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SCIENCE

Gulf Stream Cold-Core Rings: Their Physics, Chemistry, and Biology

The Ring Group

Cold-core Gulf Stream rings form when south-extending meanders of the Gulf Stream pinch off from the main current (I). The resulting eddies have cold cores of Slope Water from north of the Gulf Stream encircled by swiftly be some self-propelling mechanism that drives the ring through the surrounding water. It has been estimated that five to eight of these cold-core rings form each year (1). Each one can be thought of as having a life cycle: it forms, it ages,

Summary. Cyclonic Gulf Stream rings are energetic eddies in the warm Sargasso Sea consisting of a ring of Gulf Stream water surrounding a core of cold Slope Water. Initially a ring core has the characteristics of the Slope Water; it is rich in plants, animals, and nutrients. As a ring decays the Slope Water properties of its core are gradually replaced by those of the Sargasso Sea, where standing crops of plants, animals, and nutrients generally are low. Although the decay rate suggests a rather long lifetime (2 to 4 years), the usual death of a ring comes when it rejoins the Gulf Stream after 6 to 12 months.

flowing rings of Gulf Stream water, and are strong anomalies in the relatively uniform Sargasso Sea. The cold core is initially characterized by low temperature and salinity, high nutrient concentrations, and great biological activity. The surrounding Sargasso Sea is characterized in the upper 500 meters by warm, highly saline water low in nutrients; generally it supports a lower standing crop of plants and animals than does the Slope Water.

Cold-core rings are 100 to 300 kilometers in diameter, rotate cyclonically (counterclockwise) with surface speeds of about 150 centimeters per second (3 knots), and once out of the direct influence of the Gulf Stream, can drift for a year or more in the Sargasso Sea before they lose their identity. Often the drift is southwestward, in the same direction as the mean current; however, there may it dies. At any one time there can be ten rings in varying stages of decay (2-4).

Rings transport both nutrients and biota from near the coast of North America into the Sargasso Sea. The transport of nutrients may be important in sustaining the limited productivity of the latter region, and the rings, which occupy 10 to 15 percent of the surface area of the northern Sargasso Sea at any given time, cause major perturbations in the horizontal and vertical distribution of the zooplankton in the upper 800 to 1000 m of the water column. Many plants and animals that are translocated by the rings die as the rings age, and the fauna and flora of the rings eventually become indistinguishable from those of the surrounding Sargasso Sea. There is evidence, however, that some species are exploiters of these unusual environments

and are especially successful in the rings.

Cyclonic rings are not limited to the Gulf Stream. Similar features occur in the Kuroshio off Japan (5), and they probably occur in the East Australian Current, where anticyclonic rings have been studied (6), and in other western boundary currents.

We recently completed the first integrated investigation of the physics, chemistry, and biology of these coldcore Gulf Stream rings and have identified some of the principal processes and phenomena associated with them. In this article we discuss our findings.

Observational Program

Four multidisciplinary cruises were conducted to investigate cold-core rings, the first in December 1976, the last in November 1977 (Fig. 1). Ships-of-opportunity also were used to get additional and complementary data. Altogether, six rings were tracked and studied: Al, Bob, Charlie, Dave, Emerson, and Franklin. Results from ring Bob will be emphasized here because they were the most extensive and gave information over the entire life of that ring. Bob was formed in February and March 1977, interacted with the Gulf Stream in April and May, moved southwestward through the Sargasso Sea in June, July, and August, and coalesced with the Gulf Stream off Cape Hatteras in September.

During formation and in the early stages of their existence, Gulf Stream rings are detectable by infrared satellite imagery (see cover photo). Such portrayals of sea-surface temperature illustrate the complexity of the interactions between the Gulf Stream and its surroundings. Young rings are revealed directly because of the cold surface water at the core and the surrounding ring of warm

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Gulf Stream water. Cold-core rings that have existed throughout a summer usually are no longer evident from surface temperature observations, since the upper mixed layer has been heated by the sun. At times rings can be seen indirectly in satellite pictures when warm surface water from the Gulf Stream is entrained around and over them.

Free-drifting surface buoys monitored by the Nimbus 6 satellite proved to be a good means of tracking rings. Buoys launched in rings usually circled the ring center and stayed in the rings for months. Their looping trajectories gave the ring path. Rings were also tracked for up to 5 months by means of Sofar floats that drifted at depths of 750 to 1300 m and sent acoustic signals to shore-based hydrophones. However, the much reduced swirl or tangential velocity at these depths (10 cm/sec) was nearly the same as the translation speed of the ring, and the Sofar floats tended to be detrained making long-term tracking by this method impossible (7).

Nearly synoptic temperature surveys of rings were made over star-shaped tracks by using expendable bathythermographs (XBT's) dropped from the ship under way at 10 to 14 knots. These defined the temperature structure of the rings to 750 m and located the ring centers. These surveys took 2 days to complete and were made at the beginning and end of each 3-week investigation.

By means of an electronic system (CTD-O_2) , vertical profiles of temperature, conductivity, and dissolved oxygen were made from the surface to near the bottom (typically at about 5000 m) at chosen locations. This system was equipped with a set of 12 bottles, each of which could take a 5-liter sample on command. All water samples were analyzed for phosphate, nitrate, silicate, dissolved oxygen, and salinity, and some for chlorophyll, mercury, cadmium, and copper.

