Vol. 24: 1–13, 1985 | MARINE ECOLOGY - PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published July 11

Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area

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ABSTRACT: Monthly distribution patterns of haddock larvae are described from coastal MARMAP[1] surveys as part of a broad-based program to study recruitment processes in shelf waters from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia, an area of nearly 260,000 km^2. Within this area haddock spawn during winter and spring. Peak spawning occurs in late March-early April. The principal spawning grounds lie over the eastern half of Georges Bank. Other spawning areas include Nantucket Shoals, western Georges Bank, coastal waters of the Gulf of Maine, and the western perimeter of the Scotian Shelf. A large anticyclonic gyre and strong rotary tidal currents hold haddock larvae on Georges Bank. The gyre carries haddock larvae westward along the southern half of the bank, largely over depths between 50 and 100 m. Some are advected as far west as Nantucket Shoals but most are retained on the bank east of Great South Channel. There is no evidence of a significant loss of haddock larvae south across the shelf break nor do larvae originating on Georges Bank mix with their counterparts in the Gulf of Maine or along the western part of the Scotian Shelf.

INTRODUCTION

For the past 8 yr, biologists at NOAA's Northeast Fisheries Center (NEFC) have been working toward an understanding of the interacting ecological events that influence the size of recruiting fish populations through a comprehensive fishery ecosystem study known as MARMAP[1] (Sherman 1980). The basic research strategy of MARMAP coordinates results from broadscale surveys conducted at monthly to bimonthly intervals with finescale laboratory and field studies of larval feeding, condition and growth indices, and mortality. In addition to providing information on recruitment variability, the surveys provide an effective means, independent of fishery catch statistics, for assessing the adult spawning biomass of important coastal fishery resources (Berrien et al. 1981, Morse 1982, Berrien 1983).

This study utilizes the survey information to map monthly distribution patterns of haddock eggs and larvae in the Georges Bank region to determine where and when haddock spawned during the 6-yr period between 1977 and 1982, a period of poor recruitment (Overholtz et al. 1983). We compare our results to those of earlier studies in an attempt to account for the poor recruitment observed during the study period. In addition, we relate observed shifts in spatial and temporal distribution patterns to known hydrographic features to investigate whether transport of larvae off Georges Bank was a principal cause of early stage mortality. The importance of hydrography on the spawning strategies of shelf species off northeastern United States has been addressed by Sherman et al. (1984).

Interest in the effects of transport mechanisms on the fates of fish eggs and larvae dates to the early days of fishery science (Hjort 1914, Poulsen 1930, Rollefsen 1930) and it has been proposed that errant transport ranks with predation and starvation as a major cause of mortality during early development (Harden Jones 1968). This position is supported by Bailey (1981) and Parrish et al. (1981), who concluded that transport was a critical factor in the year-class success of Pacific hake *Merluccius productus* in the California Current system.

[1] MARMAP is an acronym for Marine Resources Monitoring, Assessment and Prediction

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But others have failed to show a relation between residual drift and the distribution of fish eggs and larvae (Saville 1956, O'Boyle et al. 1984). Several studies have been conducted to determine the influence of currents on the distribution of fish eggs and larvae spawned on Georges Bank. Some have concluded that significant mortality is attributable to transport off the shelf (Walford 1938, Chase 1955, Colton & Temple 1961); others found no convincing evidence that transport is a major source of egg and/or larval mortality (Bumpus 1976, Colton & Anderson 1983, Cohen et al. 1983). None has satisfactorily resolved the issue.

Circulation patterns in the study area are dominated by seasonally variable gyres, cyclonic in the Gulf of Maine, anticyclonic on Georges Bank (Fig. 1). Gyres in both areas are most pronounced in spring and summer and intermittently break down. Waters within the 65 m isobath on Georges Bank remain vertically mixed year-round. They are physically unique because of low volume replenishment from adjacent seasonally stratified waters. Strong semidiurnal rotary tidal currents with amplitudes of 100 cm s^{-1}, an order of magnitude greater than those in off-bank waters, create the unstratified conditions over the bank (Hopkins & Garfield 1981). Slope water south of the bank moves in a westerly direction, paralleling bathymetry (Ingham et al. 1982). From Nantucket Shoals westward, residual flow on the shelf is sluggish, moving to the west and southwest.

After the Gulf Stream turns eastward at Cape Hatteras it begins to develop meanders which occasionally form loops that eventually break from the stream as large rotating water masses known as warm core rings (WCRs). Rings splitting off the northern edge of the stream rotate clockwise and move west and south on a wayward path through slope waters at 3 to 5 km d^{-1}. Some travel as far as Cape Hatteras where they become reabsorbed in the stream. WCRs can maintain their identity for as long as 6 mo, or they can dissipate or become swallowed up by the stream in a matter of days. Rings moving westward near the shelf edge entrain shelf waters. Through this entrainment process the WCRs are suspected of pulling fish eggs and larvae as well as other planktonic organisms off the shelf into an inimical slope-water environment (Wiebe 1982).

The shelf/slope front, where cool, low-salinity shelf water meets warmer high-salinity slope water, is generally located near the edge of the shelf but it has been observed through remote sensing as far as 200 km seaward of the shelf break (Armstrong 1983). Movement of the front is dictated largely by wind conditions and WCR activity. Evidence suggests a relation between the position of the front and the abundance of larvae on Georges Bank (Bolz & Lough 1984).

