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Mesopelagic fishes in Gulf Stream cold-core rings

by Richard H. Backus and James E. Craddock[1]

ABSTRACT

Calculations of abundance of midwater fishes in the families Myctophidae, Gonostomatidae, Photichthyidae, and Sternoptychidae for the 1000 m water column were made in cold-core rings and in the nearby Sargasso Sea and Slope Water. The data were considered with respect to the depth to 15°C, which isotherm lies shallow in the Slope Water, deep in the Sargasso Sea. Myctophid-gonostomatid biomass (excluding *Cyclothone* spp.) varied inversely as the depth to 15° with that for the Slope Water in the ratio of about 4.5:1 to that for the northern Sargasso Sea. For *Cyclothone* spp. the ratio was about 2.5:1. *Benthosema glaciale*, a *subpolar-temperate* myctophid, becomes more and more restricted to the deep part of aging rings and finally disappears from them. Warm-water fishes quickly become abundant in the upper few hundred meters of aging rings. The myctophids *Lampanyctus crocodilus, L. pusillus,* and *Hygophum benoiti* appear to be rings exploiters; they were more abundant there than elsewhere. Detrainment of fish from Ring "Frank" was observed at depths near 600 m. Three-month old Ring "Al" already had entrained fish at depths greater than 250 m. The northern edge of the Gulf Stream, an important faunal boundary between temperate and subtropical parts of the western Atlantic, is a differential barrier; warm-water animals cross it to the north more easily than do cold-water animals to the south.

1. Introduction

When the Gulf Stream separates from the continent at Cape Hatteras it commences to meander. Extreme meanders are pinched off from the Stream to north and south forming eddies a hundred or more kilometers in diameter. Eddies shed to the south have cores of cold Slope Water, those shed to the north have cores of warm Sargasso Sea. Both have encircling remnants of Gulf Stream, whence the name

1. Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, 02543, U.S.A.

"ring", and both are strong anomalies in their new surroundings. Cold-core rings can retain their identity for many months while gradually becoming like their foreign environs, although a common happening is reincorporation with the Gulf Stream after a life of 6-12 months. Ring aging, that is, the change from Slope Water conditions within the ring to Sargasso Sea ones, proceeds most rapidly in the upper 200 m or so (when newly formed the rings appear to extend all the way to the bottom at about 5000 m) (Ring Group, 1981).

Cold-core rings were first recognized and studied by Fuglister (1972). Recently, they have been the object of a study in which the physics, chemistry, and biology of rings were investigated in an integrated way (Ring Group *op. cit.*). The present paper concerns the distribution of certain mesopelagic fishes in and around cold-core rings, namely those in the families Myctophidae, Gonostomatidae, Photichthyidae, and Sternoptychidae. (Henceforth we will refer to the last three families as "gonostomatids".)

Myctophid and "gonostomatid" fishes, the most abundant of mesopelagic fishes, are potentially useful in a study such as the cold-core rings one, because the Atlantic-wide distribution of the more abundant species is quite well known; that is, the type of water with which each species is associated is reasonably well established (for myctophids, Backus *et al.*, 1977 and Nafpaktitis *et al.*, 1977; for "gonostomatids", Backus *et al.*, in preparation).

2. Zoogeographic background

The North Atlantic mesopelagial can be divided into six faunal regions—four ocean-spanning ones, the Atlantic Tropical, the North Atlantic Subtropical, the North Atlantic Temperate, and the Atlantic Subarctic Regions, plus two small, marginal regions, the Mauritanian Upwelling Region and the Gulf of Mexico. The Gulf Stream (*sensu strictu*) lies at the northern edge of the Northern Sargasso Sea, a province of the North Atlantic Subtropical Region, and at the southern edge of the Slope Water, a province of the North Atlantic Temperate Region. Species of *temperate* and *subpolar-temperate* distribution find the southern limit of their western North Atlantic range at the Gulf Stream—Slope Water boundary. The same boundary sets the northern limit in the west for species of *subtropical* and *tropical-subtropical* distribution. *Tropical* and *tropical-semisubtropical* species originating in the Caribbean Sea, the westernmost province of the Atlantic Tropical Region, are swept north by the Florida Current and Gulf Stream. (Backus *et al.*, 1977).

Thus, a biotic result of ring formation is the translation across the Stream of a temperate fauna and flora into a subtropical environment in the case of cold-core rings, the opposite in the case of warm-core ones, and in both cases, the detachment from the Gulf Stream of tropical plants and animals.

Not all species are limited by the Gulf Stream-Slope Water boundary, of course.

Temperate-semisubtropical ones, for instance, live in Northern Sargasso Sea and Slope Water alike. Nonetheless, the local distribution of species in all these classes must be altered by the formation, dissipation, and reincorporation with the Gulf Stream of both cold and warm-core rings and has the promise for providing information concerning the history of parcels of water.

Jahn (1976) studied fishes from cold-core rings whose ages were estimated to range from three months to at least 10 months. He thought of rings as hybrid habitats consisting of an upper (down to about 200 m) layer of Northern Sargasso Sea and a deeper layer of Slope Water. He suggested that, for the most part, fishes preferring either Slope Water or Sargasso Sea did not show intermediate abundances in rings, but rather reacted in an "all or nothing" way; fishes either shunned the rings as if they were like the foreign habitat on the opposite side of the Slope Water-Gulf Stream boundary from their normal habitat, or they reacted as if the rings were like their accustomed habitat. Jahn explained this behavior by the ring's hybrid character and the vertical distribution of the fishes involved. However, Jahn found the abundant Slope Water species *Benthosema glaciale* and *Ceratoscopelus maderensis* to be exceptional, showing numbers in rings that decreased gradually with ring age.

Earlier, Jahn and Backus (1976) had studied sets of mesopelagic fishes from Slope Water (200 m temp. < 15°C), Gulf Stream (200 m temp. 15-17.5°C), and Northern Sargasso Sea (200 m temp. > 17.5°C). A similarity measure (Whittaker and Fairbanks, 1958) showed the Slope Water set to be about equally distinct from the Gulf Stream and Northern Sargasso Sea sets (percentage of similarity 39 and 36, respectively), while the last two were somewhat similar (PS 57). A cluster analysis showed the Gulf Stream set to be intermediate between the distinct Slope Water and Northern Sargasso Sea sets, but suggested that the Gulf Stream fauna was not simply a mixture of the other two faunas.

In the present paper we consider midwater fish data from the viewpoints of (1) the physical environments from which the fishes come, i.e., the rings, the Slope Water, and the Northern Sargasso Sea; (2) individual rings; and (3) certain individual fish species.