Biological samples were obtained by using a multiple opening and closing net system with CTD-O₂ sensors (Mocness) (8). The Mocness-1, with a mouth opening of 1 m², sampled zooplankton larger than about 333 micrometers. The Mocness-10, with a 10-m² mouth and nets with 3.0-millimeter mesh, was used to collect midwater fishes and large invertebrates. Day and night tows with these nets were taken in pairs over discrete depth intervals from the surface to 1000 m to get information about the vertical distribution and migration of organisms in rings, in the surrounding Sargasso Sea, and in the Slope Water, the source of the ring core.

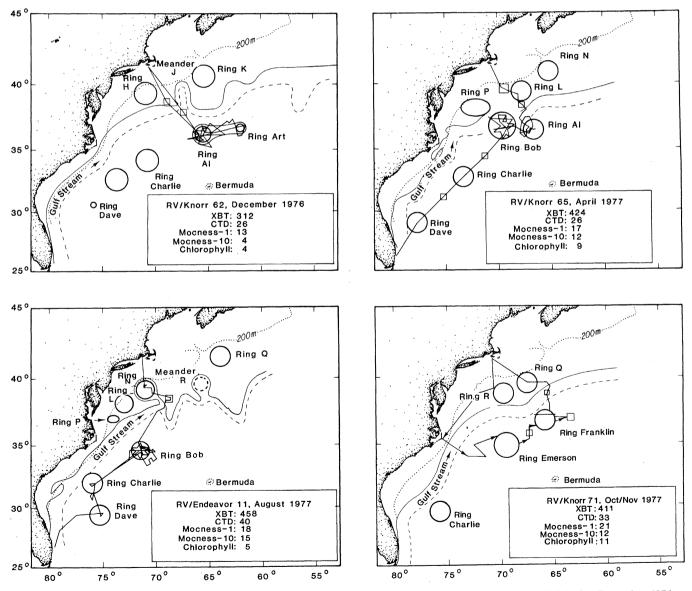


Fig. 1. Location of Gulf Stream rings and the tracks of the four principal cruises on which the rings were studied during December 1976 to November 1977.

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Formation of a Ring

Gulf Stream meanders frequently develop after the Gulf Stream turns eastward from the continent at Cape Hatteras. These meanders may grow and eventually become unstable, at which point the main Gulf Stream flow takes the shorter, straighter path. What was a meander becomes a detached ring. During ring formation, Slope Water, which lies north of the Gulf Stream, is drawn into the meander and forms the core of the ring. This Slope Water is physically, chemically, and biologically very different from the Sargasso Sea in which the ring will lie. A remnant of Gulf Stream forms a cyclonically rotating current around the Slope Water core. Surface speeds of this current can reach 150 cm/ sec (3 knots). At the time of their formation these rings appear to extend to the sea floor, that is, to about 5000 m.

The formation of ring Bob was observed in 1977 by an unusually good set of satellite infrared images. A meander formed in mid-February near 69°W (Fig. 2a). By 25 February the sides of the meander had closed, trapping cold Slope Water. By 9 March, Bob appeared to have completely separated from the Gulf Stream. An XBT section (Fig. 2b) through the center of Bob on 12 March and an airborne XBT survey on the same day (9) proved that an intense ring had formed. Subsequent satellite images in March and in the first half of April, and an XBT survey in early April (10), showed that Bob remained nearly stationary during this period.

The cross section of a cold-core ring just after formation shows bell-shaped isotherms with temperatures in the range of 10° to 16°C elevated at the ring center as much as 600 m above their normal Sargasso Sea depths (Fig. 2b) (11). A ring can persist for several years because of the elevation of the density surfaces (which are essentially parallel to the isotherms), giving a reservoir of potential energy.

The horizontal differences in density give rise to horizontal pressure gradients because of variations along ring radii of the weight of water above a given level surface. Dynamically, this force is largely balanced by the Coriolis force caused by Earth's rotation. Pressure variations can arise not only from density anomalies, which can be calculated from the CTD data, but also from deviations of the water surface from one that is gravitationally level. From observed surface velocities, the dominant force balance can be used to estimate that the sea surface is depressed about 0.5 m at the ring center. This depression has been observed recently from direct satellite altimeter measurements (12, 13). In the high swirl speed region of a ring, centrifugal force is important and amounts to about 25 percent of the Coriolis force. Imbalances among pressure, Coriolis force, and centrifugal force, plus the effect of friction and other weak forces that amount to about 1 percent of the primary three, lead to the translation and decay of the ring as described below.

The contrasting waters of the core, Gulf Stream remnant, and surrounding Sargasso Sea produce variations in properties across a ring. At the depth of the permanent thermocline (500 to 1000 m) sound velocity and heat content de-

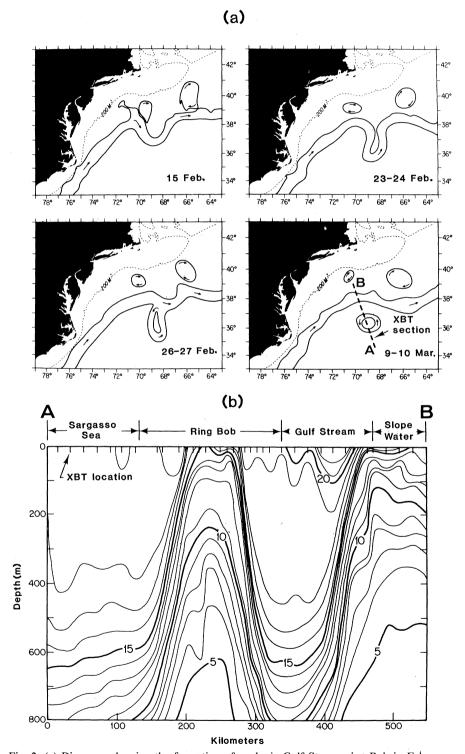


Fig. 2. (a) Diagrams showing the formation of cyclonic Gulf Stream ring Bob in February– March 1977 based on infrared images from the NOAA-5 satellite. Two anticyclonic (warm-core) rings were observed north of the Gulf Stream. (b) Vertical temperature section through ring Bob and the Gulf Stream on 12 March 1977. Ring Bob can be seen as the area of raised isotherms and cool surface temperatures.