METHODS

MARMAP surveys cover shelf waters from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia, an area of 258,067 km^2. Information on larvae in this report is based on 2,431 ichthyoplankton samples collected in 21 surveys conducted between February and July during the 6 yr period from 1977 through 1982. Two years (1979, 1980) of egg data are included to circumscribe more precisely the spawning grounds and provide added insight into temporally and spatially changing patterns of distribution during early development.

Fish eggs and larvae are sampled on 2 types of cruises: those dedicated to broadscale plankton surveys; and those where plankton samples are taken on cruises with a primary mission of assessing the distribution and abundance of fish and mollusk populations using trawl or dredge surveys respectively (Sherman et al. 1983). The station plan on the plankton surveys remains unchanged between cruises. Stations are spaced at 8 to 18 km intervals along 7 transects, with all other sampling sites located at 25 to 35 km intervals to provide uniform coverage of the shelf (Fig. 1). The ichthyoplankton stations on trawl and dredge surveys are selected from a stratified random station plan and change with each survey (Grosslein 1969). Shelf coverage and station spacing is similar to that on plankton surveys.

Plankton samples are collected by double-oblique tows with a 61 cm bongo, fitted with 0.333 and 0.505 mm mesh nets. The bongo is lowered to within a few meters of bottom or to a maximum depth of 200 m at 50 m min^{-1} and retrieved at 20 m min^{-1}. Ship speed varies between 1 and 2 kn to maintain a 45° wire angle during a tow. A flow meter in the mouth of each net provides information for computing the amount of water filtered during a tow, and a bathykymograph records a trace of the vertical tow profile and the maximum sampling depth. The 0.505 mm mesh samples are used for ichthyoplankton analysis; the 0.333 mm mesh samples, for invertebrate zooplankton studies. Plankton samples are preserved in 5 % buffered formalin.

For purposes of this study haddock larvae are divided into 3 size categories: $\leq$ 4.2 mm, 4.3 to 8.2 mm, and $\geq$ 8.3 mm, and standardized to represent the number of larvae under 10 m^2 surface area, an estimate of abundance (Smith & Richardson 1977). Based on age/growth information in Bolz & Lough (1983), larvae in the smallest size category are < 14 d old; those in the intermediate size group, 4 to 24 d; and those $\geq$ 8.3 mm, at least 20 d.

For contouring larval distributions, we plotted all stations occupied monthly during the 6 yr time series