3. Methods and materials

We mainly consider data from midwater trawl collections made on multi-disciplinary time-series cruises: *Knorr* 62, December 1976; *Knorr* 65, April 1977; *Endeavor* 11, July-August 1977; and *Knorr* 71, October-November 1977 (called hereafter "Rings cruises").

Except on *Endeavor* 11, fishes were collected with the MOCNESS-10, a scaled-up version of the MOCNESS-1 (Wiebe *et al.*, 1976). The MOCNESS-10 consists of a set of nets that can be opened and closed by command from the surface via an electrically conducting towing warp. Apparatus attached to the net frame measures and transmits temperature, depth, flow, and net-frame angle to the towing ship's laboratory. The area of the projected net mouth is about 10 m² when the net is in a common fishing attitude. The netting has circular openings about three mm in diameter. Flow and net-frame angle allow computation of the water volume filtered. Generally a set of five nets were used on the *Knorr* cruises. One net usually was fished down to 1000 m, then closed, and a second opened and fished from 1000 to 750 m, with successive nets closed and opened at 250 m depth intervals back to the surface. A single net with a time-depth recorder attached was fished down to 1000 m and back on *Endeavor* 11.

The original plan for the time-series cruises had been to chose a recently formed cold-core ring and make repeated observations in it over the course of a year. Observations were begun on *Knorr* 62 in December 1976 in a reasonably well-developed, peanut-shaped ring that we called "Al", judged (from the U.S. Naval Oceanographic Office's Experimental Ocean Frontal Analysis (EOFA)) to have formed the previous September. These observations were made, it later proved, just as the ring was dividing in two. The smaller part (min. d. 15°C-440 m), dubbed "Art", coalesced with the Gulf Stream within a few weeks and disappeared eastward. The larger, colder part (min. d. 15°C-275 m), called "Al", moved in a wide circle for about three months and then, in stages, coalesced with the Gulf Stream and disappeared (Hagan *et al.*, 1978; Richardson *et al.*, 1979). Some observations, including two midwater trawls, were made in "Al" during *Knorr* 65 (April 1977), just before the ring's final reincorporation with the Stream. At that time the ring was small and moving rapidly to the northeast.

Because of "Al's" demise, principal attention on *Knorr* 65, April 1977, was payed to "Bob", whose formation had been particularly well observed by infrared satellite imagery (EOFA) just a few weeks before. The *Knorr*-65 observations of "Bob" (min. d. 15°-40 m) were made during a period of strong interaction between the young ring and the Gulf Stream. "Bob" finally separated from the Stream for the second time early in May. Observations in "Bob" continued on *Endeavor* 11 in July and August 1977 (min. d. 15°-105 m), but by mid-September "Bob" had moved far to the west and been swallowed up by the Gulf Stream just off Cape Hatteras.

With "Bob" gone, other rings were sought on *Knorr* 71 in October and November 1977. "Emerson" ("Em"), min. d. 15°-240 m and of unknown age, proved to be a rather weak anomaly. "Franklin" ("Frank"), min. d. 15°-150 m, also of unknown age, proved more interesting and was the principal object of study on this cruise.

Because of the continually changing strategy, the distribution of the trawls is very irregular. Generally speaking, there were three classes of trawls: ones made in rings, ones made in Slope Water, and ones made in the Northern Sargasso Sea. Three subsets of rings collections can be distinguished: collections made in the center of rings (within 20 nautical miles of the very center, generally much closer), those made on the flanks of rings, that is, at places midway between the ring center and ring edge (the latter defined as the place where the relevant isotherms become flat), and those made on the ring fringe, that is, more or less close to the ring edge. When the collections have been apportioned according to ring, location with respect to ring center, season, and time of day, they are relatively few.

The myctophids and "gonostomatids" (except species of *Cyclothone*) were identified for each collection and abundances (catch per unit volume for the 1000 m water column) calculated. The range of standard lengths and displacement volume for each species lot was measured. For most myctophid species the standard length of all specimens was taken.

4. Results and discussion

A convenient way of expressing the magnitude of the cold-core ring anomaly is to give for the ring the minimum depth of the 15°C isotherm (min. d. 15°). In the Slope Water this isotherm can intersect the surface, while at the other extreme in the Sargasso Sea its depth is about 700 m. Thus, the shallower 15°C within a cold-core ring, the stronger the anomaly; for a given ring, the depth to 15° increases with time and with distance from the ring center. In the results presented below properties of collections are considered mainly as a function of depth to 15°. Furthermore, for certain considerations the collections have been divided into three sets according to the depth to 15°—those in which this depth is: (1) < 100 m, (2) 100-450 m, and (3) > 450 m. The first set (12 stations) contains all of the Slope Water stations and two from the center of newly formed ring "Bob"; the second set (15 stations) contains those from the center of five-month-old "Bob" and other rings believed not to be newly formed, plus two of the three stations classified as being on the ring flank. The third set (12 stations) contains all of the Sargasso Sea stations, the three classified as being on the ring fringe, and one of the ring flank stations.

Biomass

Figure 1 shows the biomass (ml/10,000 m³ for the water column 0-1000 m) of myctophids plus "gonostomatids" (excluding *Gonostoma elongatum* and *Cyclothone* spp.) for the several stations plotted against the depth to 15°C. The general inverse relation between biomass and depth to 15° is evident and shows the reduction in standing crop by several fold that others have described in going from Slope Water to Northern Sargasso Sea (Grice and Hart 1962 for epizooplankton, about 4:1, Jahn and Backus 1976 for mesopelagic fishes with about 60 percent of the fishing effort above 200 m, about 4.5:1; Jahn, 1976 for mesopelagic fishes 0-1000 m, about 2:1, and Ortner *et al.* 1978 for zooplankton 0-750 m, 3.5:1). The Slope Water and ring center stations are quite variable, while the ring flank, ring fringe, and Northern Sargasso Sea stations are uniformly low.