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crease across the ring by 20 m per second and 7 calories per cubic centimeter, respectively (14). The sound-velocity structure within a ring forms a horizontal lens that is slightly above the Sargasso Sea sound channel at 1200 m. This lowvelocity lens refracts sound from nearsurface sources in the ring core down into the sound channel.

At formation, cold-core rings typically have a salinity in the upper few hundred meters which is about 1 per mil lower than the salinity at the same potential temperature in the surrounding Sargasso Sea. This salinity anomaly can persist in the core of the moving ring for as much as 18 months and shows that the ring is not just a wave in the Sargasso Sea lifting up and letting fall denser, colder, fresher water. Rather, the retention of low-salinity water in the core is evidence that material has been transported with the ring from the time of its formation. Anomalies in oxygen, nutrients, and metal concentrations also are found in rings because of both the nature of their formation and the local processes of photosynthesis, respiration, and microbial degradation (15).

The several kinds of water contained in Gulf Stream rings can be distinguished by their dissolved oxygen concentration. Because of the upward displacement of isotherms in a ring a comparison of oxygen and other chemical concentrations across a ring is best referred to selected isotherms rather than to depths. This comparison is facilitated by displaying oxygen concentration as a function of temperature (Fig. 3). In the northwest Atlantic, Gulf Stream water of Caribbean origin has the lowest oxygen concentration for given temperatures between 8° and 18°C (16). Slope Water and the core of cold-core rings have the highest oxygen concentrations at given temperatures; Sargasso Sea water is intermediate. Thus, the relation between oxygen and temperature across a ring provides a basis for classifying water according to its origin. The CTD-O₂ data in the highvelocity boundary of a ring show a large amount of structure, with minima and maxima of oxygen concentrations corresponding to the interleaving of waters from the ring core and flanks with the surrounding Sargasso Sea.

Initially, the biota of the ring core has a Slope Water character. Many organisms endemic to cold water have been found in ring cores but nowhere else in the Sargasso Sea. The contrast can be attributed to the northern edge of the Gulf Stream being a sharp faunal boundary separating subtropical and tropicalsubtropical species endemic to the warm Sargasso Sea from the temperate and

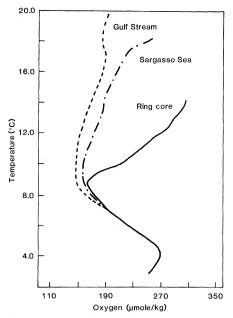


Fig. 3. Relationships between potential temperature and oxygen for three water masses associated with Gulf Stream rings. The ringcore curve is from measurements made in ring Bob in April 1977.

subpolar-temperate species (17) inhabiting the cold Slope Water. In addition, the Slope Water is characterized by a large biomass and a fauna dominated by relatively few species, whereas the Sargasso Sea has a smaller biomass and a fauna made up of a larger number of species of more equal abundance.

Migration of Cold-Core Rings

Rings show two distinct types of movement. First, rings well separated from the Gulf Stream generally move westward at about 5 cm/sec (18), although there are significant variations. The second type of movement is parallel to and with the Gulf Stream; it occurs when a ring becomes partially reattached to and interacts with the Gulf Stream. In this case, the ring either can split off again, sometimes greatly modified, or completely coalesce with the Gulf Stream. During some rings' interaction with the Gulf Stream, the rotation rate of satellite-tracked buoys looping in the rings increased while loop radius decreased; the rings were apparently "spun up" during their interaction with the stream (19). The movement of rings attached to the Gulf Stream was very fast at times, 25 cm/sec for ring Bob in April 1977.

A ring may repeatedly interact with the Gulf Stream. Often in this case it may move in large, clockwise loops with diameters of 100 to 250 km, periods of 1 to 3 months, and speeds of 5 to 10 cm/sec. The ring moves east with the Gulf Stream, moves south as it breaks away, moves west when free from the Gulf Stream, then moves north to interact with the Gulf Stream again. Motion of this kind was found by Fuglister in his 1967 study of a ring (20) and was evident with most of the rings that we studied.

We made observations in ring Bob during a period of its interaction with the Gulf Stream that persisted from 17 to 27 April 1977. A satellite-tracked buoy placed in the core of Bob at this time gave a record of Bob's subsequent movement until September (Fig. 4). In May, after Bob separated from the Gulf Stream for the second time, it began a southwestward movement through the Sargasso Sea. During this migration, the buoy looped with a period varying from 1.9 days in May to 2.9 days in August; the loops had a mean radius of 40 km and the buoy a mean speed of 125 cm/sec (Fig. 4). Since the radius of the loops remained nearly constant from May to September, we conclude that the rotation rate was gradually slowing, an indication of the ring's decay. Bob's mean southwestward translation rate was 5.5 cm/sec; there were periods of higher speed (12 cm/sec or more at the end of June) and periods when Bob remained nearly stationary (near 34.5°N, 71.5°W at the end of July). The Research Vessel Endeavor visited Bob in May and during July-August; at these times Bob was nearly circular and disconnected from the Gulf Stream (Fig. 4) (21).

