biomass, including diel changes related to vertical migration, interacts with the horizontal and vertical structure of the velocity field. Downstream transport of biomass is probably greatest in the surface

water, because both biomass and water velocities are high. cross-stream transport is highest below the oxygen minimum zone, although it also occurs in the surface water.

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Fig. 1. Location of the transect across the Gulf Stream. The short lines are the stations arranged in numerical order from PO at the southern end to P8 at the northern end. The longer lines perpendicular to the transect are the positions of the north wall of the Gulf Stream during each cruise, with each cruise identified by a different symbol.

Fig. 2. Day and night biomasses from the oblique tows in the upper 200 m along the transect. The position of the north wall of the Gulf Stream is used as the reference point, and the stations are arrayed relative to the north wall by \overline{O} aligning the 15 C isotherm for each cruise so that the geographic location of this isotherm at 200 m depth (defined as the north wall) intersects for all cruises. Biomasses in \circ the upper part of the graph and 15 C isotherms for each cruise are identified by different symbols for each cruise.

Fig. 3. Biomass concentration from the MOCNESS tows [ml -3 (1000 m)] drawn as contours across the Gulf Stream. The thick line in each plot is the depth of 50% of the cumulative water column biomass from 0 m down to 1000 m. The north wall station {P6) is at the left in each plot.

Fig. 4. Seasonal patterns of biomass concentration [ml -3 (1000 m }] in each cross-stream region from the 200 m oblique tows. Day and night values are shown by different symbols.

Table 1. Summary of cruise and sampling information.

Table 2. Median ratios of the biomass in each region relative to that of the Sargasso Sea. Areas that are not significantly different are underlined. The MOCNESS values are the integrated water column biomasses and were not tested due to small sample sizes. N = not samples.

Table 3. Summary of results from previous surveys of biomass in the western North Atlantic. The numbers are the median ratios of biomass in a region relative to the Sargasso Sea, as in Table 2 of this paper. $N = not sampled$. $X = sampled$ only in this region. The Duesse Prope. Parties and 38-8.
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Table 1 Summary of sampling dates and methods.

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Table 2 Median biomasses of each region relative to the biomass of the Sargasso Sea. Regions that are not significantly different argasso sea. Regions chat are not significantly unified.
are underlined. MOCNESS samples were not tested statistically because of small sample size.

long-core.

NS = Not Sampled

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Table 3 Total water column zooplankton biomass (0-1000 m) from the MOCNESS
tow series in [m](m-2)].

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Cross-stream Distance (k_m) Fig. 3

September MOCNESS Biomasses

May MOCNESS Biomasses

Appendix A

Copepod species distributions in September, 1982

Figures 1 through 22 are plots of selected copepod species abundances with depth across the Gulf Stream from intensive discrete depth sampling with a MOCNESS net system during September, 1982.

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Table 1. Number of a species found in a particular sample in [num(1000 m-3)]. Blank spaces indicate that the species was not found in that sample.

Table 1 cont'd. Fobie 1 mbothin

M26N2 M26N3 M26N4 M26N5 M26N6 M26N7 M26N8 M26N9 M20N2 M20N3 M20N4 M20N5 M20N6 M20N7 M20N8 M20N9

Table 1 cont'd.

MIBN2 MIBN3 MIBN4 MIBN5 MIBN6 MIBN7 MIBNB MIBN9 MI5N2 MI5N3 MI5N4 MI5N5 MI5N6 MI5N7 MI5N8 MI5N9

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Fig. 6

Fig. 9

Directory Mayreson III

Fig. 13

Fig. 15

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Fig. 16

Fig. 17

Fig.

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Appendix B

Biomass data and sampling information

Tables 1 through 8 list date, time of day, location, and zooplankton biomass measured at each station occupied during this study of the zooplankton of the Gulf Stream region.

Table 1.

Table 2.

Table 3.

Table 5.

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Table 6.

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Table 7.