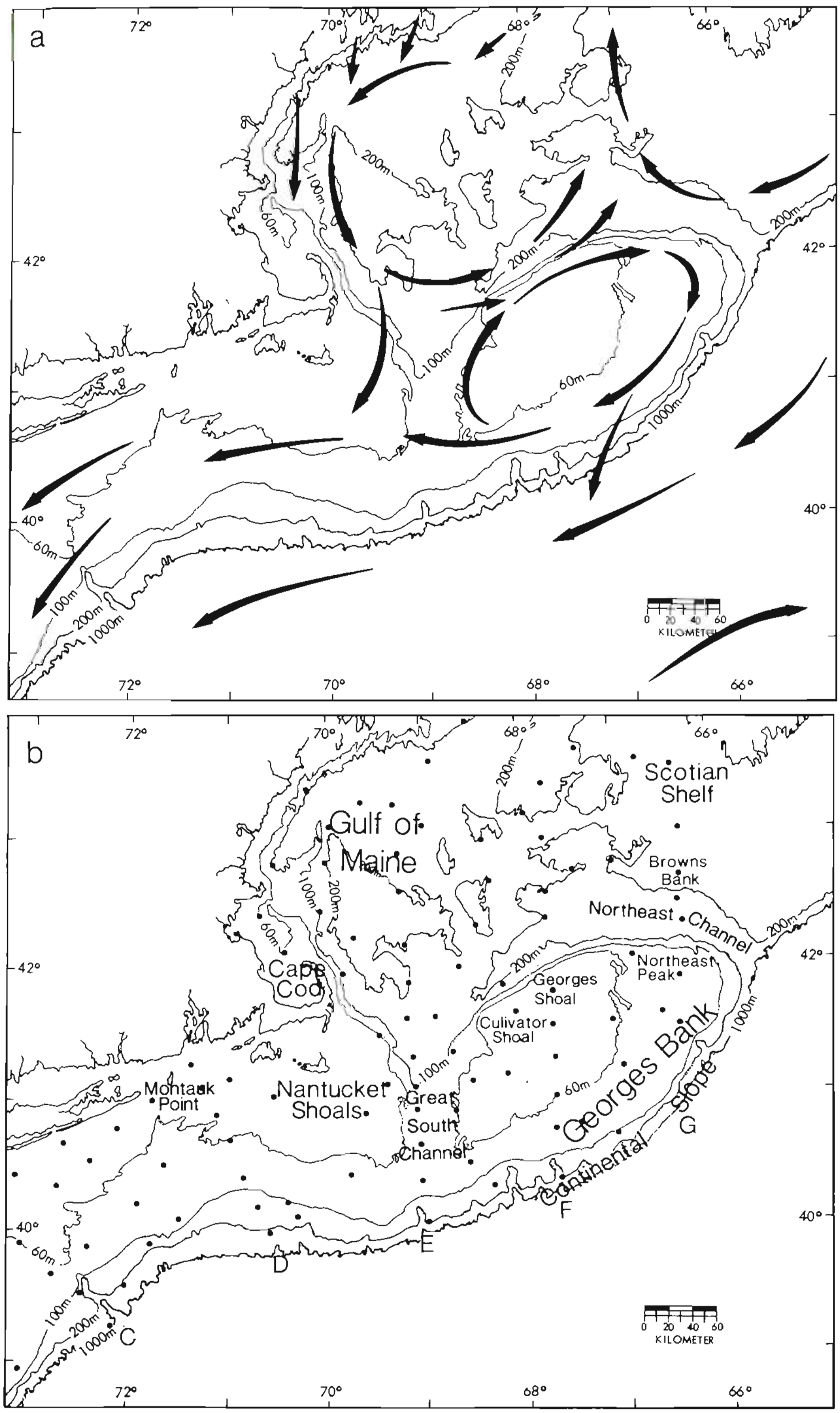

Fig. 1. (a) General surface circulation off northeastern United States showing cyclonic water movements in Gulf of Maine and anticyclonic movements on Georges Bank (from Ingham et al. 1982). (b) Northern part of MARMAP survey area showing station density. This portion of the survey area encompasses the spawning grounds of haddock. Letters designate transects

then entered the standardized larval haddock catches for each month. If larvae occurred at a station only once in a given month during the 6 yr, that single occurrence was used for contouring. When larvae occurred at the same station more than once, the highest abundance estimate was used. By treating the data in this way, we have constructed monthly composites depicting the broadest overall distribution of larvae and the most extensive occurrence of dense larval concentrations that occurred during the 6 yr period. Smith et al. (1979, 1981) show the distribution of haddock larvae by cruise for spawning seasons 1974 through 1980.

We traditionally conduct 3 surveys yearly during the haddock spawning season, but in 1977 we completed 4 and in 1978 only 2. The monthly station density composites shown in Fig. 2 to 8 produce geographically variable sampling densities because of differences in cruise scheduling; because surveys usually begin in one month and carry over into the next and the stations are then divided between 2 charts; and because inclement weather sometimes impacts on survey coverage.

RESULTS

Distribution of eggs

Haddock begin spawning on Georges Bank as early as January but in most years not until February. Thereafter spawning continues to gain momentum and the distribution of eggs and larvae spreads geographically. By March eggs are broadly distributed over Georges Bank, with the most intense spawning activity centered over the eastern half of the bank. Small patches of eggs occur as far west as Nantucket Shoals but unlike Walford (1938) we found no evidence of significant spawning west of the 68° meridian.

Spawning peaks on Georges Bank during the late March-early April period, and by April eggs occur in the Gulf of Maine and along the western perimeter of the Scotian Shelf. Spawning on Nantucket Shoals remains light. By May egg production is sharply reduced on Georges Bank, where the annual spawning cycle is nearly complete. Eggs are broadly distributed over the bank, but their center of abundance remains east of longitude 67° W. The distribution of haddock eggs in the Gulf of Maine expands in May and extends along most of the New England coastline but eggs are scattered and no dense concentrations are evident. Our results show high egg production along the western edge of the Scotian Shelf in May, with most eggs occurring on Browns and German banks. Although the spawning season effectively ends in May, scattered occurrences of eggs are sometimes encountered in June, especially in the Gulf of Maine region. Based on areal differences in egg production during the 2 yr period, the major spawning grounds are located on Georges Bank, followed by the western part of the Scotian Shelf, the Gulf of Maine, and Nantucket Shoals (Fig. 2).

Distribution of larvae

We caught larvae as early as February in 1978 and again in 1981, and based on back-calculations of larvae caught in March of 1980, a year that we did not sample in February, larvae were present on the bank in January 1980 (Smith et al. 1981). The distribution of larvae in February is limited to the eastern half of the bank, or that part of the survey area where we found spawning most intense throughout the spawning season (Fig. 3). By March the abundance of small larvae increases. Their center of abundance overlies that of eggs, a reflection of sluggish (5 cm s^{-1}) mean flow conditions along the southern part of the bank (Butman et al. 1982). However, the principal concentration of intermediate-sized larvae in March extends further westward, the first indication of an east to west displacement with time (Fig. 4).

By April, larvae $\leq$ 4.2 mm are spread over the entire eastern half of Georges Bank. Their center of abundance lies along the southern flank, west of the major egg concentrations which repeatedly occur over Northeast Peak. Small and intermediate haddock larvae first occur on the western edge of the Scotian Shelf in April (Fig. 5).

Haddock larvae are broadly distributed and at peak levels of abundance over Georges Bank and along the western edge of the Scotian Shelf in May. Recently hatched larvae remain largely over the eastern half of Georges Bank, with scattered occurrences as far west as Montauk Point, Long Island. Larvae 4.3 to 8.2 mm are also widely distributed in May, occurring from Nantucket Shoals to Northeast Peak. As with the intermediate-sized larvae, both the distribution and abundance of larvae $\geq$ 8.3 mm increase significantly on Georges Bank in May. Representatives of the largest size group occur over most of the bank but their distribution is not as concentrated on the southern edge as that of the smaller size categories (Fig. 6). When compared with the distribution of eggs in April and larvae $\leq$ 4.2 mm in April and May, there is clearly a displacement to the west of both the intermediate and large larvae by the end of May (Fig. 2, 5 & 6). Furthermore, the center of abundance of large larvae has moved toward the middle of the bank, or away from the southern edge. During the 6 yr reporting period, larvae in the $\leq$ 4.2 and $\geq$ 8.3 mm size groups occurred over