Attempts to explain the migration pattern of rings have not been totally successful. Rossby's explanation for the motion of atmospheric cyclones (22) can be equally well applied to ocean eddies. Because the locally vertical component of Earth's rotation increases with latitude, it is not possible to balance the Coriolis force on a northward current with a pressure gradient. Rather, as the fluid moves north, its own rotation rate must decrease or its vortex tubes must be stretched to compensate for the increase in Earth's rotation rate. These accelerations lead to particle trajectories being more sharply curved in the south portion of the ring than in the north so that successive loops are displaced westward. Warren (23) applied these ideas to suggest that rings should move west at the rate of a few centimeters per second. More detailed numerical studies have shown that the motion of the vortex generates asymmetries (24, 25); in turn, the nonlinear advection of the radially symmetric field by the asymmetric field (and vice versa) can substantially alter the propagation characteristics. This advection creates a northward component to the translation and an increase in the westward speed. However, in other circumstances, this advection can slow or even reverse the westward motion; this depends very sensitively on the structure and amplitude of the depth-averaged velocities. We were not able to map these velocities during our field program; therefore, we still cannot determine the importance of these effects to rings.

Aging of Cold-Core Rings

The general structure of a ring and its change with time are well shown by vertical sections of chemical, physical, and biological properties along radii of the ring (Figs. 5 and 6). Conditions in the core of a ring may remain quite similar to Slope Water conditions for 1 to 3 months after ring formation. With time, however, mixing and heating modify the surface waters, and nutrients decrease (Fig. 5).

Temperature sections for ring Bob delineate the basic features of the ring—the cold water forming the core, the steeply sloping isotherms in the high-velocity boundary region, and the flattening of the isotherms in the Sargasso Sea away from the ring. Between April and August 1977 there was a deepening of the isotherms in ring Bob at an average rate of 0.8 m per day. This subsidence represents a loss of potential energy from the ring core relative to the surrounding Sargasso Sea.

Surface salinities in the ring core do not change as much as temperature, because some of the increase in surface temperature is produced by seasonal heating. Oxygen and nitrate concentrations change through biological activity. In the Sargasso Sea the layer of minimum oxygen and maximum nutrients occurs at about 800 m. In the center of a cold-core ring the oxygen minimum-nutrient maximum is shifted upward to 300 m along with the elevated temperature and salinity surfaces. The changes in oxygen and nitrate concentration in ring Bob between April and August 1977 (Fig. 5) were primarily related to the mixing of waters of differing concentration at the boundary of the ring. The biologically produced changes in oxygen and nitrate that could be measured over this period were confined to the upper 150 m.

The changing temperature structure indicates that Bob would lose half of its potential energy (the decay is not necessarily exponential) in 1.2 to 1.5 years (26). This is consistent with earlier observations (27, 28). But it also seems that the rotation rate of Bob may have slowed

to one-half in only 5 months judging from the rotation period of the buoy in it. The disparity between these figures may indicate that changes in the size of the ring, transfer between potential and kinetic energy, or other processes are occurring.

We can identify five physical mechanisms leading to the decay of a ring: dispersion, instability, interaction with mean flow, small-scale friction, and surface windmixing and heat exchanges. Since Rossby waves are dispersive, an initial anomaly will decay as the energy spreads. Flierl (29) has shown that this process begins rapidly (half-life 90 days), but slows down after several months (half-life becomes 250 days). The nonlinearity inherent in the strong flows of a ring retards this process (24), so that the estimated half-life due to dispersion could be as long as 350 days; however, the decay at short times again depends strongly on the assumed initial structure of the depth-averaged flow.

Even if the nonlinearity were completely effective at reducing dispersion, the ring might still lose energy to mesoscale motions by an instability converting either kinetic or potential energy into energy of azimuthally varying motions (waves) which grow in strength and complexity at the expense of the ring. Although this type of decay does not appear in some theoretical models of rings, there is field evidence that energy transfer between circular rings and azimuthal waves does occur with sufficient rapidity to play a role in ring spindown (30). More recent numerical models (31) suggest that the occurrence of such instabilities in models depends on the assumed ring shape and that the observed structure indeed can be unstable. The exact processes responsible for the waves and the significance of these perturbations to ring spindown is still under investigation.

In addition to mesoscale processes, smaller scale turbulence (including internal waves, windmixing, thermal and

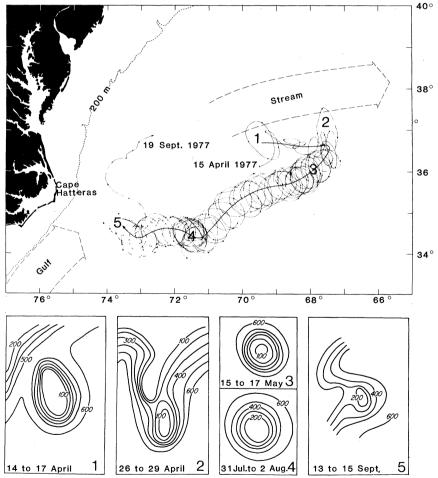


Fig. 4. Trajectory of free-drifting buoy as it looped in ring Bob from 15 April to 15 September 1977. The mean position of the Gulf Stream is shown schematically. Lower panels show depth contours (meters) of the 15°C isothermal surface in Bob at five times in Bob's existence. During April Bob became connected to the Gulf Stream and moved rapidly (up to 25 cm/sec) eastward. In May Bob separated from the stream and began its southwestward drift (5 cm/sec) through the Sargasso Sea. In September Bob rapidly coalesced with the Gulf Stream and was lost. The final coalescence may have been triggered by another ring, Dave, which was advected downstream in the Gulf Stream into the vicinity of Bob.

double-diffusive convection) can reduce the ring's kinetic and potential energy. When dissolved oxygen is plotted against temperature, the small-scale exchange processes show up as anomalies on the scale of tens of meters and show core water leaking outward and Sargasso

Sea water coming in along specific density surfaces (32).