Tow Number	GMT Time	GMT Date	Local Time	Local Date	Start N	Position Latitude Longitude W	Site
$E92-1$	2347	$11 - 21 - 82$	1847	$11 - 21 - 82$	36 36.30	51.91 73	$P - 8$
$E92-2$	0.08	$11 - 22 - 82$	1908	$11 - 21 - 82$	36.85 36	73 52.75	$P - 8$
$E92 - 3$	305	$11 - 22 - 82$	2205	$11 - 21 - 82$	36 25.77	73 41.43	$P-7$
$E92-4$	327	$11 - 22 - 82$	2227	$11 - 21 - 82$	26.10 36	73 41.80	$P - 7$
$E92-5$	705	$11 - 22 - 82$	205	$11 - 22 - 82$	15.21 36	73 31.84	$P - 6$
$E92-6$	725	$11 - 22 - 82$	225	$11 - 22 - 82$	15.99 36	73 31.84	$P-6$
$E92-7$	1129	$11 - 22 - 82$	629	$11 - 22 - 82$	05.75 36	73 21.71	$P-5$
$E92-8$	1150	$11 - 22 - 82$	650	$11 - 22 - 82$	06.67 36	73 20.89	$P-5$
$E92 - 9$	1823	$11 - 22 - 82$	1323	$11 - 22 - 82$	35 55.05	73 10.82	$P-4$
E92-10	1841	$11 - 22 - 82$	1341	$11 - 22 - 82$	55.05 35	73 10.82	$P - 4$
E92-11	2351	$11 - 22 - 82$	1851	$11 - 22 - 82$	35 44.15	73 01.06	$P-3$
$E92 - 12$	11	$11 - 23 - 82$	1911	$11 - 22 - 82$	35 44.89	73 00.96	$P-3$
E92-13	434	$11 - 23 - 82$	2334	$11 - 22 - 82$	35 33.68	51.72 72	$P-2$
E92-14	452	$11 - 23 - 82$	2352	$11 - 22 - 82$	35 33.79	72 52.15	$P-2$
E92-15	1003	$11 - 23 - 82$	503	$11 - 23 - 82$	22.86 35	72 38.60	$P-1$
$E92 - 16$	1023	$11 - 23 - 82$	523	$11 - 23 - 82$	35 23.50	38.92 72	$P-1$
$E92 - 17$	1923	$11 - 23 - 82$	1423	$11 - 23 - 82$	35 12.21	28.18 72	$P - 0$
E92-18	1944	$11 - 23 - 82$	1444	$11 - 23 - 82$	12.21 35	28.18 72	$P - 0$
E92-19	443	$11 - 26 - 82$	2343	$11 - 25 - 82$	36.61 36	73 51.90	$P - 8$
E92-20	502	$11 - 26 - 82$	0.02	$11 - 26 - 82$	37.09 36	52.06 73	$P - 8$
$E92 - 21$	814	$11 - 26 - 82$	314	$11 - 26 - 82$	36 26.10	41.34 73	$P-7$
$E92 - 22$	836	$11 - 26 - 82$	336	$11 - 26 - 82$	27.09 36	40.34 73	$P-7$
$E92 - 23$	1337	$11 - 26 - 82$	837	$11 - 26 - 82$	14.99 36	73 32.00	$P-6S$
E92-24	1355	$11 - 26 - 82$	855	$11 - 26 - 82$	15.19 36	73 30.38	$P-6S$
$E92 - 25$	2136	$11 - 26 - 82$	1636	$11 - 26 - 82$	36 05.75	73 21.70	$P-5$
E92-26	2155	$11 - 26 - 82$	1655	$11 - 26 - 82$	36 05.63	73 21.02	$P-5$
$E92 - 27$	340	$11 - 27 - 82$	2240	$11 - 26 - 82$	35 55.16	73 10.81	$P-4$
$E92 - 28$	359	$11 - 27 - 82$	2259	$11 - 26 - 82$	55.16 35	73 10.81	$P-4$
E92-29	925	$11 - 27 - 82$	425	$11 - 27 - 82$	44.40 35	01.06 73	$P-3$
E92-30	944	$11 - 27 - 82$	444	$11 - 27 - 82$	35 44.12	73 00.86	$P-3$
$E92 - 31$	1357	$11 - 27 - 82$	857	$11 - 27 - 82$	35 33.49	72 51.42	$P-2$
$E92 - 32$	1416	$11 - 27 - 82$	916	$11 - 27 - 82$	35 33.83	72 51.64	$P-2$
$E92 - 33$	2114	$11 - 27 - 82$	1614	$11 - 27 - 82$	22.64 35	72 38.37	$P-1$
$E92 - 34$	2130	$11 - 27 - 82$	1630	$11 - 27 - 82$	22.89 35	72 39.66	$P-1$

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x = Cod End Lost

Table 8.

Tab : e 8 cont'd.

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