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SPATIAL AND TEMPORAL DISTRIBUTION OF ANGUILLA ROSTRATA AND ANGUILLA ANGUILLA LEPTOCEPHALI FOUND IN NORTH AMERICAN ICHTHYOPLANKTON COLLECTIONS

by

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Abstract

Data, including specimen size and myomere number, date, place, and depth of collection, were gathered from 1903 *Anguilla rostrata* and 866 *A. anguilla* leptocephali found in North American ichthyoplankton collections. Reexamination of specimens reported by Vladykov and March (1974) revealed that the low myomere frequencies which they described are artifacts of technique.

A. Anguilla leptocephali were found as far west as 76° 31' W (a new record). The presence of other large (70 mm) *A. anguilla* leptocephali within 125 nautical miles of the Nova Scotia coast suggests that some *A. anguilla* may migrate into North American waters following metamorphosis.

Small ($<$ 20 mm) *A. rostrata* leptocephali were taken to the northeast of the Bahama Island chain and Hispaniola; the area outlined by Schmidt (1925) as positive for small *A. rostrata*. The presence of 11 to 17 mm *A. rostrata* leptocephali in the Yucatan Channel suggests that some spawning takes place in the Caribbean sea. The peak spawning period extends from late January to early March.

Large numbers of *A. rostrata* leptocephali are found in the Gulf Stream between June and October after which they begin to approach the coast. Some are found far to the east in the North Atlantic drift circulation. One 70 mm *A. rostrata* leptocephalus was collected at 20° 45' W, 49° 45' N. The *A. rostrata* growth phase averages 8 to 9 months.

A. rostrata leptocephali averaging $>$ 30 mm in length are concentrated at depths $<$ 100 m in night collections from the Gulf Stream. The depth distribution of daytime sampling effort was to deep to collect *A. rostrata* leptocephali.

INTRODUCTION

Ancillary to his study on the breeding place of the European eel, *Anguilla anguilla*, Schmidt (1922, 1925) reported on the distribution and biology of American eel, *A. rostrata*, leptocephali. He concluded that *A. rostrata* spawns during the late winter in the area north of the West Indian Islands, that the leptocephalus phase lasts for approximately one year, and that metamorphosis to the elver phase occurs at a smaller size than is the case for *A. anguilla*. Though many of Schmidt's ideas may be correct, few data were presented to substantiate the conclusions.

Vladykov (1964) posed questions concerning the location of spawning and mechanism of larval transport for *A. rostrata*. His analysis of the works of Schmidt (1922, 1925), Jensen (1937), and Bertin (1956), led him to suggest that the spawning ground must be located much farther south than the area suggested by Schmidt. Also, he questioned how the leptocephali and elvers of *A. rostrata* cross the Gulf Stream without being swept away into the northeast Atlantic. On the basis of their examination of *A. rostrata* leptocephali in Canadian and United States oceanographic collections, Vladykov and March (1974) determined that the spawning period must extend from February to July. Furthermore, they strongly suggest that *A. rostrata* leptocephali may spend more than one year at sea before metamorphosis. The question of the location of the spawning ground was not raised in this paper.

Smith (1968) found no specimens of *A. rostrata* in collections made during July in the southern Caribbean Sea between Panama and Trinidad. Three collections made south of 25° N and west of 80° W in Straits of Florida waters flowing from the west were also negative; however, Smith rightly points out that this sampling is insufficient. Farther north and east in the Straits of Florida and adjacent Bahamian waters *A. rostrata* leptocephali were frequently collected between April and August.

It is apparent that many questions exist concerning spawning and leptocephalus migration in *A. rostrata*. In an attempt to answer some of these questions we have gathered data on *Anguilla* leptocephali from available North American sources. This paper reports the preliminary findings of our investigation including time of spawning, spawning areas, rate of leptocephalus growth, occurrence in the Gulf Stream and vertical distribution. Though we are primarily concerned with *A. rostrata*, mention of *A. anguilla* found in these collections is included.

MATERIALS AND METHODS

Specimens and station data were acquired from the following sources:

1) The collections of the Woods Hole Oceanographic Institution held by the Division of Fishes of the Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts, U.S. A. (This includes material collected between August 1953 and February 1979; most of the specimens utilized by Vladykov and March (1974) were reexamined.)

2) Miscellaneous collections of U.S. and Canadian research vessels also held by the Museum of Comparative Zoology;

3) The MARMAP collections of the U.S. National Marine Fisheries Service, Narragansett, Rhode Island, U.S.A.;

4) The Scotian Shelf Survey collections of the Huntsman Marine Laboratory, Saint Andrews, New Brunswick, Canada; and

5) Collections held by Dr. J.W.H. Hain of the University of Rhode Island, Graduate School of Oceanography, Narragansett, Rhode Island, U.S.A.;

6) A publication of Smith (1968). Dr. David Smith kindly provided further station data on this material as well as specimen and station data for new collections of the Marine Biomedical Institute, University of Texas, Galveston, Texas, U.S.A.

A complete listing of specimen and station data utilized in this study will be forthcoming (Kleckner and McCleave, in preparation).

Total length of each specimen was measured from the tip of the mandible to the extremity of the caudal fin. Anteriorly, all myomeres were counted including the five incomplete epaxial myomeres of the branchial region. Caudally, myomeres were difficult to differentiate in smaller specimens. The spinal ganglia, which underlie the myosepta, were used to differentiate myomeres in this region. They were counted beginning with the space between the second and third from the last ganglia and working anteriorly until the separate myomeres are distinct. A myomere was not seen lateral to the space between the first and second from the last spinal ganglia, even in large, well preserved specimens.

Specimens of 102 to 110 and 112 to 119 myomeres are considered to be A. rostrata and A. anguilla respectively. Five specimens with 111 myomeres are omitted from the analysis. Developmental phase was assigned according to Tesch (1977; Table 2).

Figure 1 includes additional data taken from Schmidt (1925; Figs. 13 & 14) for Dana stations 857 (listed incorrectly as 837 in Figure 13 and 827 in the body of the paper (J. Boëtius, personal communication)), 891 and 948. The distribution limits outlined in Figures 2 and 3 are based solely on positive collections. Discrete depth samples discussed were collected with a 3 m multiple opening/closing net system (MOC10) by R.H. Backus and J.E. Craddock of the Woods Hole Oceanographic Institution.

RESULTS AND DISCUSSION

A total of 2009 A. rostrata leptocephali were found in the North American collections (Table 1); 985 are new records. The 899 A. anguilla leptocephali include 580 newly recorded specimens.