The small-scale eddy friction processes, according to the simplest model of Molinari (33), can generate large-scale meridional circulations within the upper kilometer of the water column that bring

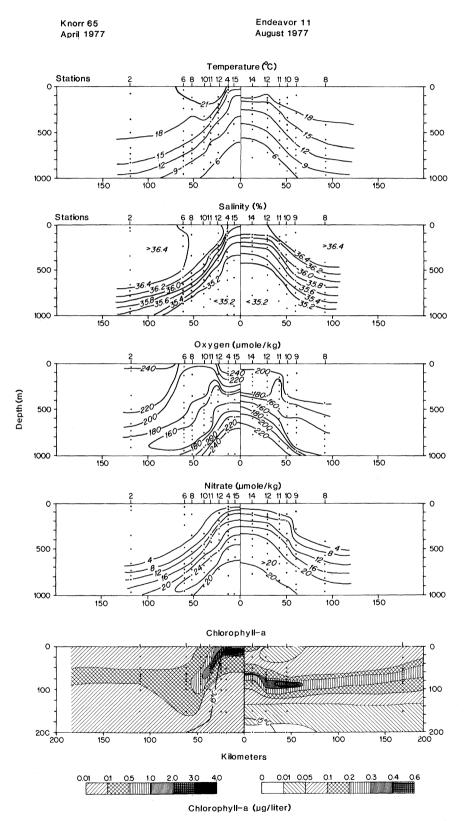


Fig. 5. Vertical sections of temperature, salinity, oxygen, nitrate, and chlorophyll a along a radius of ring Bob. The left side of each section is for April 1977, the right side of each for August 1977.

water in at the surface and out at about 500 m (34). That this circulation and associated water mass formation occurs is evident both from the water properties (35) and from the distribution of coldwater species such as the euphausiid Nematoscelis megalops, which suggests outward motion between 500 and 800 m (36). One consequence of the detrainment of cold-water species from the core of a ring is their injection deep into the northern Sargasso Sea (36, 37). A number of investigators have collected such species without realizing that they are nonreproducing expatriates from a home range that may be hundreds of kilometers to the north.

The sharp biological contrasts that exist at ring formation also decline with time. However, these time-related biological transformations appear accelerated compared to the physical ones. Chlorophyll a sections give a measure of the phytoplankton biomass and were highest in the core of ring Bob at temperatures of about 16°C (Fig. 5). Between April and August the chlorophyll a concentration in the ring core decreased by a factor of 8. In general, rings have a 1.3 to 1.8 times higher zooplankton biomass than the surrounding Sargasso Sea for at least a year after formation (38, 39). Biomass was higher in the rings sampled in 1977 by factors of 1.7 and 2.8, except in ring Emerson, one of the oldest rings sampled, where it was the same as in the Sargasso Sea.

The highest biomass occurs near the center of a ring and progressively declines toward the ring edge (Fig. 6). Also, the vertical distribution of biomass is different from that in the Sargasso Sea and Slope Water. In most rings a larger fraction of the water-column biomass is found between 200 m and 800 to 1000 m than in that part of the water column in the Sargasso Sea (Fig. 6). Often in older rings the surface layer (0 to 200 m) has significantly less biomass than the surrounding waters, and the generally higher standing crop of the ring is due entirely to the large subsurface biomass.

Two processes appear to be responsible for this unusual vertical distribution. Fi. st, as a ring warms a number of Slope Water species move down in the water column in an attempt to maintain themselves in their preferred environment. Second, the more rapid physical modification of the surface layer results in a more rapid transformation of the nearsurface plankton to the smaller, less abundant forms typical of the Sargasso Sea.

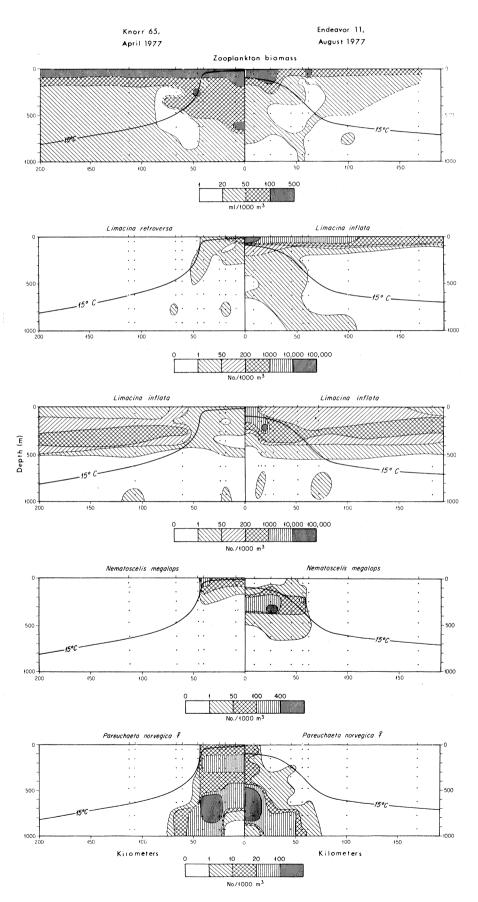
The shift in vertical distribution that occurs as a ring ages is well illustrated by the Slope Water indicator species *Nema*- toscelis megalops. This animal is found south of the Slope Water mainly because of cold-core rings. In the Slope Water, *N. megalops* typically lives in the upper 600 m with most individuals occurring above 300 m by both day and night. A similar vertical distribution is observed in young rings, but by the time a ring is 6 months old, more of the population lives below 300 m and individuals appear as deep as 800 m. In older rings most of the population occurs below 300 m. It appears that the downward shift is an attempt by *N. megalops* to remain in an optimal temperature regime (*36*).