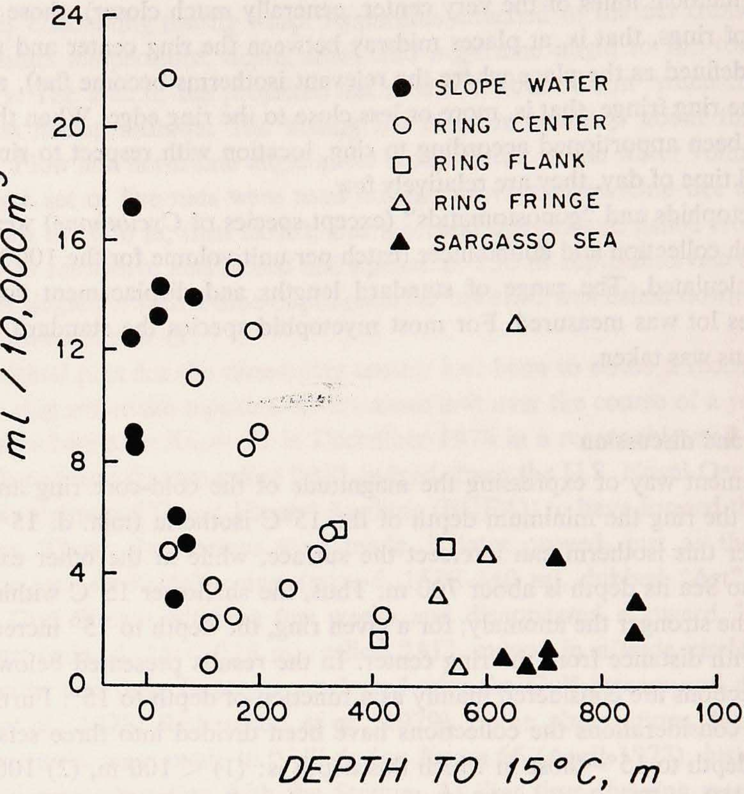

Figure 1. Myctophid-"gonostomatid" biomass as a function of depth to 15°C. The four points to the left of depth zero represent stations at which the surface temperature was less than 15°.

On *Knorr* 65 (April 1977) the myctophid-"gonostomatid" biomass showed a ratio of about 4.5:1 between Slope Water (6.0, 13.1, and 14.2) and Northern Sargasso Sea (1.9 and 2.9) (Fig. 1). Newly formed "Bob" (4.8 and 21.7) appeared to be like the Slope Water. On *Endeavor* 11 (August 1977) the Slope Water (3.1 and 5.1)-Northern Sargasso Sea (0.7, 0.8, 1.0, and 1.1) ratio was about 4:1. Ring "Bob", now a few months old, was intermediate (0.7, 2.0, 2.2, 2.5, and 3.6). (One-sided Mann-Whitney U tests show that it is probable ($p=.1$) that the average value for the ring set is intermediate between the other two.)

Biomass data for the deep-living *Cyclothone* spp. (Fig. 2) suggests a relationship among the sets similar to that for myctophids-"gonostomatids", but the Slope Water-Northern Sargasso Sea ratio appears to be less—2 or 3:1, rather than 4 or 5:1. The catches for MOC10-27, 28, 32, and 33, in the center and on the flank of newly formed "Bob", are exceptionally large. The myctophid-"gonostomatid" biomasses for these same stations are not unusual except for MOC10-28, which is the largest for any station.

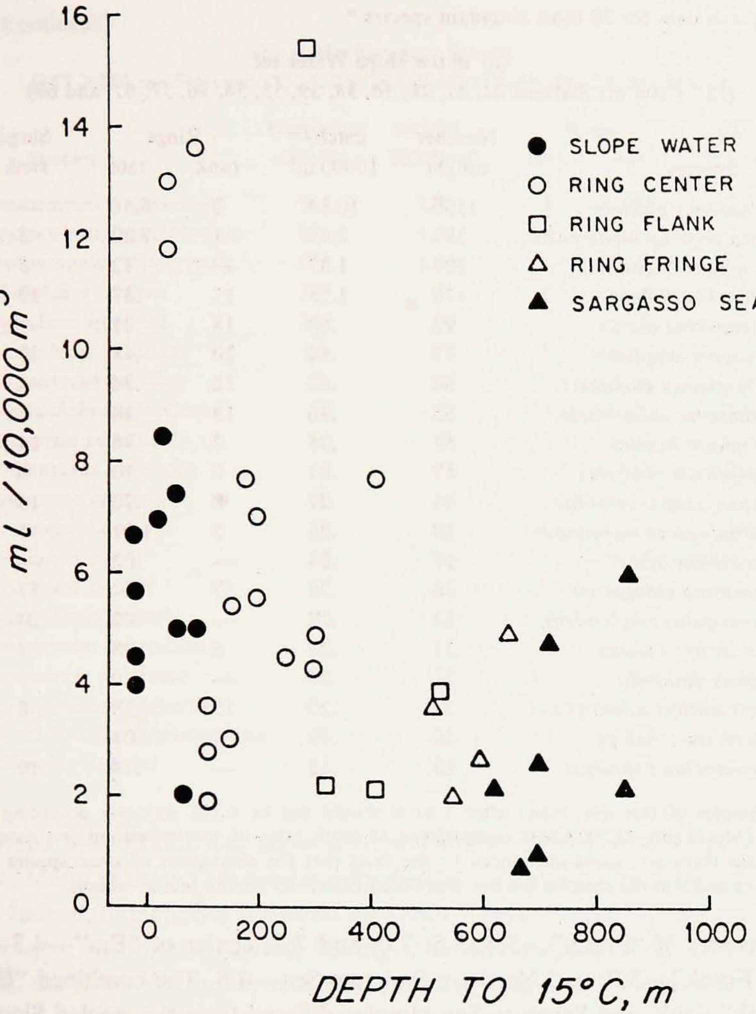

Figure 2. *Cyclothone* spp. biomass as a function of depth to 15°C. The four points to the left of depth zero represent stations at which the surface temperature was less than 15°. The four high points, from the center and flank of Ring "Bob", are considered exceptional. They may be within the normal range of variation for the Slope Water, although they exceed the Slope Water values observed on the Rings Cruises.