Myomere Frequency Distribution. The mean myomere counts of 106.83 and 114.48 for A. rostrata and A. anguilla, respectively, are lower than those of Jesperson (1942) (108.17 and 115.58) and higher than those of Vladykov and March (1974) (105.13 and 111.76) (Table 1). Omission of five specimens with 111 myomeres imparts a small bias to our calculations. Variation in mean myomere counts between studies is clearly due to systematic differences in counting technique. We have reexamined most of the specimens studied by Vladykov and March (1974); their counts (as listed on the sample labels) were consistently lower than our determinations. Furthermore, the relative myomere frequency distribution pattern is the same for all three studies (Table 1). The myomere frequency distribution of A. rostrata is peaked at a single myomere count (Vladykov and March = 105; our study = 107; Jesperson = 108), while that of A. anguilla is peaked at two adjacent myomere counts (111 & 112; 114 & 115; 115 & 116 respectively).

Length Versus Day of Collection. The regression equation, Length = -9.737 + 0.256 (Day) (Fig. 1), gives an estimate of the growth rate for 0+ year class specimens collected during the first 280 days of the year. It is based on a total of 2,672 specimens. The growth rate (regression coefficient) has a 95% confidence interval of 0.252 to 0.261 mm/day. A. rostrata measuring less than 15 mm in length were collected between February 14 and April 27.

Yamamoto et al. (1975a,b) reported that hatched A. japonica leptocephali attain a length of about 6 mm approximately seven days after fertilization. The yolk sac was almost totally absorbed and the initial rapid growth rate had declined by day seven. If A. rostrata follows a similar pattern the peak spawning period may be estimated as one week prior to the day when the regression equation predicts A. rostrata attains a length of 6 mm, about day 51 (February 20). The 13 mm specimen collected on February 14 (45th day) may have been spawned on about January 11; the 7 mm specimens collected on April 27 (119th day) may have been spawned on about April 16 (108th day). The absolute values of these predictions are crude. However, they do clearly indicate that the peak A. rostrata spawning period is during February with spawning occurring from January into April. One 17 mm specimen collected on August 9 (Smith, 1968) may have been spawned during late June. Schmidt (1923) indicated that A. rostrata spawns during February and that the leptocephali attain their full length of 60 to 65 mm towards the end of the year.

Our data indicate that the majority of the population attain the maximum size during October (Figure 1). A small fraction of the population is still present as leptocephali during the following April. Metamorphosing leptocephali were taken from October to March and glass eels from February through May in oceanic collections.

The two to three year leptocephalus phase of A. anguilla negates the value of a size versus date of collection plot for this species. Only one small specimen (14 mm) taken during April was found in the North American collections. A. anguilla leptocephali of 40 to 50 mm in length were collected during all seasons.

Spatial and Temporal Distribution. With one exception A. rostrata leptocephali were collected between 18° 57' N to 42° 35' N and 45° 56' W to 87° 4' W. One 70 mm specimen (109 myomeres) was collected during August at 49° 43' N, 20° 45' W. This is the eastern most collection of an A. rostrata leptocephalus reported to date. It is also the largest specimen in the collections examined by us. A. rostrata elvers and adults are collected occasionally in Europe (Boëtius 1976, 1980).

Few A. rostrata leptocephali have been collected in the Gulf of Mexico and Caribbean Sea (Schmidt 1925, Smith 1968). Only 16 were found in the collections available to us. For this reason the collection of eight 11 to 17 mm long A. rostrata leptocephali on the west side of the Yucatan Channel (Fig. 2A) by Dr. David Smith is of great interest. Their location and small size strongly suggest they were spawned within the Caribbean Sea. Had they been spawned near the Windward Passage in the Atlantic and then drifted with the prevailing westward currents to the south of Cuba (Wüst 1964) the strong northward flow through the Yucatan Channel would have held them to its eastern side. Also, assuming an average current through the Caribbean of 1.9 km per hr (Wüst 1964) from the Lesser Antilles to the Yucatan Channel (>2800 km) and a rate of growth as discussed in the previous section, these specimens could not have been transported to this location rapidly enough to account for their small size. The collection of so few A. rostrata leptocephali in the Gulf of Mexico and Caribbean Sea suggests that spawning in the Caribbean is limited.

Small 0-group A. rostrata leptocephali ($\leq$ 15 mm TL) were collected in the Atlantic to the east of the Bahama Islands and north of Hispaniola during February and March (Fig. 2A). This region coincides with the area outlined by Schmidt (1925) as positive for A. rostrata of this size. Larger 0-group leptocephali were collected within the Bahama Island chain south of Grand Bahama Island during April, May, and June (Figs. 2A, B). They were first collected in the Straits of Florida during May and in the Gulf Stream during June (Fig. 2B). Large collections were taken within 200 km northeast of Grand Bahama Island during August (Fig. 2C). A. rostrata leptocephali were much less abundant closer to Bermuda. Thus, our data indicate A. rostrata leptocephali may enter the Gulf Stream by one of two routes. They may drift first to the southwest into the Bahama Island chain and then to the northwest through the chain to the Straits of Florida or they may drift directly to the northwest joining the Gulf Stream north of Grand Bahama Island. Currents east of the Bahamas are very complex. Day (1954) found that drift bottles released to the northeast of the Bahamas tended to drift to the southwest. The so-called Antilles Current may not be as strong or constant as originally believed (Ingham 1975, Gunn and Ingham 1977).

In the Gulf Stream, A. rostrata leptocephali are abundant from July through September. The apparent northward shift in their distribution during September (Fig. 2C) may be due to sampling effort. By October collections of A. rostrata leptocephali in the Gulf Stream begin to drop off dramatically (Fig. 2D). The few metamorphosing leptocephali in these collections were first taken during October. Thus, the decreased numbers of A. rostrata leptocephali in the Gulf Stream may be due to metamorphosis and directed movement towards the coast. A few 1+ year group A. rostrata are still present in the Gulf Stream during February (Fig. 2A). Other apparent straglers were found scattered about the western North Atlantic from December through April (Figs. 2A, D).

Relative to the final delineation of the A. rostrata spawning area a major spatial and temporal gap in coverage exists in the region between 20° N to 25° N and at least 60° W to 70° W during February and March. A large collection of A. rostrata averaging 20 mm in length taken by Schmidt (1925) during April at 22° 14' N, 67° 22' W suggests that spawning may occur in this area.