This change in the vertical distribution of N. megalops in aging rings brings about changes in the physiology of the species that contribute to its extinction in the ring. In rings aged 6 to 9 months we have observed significant differences in some of the animal's biochemical constituents, such as carbon and nitrogen as percentages of wet weight and total lipids. Compared to populations in Slope Water, N. megalops in aging rings showed decreases of 5 to 20 percent in respiration rates. Furthermore, in old rings adult males disappear, the production of eggs seems to cease, and growth rates are markedly reduced compared to Slope Water populations (40). Thus, as a ring decays, N. megalops is driven to deeper waters where there is insufficient food for growth and reproduction: starvation ensues. In the oldest ring sampled (age 17 months) no N. megalops were caught, although this ring had contained them earlier (36). This extinction can be ascribed to the combination of physical dispersal out of the ring and the effects of the ecological transformation within the ring just described.

Nematoscelis megalops is not unique as an expatriate in rings. The large carnivorous copepod Paraeuchaeta norve-

Fig. 6. Vertical sections of zooplankton biomass [measured as displacement volume (55)] and the abundance of warm-water (Limacina inflata) and cold-water (Limacina retroversa, Nematoscelis megalops, and Pareuchaeta norvegica) zooplankton indicator species from the center of ring Bob out to 150+ km for April 1977 (left) and August 1977 (right). Collections were made with a Mocness; the solid dots denote the center of the oblique portion of the tow taken with one of eight nets. The ring extended out to about the 80km mark as indicated by the depth of the 15°C isotherm; beyond was the Sargasso Sea. The cold-water pteropod Limacina retroversa already had disappeared from ring Bob by August. The left-right pair for L. inflata show daytime distributions. The vertical pair allows a day (above)-night (below) comparison for August and shows diel vertical migration. By August Nematoscelis and Pareuchaeta had become less abundant and lay deeper in the water column.

gica, the pteropod Limacina retroversa, and the myctophid fish Benthosema glaciale show similar patterns. The adults and stage V copepodids of P. norvegica are most numerous between the 5° and 7° C isotherms, rarely occurring above 10° C in the Slope Water. Their center of distribution is 100 to 200 m below that of *N. megalops*. In cold-core rings this preference is maintained. They live



deeper with increasing distance from the ring center in conformity to the dipping isotherms (Fig. 6).

When ring Bob was 1 month old, L. retroversa was present in the center and at one fringe station (Fig. 6). Sampling of Bob at age 5 months yielded only two individuals. The disappearance of L. retroversa within this short time probably can be attributed to the warming of the upper 100 m and the reduction in the phytoplankton standing crop that serves as its food supply.

Benthosema glaciale, a subpolar-temperate species (17), is abundant in the Slope Water and in the core of newly formed rings. Its numbers diminish as the depth of the 15°C isotherm increases, that is, with ring age and with distance from ring center. In its normal range B. glaciale commonly migrates at night to a depth of 50 to 100 m. As the 15°C isotherm sinks beyond about 150 m the fish rapidly becomes more and more restricted to the deeper parts of the water column. When the 15°C isotherm is deeper than about 250 m there are no specimens above 500 m; when the 15°C isotherm sinks deeper than about 525 m there are none at all.

The second process causing a downward shift in biomass in the ring water column also comes from the relatively rapid changes that take place in the surface waters of the ring. There is a shift toward lower phytoplankton standing crops, smaller cell size, greater phytoplankton diversity, and somewhat lower production (41, 42). The decrease in plant biomass and its rearrangement in ring Bob were dramatic (Fig. 5). These changes in the phytoplankton are accompanied by replacement of Slope Water herbivores by their generally less abundant Sargasso Sea counterparts.

There are other species that appear to exploit the changing conditions and, at least in rings of intermediate age, become more rather than less abundant. Limacina inflata is a warm-water species characteristic of the Sargasso Sea. Sometimes it is found in the Slope Water, probably carried there mainly by the action of warm-core rings. This species shows a diel vertical migration from daytime depths of 200 to 400 m to nighttime ones of 100 m and shallower (Fig. 6). At age 1 month. Bob had a small population of L. inflata with smaller numbers in the center than on the fringe. These individuals may have been in the ring initially or been carried there from the surrounding Sargasso Sea during the first month. At 5 months, the water-column abundance of L. inflata had increased by 300 times. In the Sargasso Sea, L. inflata in the water column had dropped to about 30 percent

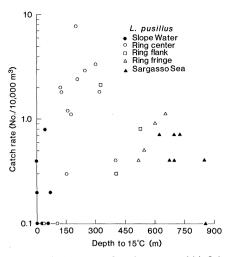


Fig. 7. Catch rates for the myctophid fish Lampanyctus pusillus plotted against depth to 15°C. Five collections with catch rate zero, all situated in the cool water represented at the left of the figure, have been omitted. Intercomparisons of three sets—collections with depths to 15° C less than 150 m, equal to or greater than 150 m but less than 450 m, and greater than 450 m, respectively—were made with Mann-Whitney U tests. The central set, consisting of ring center and ring flank collections, was different from the adjacent colderwater and warmer-water sets (P = .02 and .05, respectively, in two-sided tests).

of its April abundance, but this apparently was its normal seasonal decrease.

