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The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring

by Donald B. Olson[1] and Richard H. Backus[2]

ABSTRACT

Net hauls made in and around a warm-core Gulf Stream ring in April and June 1982 suggest a concentrating of the mesopelagic fish *Benthosema glaciale* (family Myctophidae) in the frontal zone at the east edge of the ring. In April, *Benthosema* was found in very small numbers in the two-month old ring, as was to be expected from the subpolar-temperate distribution of this fish and the warm-water origin and age of the ring. By June, age-0 fish had been recruited to the population susceptible to capture by the midwater trawl. These young fish were about five times as abundant at the frontal zone of the ring and about twice as abundant in the ring center as in the adjacent Slope Water. It is proposed that the increased abundance at the ring front results from a concentrating of the original Slope Water population by convergence. The increase of *B. glaciale* in the center of the ring may be associated with the inwardly spiralling streamers observed in satellite images.

A simple advection/diffusion model for both the fish and a passive tracer of the fluid is used to consider a mechanism that might have concentrated the fish at the ring edge. It is assumed that the fish can counter the vertical flow in order to maintain their preferred depth. Swimming in the horizontal is assumed to be random. The result of this behavior is that the fish and the passive tracer are affected differently in flow fields such as those in rings. Solutions to the model equations lead to the conclusion that the abundance of fish at the ring front can be accounted for by convergence. The model and the divergence pattern in the ring, calculated from hydrographic data, show the time necessary to effect the hundred-fold increase in abundance that was observed in the ring front between April and June to be on the order of two weeks to a month. We suggest that the concentrating mechanism described is widely applicable to a variety of frontal phenomena and to a variety of planktonic plants and animals.

1. Introduction

A general observation for the world's oceans is that plants and animals have high abundances near fronts. This observation is rationalized in several ways. Fronts are zones of increased mixing both laterally and vertically, the result of which often is increased primary and secondary production. Enlarged standing stocks of phytoplankton in the vicinity of fronts are reported by Bainbridge (1957), Dufour and Stretta

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[1] Division of Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science. (MPO/RSMAS). University of Miami, 4600 Rickenbacker Causeway, Miami, Florida, 33149, U.S.A.

[2] Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 02543, U.S.A.

(1973), Pingree *et al.* (1975), Savidge (1976), and Fournier *et al.* (1979). The increased primary production can be explained tentatively by an intensified flux of nutrients. If the frontal region is sufficiently long-lived, populations of herbivorous zooplankters will increase. (Dufour and Stretta, 1973, noted increases in zooplankton at the Cape Lopez front in the Gulf of Guinea.) Finally, species that can detect the front or its anomalous biotic condition may congregate there in order to take advantage of the increase in their prey. This appears to be the case in birds (Ainley and Jacobs, 1981; Kinder *et al.*, 1983) and in tunas (Dufour and Stretta, 1973; Laurs and Lynn, 1977; Sund *et al.*, 1981). Why large migratory fishes prefer fronts is discussed by Magnuson *et al.* (1980). Magnuson *et al.* (1981) found that certain benthic and near-bottom fishes and decapod crustaceans were more abundant at collection sites near Cape Hatteras when a Gulf Stream/shelf water front was present than when the front was absent. Tranter *et al.* (1983) noted increases in chlorophyll *a*, zooplankton biomass, and the density of certain copepod species where a cool-water "crescent" bordered a warm-core ring shed by the East Australian Current.

Another way in which animals can be concentrated at fronts stems from the flow that accompanies these features (Dufour and Stretta, 1973; Okubo, 1978). Active fronts are associated with horizontal convergence. For a tracer following parcels of water, the concentration of the tracer in any parcel is not changed directly by the convergence, but for constituents, such as certain living things, that are capable of eliminating one component of the flow field, the concentration can be increased along the front directly by the flow. The vertical motions at fronts are small enough to be overcome by most animals (and probably by certain plants in some cases). This coupled with the ability of many species either to maintain an approximately constant level in the water column or to migrate dielly between certain more or less fixed levels provides a means for concentration in frontal zones without any regular horizontally-directed movement on the part of the organism.

Here, we present a set of observations that suggests the concentrating of a Slope Water fish, *Benthosema glaciale* (family Myctophidae, the lanternfishes), at the frontal boundary between warm-core ring 82-B and cold shelf and Slope Water entrained by the ring. The mechanism responsible for the presumed concentrating is explored by the use of an analytical model that includes both advection and diffusion in a flow field like that found in the ring and its surroundings. We also suggest that advection of ring-front fluid into the ring core by "streamers" led to an increase in fish inside the ring.

Gulf Stream rings are formed downstream from Cape Hatteras where the Stream meanders widely. Extreme meanders are pinched off from the Stream to north and south, forming eddies that extend from sea surface to sea bottom and are a hundred or more kilometers in diameter. Eddies shed to the south have cores of cold Slope Water; those shed to the north, cores of warm Gulf Stream or Sargasso Sea water. Both have encircling remnants of Gulf Stream, whence the name "ring," and both are strong anomalies in their new surroundings.

In 1976 and 1977 *cold-core* rings were the subject of a multidisciplinary investigation supported by the Office of Naval Research and the National Science Foundation (The Ring Group, 1981). An even more intensive and extensive study of the physics, chemistry, and biology of *warm-core* rings was conducted by 25 NSF-supported investigators between September 1981 and October 1982 (Joyce and Wiebe, 1983). At times, four ships were simultaneously engaged along with aircraft (NASA) and real-time satellite coverage. One ring, 82-B, was visited during three-week periods in April, June, and August 1982.

Before the comprehensive warm-core rings investigation began, it was supposed that at their genesis these eddies were relatively simple bodies with cores of Sargasso Sea and surrounding rings of Gulf Stream that would be gradually mixed away until they were more or less indistinguishable from the foreign environment into which they had been cast—the North American Slope Water. Within a few days of the start of the first field study in September 1981, however, ring 81-D, then about two months old, was observed to interact strongly with the Gulf Stream resulting in substantial physical and biological changes to the ring center (Joyce *et al.*, 1984). Interactions between warm-core rings and water on the continental shelf have also been observed (Ramp *et al.*, 1983; Bisagni, 1983), and interactions of both classes now are thought to be common.

Because water generally is not moved without its plants and animals, and because there are considerable biotic differences between Slope Water, Gulf Stream, and Northern Sargasso Sea (especially between the first and last), it is often possible in the Gulf Stream region to identify the source of a parcel of water by its fauna and flora. This can be true even in the situation where the water itself is indistinguishable in temperature/salinity properties as in the case of water cooler than about 10°C along the Slope Water/Gulf Stream margin. By such faunistic and floristic means, it should be possible to make deductions about the mechanics of the Gulf Stream rings. Principal limitations to the method are uncertainties about the geographic distribution of organisms and the fact that the generation time for many is too short for distinguishing *in situ* proliferation from an exchange of waters through advection. The small mesopelagic fishes of the family Myctophidae (lanternfishes) are exempt from both of these objections. Their distribution in the North Atlantic is quite well known (Backus *et al.*, 1977; Nafpaktitis *et al.*, 1977), and although a few species have life-cycles as short as a year, most, including *B. glaciale,* take longer to grow from egg to sexual maturity (Nafpaktitis *et al.*, 1977; Karnella, 1983).

2. Data

Expendable bathythermograph (XBT) observations were taken from the several ships surveying ring 82-B in April and June 1982. These have been composited in a coordinate system that is based on the ring center as it moves through the Slope Water and have been averaged to provide the mean radial thermal structure for April and

June. (The coördinate system was derived from a combination of satellite, XBT, and drifter data relating to the position of the ring center (Hooker and Olson, 1985).) Additional physical information on the evolution of the near-surface structure of the ring and the entrainment around it have been derived from data collected by the NOAA polar orbiter as part of the experiment by the RSMAS/MPO Remote Sensing Center in Miami. Brown *et al.* (1983) described the way in which the satellite data are corrected and processed.