The pattern of distribution of A. anguilla leptocephali from the North American collections (Figs. 3A, B, C) are due almost entirely to sampling effort. The one small A. anguilla in these collections was taken at 25° 58' N, 63° 26' W within the hypothesized spawning area (Schmidt 1925) (Fig. 3A). By comparison with Fig. 2A it can be seen that small A. anguilla were absent from the area northeast of the Bahama Islands where small A. rostrata were collected. A. anguilla are numerous in the summer Gulf Stream collections (Fig. 3B). There appears to be a tendency for them to be centered farther to the east than A. rostrata in the Gulf Stream.

The capture of two 70 mm A. anguilla leptocephali south-southeast of Nova Scotia during August (Fig. 3C) opens the possibility that A. anguilla may occasionally metamorphose and move inshore in this region. One specimen measuring 36 mm in length was collected during August at 26° 38' N, 79° 31' W. This is the western most collection of A. anguilla to date. Comparisons of leptocephalus length relative to point of collection did not reveal significant differences with figures presented by Schmidt (1925).

Vertical Distribution. A series of discrete depth MOC10 collections taken at night in the Gulf Stream during July and August show that A. rostrata leptocephali are most abundant in the upper 70 m (Table 2). The number of specimens collected relative to volume of water filtered is 3 times higher for collections from 0 to 70 m than for trawls fished at 0 to 110 m. Collections taken 60 m to 140 m and 90 m to 1000 m deep have low relative catch rates. The deepest positive collection was fished 500 to 600 m deep. It took one specimen. Schmidt (1925) reported that A. anguilla averaging 25 mm in length were concentrated between 0 and 50 m. The MOC10 collection with the highest catch rate for A. rostrata (33.8 specimens 10^4 m^3 of water) was fished at this depth.

ACKNOWLEDGMENTS

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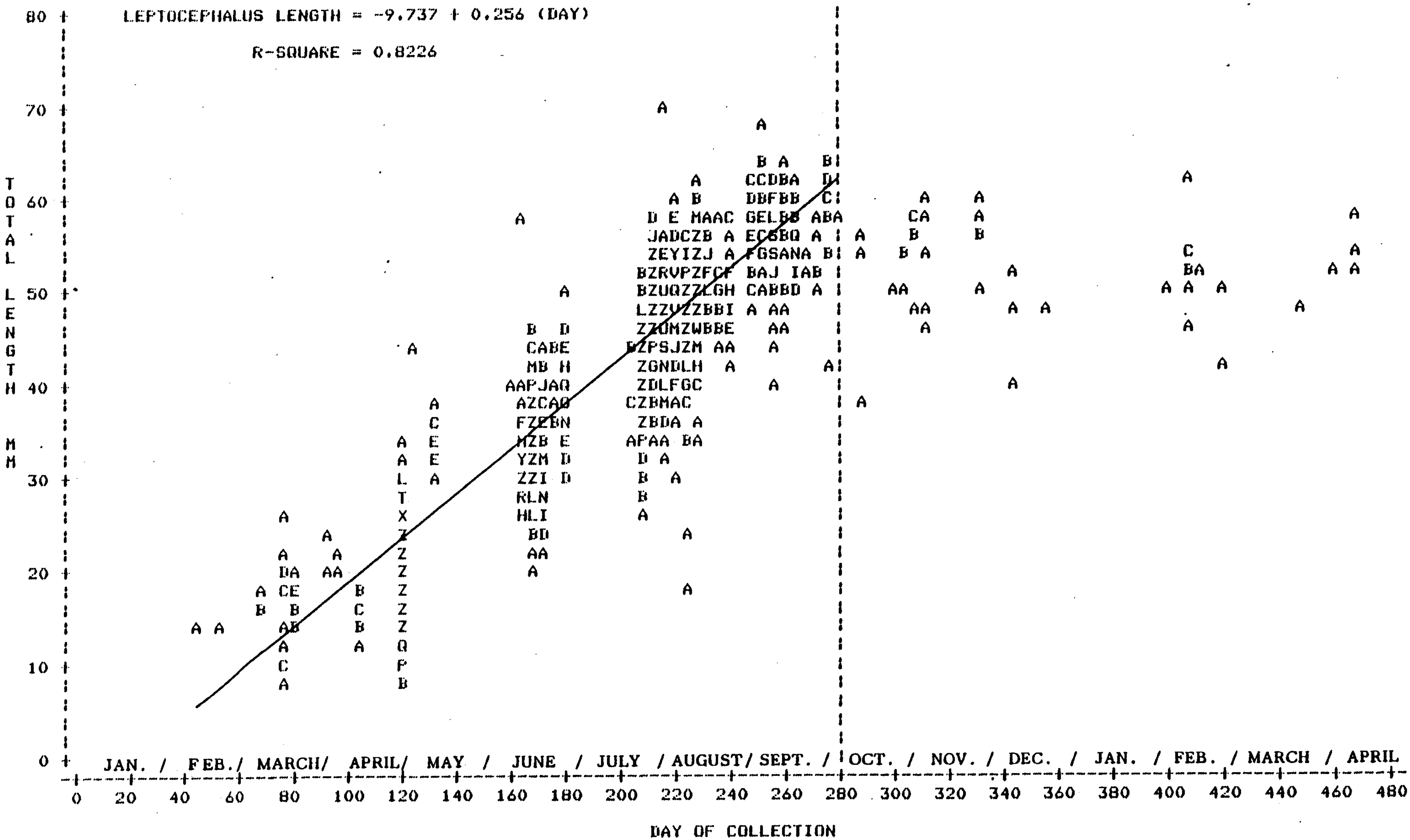
Table 1. Between study comparison of *Anguilla rostrata* and *A. anguilla* myomere frequency distributions.

	Anguilla rostrata			Anguilla anguilla		
Number of myomeres	Vladykov and March (1974) %	Present study %	Jesperson (1942) %	Vladykov and March (1974) %	Present study %	Jesperson (1942) %
101	0.5					
102	1.5	0.4				
103	10.1	0.6				
104	20.8	3.5	0.3			
105	27.9	12.0	2.1			
106	23.8	21.3	6.3			
107	10.8	31.7	17.8			
108	3.9	19.4	35.3			
109	0.7	8.8	23.8	2.9		
110	0.1	2.3	11.9	14.3		
111			2.4	27.5		
112				26.2	7.7	0.2
113				20.5	17.8	4.2
114				6.2	26.1	13.8
115				2.1	25.9	29.4
116				0.3	13.8	30.1
117					6.9	16.3
118					1.4	5.3
119					0.3	0.6
$\overline{X}$	105.13	106.83	108.17	111.76	114.48	115.58
n	736	1903	286	385	889	472

Table 2. Vertical distribution of *Anguilla rostrata* leptocephali collected in night discrete depth MOC10 trawls between 26° to 35° N and 74° to 80° W.