A few species of midwater fishes seem also to be ring exploiters, being more abundant in the rings than in adjacent waters. Examples are the myctophids Hygophum benoiti and Lampanyctus pusillus (Fig. 7), members of a group of species with a temperate-semisubtropical distribution (43). Their normal range includes both the temperate Slope Water and the subtropical northern Sargasso Sea. On the basis of its geographical distribution, it has been suggested of H. benoiti that "this is a species that flourishes along regional (oceanographic) boundaries" (44). Both H. benoiti and L. *pusillus* appear to be well suited for life in the temporary habitats provided by rings. They require few resources, being diminutive even as myctophids go (about 30 mm at sexual maturity); they complete their life cycles rapidly (in a year or less); and both have the flexibility of a protracted spawning season, L. pusillus the year round and H. benoiti for 4 or 5 months in winter and spring (45).

Death of a Ring

The ultimate fate of rings is coalescence with the Gulf Stream. Although some rings may move south into the southern Sargasso Sea, this has not been observed for rings tracked with buoys. No rings have been identified south of 30° N except in the extreme west, although weak temperature anomalies suggesting rings have been observed near the Bahamas at 25° N (2, 3, 27).

We have observed two ways in which rings coalesce with the Gulf Stream and are lost. One way occurs when a relatively intense ring becomes attached to the Gulf Stream and the main current is diverted and flows around the ring. In the final stage the ring merges completely with the Gulf Stream to produce an open meander. It is possible then for the meander to form a ring again or to dissipate. The dissipation resembles ring formation but the steps are in reverse order. During this sort of coalescence it is possible for water from the ring center to be transported back into the Slope Water. When this occurs, surviving populations in the ring core may be reunited with their home-range counterparts. The potential for an important effect on the home-range population is present if the stressed ring populations have undergone genetic selection or if returning individuals have been rendered sterile. We have observed this mode of ring coalescence at least four times, including once during the early life (in April 1977) of ring Bob.

The second way in which rings coalesce with the Gulf Stream occurs when a relatively weak ring becomes attached to the Gulf Stream and is advected downstream. In this case the ring core does not seem to rejoin the Slope Water. On two occasions buoys in rings continued to loop as they were swept eastward. We suggest that such rings eventually were deformed by the strong horizontal and vertical shear of the Gulf Stream and were incorporated into it.

Ring Bob coalesced with the Gulf Stream in September 1977 (Fig. 4) at the age of 7 months. The event was evident from buoy trajectories (18), XBT surveys, and a 3-week series of observations gathered with inverted echo-sounders moored to the bottom (46). The observations suggest that when the ring rejoined the Gulf Stream, a large Sshaped meander was rapidly formed that failed to intensify to the point of ring regeneration. The advection of another, older ring, Dave, up the Gulf Stream from the south and into the vicinity of Bob may have played a part in the final coalescence of Bob. The possible interaction between the two rings prior to coalescence is suggested by the trajectory of a buoy, originally in Dave, which looped once around Bob and then moved downstream in the Gulf Stream. Other buoys in Bob were captured by the Gulf Stream, with those in the outer, highvelocity part of the ring entering the stream first. The buoy nearest the ring core traveled across the Gulf Stream into the Slope Water during coalescence and then was swept away by the stream. This slower incorporation of ring-core waters into the Gulf Stream was also apparent in shipboard surveys made during the event (46).

These observations provide the first detailed description of the final coalescence of a ring with the Gulf Stream, the fate of most rings. Although rings, such as Bob, have rejoined the Gulf Stream at Cape Hatteras, the process takes place all along the current from northern Florida to the New England Seamount chain.

Because it is difficult to maintain continuous contact with rings we have little certain information about their longevity. Estimates of ring age have been derived by tracking satellite buoys placed in rings and by identifying and collecting successive observations of rings (satellite images, and temperature profiles, for example) and thereby constructing their long-term paths. In addition, we can combine estimates of ring production and the number of rings present at any given time and also estimate lifetimes by extrapolating rates of ring decay.

Rings were tracked by means of satellite buoys for up to 8 months, but in most cases the whole life of the ring was not observed. The rings identified in historical data sets had lifetimes of up to 2 years. The other procedures give estimates of 2 to 4 years, but these are thought to be on the high side. Our best estimate for a mean lifetime is 1 to 1.5 years, with a probable maximum lifetime of 3 years.

Significance of Rings in the

North Atlantic System

Our oceanographic studies have provided an initial understanding of the behavior of individual Gulf Stream rings. With these data we can begin to assess the influence of rings on the oceanic distributions of physical, chemical, and biological properties. The Gulf Stream itself represents an interface between two regions with very different properties. In the ring formation process, a large volume of water is transported across this interface. As the ring decays there is partial exchange of this water with the surroundings; thus the rings generate a flux of properties from the Slope Water to the Sargasso Sea. Furthermore, because the rings bodily carry water with them, the transfer of properties takes place well within the Sargasso Sea, not just at the boundary. When a ring recombines with the Gulf Stream, modified core water can be injected into the Slope Water. Finally, rings can also alter the distribution of properties in the Sargasso Sea by less direct means: they can stir the region horizontally and vertically (47) and also affect the flux of properties through the surface.