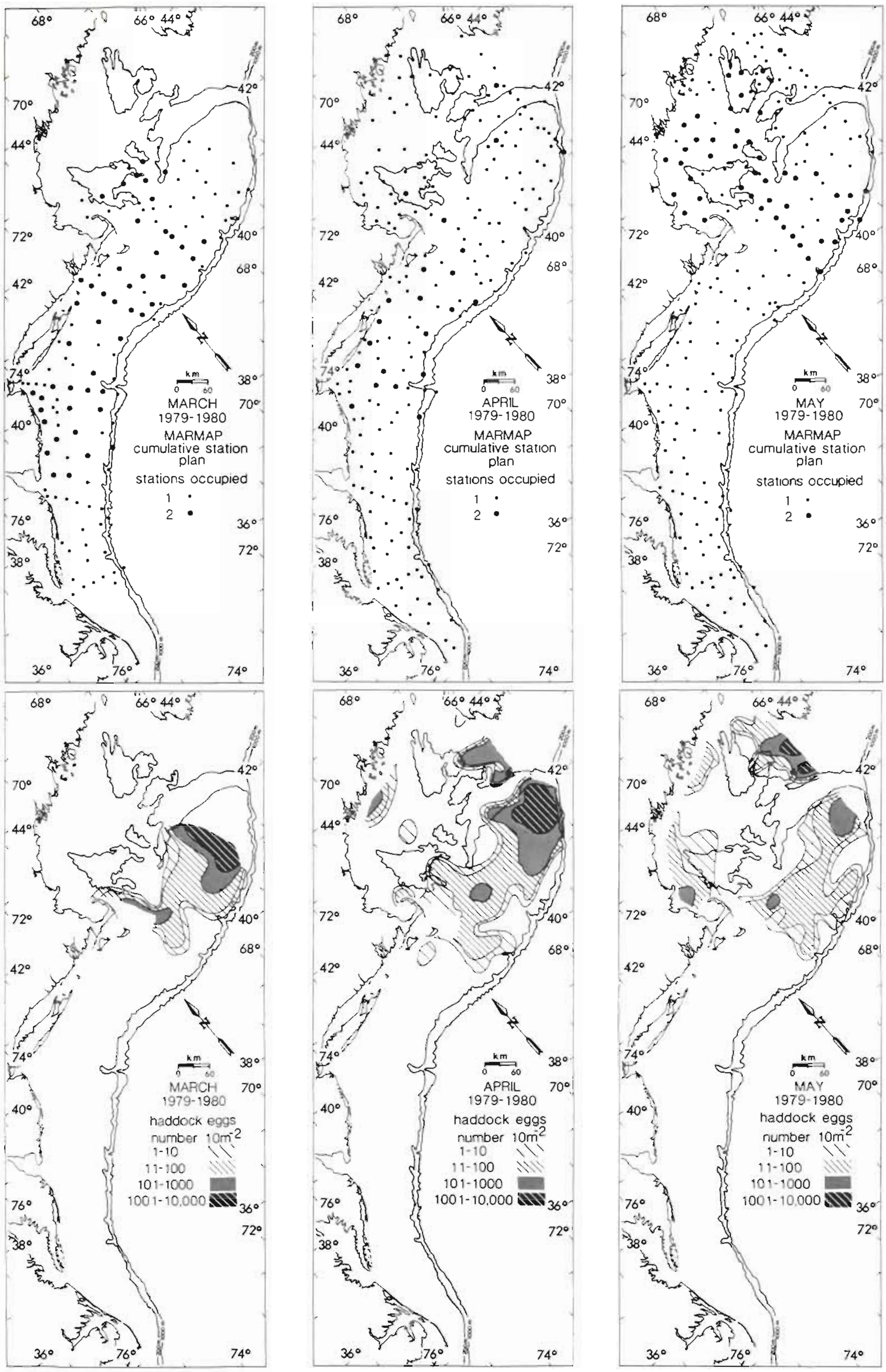

Fig. 2. Cumulative MARMAP stations occupied off northeastern United States during March, April and May 1979 and 1980 (top); and distribution of haddock eggs during each of the 3 mo (bottom)