Data on the abundance and biomass of *Benthosema glaciale* come from midwater trawls made with the MOCNESS-20 (MOC-20), a scaled-up version of the MOCNESS-1 (Wiebe *et al.*, 1976) in which the area of the projected net mouth is about 20 m^2 when the apparatus is in a common fishing attitude. The MOC-20 consists of a set of 3-mm mesh nets that can be opened and closed by command from the surface via a signal-conducting towing warp. Apparatus attached to the net frame measures and transmits depth, temperature, salinity, flow, and net-frame angle to the towing ship's laboratory. Flow and net-frame angle allow computation of the water volume filtered. On the April/May and June cruises discussed (*Oceanus* 118 and 121) a set of five or six nets was used. One net was fished to 1000 m, then closed and a second net opened. The second and successive nets were closed and opened at intervals as the apparatus was brought back to the surface. A surface-to-surface cycle with the gear is referred to as a "station," the contents of a single net as a "collection." In addition to being described by latitude and longitude, stations are located in the same radial coordinate system used to composite the physical data (Table 1). Abundance (i), fish specimens per unit volume of water, is the integrated value for the 1000-m water column having an area of one square meter at the sea surface; it is expressed as specimens per m^2 (of sea surface). Biomass (m), fish volume (ml) per unit volume of water, is derived and expressed in the same way.

3. Biology and distribution of *Benthosema glaciale*

The biological data given here pertain to *Benthosema glaciale*, a "subpolar-temperate" species in the scheme of zoogeographic classification for Atlantic myctophids given by Backus *et al.* (1977). The southern limit of its range is at the boundary between temperate and subtropical North Atlantic—in the west, at the Gulf Stream's north edge (Fig. 1). A few fish are carried across the Slope Water/Gulf Stream boundary by the Western Boundary Undercurrent (unpublished data of the second author) and by Gulf Stream cold-core rings (Backus and Craddock, 1982). Eighteen measurements of the 1000-m water-column abundance, i, of *B. glaciale* in the Slope Water made by the second author and colleagues during warm-core ring cruises varied from 0.36 to 4.41 specimens/m^2 and have a mean of 1.24 specimens/m^2 (Fig. 2). Water-column biomass for *B. glaciale* at the same stations ranged from 0.13 to 1.38 ml/m^2 and have a mean of 0.64.

B. glaciale was found in *cold-core* rings as long as depths to 15°C were less than about 515 m (Backus and Craddock, 1982). Ring-center stations with depths to 15°C of about 200 m or less had abundances like Slope Water ones. Abundance decreased as depth to 15°C increased between about 200 and 515 m, and the fish became confined to increasingly deeper layers in the ring. Eleven ring-fringe and Sargasso Sea stations with depths to 15°C of 515 m or more caught no *B. glaciale*.

Like many mesopelagic fishes, *B. glaciale* is thought to make a diel vertical migration, coming close to the sea surface at night and going deep by day. Halliday (1970) suggested that the center of abundance in the Slope Water south of Nova Scotia moves from deeper than about 450 m by day to about 50–90 m by night, but the data upon which this was based were far from ideal for the purpose. More certain is the report by Goodyear *et al.* (1972), who found the western Mediterranean population to move from around 500 m by day to 50–70 m by night. Unpublished data of the second author and colleagues from 16 Slope Water stations made during warm-core rings cruises show no evidence for a vertical migration of fish of age I+ or older, although there is clear evidence for such a migration by fish of age 0. Among the latter, the situation is very complicated with some fish at a station migrating, others not. As in other small and relatively weak macroplanktonic (or micronektonic) fishes, swimming in the horizontal by *B. glaciale* is thought to be limited to short, more or less random excursions in response to food, predators, and each other.

B. glaciale is about 25 mm long at one year and reaches sexual maturity at age two, by which time their modal length is between 40 and 50 mm (Halliday, 1970). The longest fish in Halliday's records were less than 70 mm at an age (based on otolith rings) of four years. According to Halliday, spawning takes place in early spring.

4. The early history of ring 82-B

Warm-core ring 82-B was formed from a Gulf Stream meander in late February 1982. It was cursorily surveyed by R/V *Oceanus* in mid-March (P. H. Wiebe, pers. comm.). Following this, the Sargasso-Sea core of the ring was modified by atmospheric cooling and the entrainment of surrounding water (Schmitt and Olson, 1985). The first cruises whose main purpose was to examine 82-B took place from mid-April to early May, during which time the ring was isolated both from the strong influence of the Gulf Stream and from gross irregularities of the bottom such as the New England seamounts. In mid-May, parts of an extensive streamer-field, consisting of shelf water entrained and drawn off-shelf and entrained Slope Water, appeared to spiral into the ring center (Fig. 3). That these streamers were actually near-surface (0 – ca. 100 m) water being added to the ring from outside is evident from a decrease in ring-surface salinity. These bands of entrained water eventually diffused to cover the surface of the ring. By late June the entrainment of shelf and Slope Water into the ring core was at an end, and the ring was entering a period of interaction with the Gulf Stream.

Table 1. Catch (*Benthosema glaciale*) and station data in and around warm-core ring 82-B, April, June 1982

MOC 20	Position latitude N, longitude W	Date	d10° (m)	d15° (m)	From r ctr (km)	From r ctr (°)	Area Time of day	i			*m*
								Age 0	Age I++	Age 0 + Age I++	
9	39°09.2′, 69°41.7′ to 39°11.3′, 69°38.9	21 Apr	234	—	146 151	080 079	SW d	0	1.22	1.22	1.31
10	38°57.9′, 71°15.8′ to 39°00.7′, 71°15.7′	22 Apr	568	408	11 15	071 052	rc n	0	0.02	0.02	0.02
11	38°54.6′, 71°36.8′ to 38°50.5′, 71°35.1′	23 Apr	561	439	13 13	262 226	rc d	0	0.01	0.01	0.03
12	38°39.4′, 72°05.3′ to 38°38.4′, 72°01.8′	24 Apr	442	209	57 53	239 234	hvr d	0	0.04	0.04	0.04
14	38°31.2′, 72°23.6′ to 38°30.1′, 72°19.5′	26 Apr	370	—	82 77	237 234	hvr n	0.05	0.11	0.16	0.20
15	38°34.6′, 72°31.7′ to 38°35.3′, 72°27.5′	26 Apr	342	—	87 80	244 243	hvr d	0.07	0.10	0.18	0.16
17	38°48.3′, 71°44.5′ to 38°51.0′, 71°53.0′	30 Apr	553	417	11 17	198 252	rc n	0.01	0.03	0.04	0.06
18	39°27.1′, 71°08.4′ to 39°28.0′, 71°01.7′	1 May	255	—	74 82	034 039	SW n	0.22	0.14	0.36	0.18
19	39°13.5′, 71°17.6′ to 39°07.5′, 71°17.4′	15 Jun	285	90	290 283	041 043	SW n	1.09	0.06	1.14	0.13
20	38°58.9′, 71°29.5′ to 38°55.7′, 71°34.2′	16 Jun	246	60	272 265	041 041	SW d	1.48	0.19	1.67	0.34

21	37°05.7′, 73°37.0′	18	549	420	2	350	rc	2.65	0	2.65	0.08
	to	Jun					n				
	36°59.7′, 73°36.1′				9	169					
23	36°58.6′, 73°37.3′	20	543	399	10	117	rc	2.09	0.03	2.12	0.11
	to	Jun					n				
	37°01.7′, 73°34.3′				14	084					
24	36°54.6′, 73°36.2′	20	530	380	17	129	rc	3.84	0	3.84	0.09
	to	Jun					d				
	36°57.1′, 73°35.0′				17	110					
26	37°00′, 73°07.1′	21	353	27	61	087	entr	8.76*	0.08	8.84	0.31
	to	Jun					d				
	37°03.4′, 73°04.7′				66	082					
27	37°07.5′, 73°08.7′	23	215	—	73	072	entr	20.82	0.25	21.07	0.71
	to	Jun					d				
	37°12.8′, 73°11.8′				73	063					
28	36°59.8′, 73°48.9′	24	514	362	15	046	rc	13.44	0.02	13.46	0.44
	to	Jun					d				
	36°56.3′, 73°56.1′				4	355					
30	37°05.5′, 73°45.1′	26	441	249	29	022	hvr	5.13	0.15	5.28	0.41
	to	Jun					d				
	37°11.6′, 73°46.7′				39	012					
31	37°02.6′, 73°31.3′	27	406	101	38	051	hvr	2.60	0.07	2.68	0.22
	to	Jun					d				
	37°06.8′, 73°30.2′				44	044					
33	37°41.0′, 72°54.8′	28	224	58	127	040	SW	4.21	0.20	4.41	0.46
	to	Jun					n				
	37°46.9′, 72°50.7′				139	039					
34	39°22.3′, 71°36.0′	30	282	67	347	035	SW	1.32	0.38	1.70	0.59
	to	Jun					n				
	39°26.7′, 71°34.4′				356	035					

i is the 1000-m water-column abundance in specimens per m^2 of sea surface. *i* is given for juvenile fish (age 0), probably spawned in March or April 1982, and for fish older than one year (age I++). *m* is the 1000-m water-column biomass in milliliters per m^2 of sea surface. SW = Slope Water, rc = ring center, hvr = the high-velocity region of the ring, entr = the entrainment, d = day, and n = night.