On *Knorr* 71 (October-November 1977), the center of "Frank" (min. d. 15°C-150 m) had a myctophid-"gonostomatid" biomass (8.5, 9.0, 12.7, and 14.9 ml/10,000 m^3) comparable to that of the Slope Water (8.6, 9.0, 12.5, and 17.2), while the center of "Em", min. d. 15°C-240 m, (3.5 and 4.7), the flank of "Frank" (4.9), and the Sargasso Sea (4.6) were lower and similar to one another. The *Cyclothone* spp. biomass varied among these sets in the same way: Slope Water—4.0, 4.5, 5.7,

Table 1. Catch data for 20 most abundant species.*

(a) in the Slope Water set
(15° <100 m: Stations 24, 27, 28, 36, 38, 39, 53, 54, 56, 57, 67, and 68)

Rank	Species	Number caught	catch/ 10000 m³	Rings rank	Rings rate	Sargasso Sea rank	Sargasso Sea rate
1.	*Benthosema glaciale*	1550	10.14	2	5.56	—	.03
2.	*Ceratoscopelus maderensis*	381	2.49	1	7.29	3	1.00
3.	*Hygophum hygomii*	209	1.37	—	.12	5	.95
4.	*Lobianchia dofleini*	176	1.15	11	.37	19	.24
5.	*Lampanyctus alatus*	92	.60	18	.21	—	.14
6.	*Sternoptyx diaphana*	77	.50	20	.18	12	.42
7.	*Lepidophanes guentheri*	64	.42	12	.34	—	.20
8.	*Benthosema suborbitale*	55	.36	19	.18	—	.14
9.	*Hygophum benoiti*	53	.35	7	.96	14	.34
10.	*Notolychnus valdiviae*	47	.31	9	.50	6	.73
11.	*Lampanyctus crocodilus*	41	.27	8	.70	16	.32
12.	*Ceratoscopelus warmingii*	39	.26	5	1.01	1	2.38
13.	*Myctophum affine*	37	.24	—	.02	—	.02
14.	*Gonostoma elongatum*	36	.24	17	.24	11	.44
15.	*Notoscopelus resplendens*	34	.22	—	.02	20	.24
16.	*Bolinichthys indicus*	31	.20	6	.98	4	.97
17.	*Diaphus dumerilii*	31	.20	—	0	—	.02
18.	*Diogenichthys atlanticus*	31	.20	15	.28	8	.55
19.	*Hygophum taaningi*	29	.19	—	.08	—	.15
20.	*Lampanyctus cuprarius*	28	.18	—	.14	10	.45

* With samples of this size, ranks after 5 or 6 should not be taken seriously according to Miller and Wiebe (McGowan, 1971). Close comparisons of catch rates of species among sets should not be made, because there are biases introduced by the facts that the abundance of some species is a function of season and that the samples are not distributed uniformly among sets by season.

and 6.7; center of "Frank"—5.4, 5.5, 7.0, and 7.7; center of "Em"—4.3 and 4.5; flank of "Frank"—3.9; and Northern Sargasso Sea—4.8. The combined "Em" center, "Frank" flank, and Sargasso Sea samples differed from the pooled Slope Water and "Frank" center ones according to Mann-Whitney U tests ($p=.01$ for the myctophid-"gonostomatid" biomass and $p=.1$ for the *Cyclothone* spp. biomass in two-sided tests).

The samples are too few and their depth resolution too coarse to show whatever systematic change there may be in the depth distribution of the mid-water fish biomass in going from Slope Water to rings to Sargasso Sea, although a downward shift is suggested as has been noted for zooplankton taken with the MOCNESS-1 (Ring Group, 1981).

The three fish faunas

a. Slope Water. The hydrographic complexity of the Slope Water (Wright, 1978) is paralleled by its ichthyofaunal complexity. The 20 most abundant species in the

Table 1. (continued)

(b) in the Sargasso Sea set

(15° >450 m: Stations 23, 25, 26, 29, 30, 43, 44, 45, 46, 52, 63, and 64)

Rank	Species	Number caught	catch/ 10000 m³	Rings rank	Rings rate	Slope Water rank	Slope Water rate
1.	*Ceratoscopelus warmingii*	311	2.38	5	1.01	12	.26
2.	*Argyropelecus hemigymnus*	171	1.31	4	1.53	—	.16
3.	*Ceratoscopelus maderensis*	131	1.00	1	7.29	2	2.49
4.	*Bolinichthys indicus*	127	.97	6	.98	16	.20
5.	*Hygophum hygomii*	125	.95	—	.12	3	1.37
6.	*Notolychnus valdiviae*	96	.73	9	.50	10	.31
7.	*Lampanyctus pusillus*	78	.60	3	1.62	—	.16
8.	*Diogenichthys atlanticus*	72	.55	15	.28	18	.20
9.	*Bonapartia pedaliota*	66	.50	—	.04	—	0
10.	*Lampanyctus cuprarius*	59	.45	—	.14	20	.18
11.	*Gonostoma elongatum*	58	.44	17	.21	14	.24
12.	*Sternoptyx diaphana*	55	.42	20	.18	6	.50
13.	*Pollichthys mauli*	52	.40	—	.08	—	0
14.	*Hygophum benoiti*	45	.34	7	.96	9	.35
15.	*Lepidophanes gaussi*	43	.33	—	.13	—	.01
16.	*Lampanyctus crocodilus*	42	.32	8	.70	11	.27
17.	*Vinciguerria attenuata*	42	.32	10	.49	—	.10
18.	*Argyropelecus aculeatus*	36	.28	13	.31	—	.07
19.	*Valenciennellus tripunctulatus*	35	.27	14	.30	—	.18
20.	*Lobianchia dofleini*	32	.24	11	.37	—	1.15

set described here (Table 1a) show diverse patterns so far as their Atlantic-wide ranges go. Many of them (14) are broadly distributed in the tropical and subtropical Atlantic. Indeed, four species (*Diaphus dumerilii, Lampanyctus alatus, Lepidophanes guentheri,* and *Myctophum affine*), having otherwise *tropical* ranges, may also reproduce in the Slope Water. However, the basically temperate character of the Slope Water fauna is well shown by the fact that the four most abundant species in the set of 20 most abundant, accounting for 77% of the specimens in the set, are of *subpolar-temperate* (*Benthosema glaciale*, 51% of the total number of specimens in the set), *temperate* (*Ceratoscopelus maderensis*, 13%), and *temperate-semisubtropical* (*Hygophum hygomii* and *Lobianchia dofleini*, 13%) distribution pattern.