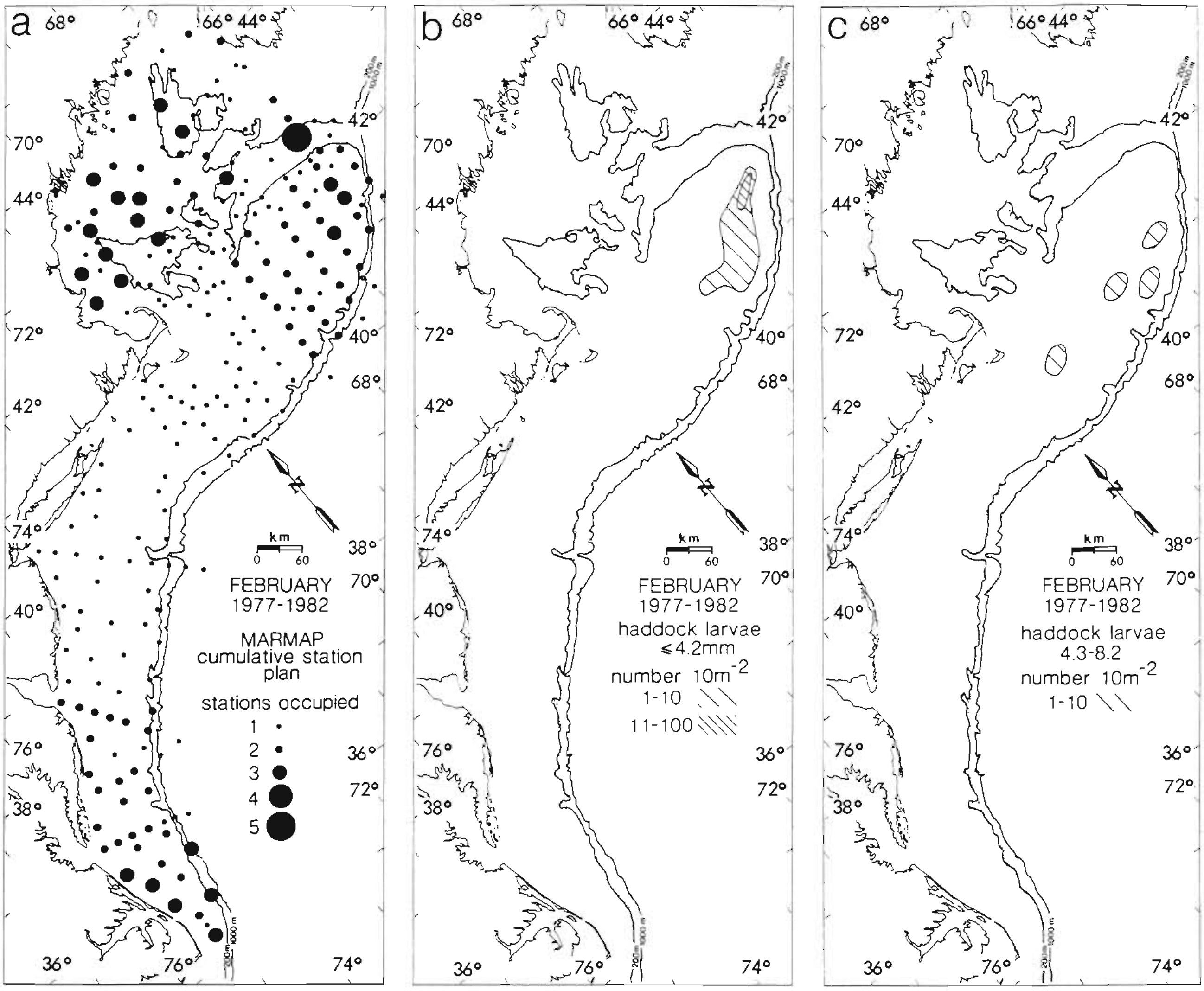

Fig. 3. (a) Cumulative MARMAP stations occupied off northeastern United States during Feb 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.3 mm, (c) 4.3 to 8.2 mm

weighted mean depths of 90 and 78 m, respectively. This trend toward shoaler depths with growth was also reported by Walford (1938) and Lough (1984).

Low densities of small larvae remain only over the central portion of Georges Bank and on the western Scotian Shelf in June, with isolated occurrences in the Gulf of Maine and on Nantucket Shoals. Larvae in the intermediate size group continue to occupy a large part of the bank but their overall distribution begins to recede in June. The distribution of larvae ≥ 8.3 mm extends westward over Georges Bank to waters south of Nantucket Shoals. Although the western extremity of their distribution broaches Great South Channel, most of the large larvae remain east of the channel (Fig. 7).

By July, nearly all surviving haddock larvae have outgrown the plankton. Colton (1965) reported the average length of young haddock during the July/August period to be 84 mm, or more than 4 times the size of the largest haddock larvae taken in the bongo net. Scattered occurrences of small larvae remain in evidence in the Gulf of Maine, intermediate-sized larvae in the vicinity of Great South Channel, and larvae ≥ 8.3 mm persist in both of the above locations (Fig. 8).

It is worthy of note in Fig. 2 to 8 that eggs and larvae originating on the Georges Bank, Gulf of Maine, and Scotian Shelf spawning grounds are geographically isolated. We see no evidence in our data that they intermix. Depth and strong currents associated with the Northeast Channel seem to provide a natural boundary for separating spawning products originating on the Georges Bank and Scotian Shelf spawning