*There are no data for the interval 750–1000 m. *i* and *m* were calculated assuming that there were no *Benthosema* in the interval, which is close to being so, judging from catches in this interval at similar stations.

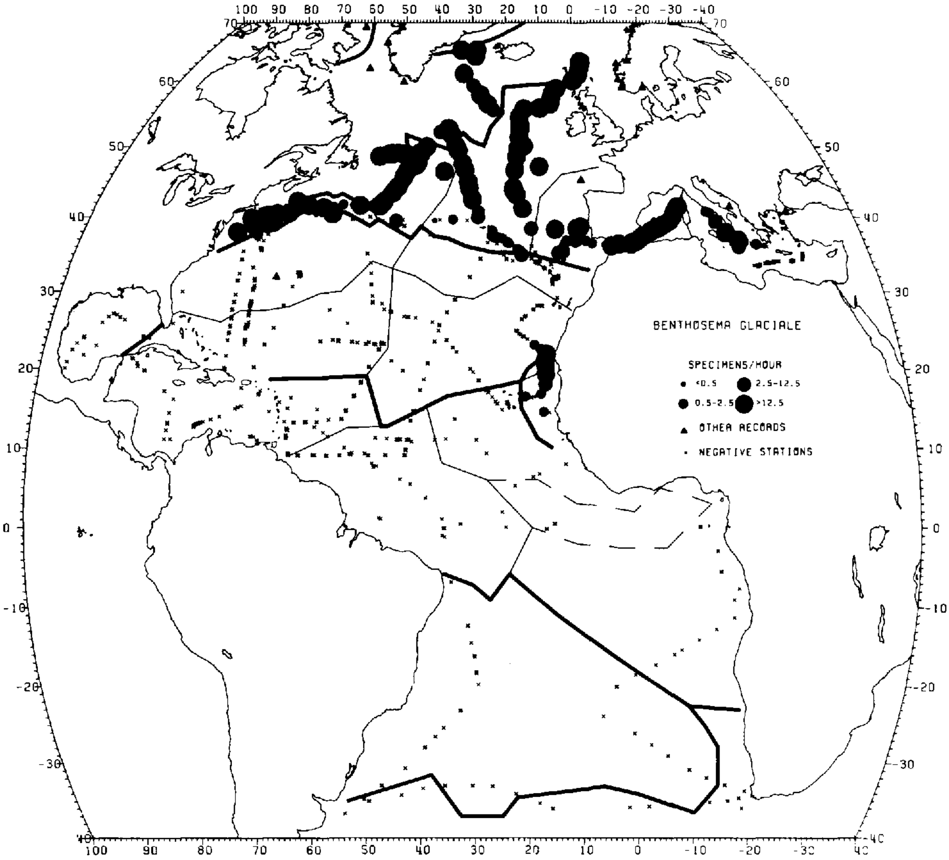

Figure 1. Distribution of *Benthosema glaciale,* a subpolar-temperate lanternfish (family Myctophidae) from Nafpaktitis *et al.*, 1977. The radii of the balls are proportional to catch rate. X's mark the stations at which *B. glaciale* was not caught although the net was towed at the right depth for doing so (based on the positive catch data).

5. ***Benthosema glaciale*** in warm-core ring 82-B

MOC-20 stations were first occupied in and around ring 82-B on *Oceanus* cruise 118 in April/May 1982. Two stations were made in the Slope Water where the abundance (*i*) and biomass (*m*) of *B. glaciale* were 0.36 and $1.22/m^2$ and 0.18 and $1.31/m^2$ respectively. All of the fish taken at the Slope Water station on 21 April were more than a year old (Table 1), but at the Slope Water station occupied 10 days later (and 70 km nearer the ring) about two-thirds of the fish were of age 0. There were very few *B. glaciale* in the ring (Table 1 and Fig. 4). At ring-center stations 10, 11, and 17 (at radii from the ring center of 12 to 22 km), *i* was 0.02, 0.01, and $0.04/m^2$, and *m* 0.2, 0.3, and $0.6/m^2$. Catch rates at three stations in the high-velocity region (hvr) of the ring were somewhat higher than the ring-center stations, but still low—*i* was 0.04,

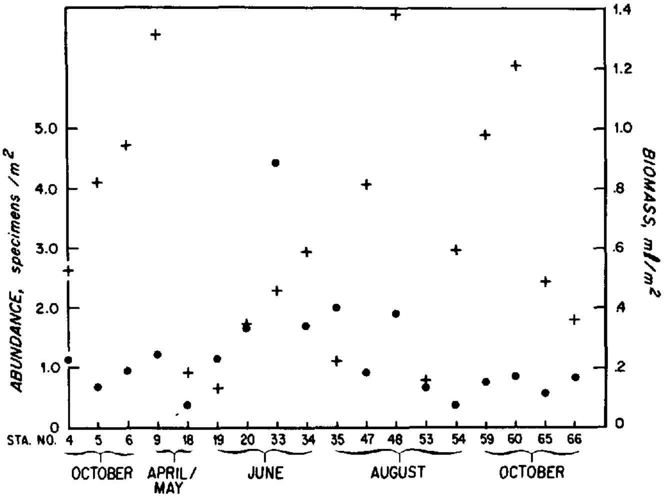

Figure 2. Water-column abundance, *i* (dots), and biomass, *m* (crosses), of *Benthosema glaciale* at MOC-20 stations occupied in the Slope Water during the warm-core rings program.

0.16, and 0.18/m^2 and *m* 0.04, 0.20, and 0.16/m^2 at stations 12, 14, and 15 with radii from 58 to 86 km. Fish of age I+ or older predominated at all six ring stations, although a few age 0 fish occurred at three of the six (Table 1). Two-sided Mann-Whitney U-tests (nonparametric) show that the Slope Water sets for *i* and *m* differ from the ring sets (combined center and hvr) at the 0.1 and 0.2 significance levels respectively and that the hvr and ring center sets differ from one another at the 0.2 level. (In this and in the U-tests subsequently reported it makes no difference to the result whether abundances of age-0 fish or fish of all ages are used.) Thus, the abundance of *B. glaciale* in April appears to have diminished from the Slope Water to the high-velocity region of the ring to the ring center.