Depth range (m)	Number of samples	Number of specimens	Volume filtered (X 10^4 m^3)	Number of specimens per 10^4 m^3 of water
0 - 70	5	199	20.6	9.66
0 - 110	5	72	24.2	2.98
60 - 140	5	69	22.7	3.04
90 - 1000	24	14	85.4	0.16
Total	39	354		

FIG. 1. PLOT OF ANGUILLA ROSTRATA LEPTOCEPHALUS LENGTH VERSUS DAY OF COLLECTION.
LINEAR REGRESSION OF LENGTH ON DAY OF COLLECTION FOR 0+ AGE CLASS DURING GROWTH PHASE.
LEGEND: A = 1 OBSERVATION, B = 2 OBSERVATIONS, ... Z = 26 OR MORE OBSERVATIONS.



NOTE: 593 OBS HIDDEN

Figure 2A, B, C, and D. Spatial and temporal distribution of *Anguilla rostrata* leptocephalus collections including month of collection, number of specimens (in parentheses) and length range (mm). (Note: one 70 mm specimen collected during August at 49° 43' N, 20° 45' W is omitted from Fig. 2C.)

Figure 3A, B, and C. Spatial and temporal distribution of *Anguilla anguilla* leptocephalus collections including month of collection, number of specimens (in parentheses) and length range (mm).

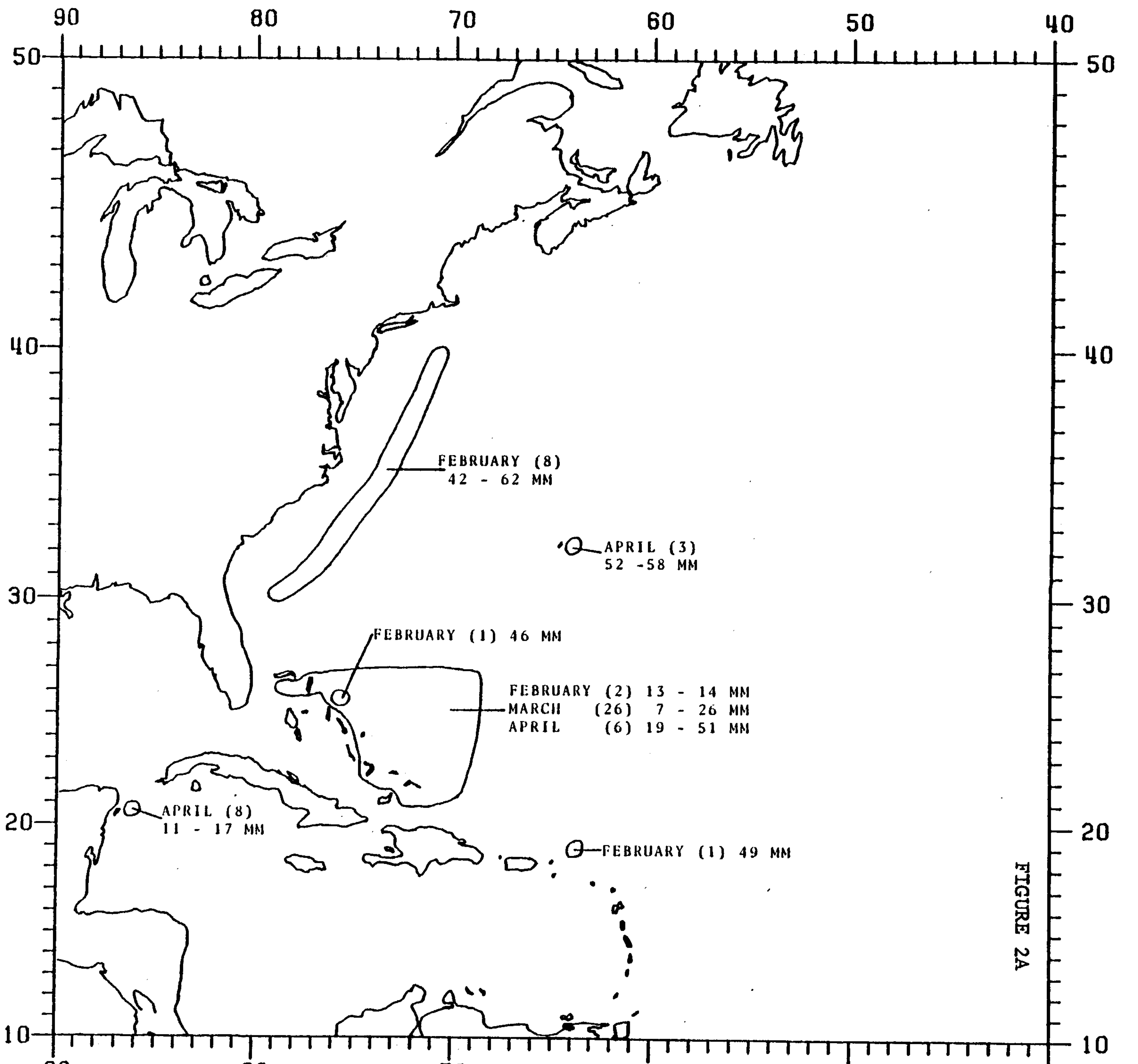
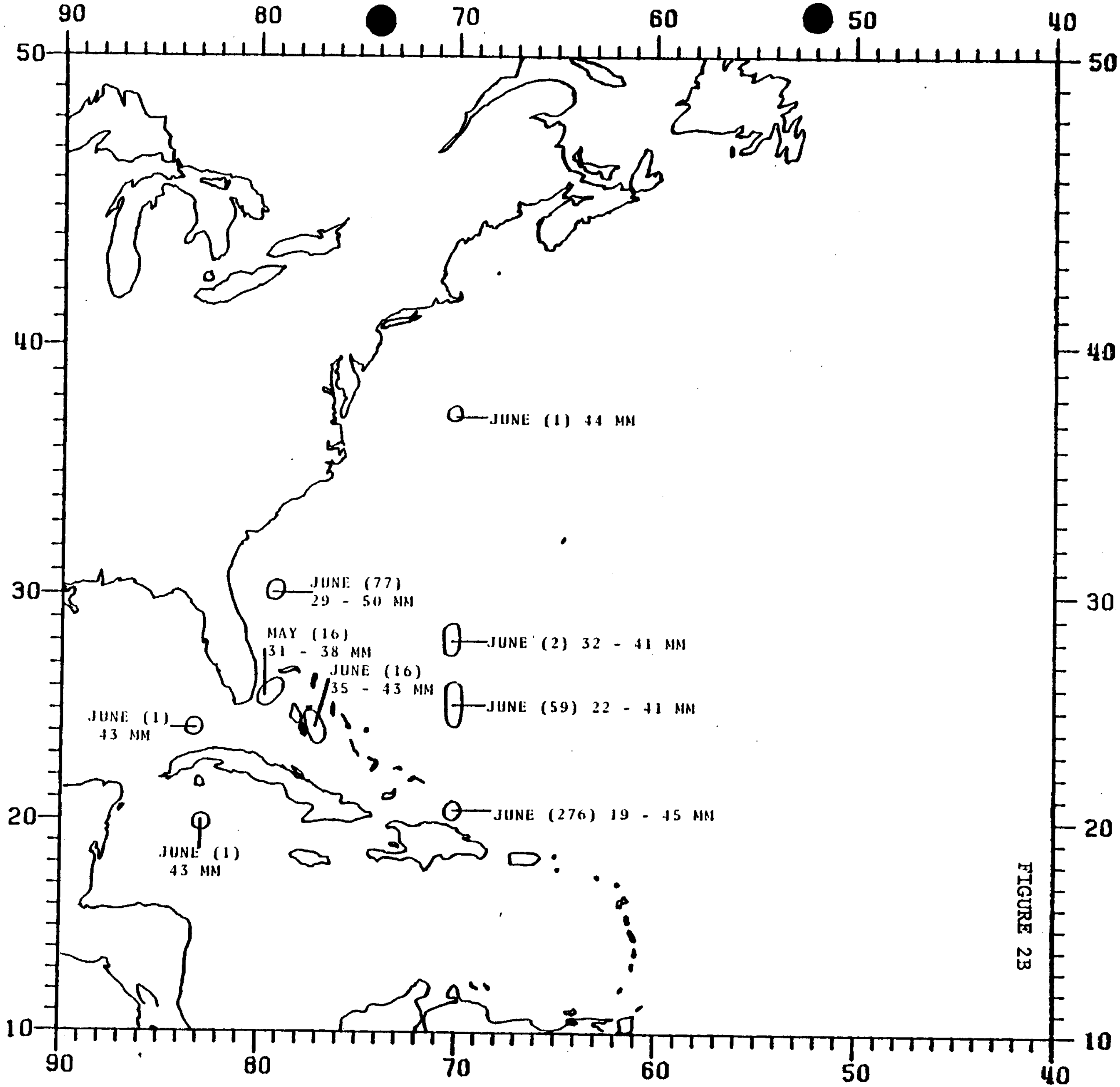