Jahn and Backus (1976) described the Slope Water midwater fish fauna from two dozen collections (in which the depth to 15°C was less than 200 m.) The three most abundant species in their set (*Lobianchia dofleini, Benthosema glaciale*, and *Ceratoscopelus maderensis*) are among the top four in the Slope Water set at hand.

b. Northern Sargasso Sea. The 20 most abundant species in the "Sargasso Sea" set (Table 1b) show more equitable abundances of species compared with the Slope Water. This difference had been noted earlier by Jahn and Backus (*op. cit.*). The

Table 1. (continued)

(c) in the Rings set

(15° depth 100-450 m: Stations 20, 22, 35, 42, 47, 48, 49, 50, 51, 58, 59, 61, 62, 65, and 66)

Rank	Species	Number caught	catch/ 10000 m³	Slope Water rank	Slope Water rate	Sargasso Sea rank	Sargasso Sea rate
1.	*Ceratoscopelus maderensis*	1223	7.29	2	2.49	3	1.00
2.	*Benthosema glaciale*	933	5.56	1	10.14	—	.03
3.	*Lampanyctus pusillus*	272	1.62	—	.16	7	.60
4.	*Argyropelecus hemigymnus*	256	1.53	—	.16	2	1.31
5.	*Ceratoscopelus warmingii*	169	1.01	12	.26	1	2.38
6.	*Bolinichthys indicus*	164	.98	16	.20	4	.97
7.	*Hygophum benoiti*	161	.96	9	.35	14	.34
8.	*Lampanyctus crocodilus*	117	.70	11	.27	16	.32
9.	*Notolychnus valdiviae*	84	.50	10	.31	6	.73
10.	*Vinciguerria attenuata*	82	.49	—	.10	17	.32
11.	*Lampanyctus photonotus*	70	.42	—	.07	—	.23
12.	*Lobianchia dofleini*	62	.37	4	1.15	19	.24
13.	*Lepidophanes guentheri*	57	.34	7	.42	—	.20
14.	*Argyropelecus aculeatus*	52	.31	—	.07	17	.28
15.	*Valenciennellus tripunctulatus*	51	.30	—	.18	18	.27
16.	*Diogenichthys atlanticus*	47	.28	18	.20	8	.55
17.	*Diaphus mollis*	43	.26	—	.04	—	.16
18.	*Gonostoma elongatum*	36	.21	14	.24	11	.44
19.	*Lampanyctus alatus*	36	.21	5	.60	—	.14
20.	*Benthosema suborbitale*	30	.18	8	.18	—	.14

four most abundant species account for only 45% of the total, while 10 to 11 species are required to account for the 77% of the total that the four most abundant species in the Slope Water set comprised.

The distribution patterns for the first ten fish on the list are, with one exception, those to be expected for a subtropical faunal province: *tropical—subtropical* (*Ceratoscopelus warmingii* and *Bonopartia pedaliota*, 23% of total specimens), *tropical-subtropical-temperate* (*Argyropelecus hemigymnus* and *Notolychnus valdiviae*, 16%), *temperate-semisubtropical* (*Hygophum hygomii* and *Lampanyctus pusillus*, 13%), *subtropical* (*Bolinichthys indicus* and *Lampanyctus cuprarius*, 12%), and *tropical-subtropical—Slope Water* (*Diogenichthys atlanticus*, 4%). A *temperate* species, *Ceratoscopelus maderensis*, 8%, is the exception. It occurs in the Sargasso Sea set by virtue of a single very large lot and is discussed below.

Jahn and Backus (*op. cit.*) described the midwater fish fauna of the Northern Sargasso Sea from 20 collections. The most abundant species in their set, *Ceratoscopelus warmingii*, is the same in ours, and their top four fall within our top eight.

c. Rings. The Rings set of most abundant species (Table 1c) comes from a very variable environment and, therefore, is to some extent an artificial assemblage. It shows a mix of distribution patterns as is to be expected. Nevertheless, it is probably significant that the top six species in the set include the two most abundant from the Slope Water set (*Benthosema glaciale* and *Ceratoscopelus maderensis*) *and* the four most abundant from the Sargasso Sea set (*Ceratoscopelus warmingii, Argyropelecus hemigymnus, Ceratoscopelus maderensis,* and *Bolinichthys indicus*). The third most abundant species in the Rings set, *Lampanyctus pusillus,* is thought to be an exploiter of rings and is more abundant there than in either Slope Water or Sargasso Sea (see below).

The first four most abundant species comprise 69% of the total number of specimens in the set, the first 10, 89%. Thus, the Rings set is more like the Slope Water one than the Sargasso Sea one so far as equitability of abundances of species goes.

The similarity of the three sets to one another was calculated. The greatest similarity exists between Slope Water and Rings (50.0%), with *Benthosema glaciale* and *Ceratoscopelus maderensis* making the greatest contributions to the similarity (24.0 and 12.5%, respectively). The similarity of the Rings set to the Sargasso Sea set was 42.6%. There were no outstanding contributors to the similarity in keeping with the more equitable distribution of abundances of species in the Sargasso Sea. The similarity of Slope Water and Sargasso Sea sets was lowest—30.4%. It would have been lower still but for the exceptional occurrence of *Ceratoscopelus maderensis* in the Sargasso Sea already noted.

Faunal changes with ring age

a. The disappearance of the cold-water fishes. The *subpolar-temperate* species *Benthosema glaciale* was of premier abundance in the Slope Water set and second in abundance in the Rings set. It is known to spawn in the Slope Water (Halliday, 1970) and others have noted both its great abundance and the high fidelity with which it is found in collections there (Jahn and Backus, 1976; Nafpaktitis *et al.*, 1977). In contrast, it occurs so little in the Northern Sargasso Sea (Nafpaktitis *et al.*, *op. cit.*) as to suggest that it gets there principally through the agency of cold-core rings. In the "Ocean Acre" at Bermuda less than a hundred specimens of *B. glaciale* were taken; their sizes showed them to be expatriates, presumably from the Slope Water; none was taken shallower than 750 m and all adults were male (Karnella, in preparation). Furthermore, the species shows a well-developed diel vertical migration. Halliday (1970) found the center of abundance of the Slope Water population south of Nova Scotia to move from deeper than 250 fm (457 m) by day to between 25 and 50 fm (46-91 m) by night. A similar movement is reported for the western Mediterranean population—from a daytime maximum around 500 m to a nighttime one between 50 and 70 m (Goodyear *et al.*, 1972). For these reasons the species is well suited for illustrating the behavior and fate of certain Slope Water animals of the upper few hundred meters that are intolerant of conditions in the Sargasso Sea.