In June during *Oceanus* cruise 121 the abundance of *B. glaciale* in and near the ring had increased markedly (Table 1, Fig. 4) due to the appearance in the catch of age-0 fish from the early spring spawning. These small fish were predominant at all stations, making up 78–96% of the *B. glaciale* caught in the Slope Water and 97–100% of those caught in and at the edge of the ring. (Note the difference in scale in Figs. 4a and b in order to accommodate the much greater numbers.) Slope Water biomasses in June ($m = 0.13$, 0.34, 0.46, and 0.59/m^2) were at the low end of the range for all Slope Water observations. Slope Water abundances at this time ($i = 1.14$, 1.67, 1.70, and 4.41/m^2) were ordinary except for that at station 33 ($i = 4.41/\text{m}^2$), where it was more than twice that of the Slope Water station having the next highest abundance whatever the season (station 35 in August 1982) (Fig. 2). All four Slope Water stations were northeast of the ring center—the same direction in which lay the source of the cold water being entrained by the ring. Unlike the other three Slope Water stations

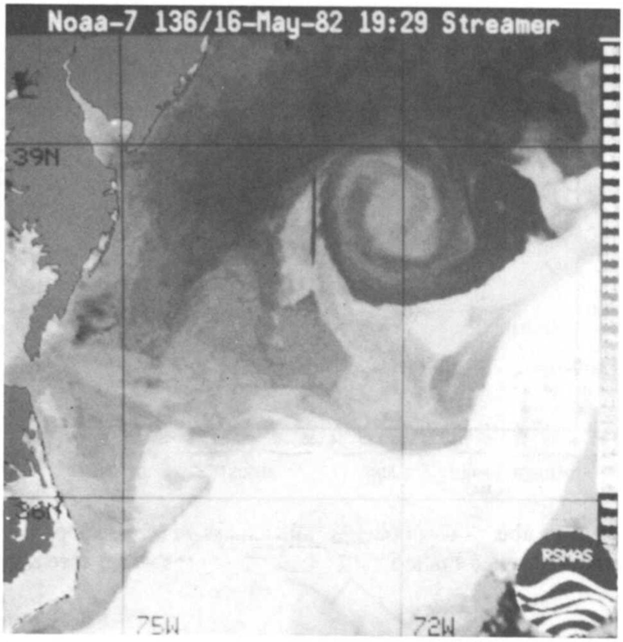

Figure 3. Satellite thermal image showing warm-core ring 82-B (centered near 38.5N, 72W) when it was entraining shelf and Slope Water into its core. The gray scale is such that darker areas are colder. The image is a composite of several images centered on May 16, 1982. The ring front is the banded region with large contrasts in temperature. Along the eastern side of the ring, cool water is being drawn off the continental shelf. The Gulf Stream is apparent at the lower right. The plankton tows made on *Knorr* cruise 94 on May 19 and 21 (see text) were in the streamer of fluid spiralling into the ring core. The image was processed by R. Evans, O. Brown, and J. Brown at the University of Miami RSMAS/MPO Remote Sensing Laboratory.

occupied during the June cruise, which were 265–347 km distant from the ring center, station 33 was only about 130 km distant from ring center—thus much nearer to the entrainment feature. Mann-Whitney U tests indicate that the April and June Slope Water sets for both i and m did not differ.

After making two MOC-20 stations in the Slope Water, the June cruise of *Oceanus* occupied three ring-center stations—21, 23, and 24, east-southeast of the ring center at radii of 2–17 km—where many small *B. glaciale* were found, but virtually no large ones (three fish older than age 0 at Sta. 23 only). Abundances in the ring center (i = 2.65, 2.12, and 3.84/m^2) were 100 times the April ring-center ones, although biomass (m = 0.08, 0.11, and 0.09/m^2) had only increased about 2.5 times. U tests show that these first June sets in the ring center differ from the April ones in both abundance and biomass at a significance level of 0.1. Compared to the Slope Water in June, these first ring-center stations had higher abundances if one disregards the anomalous Slope

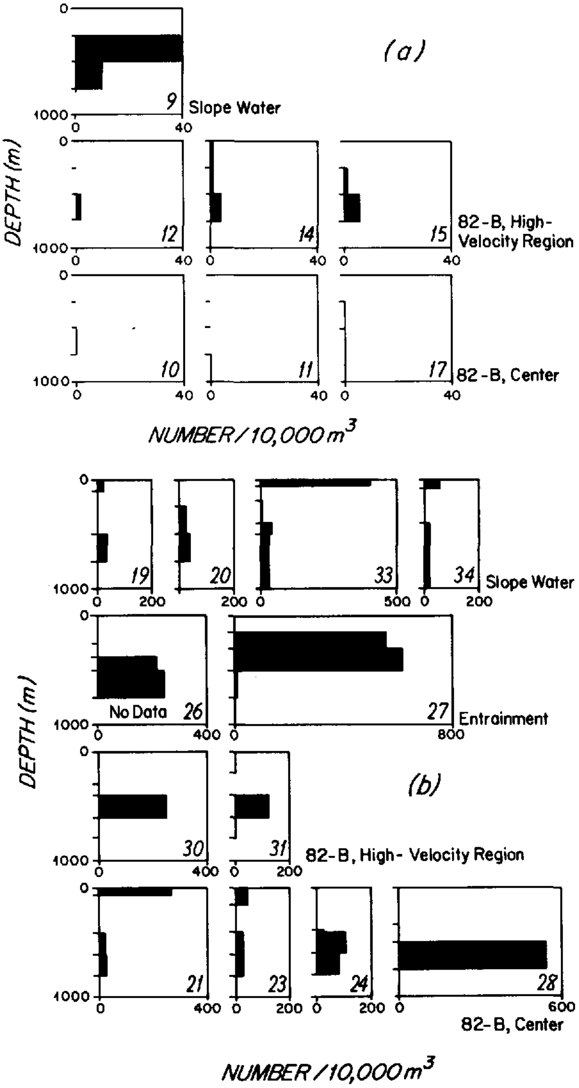

Figure 4. Abundance of *Benthosema glaciale* at certain MOCNESS-20 stations in and around Gulf Stream warm-core ring 82-B in (a) April and (b) June, 1982. Note the change in scale between (a) and (b). The ticks on the ordinate represent depths at which nets were closed and opened. Stations 9, 11, 12, 15, 20, 24, 26–28, 30 and 31 were made by day, Stations 10, 14, 17, 19, 21, 23, 33, and 34 by night.

Water station 33, but lower biomasses in keeping with the fact already noted that a larger percentage of the ring-center *B. glaciale* were age-0 fish. (Mann-Whitney U tests show that the abundance sets differ at the 0.1 level if station 33 is omitted from the analysis, but not otherwise, and that the biomass sets differ at the 0.1 level.)

Following this first visit to the ring center, *Oceanus* withdrew 60–70 km to the east of the ring center into the boundary region between the ring and the principal entrainment of cold water, where two MOC-20 stations, 26 and 27, were made. The abundances of *B. glaciale* at these entrainment stations ($i = 8.84$ and $21.07/\text{m}^2$) were much in excess (5–10 times) of Slope Water abundances, but because the fish were almost all small ones, biomass here ($m = 0.31$ and $0.71/\text{m}^2$) and in the Slope Water were much the same. (U tests show that the entrainment and Slope Water abundance sets differ at the 0.1 level, but that the biomass sets cannot be distinguished.) The second entrainment station, 27, had the least depth to 10°C observed on the June cruise and surface water colder than 15°C—the only such station occupied on that cruise. Salinity decreased rapidly from about 35 per mille to about 33 per mille in the upper 50 m at station 26 and in the upper 150 m at 27. Very cold water in the surface layers at stations 26 and 27 originated on the continental shelf where *B. glaciale* is not found, showing that the cold water itself is not the source of the fish.

After sampling the entrainment, *Oceanus* returned to the ring center and occupied station 28 at a radius of 4 to 15 km north-northeast of the ring center. This station came about 20 km from and four days after the last of the earlier ring-center stations. Water-column biomass, 0.44, and abundance, 13.46, were comparable to values seen in the entrainment and about five times those seen at the ring-center stations made a few days before (Table 1). As at the earlier ring-center stations, almost all fish were small (two large fish out of about 1500). A final pair of ring stations were made in the high-velocity region (stations 30 and 31, northeast of ring center at radii of 29 to 45 km). Abundances here ($i = 5.28$ and $2.68/\text{m}^2$) were substantially higher than Slope Water ones, lying in the lower half of the range of abundances from entrainment to ring center. U-tests show that a set consisting of all the June abundances for ring center and high-velocity region differs both from the entrainment set and the Slope Water set for June at the 0.2 level, although the second comparison is significant at the 0.01 level if the anomalous station 33 is omitted from the Slope Water set. No difference is indicated if the high-velocity region stations are pooled with the entrainment ones and these abundances compared with those of the ring center. However, abundance at entrainment plus high-velocity region stations differs from that in the Slope Water at a significance level of 0.1. Taken together, the observations from all of the ring stations probably indicate great patchiness in the ring, although temporal changes over the nine-day observation period cannot be wholly excluded. In summary, intercomparison of June observations suggests that the abundance of *B. glaciale* is lowest in the Slope Water, highest at the ring edge, and intermediate in the ring center.