90
80
70
60
50
40
50
40
30
20
10
FEBRUARY (8)
42 - 62 MM
APRIL (3)
52 -58 MM
FEBRUARY (1) 46 MM
FEBRUARY (2) 13 - 14 MM
MARCH (26) 7 - 26 MM
APRIL (6) 19 - 51 MM
APRIL (8)
11 - 17 MM
FEBRUARY (1) 49 MM

FIGURE 2A



90
80
70
60
50
40
50
40
30
20
10
JUNE (1) 44 MM
JUNE (77)
29 - 50 MM
MAY (16)
31 - 38 MM
JUNE (16)
35 - 43 MM
JUNE (2) 32 - 41 MM
JUNE (59) 22 - 41 MM
JUNE (1)
43 MM
JUNE (276) 19 - 45 MM
JUNE (1)
43 MM

FIGURE 2B

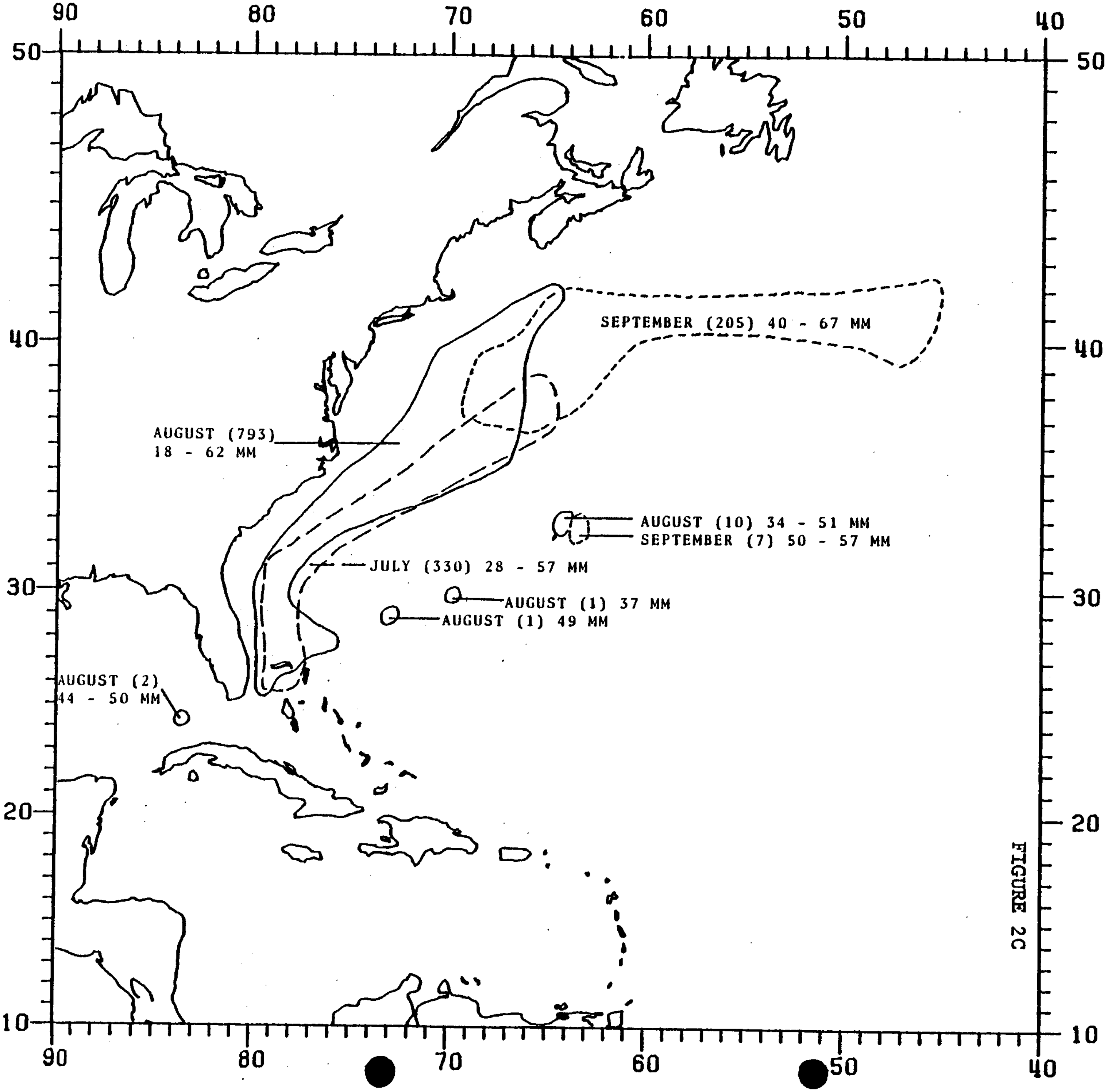

90
80
70
60
50
40
50
40