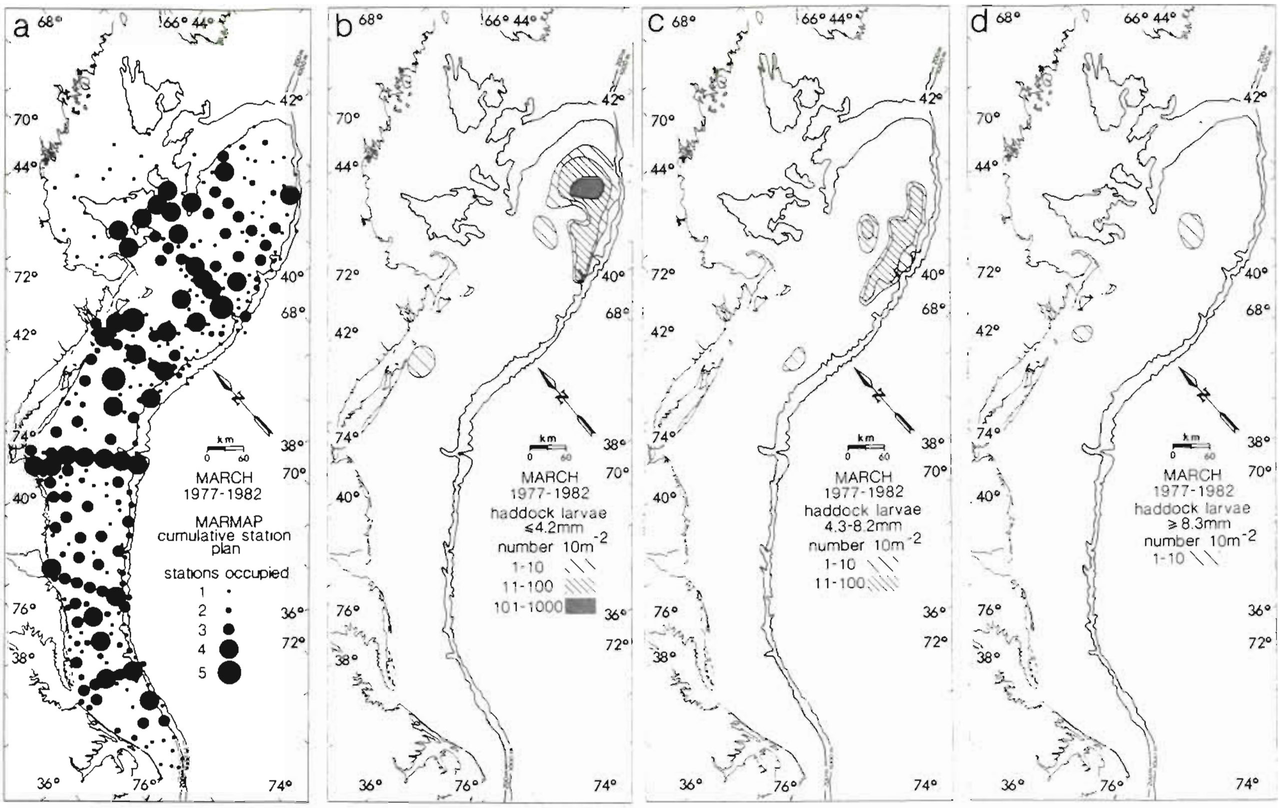

Fig. 4. (a) Cumulative MARMAP stations occupied off northeastern United States during Mar 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.2 mm, (c) 4.3 to 8.2 mm, (d) ≥ 8.3 mm

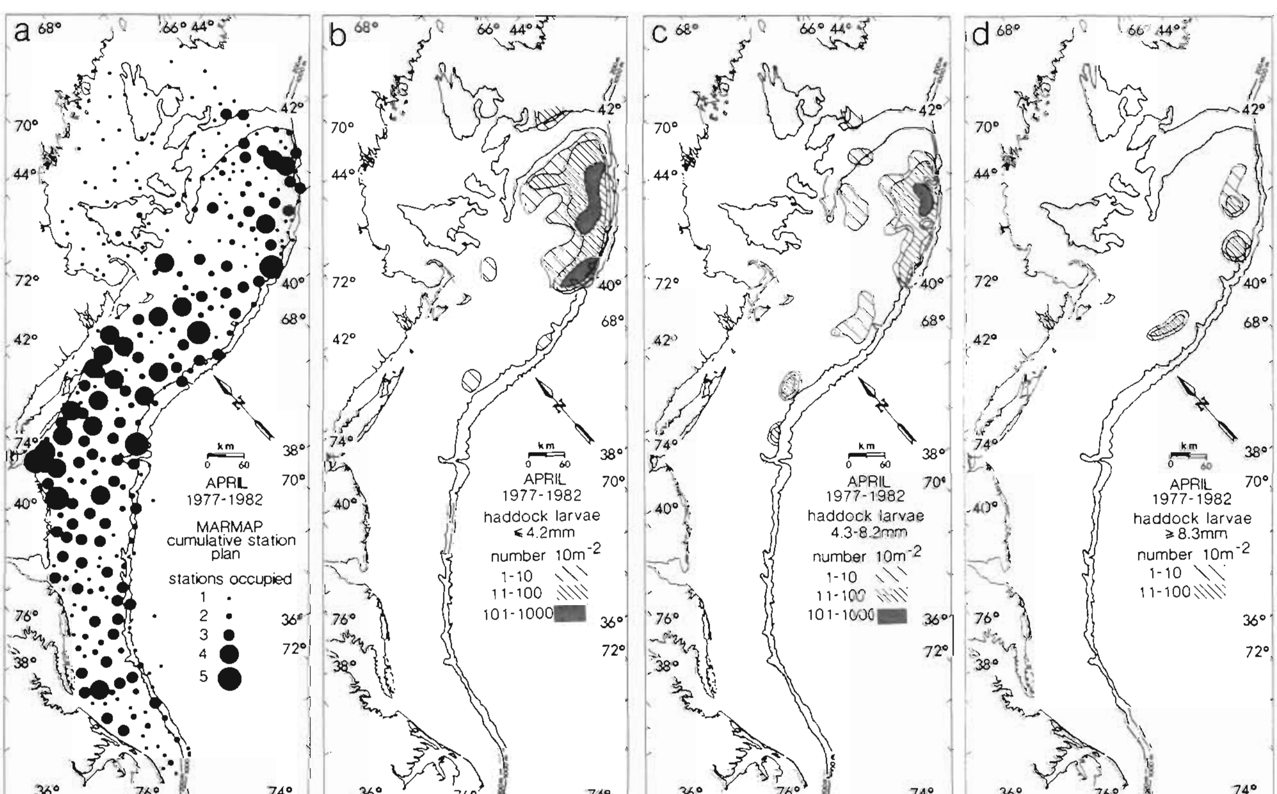

Fig. 5. (a) Cumulative MARMAP stations occupied off northeastern United States during April 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.2 mm, (c) 4.3 to 8.2 mm, (d) ≥ 8.3 mm