Certain other statistical analyses of the abundance data were made in addition to the

Mann-Whitney U-tests already recounted. The data were pooled according to season—April/May and June—and water mass—Slope Water, ring edge (high-velocity region or high-velocity region plus entrainment) and ring center (ring core). For parametric tests the data were log-transformed. A two-way parametric analysis of variance (Anova) showed that abundances by season, by water mass, and by the interaction of the two all differed at levels of 0.06 or higher. A Friedman test, a two-way nonparametric Anova, showed abundance differing by water mass and by season at a significance level of 0.001 with rank in the order given. A one-way parametric Anova for the effects of water mass in April showed that Slope Water abundance differed from abundance in the high-velocity region and in the ring center (at the 0.05 significance level), but the abundance in the two parts of the ring did not differ. In June, the only difference in abundance lay between the Slope Water and the ring edge (probability = 0.05). Student's *t*-tests showed with a probability of 0.01 that both the ring edge and the ring center change between April and June.

Thus, though the samples are few, they support that hypothesis that there was a concentrating in the frontal region at the east edge of the ring of *Benthosema glaciale* of Slope Water origin and that they were advected by some mechanism into the ring center prior to the June observations. Although some of the few fish found in the ring in April were large enough to be sexually mature, it is virtually certain that these mature fish, had they spawned in the ring, were not numerous enough to explain the large numbers of 0+ fish seen in the ring in June.

6. A mechanism for concentrating depth-keeping species

Most mesopelagic animals, such as the one discussed here, *Benthosema glaciale*, live within restricted (sometimes quite narrow) strata in the water column. Many such animals (age-0 *Benthosema* included) are diel vertical migrators, living within one layer by day, another (or others) by night. Whether vertical migrator or not, mesopelagic animals appear to keep depth by swimming up or down in the water column so as to stay within some range of intensities of ambient light that is appropriate to the time of day (although not so narrow a one as generally has been supposed according to Roe (1983)). When such a depth-keeping species is subjected to a converging (diverging) horizontal flow at the level at which it is swimming, it is concentrated (thinned). This is illustrated by the flow in the entrainment field of a warm-core ring (Fig. 5), although the mechanism is applicable to fronts in general. Fluid is swept in along the edge of the continental shelf, then deformed to produce a sharp front that curves around the ring. Parcels of fluid are horizontally compressed. Since the flow is three-dimensionally nondivergent, this horizontal reduction of a parcel is compensated by a stretching of the parcel in the vertical. Depth-keeping species can easily compensate for the vertical velocities involved, which typically are less than 0.0005 m s^{-1}. The animals, therefore, only are subject to a horizontal

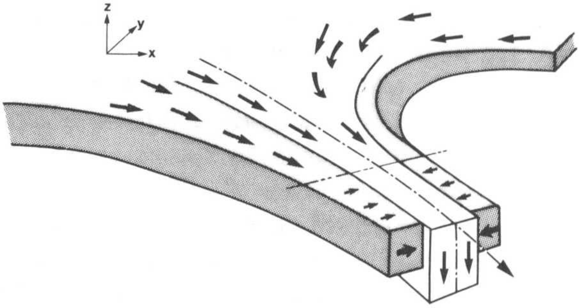

Figure 5. Schematic of the frontal zone on the northeast quadrant of a warm-core ring. Fluid moving around the ring in the foreground meets water swept into the edge of the ring. Convergence in the front compresses fluid columns horizontally as shown in the lower right. This compression is compensated for by vertical stretching of the columns.

reduction of the volume that they are occupying, and, in the absence of any organized horizontal motion by the animals, their concentration will increase. Similarly, the same species will be thinned if the convergent flow is replaced by a divergent one.

The concentration rate in the absence of diffusion can be calculated from a Lagrangian version of the divergence in the horizontal plane. In this frame, i.e., a frame following the parcels of fluid, the divergence, D, is given by

$$D = 1/A \; dA/dt, \qquad (1)$$

where A is the area of the fluid parcel in the horizontal. Here the variable divergence is chosen, consistent with common physical usage—convergence is negative divergence. The concentration of animals, C, is then related to the divergence by

$$D = 1/A \; dA/dt = -1/C \; dC/dt. \qquad (2)$$

The concentration of animals decreases (increases) exponentially in time for a constant divergence (convergence). The divergence and the net concentration rate for a population in the flow field in Figure 5 can be computed by comparing the cross-sectional area of a fluid column as a function of time.

In the ocean the tendency for a property to be concentrated by a flow field typically is opposed by an outward diffusion of the property due to turbulence. In the case of an animal swimming randomly in the horizontal, turbulent diffusion, which is a property of the fluid flow, is enhanced by the behavior of the animal. Therefore, the effective diffusivity for such an animal should be larger than that for a passive tracer in the fluid.

The relative role of convergence and diffusion in determining the concentration, S, can be obtained by scaling the conservation equation,

$$S_t + \nabla \cdot (\mathbf{u} S) = K \nabla^2 S, \qquad (3)$$

where the term S_t denotes the partial derivative of S with respect to time, $\mathbf{u}$ is the full three-dimensional velocity vector, and K the diffusivity for S. This equation can be expanded to

$$S_t + \mathbf{u} \cdot \nabla S + S \nabla \cdot \mathbf{u} = K \nabla^2 S. \tag{4}$$

The ocean is approximately incompressible, $\nabla \cdot \mathbf{u} = 0$; thus, the equation for S simplifies to

$$S_t + \mathbf{u} \cdot \nabla S = K \nabla^2 S. \tag{5}$$

In the case of the animals, however, the vertical components are cancelled by the swimming behavior. The concentration of fish, C, is then governed by the equation

$$C_t + \mathbf{u} \cdot \nabla_H C + C \nabla_H \cdot \mathbf{u} = K \nabla_H^2 C, \tag{6}$$

where the subscript, H, denotes the horizontal component of the operator or vector.

For the scaling of Eqs. (5) and (6), it is assumed that the velocity field has magnitude, U, and length scale, L, associated with a horizontally divergent flow such that

$$D \sim U/L.$$

It is also assumed that the divergence term in Eq. (6) is the same order of magnitude as the advective terms in Eqs. (5) and (6). If the scale of the property concentrations is also L, then the equations can be scaled to give a nondimensional measure of the importance of the diffusion term. This scaling parameter is

$$K/(UL) \sim K/(DL^2).$$

For divergent patterns of scale

$$L > (K/D)^{1/2},$$

divergence is more important than diffusion, while at shorter scales the diffusion of properties dominates advection. For the situation in which the length scales of the divergence field and the concentration of properties do not match initially, the concentration will vary in time in a manner such that the length scale approaches $(K/D)^{1/2}$. In general, for the problems of interest, the scaling given above is the correct scaling for the case in which the divergence initially dominates, as will become obvious below. Estimates of this length scale for values of K and D, which are representative of the range found in the ocean, are given in Table 2. Both K and D vary considerably in the ocean depending on the scale of motion considered with larger scales having lower D but higher K. The time scale for an e-fold increase in the concentration of C as computed from the solution to Eq. (2),

$$C = Co \exp\left[-Dt\right],$$

Table 2. Critical length, L_c, and time scales, τ, for different combinations of convergence and diffusivity. For discussion of calculations see text.

K m^2 s^{-1} $\nabla_H \cdot V$s^{-1}	10	50	100	τ days
10^{-6}	$L_c = 3$ km	7	10	12
10^{-7}	10	22	32	116
10^{-8}	32	71	100	1160

is shown in the last column of the table. These time scales assume that the length scales in the problem are such that the diffusion is unimportant.