30
20
10
SEPTEMBER (205) 40 - 67 MM
AUGUST (793)
18 - 62 MM
AUGUST (10) 34 - 51 MM
SEPTEMBER (7) 50 - 57 MM
JULY (330) 28 - 57 MM
AUGUST (1) 37 MM
AUGUST (1) 49 MM
AUGUST (2)
44 - 50 MM

FIGURE 2C

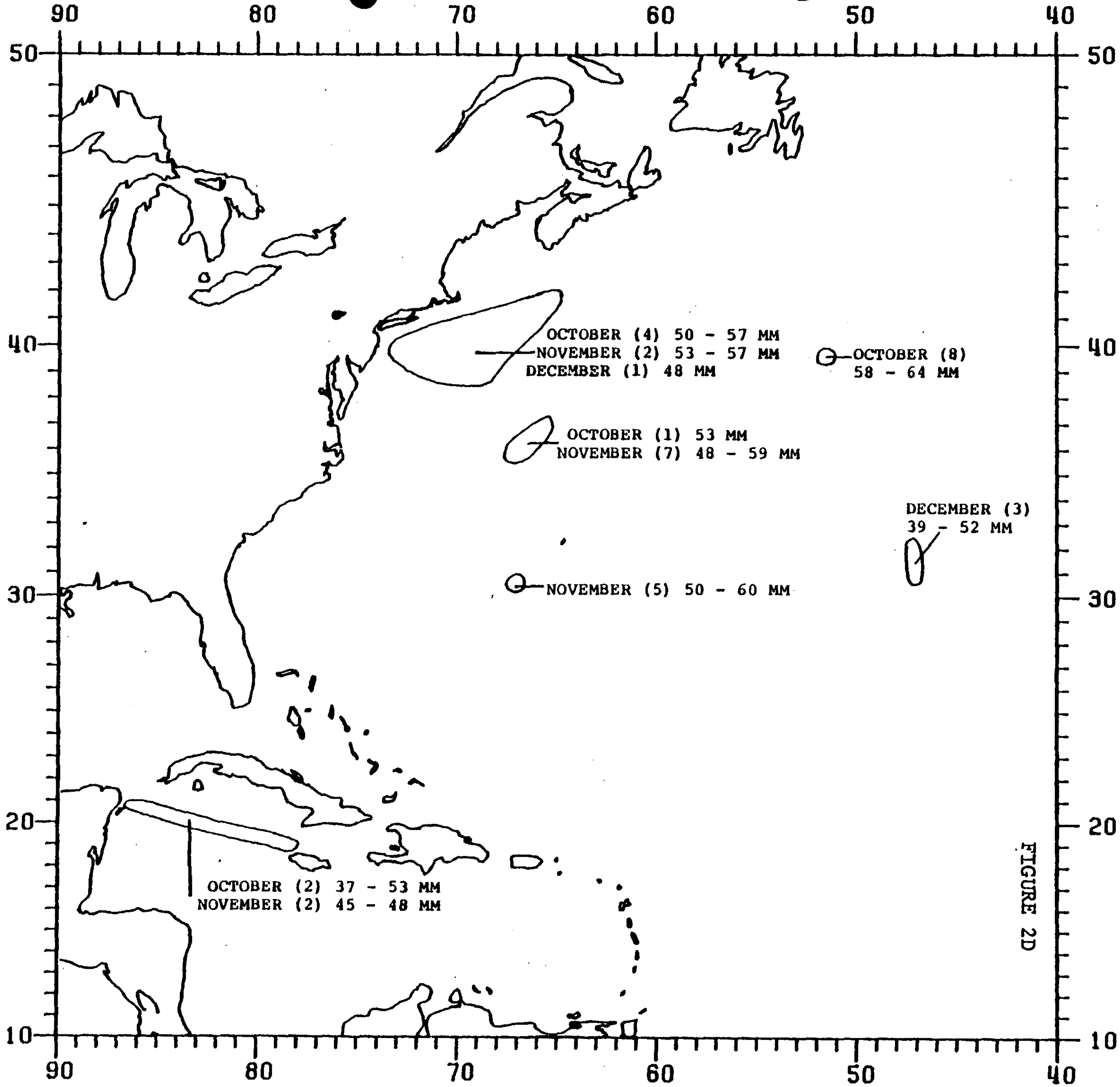

90
80
70
60
50
40
50
40
30
20
10
OCTOBER (4) 50 - 57 MM
NOVEMBER (2) 53 - 57 MM
DECEMBER (1) 48 MM
OCTOBER (8)
58 - 64 MM
OCTOBER (1) 53 MM
NOVEMBER (7) 48 - 59 MM
DECEMBER (3)
39 - 52 MM
NOVEMBER (5) 50 - 60 MM
OCTOBER (2) 37 - 53 MM
NOVEMBER (2) 45 - 48 MM