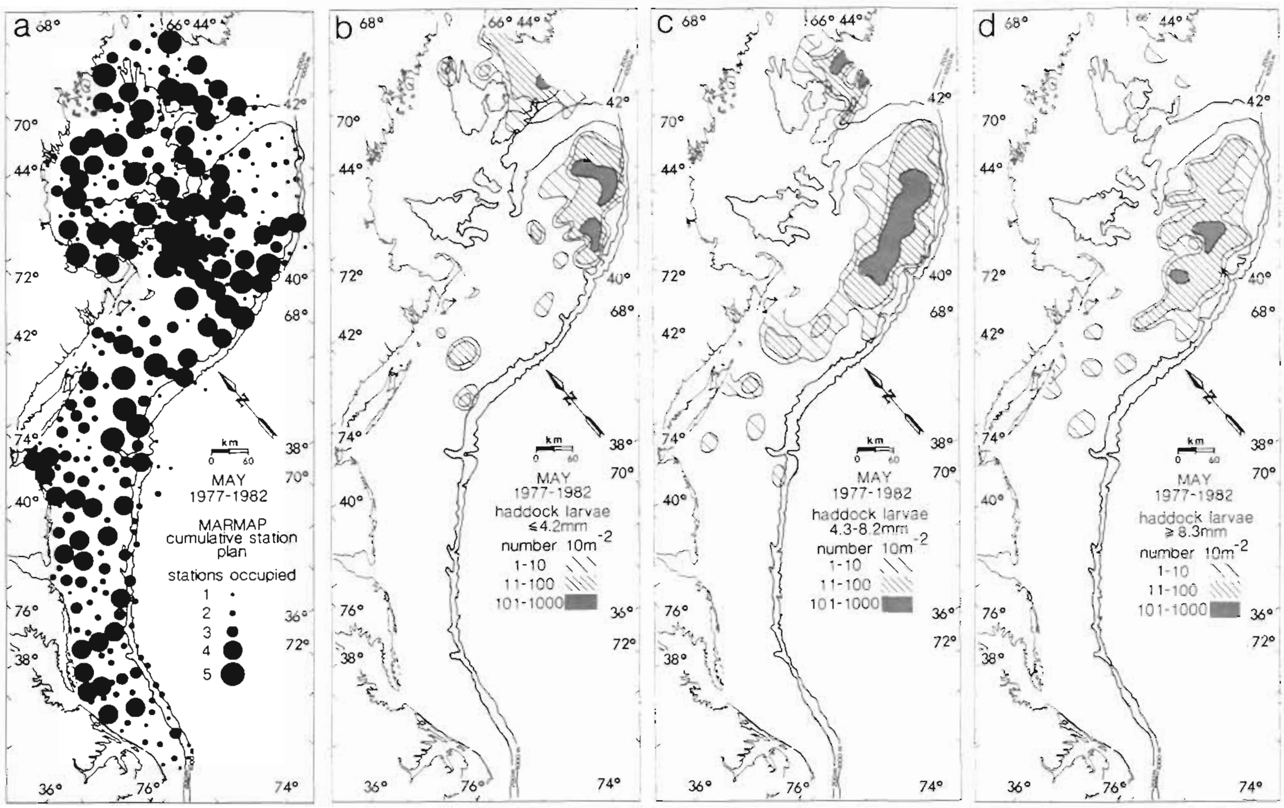

Fig. 6. (a) Cumulative MARMAP stations occupied off northeastern United States during May 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.2 mm, (c) 4.3 to 8.2 mm, (d) ≥ 8.3 mm