7. A model of the process in a simplified flow-field

The equations for the concentration of fish and some conservative tracer of the fluid can be solved to give an appreciation of the mechanism. Here Eqs. (5) and (6) are solved for the case where the imposed flow field is two dimensional with $u = Dx$ and a vertical velocity of $w = -Dz$ with horizontal diffusion. Similar solutions for the evolution of a tracer under the influence of both strain and diffusion are given by Chatwin (1974) and Young *et al.* (1982). Chatwin considers an initial delta-function distribution, while Young *et al.* consider sinusoidal initial fields. For initial Gaussian distributions of S and C, the solutions to (5) and (6) are

$$S = S(t) \exp\left[-\alpha x^2 - \gamma z^2\right]$$

and (7)

$$C = C(t) \exp\left[-\alpha x^2 - \gamma z^2\right],$$

where α and γ are the inverse squared length scales associated with the width of the distribution in x and z. Substitution of these back into the equation above yields the following expressions for $S(t)$ and $C(t)$ in terms of the time-dependent parameters α and γ. These are

$$S_t(t)/S(t) + 2K\alpha - [\alpha_t - 4K\alpha^2 + 2D\alpha]\, x^2 + [2D\gamma - \gamma_t]\, z^2 = 0 \tag{8}$$

and

$$C_t(t)/C(t) + [2K\alpha + D] - [\alpha_t - 4K\alpha^2 + 2D\alpha]\, x^2 - \gamma_t z^2 = 0. \tag{9}$$

Now if $C(t)$, $S(t)$, and the coefficients are to be a function of time alone, as assumed initially, it is necessary that the terms in brackets modifying the x^2 and z^2 vanish. This solvability condition leads to three equations to be solved simultaneously. The set for S

is

$$\begin{gathered} S_t(t) + 2K\alpha S(t) = 0, \\ \alpha_t + 2D\alpha + 4K\alpha^2 = 0, \end{gathered} \tag{10}$$

and

$$\gamma_t + 2D\gamma = 0.$$

The equivalent equations for C are

$$\begin{gathered} C_t(t) + [2K\alpha + D]\, C(t) = 0, \\ \alpha_t + 2D\alpha + 4K\alpha^2 = 0, \end{gathered} \tag{11}$$

and

$$\gamma_t = 0.$$

Eqs. (10) and (11) can be solved analytically by first integrating the common α equation to give

$$\alpha = \frac{\alpha_0}{\left(1 + \dfrac{2K\alpha_0}{D}\right) e^{2Dt} - \dfrac{2K\alpha_0}{D}} \tag{12}$$

where α_0 is the initial condition at $t = 0$. Then substituting for α and the solution for γ into the S and C equations to yield the final solutions

$$S = S_0 \frac{e^{Dt}}{\sqrt{\left(1 + \dfrac{2K\alpha_0}{D}\right) e^{2Dt} - \dfrac{2K\alpha_0}{D}}} \cdot \exp\left\{ - \frac{\alpha_0}{\left[\left(1 + \dfrac{2K\alpha_0}{D}\right) e^{2Dt} - \dfrac{2K\alpha_0}{D}\right]} X^2 - \alpha_0 e^{2Dt} Z^2 \right\}$$

and

$$C = C_0 \frac{1}{\sqrt{\left(1 + \dfrac{2K\alpha_0}{D}\right) e^{2Dt} - \dfrac{2K\alpha_0}{D}}} \cdot \exp\left\{ - \frac{\alpha_0}{\left[\left(1 + \dfrac{2K\alpha_0}{D}\right) e^{2Dt} - \dfrac{2K\alpha_0}{D}\right]} X^2 - \alpha_0 Z^2 \right\} \tag{13}$$

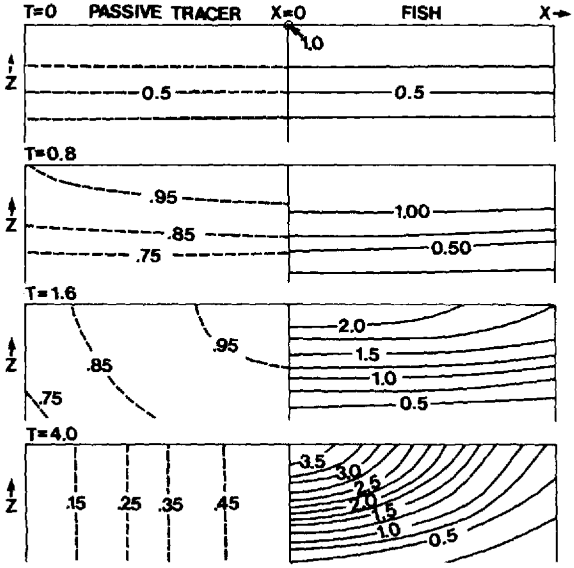

Figure 6. The spatial fields of a passive tracer (left) and for an animal maintaining depth in the face of vertical advection. Time in nondimensional units increases downward. The initial fields are very flat Gaussians as is obvious from the almost straight concentration lines at $t = 0$. The initial half-width for the Gaussian is 282 km in a flow with a diffusion to divergence ratio of 0.0025.

These solutions have a limiting case in which the distribution of fish becomes stationary in time and the tracer, S, obtains a steady-state form in the horizontal. It occurs when

$$\alpha = -D/2K \quad \text{(convergent steady state)}$$

such that $\alpha_t = 0$. In this situation, the solutions for S and C are

$$S = S_0 \frac{e^{Dt}}{\sqrt{-2K/D\alpha_0}} \exp\left\{-\frac{D}{2K}X^2 - \alpha_0 e^{2Dt} Z^2\right\}$$

and

$$C = C_0 \frac{1}{\sqrt{-2K/D\alpha_0}} \exp\left\{-\frac{D}{2K}X^2 - \alpha_0 Z^2\right\}. \tag{14}$$

Therefore, when the scale of the property distributions reaches the critical scale-length, $Lc = (|2K/D|)^{1/2}$, the concentration of fish reaches a steady state. The tracer continues to decrease under the influence of the constant dilution of the fluid by the vertical velocity.

In the case where the distributions begin with larger scales, the solutions converge to

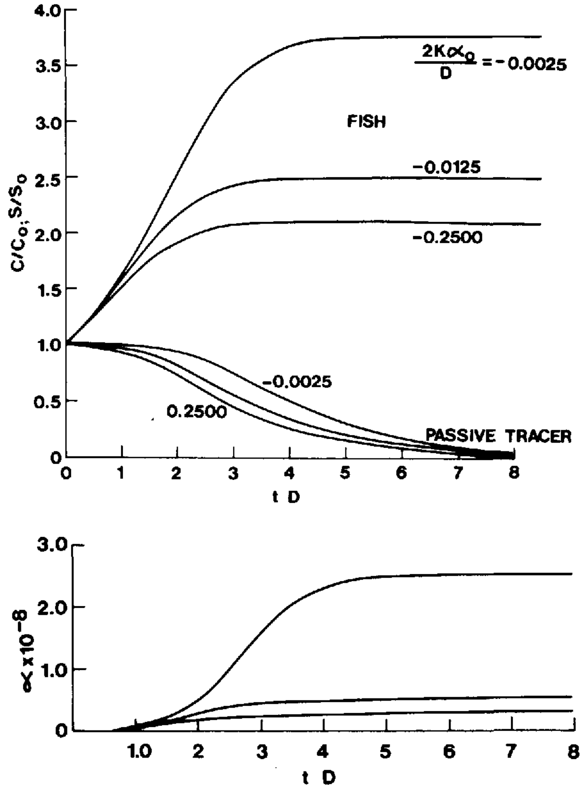

Figure 7. (a) Evolution of fish and passive tracer distributions at the axis of the strain field assumed in the model. Different curves correspond to alternate nondimensional ratios of diffusion to divergence in the flow. (b) Change in the horizontal scale of the Gaussian describing the distributions with time. The upper curve is for a nondimensional ratio of diffusion to divergence of 0.0025. The other curves are for the same ratios as given in (a) in ascending order.

the limiting cases in Eq. (12) for $D < 0$. The evolution of the distributions of fish and a passive tracer, based on Eqs. (13), are shown in Figures 6 and 7. The temporal behavior of C and S as a function of x and z is shown in Figure 6. The equations have been solved in their nondimensional form, and the results presented in terms of the ratio of the concentrations to the initial values at $x = 0$ and $z = 0$. The time-dependence of the variables for different values of the ratio of the critical length-scale to the scale of the distribution is given in Figure 7. The sections in Figure 6 are for the case in which $2\ K\alpha 0/D = -0.0025$. As expected the fish and the tracer evolve very differently. The time-dependence of α for both the fish and S is given in Figure 7b. The solutions reach the asymptotic limits in Eq. (14) in one to two nondimensional time scales (tD). The distribution of S becomes more uniform with depth in the model due to the constant

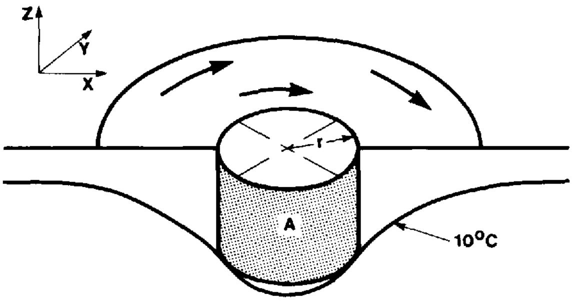

Figure 8. A representation of the areas used in the computation of divergence from the distribution of the depth of the 10° isotherm as a function of radius in ring 82-B in April and June. The divergence is computed from the relative change of the area of the cylinders indicated by the shading. See text.

deformation of the tracer field. The addition of a vertical diffusivity would enhance this trend.