Estimates can be made of the importance of transport by rings of heat, salt, and nutrients, but further research will be needed before firm statements can be made. Consider the role of rings in the salt balance of the northwestern Sargasso Sea (48). In the formation of a cold ring and the balancing formation of a warm one (thereby preserving mass), we estimate that 3×10^{15} grams of salt are removed from the saltier Sargasso Sea to the fresher Slope Water (using a ring volume of 3×10^{13} m³ and a difference between the salinity of the cold ring and the warm ring of 0.1 per mil on the average). If eight rings form per year, 2 \times 10¹⁶ g of salt per year are so transported to the Slope Water and lost to the Sargasso Sea. This estimate is an upper bound since some anomalous (fresher) water may be recombined with the Slope Water as the ring dies, rather than being spread over the Sargasso Sea. For comparison, let us consider the addition of salt due to surface evaporation over the northwestern Sargasso Sea. Evaporation would lower the water level by about 1 m each year, giving a salt flux of 35 kilograms of salt per square meter per year for a net addition of 10^{17} g of salt per year. Thus, rings appear to play a significant role in the salt balance of the northwestern Sargasso Sea.

For heat, we estimate that rings carry 10²¹ calories per year northward across the Gulf Stream, which is comparable to the amount of heat entering the northwestern Sargasso Sea through the surface. For potential vorticity (the dynamical analog of angular momentum), which determines the circulation patterns, the input from rings, 1 m² per square second, is comparable to the input from the variations in the wind stress, generally considered to be the driving force for the circulation above the thermocline. Thus, our calculations suggest that the strong westward "recirculation" that has been described for this area of the Sargasso Sea (49-51) is actually ring-driven.

Flux comparisons for biological variables come out rather differently. The net addition of living organic material to the northern Sargasso Sea by cold-core rings is about 5×10^{11} g of carbon per year [Slope Water standing stock in the upper 1000 m is about 3 g of carbon per square meter, that of the Sargasso Sea about 1 g of carbon per square meter (39)], while

the loss of organic matter through the thermocline is about ten times as large [1 g of carbon per square meter per year \times $3 \times 10^{12} \text{ m}^2$ (52)]. However, since most biological properties are not conservative, we must also consider that the effect of a ring is not just to produce a flux of organic material but also to provide a site of enhanced production for much of its lifetime. One measure of this is to compare the net productivity over the region of the Sargasso Sea affected by rings to the net productivity that would occur if there were no rings. At any time roughly 10 percent of the region contains rings having a primary productivity about 50 percent above that of the Sargasso Sea. Thus, the regional primary productivity would be 5 percent lower in the absence of rings; in other words, 14 percent of the production occurs in the 10 percent of the region that is occupied by the rings (39).

Rings can be more important in the ecology of certain kinds of organisms: Foraminifera, for example, have a standing stock in rings as much as 18 times as large as that in the Sargasso Sea, so that about two-thirds of the population in this region is contained in rings. Thus, the flux of foraminiferan tests to the sea floor in this region is three times larger than it would be if there were no rings, a statistic of considerable importance for our ability to judge the position of the Gulf Stream from the deep-sea sedimentary record (53).

Thus, the thread running from the 15th-century mariner's mythology to the oceanography of the 1950's-the view of the Sargasso Sea as a virtually stagnant and homogeneous pool-has been cut. Mesoscale eddy studies such as MODE (54) have shown the ubiquity of variability in ocean currents and water properties, while our studies of rings have shown just how large these variations can be. Although rings do represent the most energetic form of mesoscale eddy, it is their unique origin that prompted our study. Our data have begun to resolve the complex physical, chemical, and biological changes occurring during the life of a ring. Because of its traceable core of trapped water, a ring offers an ideal environment for studying the exchanges of water properties and examining the biological-chemical cycles occurring as an ecosystem is stressed. Our estimates of the importance of rings in determining the circulation, water characteristics, and ecology of the Sargasso Sea suggest that the study of rings will lead to a broader understanding not only of mesoscale oceanographic processes but also of the circulation and structure of the ocean as a whole.

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Psychoneuroendocrine Influences on Immunocompetence and Neoplasia

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"Stress" is a widely used term for describing emotional and biological responses to novel or threatening situations. There is, thus, an extensive variety of experimental or other circumstances in which "stress" serves as a convenient word to express complex and incompletely understood psychological and physiological phenomena (1-3).

In studies at this laboratory, we use the term "stress" in a more restricted experimental sense to relate specific

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stress-inducing stimuli, or stressors, to their physiological consequences. The latter include specific biochemical, cellular, and tissue alterations that are associated with an emotional activation of the adrenal cortex by way of the pituitary and its secretion of adrenocorticotropic hormone (4, 5). Within the biological systems that we have used, several key parameters characterize the physiological manifestations of stress, and relate to pathological and other changes that may be observed in stressed experimental animals.

Although emotional stress brings about many biochemical changes, in our studies with mice we have focused our attention on the adrenal cortex and have

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measured with precision the most conspicuous, and what appears to be the most relevant, of the biochemical substances elaborated by this organ in response to anxiety, namely, corticosterone. Immediately after an animal is subjected to an emotional stimulus, or perceives a situation that generates anxiety, the adrenal cortex in response to signals from the hypothalamus, via the pituitary, produces increased quantities of corticosterone. The rapidity of the appearance of corticosterone in the plasma can be readily measured by appropriate microassay techniques (6-8).

Immunological and Pathological

Consequences of Stress

Secondary manifestations that result from increased corticosterone in the blood plasma that are readily observed include (i) lymphocytopenia, or decreased circulating lymphocytes, (ii) thymus involution, and (iii) related loss of tissue mass of the spleen and peripheral lymph nodes. Details of these cellular and tissue stress effects will be discussed later, but it is relevant to note here that the physiological consequences of such stress-mediated events have significant

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