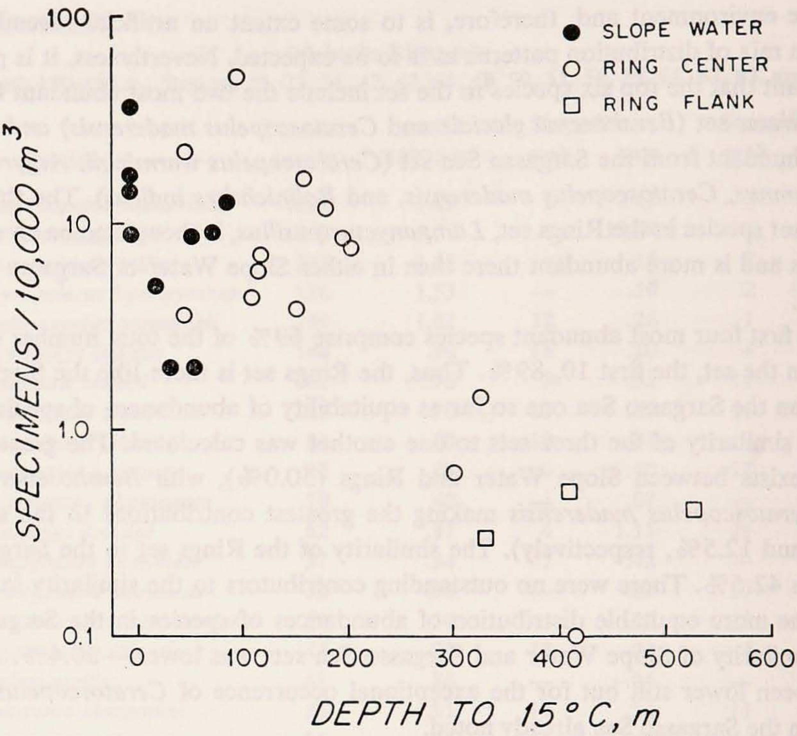

Figure 3. Catch rate for the myctophid *Benthosema glaciale* as a function of depth to 15°C. The four points to the left of depth zero represent stations at which the surface temperature was less than 15°. Eleven ring-fringe and Sargasso Sea stations with depths to 15° of 515 m or more have no *B. glaciale*.

Jahn (1976, p. 76) states that in cold-core rings *B. glaciale* "decreases gradually in numbers with ring age." This agrees with our findings. In the collections reported here there is a strong inverse relationship between catch rate and depth to the 15° isotherm (Fig. 3). The species occurred at all stations made in the Slope Water, in ring centers and on ring flanks with the exception of the station made near the center of old ring "Dave" (MOC10-40, min. d. 15°-305 m and where the maximum depth reached by the net was less than 400 m). As the depth to 15° deepened beyond about 150 m, the fish rapidly became more and more restricted to the deeper parts of the water column. At 15°-isotherm depths greater than about 250 m no specimens were found shallower than 500 m. At stations with 15°-isotherm depths greater than about 525 m, that is, on the ring fringe and in the Sargasso Sea, none at all were found within the depth range sampled.

A similar change in vertical distribution and abundance with ring age has been described for other *subpolar-temperate* animals, e.g., the euphausiid *Nematoscelis* *megalops* (Wiebe and Boyd, 1978), and the copepod *Paraeuchaeta norvegica* (Ring Group, 1981).

Another abundant myctophid normally finding the southern limit of its range in the western North Atlantic at the boundary between Slope Water and Gulf Stream is *Ceratoscopelus maderensis*. Called *temperate-semisubtropical* by Backus *et al.* (1977) and Nafpaktitis *et al.* (1977) before the role of cold-core rings in dispersing the species was understood, it is better classed as *temperate*. This species was abundant in all three sets, although its occurrence in the Sargasso Sea set was almost wholly limited to a single large lot.

As an adult, at least, *C. maderensis* forms schools that occur irregularly in the Slope Water (Backus *et al.*, 1968). Jahn (1976) described the fish as "an abundant Slope Water species showing extreme fluctuations in numbers." These facts of its existence suggest that the *C. maderensis* may appear irregularly in the cores of newly formed cold-core rings; the observations reported here bear this out.

Generally speaking, juvenile *C. maderensis* 15-20 mm long were abundant in Slope Water and in the center of rings from August to December. In rings, catch decreased with distance from the ring center as expected. The most interesting data come from *Knorr* Cruise 71 in October-November when day-night pairs of Slope Water stations at two widely separated localities gave 1.1 (night) and 1.5 (day) and 6.2 (night) and 7.7 (day) specimens per 10,000 m^3. At this time, "Emerson" (min. d. 15°-240 m) lacked *C. maderensis* entirely, while "Frank" (230 n. mi. southeast with min. d. 15°-150 m) gave the highest catch-rates observed during the Rings cruises—7.6, 10.2, 15.1, and 22.9 specimens per 10,000 m^3. A moderately high rate (3.5) obtained on the flank of Frank (MOC10-64 about 40 n. mi. east of the ring center, d. 15° 510-540 m), while the only Sargasso Sea stations from all the Rings cruises to have significant numbers of *C. maderensis* were MOC10-60 (d. 15°-740 m) about 100 n. mi. southwest with catch-rate 4.9 and MOC10-63 (d. 15°-720 m) 70-75 n. mi. east of the center of "Frank" with catch-rate 1.6. It is suggested that the fish at these stations had been detrained earlier from "Frank". Those in 63 mostly lay in the interval 750-1000 m (84 per cent), while those in the center of "Frank" mostly lay in the interval 500-750 m by day and by night. These data support the model by Schmitz and Vastano (1975) of the upper 1000 m of aging cold-core rings, which suggests that water flows in above about 600 m with a compensating outward flow below this depth, as well as the observations of Wiebe and Boyd (1978), who suggested outward motion between 500 and 800 m from the occurrence of supposedly detrained *Nematoscelis megalops*.

b. The invasion by warm-water fishes. The invasion of an aging ring by the mid-water fishes of the Northern Sargasso Sea is not so conspicuous as the disappearance of cold-water fishes from the ring. This is so, because certain warm-water fishes are regular inhabitants of the Slope Water (as has been noted above) and, as such, can