8. The actual divergence field in the ring

The relationship in Eq. (1) can be used to estimate the actual divergence field in the ring during the period leading up to the observations of high fish concentrations in late June 1982. This is based on volumetric computations with hydrographic data for April and June (Olson *et al.*, 1985). The computations of interest here consist of the time rate of change of the surface area of vertical cylinders bound by the azimuthally averaged 10°C isotherm and the sea surface as a function of radius from ring center (Fig. 8). The normalized changes in these areas provide the two-dimensional divergence in the ring as a function of radius (Fig. 9). In the core of the ring at temperatures greater than 10°C, the flow over the month and a half separating the two surveys of the ring is divergent. Beyond a radius of 90 km there is a zone of convergence coincident with the front separating the ring and the entrained shelf water.

The convergences calculated in these outer parts of the ring (Fig. 9) are sufficient to account for the observed increase in the *Benthosema* population. If the simple time-scale appropriate for the situation in which convergence dominates diffusion is used (Table 2), the concentration found in the net hauls to the east of the ring could have developed in a month. If we assume that the actual convergence field is stronger on the east side of the ring where the best-developed near-surface fronts are located, the observed increase in fish density could have been accomplished in two weeks or less.

9. Discussion and conclusions

We report an increase in the abundance of a midwater fish at the front of a warm-core Gulf Stream ring and the fish's rapid appearance in the core of the ring. A

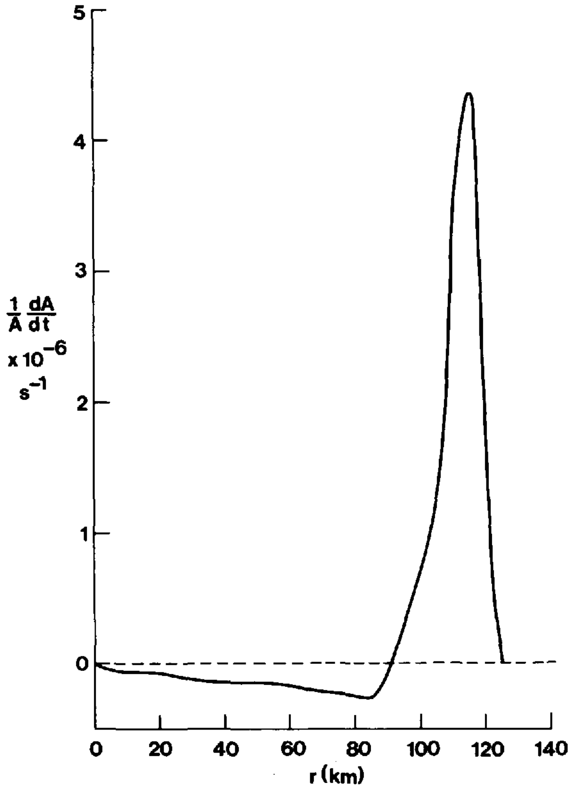

Figure 9. The distribution of divergence in waters warmer than 10°C in warm-core ring 82-B between April and June. The calculation is explained in the text.

model based on the assumption that the fish swims only randomly in the horizontal but moves vertically so as to maintain its preferred depth is used to test the ability of horizontal flow to produce the presumed concentration. The results show that a convergence field of the sort typically associated with fronts can account for the concentrations seen during the June cruise to ring 82-B even in the presence of reasonably large diffusion of the fish ($K \sim 100\ m^2s^{-1}$).

We suggest that the concentrating mechanism described is widely applicable to a variety of frontal phenomena in the world ocean and to a variety of planktonic plants and animals so long as they are depth-keepers. (We use the term "depth-keeper" loosely to mean any organism that stays or tends to stay within a certain depth range by swimming or by changes in its buoyancy.) The group of pelagic animals that are diel vertical migrators is very large. A. C. Hardy (1965) says of such migration, "It is a habit that has been evolved quite independently in almost every major group of animals in the plankton, some making shorter, others longer migrations: protozoons, coelenterate medusae, siphonophores, ctenophores, arrow-worms, the polychaete worm *Tomo-*

pteris, the pteropods, all the many different groups of crustaceans, salps, doliolids and *Oikopleura,* and most young fish." The group of animals that are depth keepers though not diel vertical migrators must also be very large, and, indeed, perhaps all planktonic animals are depth keepers of one kind or another.

Depth-keeping in the phytoplankton is not so well studied, but appears to be more restricted than in animals as might be supposed. Most of the known vertical migrants are dinoflagellates (Sournia, 1974), although one of the first species noted was a diatom—*Coscinodiscus bouvet*—individual cells of which moved up and down 50 m (Hardy, 1935). Marshall (1968) describes changes with time of day in the vertical distribution of the coccolithophorid *Coccolithus huxleyi* that were probably caused by vertical migration and calls attention to the laboratory experiments of Mjaaland (1956), who recorded phototactic movement in *C. huxleyi* and its concentrating at certain light levels.

Because every divergence (convergence) would seem to be accompanied by its convergence (divergence) and because depth-keeping organisms resist being carried too far up by an upwelling flow as well as too far down by a down-welling one, the concentrating of some assemblage of plants and animals at fronts and at the edges of cells in any system of convergences and divergences (e.g., in Langmuir circulation) would seem to be inevitable. Exactly what is concentrated will depend upon what depth-keeping species are at hand, their vertical arrangement, and the depths and velocities at which the converging and diverging flows are taking place.

In the case studied here, we suggest from observation that the fish *Benthosema glaciale* was concentrated at the edge of ring 82-B and explain by means of a model how it could have been concentrated there. However, neither the observations nor the model can show how the fish got from the ring edge to the ring center. We further suggest that the fish were carried into the ring center by streamers of cold water shown in Figure 3. At this stage these features are not well understood and may be either a manifestation of diffusion in the presence of shear (Holloway and Kristmannson, 1984; Haidvogel and Keffer, 1984; and Dewar and Flierl, 1985) or near-surface convergence in the ring core. By chance, two plankton tows made in ring 82-B during *Knorr* cruise 94 on May 19 and 21 1982 fell in such a streamer; *B. glaciale* was caught in both tows. (No tows were made in the ring outside the streamer at that time.) It may be that streamers are important in the rapid and extensive modification of warm-core rings.

For placing the results of this effort in their proper perspective, it is important to point out that both the observational data—though on the "cutting edge" of technology with the MOC-20 and satellite ring-mapping—and the analysis are quite primitive. The extent of empirical and theoretical knowledge of divergence and diffusion is limited. The need for refined biological sampling and more information on the biology of most oceanic species is obvious. Refinements—both physical and biological—should result from further analysis of various components of the Warm-core Rings data set. More sophisticated time/space sampling of both physical and biological parameters is needed in the future in order to provide better insight into the paradigm of increased biotic activity at fronts. The results of such studies should also provide new information on the phenomena of frontogenesis and macroscale diffusion in the ocean.

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REFERENCES

Ainley, D. G. and S. S. Jacobs. 1981. Seabirds, pack ice, and the Antarctic Slope Front in the Ross Sea. Deep-Sea Res., *28,* 1173–1185.