FIGURE 2D

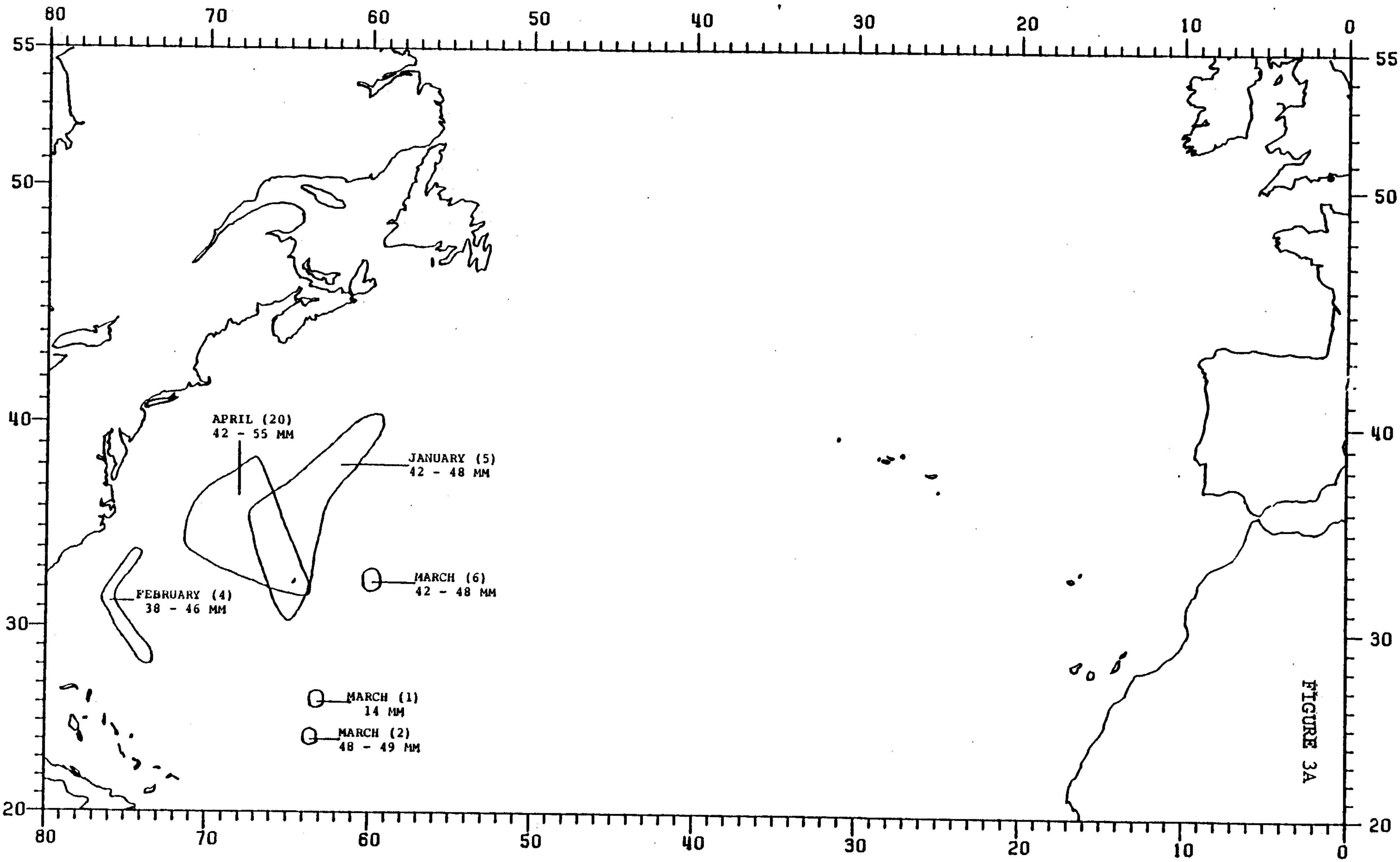

APRIL (20)
42 - 55 MM
JANUARY (5)
42 - 48 MM
MARCH (6)
42 - 48 MM
FEBRUARY (4)
38 - 46 MM
MARCH (1)
14 MM
MARCH (2)
48 - 49 MM
80
70
60
50
40
30
20
10
0
55
50
40
30
20