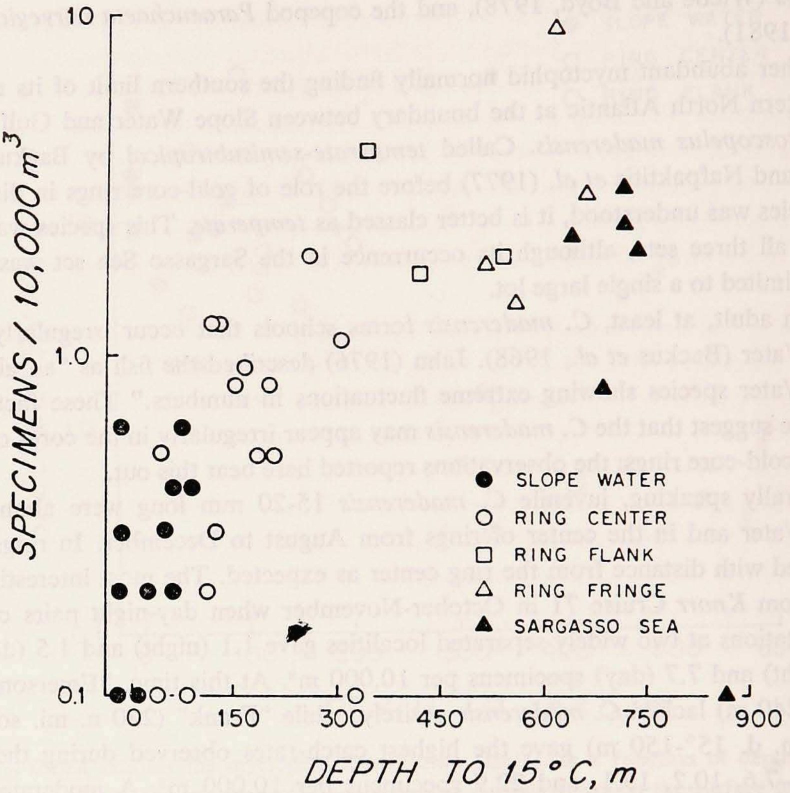

Figure 4. Abundance of the myctophid *Ceratoscopelus warmingii* as a function of depth to 15°C. The four points to the left of depth zero represent stations at which the surface temperature was less than 15°.

already occur in the center of a ring at the time of its formation. Thus, the *tropical-subtropical* myctophid *Ceratoscopelus warmingii*, the most abundant species in the Sargasso Sea set, is found, though in much lesser abundance, in the Slope Water set (Table 1); but *C. warmingii*'s abundance increases rapidly as the depth to 15°C increases (Fig. 4) and abundance in the Rings set is intermediate (Table 1).

The second most-abundant species in the Sargasso Sea set, the hatchetfish *Argyropelecus hemigymnus*, is of low abundance in the Slope Water, while Sargasso Sea and Rings abundances are higher and not different from one another. (The probabilities in Mann-Whitney U tests that the Slope Water set differs from the Rings and Sargasso sets are both $< .01/2$.) A moderate catch-rate of *A. hemigymnus* already obtained at MOC10-20 in the center of 3-month old "Al". Thus, the incorporation of this species into rings seemed to take place rapidly even though the species occurred but little above 250 m.

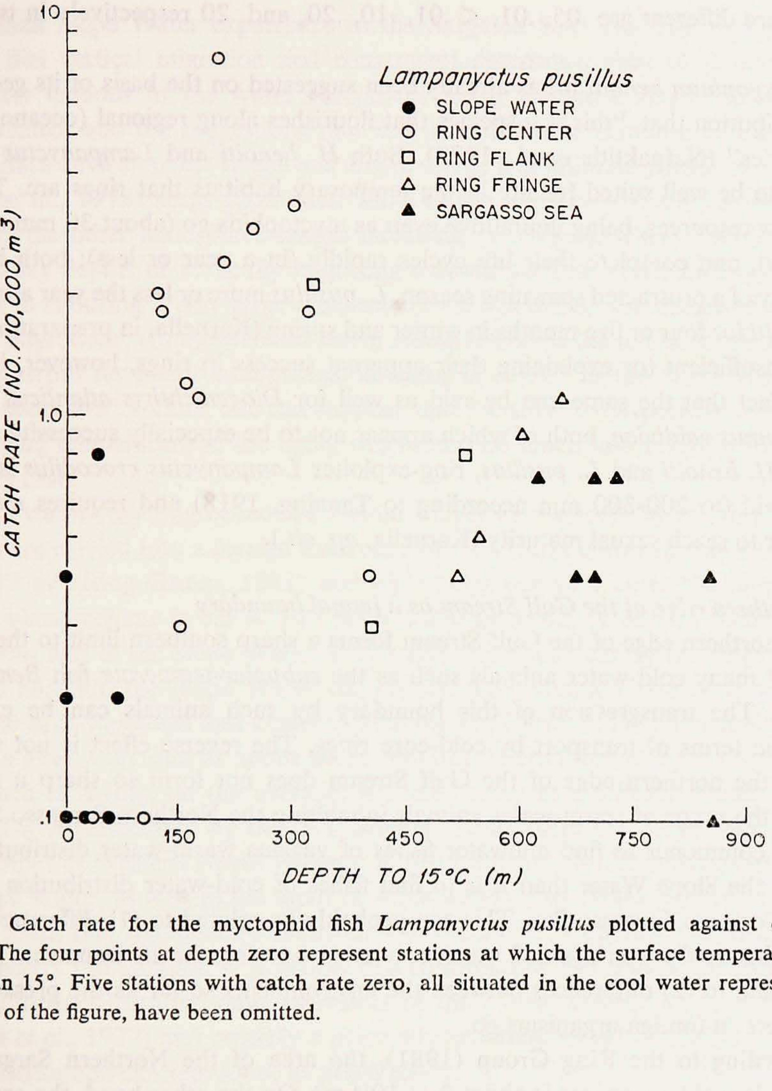

Figure 5. Catch rate for the myctophid fish *Lampanyctus pusillus* plotted against depth to 15°C. The four points at depth zero represent stations at which the surface temperature was less than 15°. Five stations with catch rate zero, all situated in the cool water represented at the left of the figure, have been omitted.

Ring-exploiting fishes

One might look for species that take advantage of the special, changing conditions in the disturbed environments that are rings. To do this we have examined the relative abundance in rings, Slope Water, and Northern Sargasso Sea of those species that are both abundant and whose normal range includes both the Slope Water and the Northern Sargasso Sea. Three species *Lampanyctus crocodilus, L. pusillus* (Fig. 5), and *Hygophum benoiti*, are more abundant in rings than in the other two environments judging from Mann-Whitney U tests (for the Slope Water-rings and Sargasso Sea-rings comparisons for the three species the probabilities that the abundances are different are .05, .01, < .01, .10, .20, and .20 respectively in two-sided tests).

Of *Hygophum benoiti* it has already been suggested on the basis of its geographical distribution that, "this is a species that flourishes along regional (oceanographic) boundaries" (Nafpaktitis *et al.*, 1977). Both *H. benoiti* and *Lampanyctus pusillus* appear to be well suited for life in the temporary habitats that rings are. They require few resources, being diminutive even as myctophids go (about 30 mm at sexual maturity), and complete their life cycles rapidly (in a year or less); both have the flexibility of a protracted spawning season, *L. pusillus* more or less the year around and *H. benoiti* for four or five months in winter and spring (Karnella, in preparation). That this is insufficient for explaining their apparent success in rings, however, is shown by the fact that the same can be said as well for *Diogenichthys atlanticus* and for *Notolychnus valdiviae*, both of which appear not to be especially successful in rings. Unlike *H. benoiti* and *L. pusillus*, ring-exploiter *Lampanyctus crocodilus* is a large myctophid (to 200-300 mm according to Taaning, 1918) and requires more than one year to reach sexual maturity (Karnella, *op. cit.*).