Backus, R. H. and J. E. Craddock. 1982. Mesopelagic fishes in Gulf Stream cold-core rings. J. Mar. Res., *40,* (Suppl.), 1–20.

Backus, R. H., J. E. Craddock, R. L. Haedrich, B. H. Robison and C. Karnella. 1977. Atlantic mesopelagic zoogeography. Memoir Sears Foundation for Marine Research, *1* (7), 266–287.

Bainbridge, R. 1957. The size, shape and density of marine phytoplankton concentrations. Cambridge Philosoph. Soc., Biol. Rev., *32,* 91–115.

Bisagni, J. J. 1983. Lagrangian current measurements within the eastern margin of a warm-core Gulf Stream ring. J. Phys. Oceanogr., *13,* 709–715.

Brown, O. B., D. B. Olson, J. W. Brown and R. H. Evans. 1983. Satellite infrared observations of the kinematics of a warm-core ring. Aust. J. Mar. Freshw. Res., *34,* 534–545.

Chatwin, P. C. 1974. The dispersion of contaminant released from instantaneous sources in laminar flow near stagnation points. J. Fluid Mech., *66,* 753–766.

Dewar W. K. and G. R. Flierl. 1985. Particle trajectories and simple models of transport in coherent vortices. Dyn. Atmos. Oceans, (submitted).

Dufour P. and J. M. Stretta. 1973. Fronts thermiques et thermohalins dans la région du Cap Lopez (golfe du Guinée) juin-juillet 1972: Phytoplancton, zooplancton, micronekton et pêche thonière. Doc. Sci., Cent. Rech. Océanogr. Abidjan, *4,* 99–142.

Fournier, R. O., M. Van Det, J. S. Wilson and N. B. Hargreaves. 1979. Influence of the shelf-break off Nova Scotia on phytoplankton standing stock in winter. J. Fish. Res. Board Canada, *36,* 1228–1237.

Goodyear, R. H., B. J. Zahuranec, W. L. Pugh and R. H. Gibbs, Jr. 1972. Ecology and vertical distribution of Mediterranean midwater fishes, *in* Mediterranean Biological Studies: Final Report, *1,* Part 3, Smithsonian Institution, Washington, D.C., 91–229.

Haidvogel, D. B. and T. Keffer. 1984. Tracer dispersal by mid-ocean mesoscale eddies. Part I. Ensemble statistics. Dyn. Atmos. Oceans, *8*, 1-40.

Halliday, R. G. 1970. Growth and vertical distribution of the glacier lanternfish, *Benthosema glaciale*, in the northwestern Atlantic. J. Fish. Res. Board Canada, *27*, 105–116.

Hardy, A. C. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927; part 2, the phytoplankton. Discovery Reports, *11*, 39–87.

—— 1965. The Open Sea: Its Natural History. Part 1: The World of Plankton, Houghton Mifflin, Boston, MA. 335 pp.

Holloway, G. and S. S. Kristmannsson. 1984. Stirring and transport of tracer fields by geostrophic turbulence. J. Fluid Mech., *141*, 27–50.

Hooker, S. B. and D. B. Olson. 1984. Center of mass estimation in closed vortices: a verification in principle and practice. J. Atmos. Ocean. Tech., *1* (3), (in press).

Joyce T., R. Backus, K. Baker, P. Blackwelder, O. Brown, T. Cowles, R. Evans, G. Fryxell, D. Mountain, D. Olson, R. Schlitz, R. Schmitt, P. Smith, R. Smith, and P. Wiebe. 1984. Rapid evolution of a Gulf Stream warm-core ring. Nature, *308* (5962), 837–840.

Joyce, T. M. and P. H. Wiebe. 1983. Warm-core rings of the Gulf Stream. Oceanus, *26*, 34–44.

Karnella, C. 1983. The ecology of lanternfishes (Myctophidae) in the Bermuda "Ocean Acre." Ph. D. thesis, George Washington University, 499 pp.

Kinder, T. H., G. L. Hunt, Jr., D. Schneider and J. D. Schumacher. 1983. Correlations between seabirds and oceanic fronts around the Pribilof Islands, Alaska. Estuar. Coast. Shelf Sci., *16*, 309–319.

Laurs, R. M. and R. J. Lynn. 1977. Seasonal migration of North Pacific albacore, *Thunnus alalunga*, into North American coastal waters: Distribution, relative abundance, and association with transition zone waters. Fish. Bull., *75*, 795–822.

Magnuson, J. J., S. B. Brandt and D. J. Stewart. 1980. Habitat preferences and fisheries oceanography, *in* Fish Behavior and its Use in the Capture and Culture of Fishes, ICLARM Conf. Proceedings, *5*, Int. Cent. Living Aquatic Resource Manag., Manila, 371–382.

Magnuson, J. J., C. L. Harrington, D. J. Stewart and G. N. Herbst. 1981. Responses of macrofauna to short-term dynamics of a Gulf Stream front on the continental shelf, *in* Coastal Upwelling, F. A. Richards, ed., Coastal and Estuarine Sciences, *1*, American Geophysical Union, Washington, DC, 441–448.

Marshall, H. 1968. Coccolithophores in the northwest Sargasso Sea. Limnol. Oceanogr., *13*, 370–376.

Mjaaland, G. 1956. Laboratory experiments on *Coccolithus huxleyi*. Oikos, *7*, 251–255.

Nafpaktitis, B. G., R. H. Backus, J. E. Craddock, R. L. Haedrich, B. H. Robison and C. Karnella. 1977. Family Myctophidae. Memoir Sears Foundation for Marine Research, *1* (7), 13–265.

Okubo, A. 1978. Advection-diffusion in the presence of surface convergence, *in* Oceanic Fronts in Coastal Processes, M. J. Bowman and W. E. Esaias, eds., Springer-Verlag, New York, 23–28.

Olson, D. B., R. W. Schmitt, M. A. Kennelly and T. M. Joyce. 1985. A two-layer model of the long-term physical evolution of warm-core ring 82-B. J. Geophys. Res., (submitted).

Pingree, R. D., P. R. Pugh, P. M. Holligan and G. R. Forster. 1975. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. Nature, *258*, 672–677.

Ramp, S. R., R. C. Beardsley and R. Legeckis. 1983. An observation of frontal wave development on a shelf-slope/warm core ring front near the shelf break south of New England. J. Phys. Oceanogr., *13*, 907–912.

Ring Group, The. 1981. Gulf Stream cold-core rings: their physics, chemistry, and biology. Science, *212,* 1091–1100.

Roe, H. S. J. 1983. Vertical distributions of euphausiids and fish in relation to light intensity in the northeastern Atlantic. Mar. Biol., *77,* 287–298.

Savidge, G. 1976. A preliminary study of the distribution of chlorophyll *a* in the vicinity of fronts in the Celtic and Western Irish Seas. Estuar. Coast. Mar. Sci., *4,* 617–625.

Schmitt, R. W. and D. B. Olson. 1985. Wintertime convection in warm-core rings: Thermocline ventilation and the formation of mesoscale lenses. J. Geophys. Res., (submitted).

Sournia, A. 1974. Circadian periodicities in natural populations of marine phytoplankton. Adv. Mar. Biol., *12,* 325–389.

Sund, P. N., M. Blackburn and F. Williams. 1981. Tunas and their environment in the Pacific Ocean: A review. Oceanogr. Mar. Biol. Ann. Rev., *19,* 443–512.

Tranter, D. J., G. S. Leech and D. Airey. 1983. Edge enrichment in an ocean eddy. Aust. J. Mar. Freshwater Res., *34,* 665–680.

Wiebe, P. H., E. M. Hulburt, E. J. Carpenter, A. E. Jahn, G. P. Knapp III, S. H. Boyd, P. B. Ortner and J. L. Cox. 1976. Gulf Stream cold core rings, large scale interaction sites of open ocean plankton communities. Deep-Sea Res., *23,* 695–710.

Young, W. R., P. B. Rhines and C. J. R. Garrett. 1982. Shear-flow dispersion, internal waves and horizontal mixing in the ocean. J. Phys. Oceanogr., *12,* 515–527.

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