FIGURE 3A

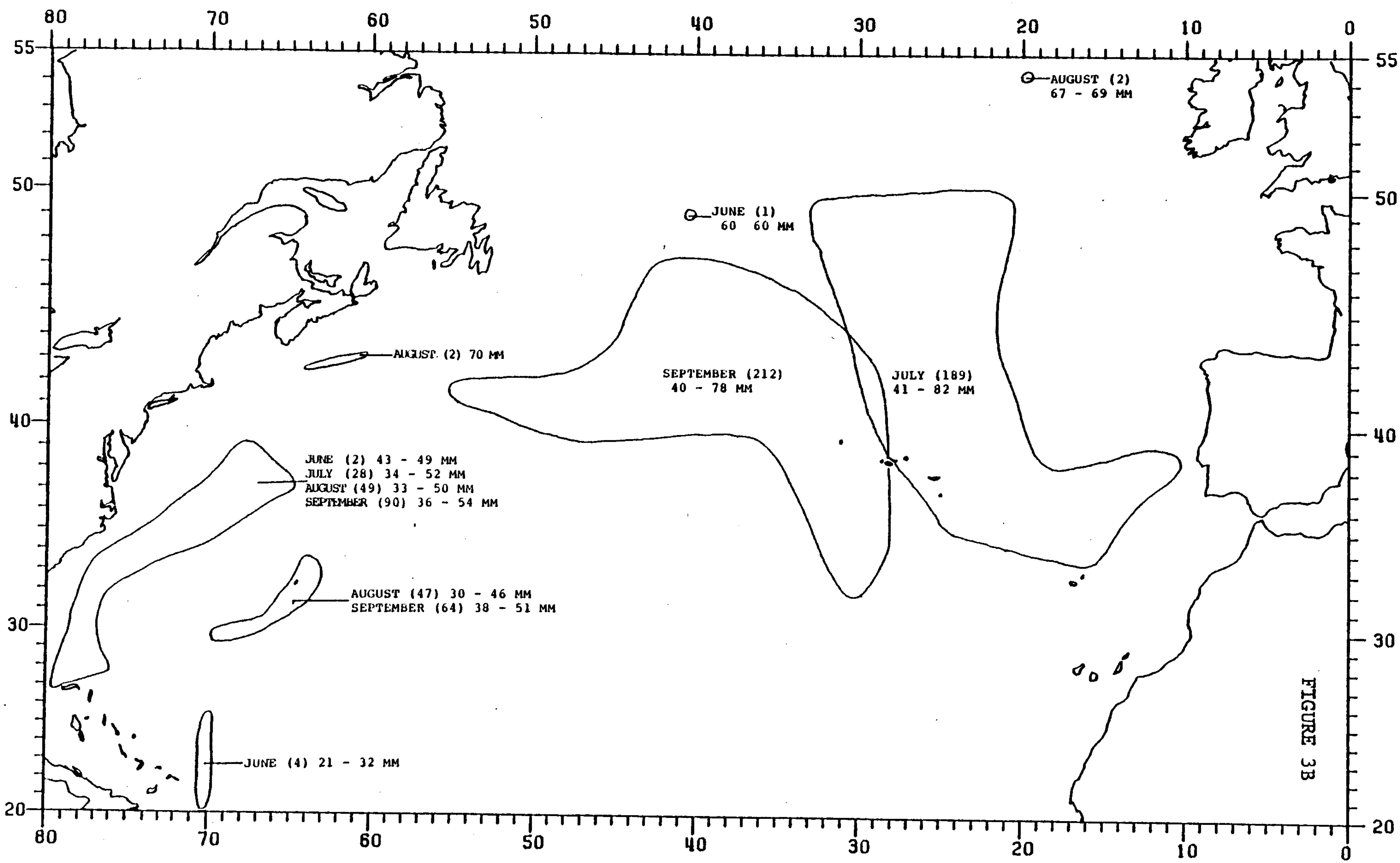

AUGUST (2) 67 - 69 MM
JUNE (1) 60 60 MM
AUGUST (2) 70 MM
SEPTEMBER (212) 40 - 78 MM
JULY (189) 41 - 82 MM
JUNE (2) 43 - 49 MM
JULY (28) 34 - 52 MM
AUGUST (49) 33 - 50 MM
SEPTEMBER (90) 36 - 54 MM
AUGUST (47) 30 - 46 MM
SEPTEMBER (64) 38 - 51 MM
JUNE (4) 21 - 32 MM
80 70 60 50 40 30 20 10 0
55 50 40 30 20

FIGURE 3B

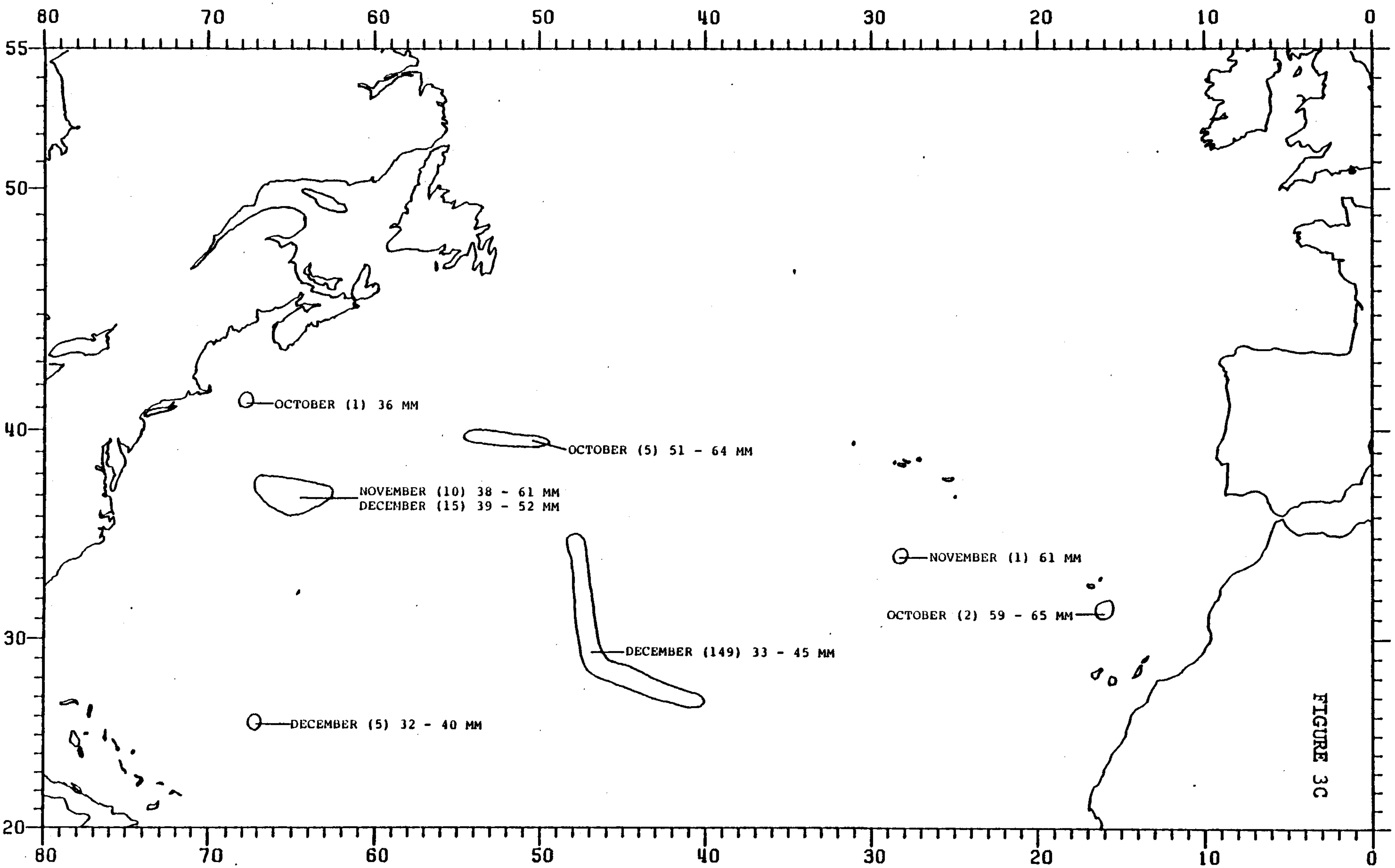

80
70
60
50
40
30
20
10
0
55
50
40
30
20
OCTOBER (1) 36 MM
OCTOBER (5) 51 - 64 MM
NOVEMBER (10) 38 - 61 MM
DECEMBER (15) 39 - 52 MM
NOVEMBER (1) 61 MM
OCTOBER (2) 59 - 65 MM
DECEMBER (149) 33 - 45 MM
DECEMBER (5) 32 - 40 MM

FIGURE 3C