The northern edge of the Gulf Stream as a faunal boundary

The northern edge of the Gulf Stream forms a sharp southern limit to the normal range of many cold-water animals such as the *subpolar-temperate* fish *Benthosema glaciale*. The transgression of this boundary by such animals can be explained readily in terms of transport by cold-core rings. The reverse effect is not so clear; that is, the northern edge of the Gulf Stream does not form so sharp a northern limit to the range of warm-water animals inhabiting the Northern Sargasso Sea, and it is far commoner to find midwater fishes of various warm-water distribution patterns in the Slope Water than it is to find fishes of cold-water distribution patterns in the Northern Sargasso Sea. This can probably be related to (1) differences in the effects that cold-core rings and warm-core rings have on the environments that they invade and to (2) differences between the environments so far as the pressures that they exert on foreign organisms go.

According to the Ring Group (1981), the area of the Northern Sargasso Sea affected by cold-core rings is about 3×10^{12} m². On the other hand, the area of the Slope Water, into which warm-core rings intrude, is only about 0.5×10^{12} m² (Jahn, 1976). If mass is balanced by the formation of a warm-core ring for each cold-core ring formed, then the gross effect of warm-core rings on the Slope Water is about six times that of cold-core rings on the Northern Sargasso Sea. Thus, even if the midwater fish biomass of the Slope Water be three times that of the Northern Sargasso Sea, expatriates from the Sargasso Sea would be twice as available to samplers in the Slope Water as Slope Water expatriates to samplers in the Sargasso Sea assuming equal survival and uniform dispersal.

Further, one can suppose that Sargasso Sea expatriates in the Slope Water survive longer than Slope Water expatriates in the Sargasso Sea. The interruption of the normal diel vertical migration and consequent downward shift of populations of cold-water animals in the water column of aging cold-core rings has been well demonstrated, and the suggestions that this behavior is in response to too warm a near-surface environment (Wiebe and Boyd, 1978) and ultimately leads to starvation (Boyd, *et al.*, 1978) seem good ones. Most of the expatriate species in warm-core rings, on the other hand, have ranges including the tropics, where temperatures at the mid-day depths of vertically migrating animals are low; thus, such animals are adapted to enduring a very large temperature change during the course of their diel vertical migrations. (In the western North Atlantic tropics the temperature at 700 m, mid-day depth for many mesopelagic animals, is 6-7°C; in the Slope Water, little cooler, about 4-5°.) Thus, one can suppose that the stress on expatriate animals due to changing temperature in the aging ring would be much less severe in the warm-core ring case.

But, a warm-core ring cannot be viewed simply as a vehicle by which plants and animals are carried into a foreign environment. If a warm-core ring has a volume of 3×10^{13} m^3 (Ring Group, 1981) and eight rings per year enter the Slope Water (*ibid.*), whose volume is 0.5×10^{12} m^2 $\times$ 1000 m or 0.5×10^{15} m^3 (Jahn, 1976), then about half of the Slope Water will be replaced each year by the rings were the rings to mix into the Slope Water completely. The common fate of a warm-core ring is to drift westward and coalesce with the Gulf Stream in the vicinity of Cape Hatteras after a lifetime of about seven months. There seem to be no estimates of how much of a ring, on the average, is mixed away in the Slope Water and how much of it is reabsorbed by the Gulf Stream. Thus, there is a large, virtually continual, input of Western North Atlantic Water from the Northern Sargasso Sea into the Slope Water, as well as the input of some water of tropical origin from the Gulf Stream itself, that significantly contributes to the Slope Water's character as a habitat for plants and animals. It is mainly this contribution that makes the Slope Water faunally distinct from the other provinces of the North Atlantic Temperate Region (Backus *et al.*, 1977) and possibly a place where certain animals of otherwise warm-water distribution can reproduce as noted above.

5. Summary

1. About 140 collections from which abundance could be calculated were made with midwater trawls at 40 stations in and around cold-core rings on cruises between December 1976 and November 1977. The data were considered in relation to the depth to 15°C, which increases in going from the Slope Water to the Northern Sargasso Sea and so is expressive of the strength of the cold-core ring anomaly.

2. Both myctophid-"gonostomatid" and *Cyclothone* biomass decrease with increasing depth to 15° and are about 4.5:1 and 2.5:1 respectively comparing Slope Water and Northern Sargasso Sea. Rings values are very variable.

3. Slope Water (d. 15° < 100 m), Northern Sargasso Sea (d. 15° > 450 m), and Rings (d. 15° 100-450 m) fish faunas are described. Four species of cold-water species make up 77% of the individuals caught in the Slope Water, but many species of warm-water fishes occur there in low numbers. Species abundances are more equitable in the Northern Sargasso Sea than in the Slope Water and 10 to 11 species are needed there to account for 77% of the individuals caught. The species caught in the Northern Sargasso Sea are of distribution patterns to be expected for a subtropical faunal province. The Rings fauna is a mixture and contains the most abundant species from both the Slope Water and Northern Sargasso Sea sets.

4. *Benthosema glaciale,* a *subpolar-temperate* species and the most abundant species in the Slope Water, became more and more restricted to the deepest parts of an aging cold-core ring and finally disappeared altogether, as has been observed for other cold-water animals. Specimens of the cold-water myctophid *Ceratoscopelus maderensis,* thought to have been detrained from a ring, were caught in the Sargasso Sea. Warm-water fishes rapidly became abundant in the upper few hundred meters of aging cold-core rings.

5. Three myctophids, *Lampanyctus crocodilus, L. pusillus,* and *Hygophum benoiti,* more abundant in the Rings set than in either Slope Water or Northern Sargasso Sea sets, appeared to be exploiters of rings.

6. There was evidence from Ring "Frank", of unknown age, that cold-water animals had been detrained from the ring at depths near 600 m and from three-month old Ring "Al" that the entrainment of warm-water animals can take place at depths in excess of 250 m in rings of this age.

7. Because the area into which warm-core rings intrude is much smaller than the area into which cold-core rings intrude, the gross effect of the former is thought to be much greater than the latter. This notion is used to explain, in part, why warm-water fishes are more evident in the Slope Water than cold-water fishes are in the Northern Sargasso Sea.

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