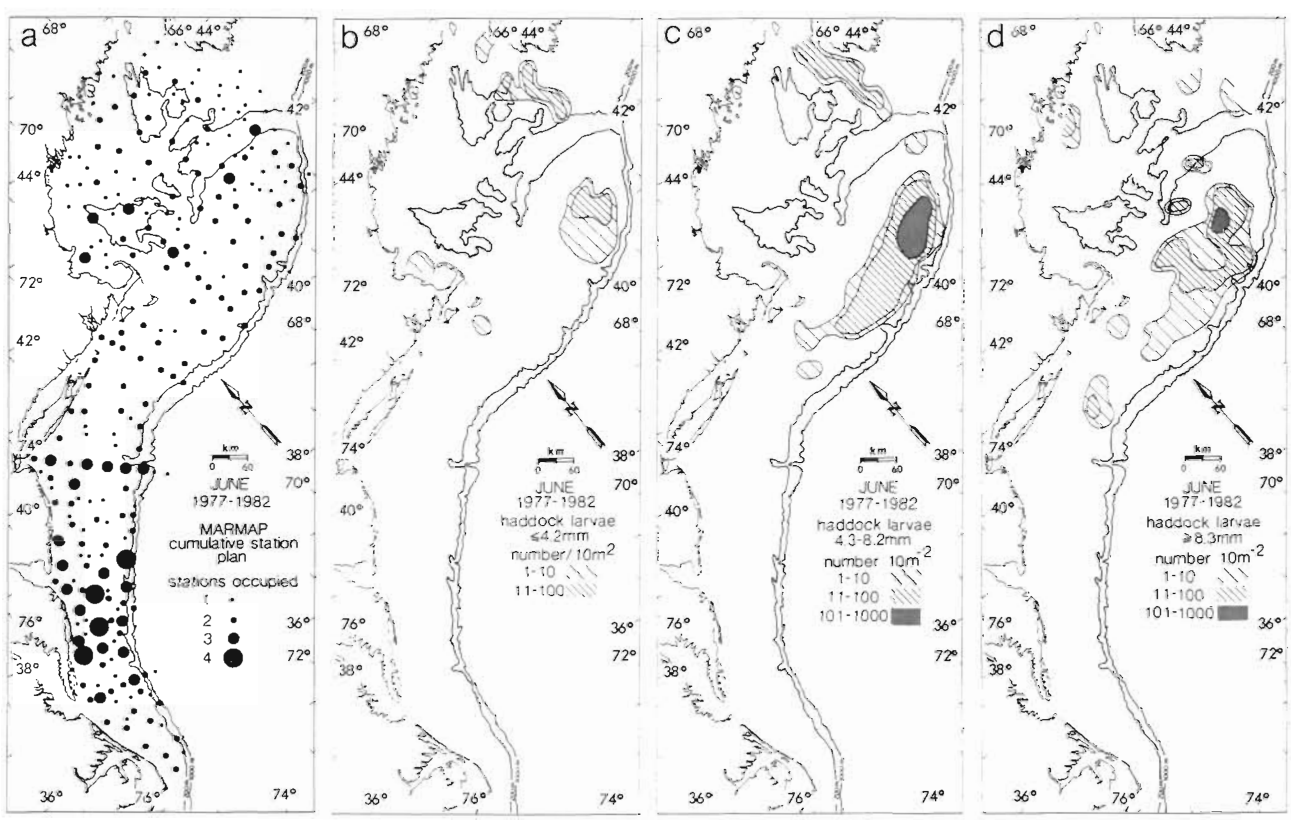

Fig. 7. (a) Cumulative MARMAP stations occupied off northeastern United States during Jun 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.2 mm, (c) 4.3 to 8.2 mm, (d) ≥ 8.3 mm

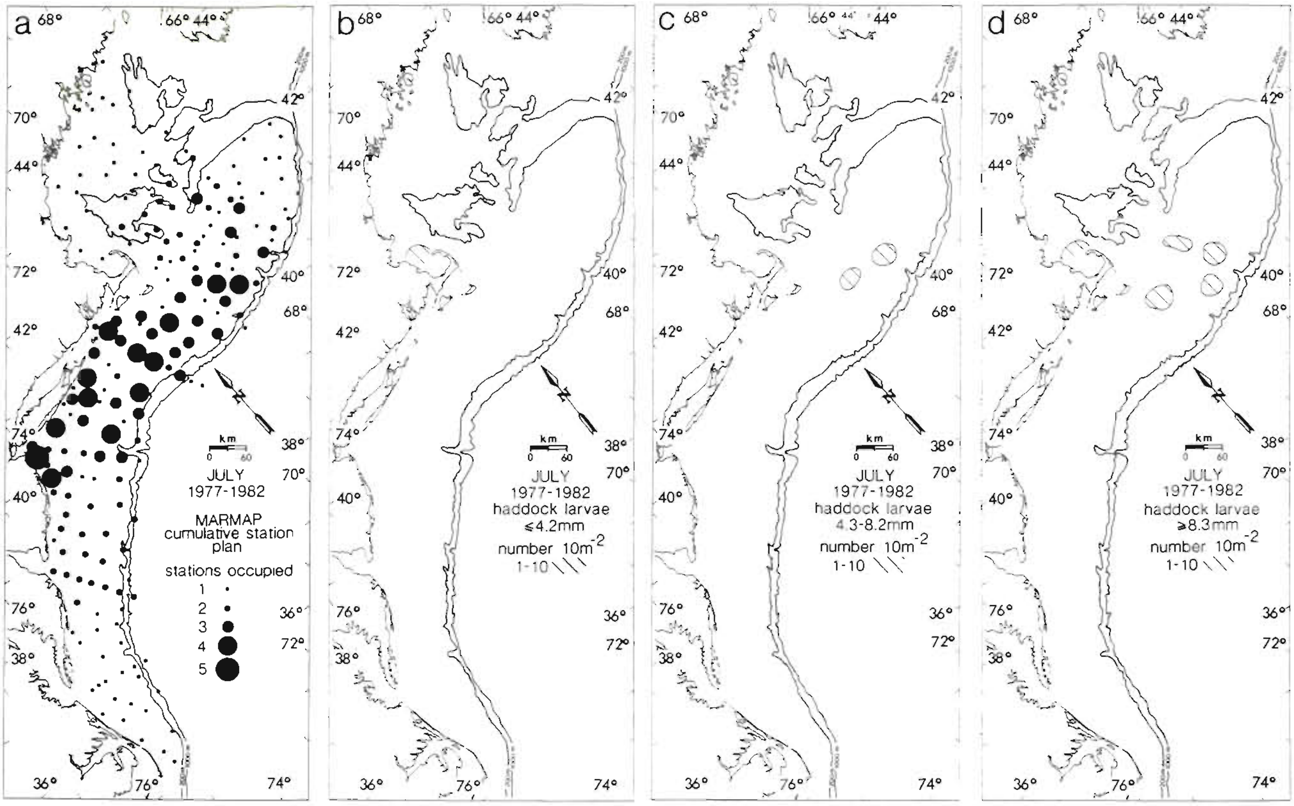

Fig. 8. (a) Cumulative MARMAP stations occupied off northeastern United States during Jul 1977–82, and resultant distribution pattern of haddock larvae, (b) ≤ 4.2 mm, (c) 4.3 to 8.2 mm, (d) ≥ 8.3 mm

grounds, while the broad, deep central basin of the Gulf of Maine isolates eggs and larvae on the Scotian Shelf from those in coastal New England waters.

An examination of the modal lengths of haddock larvae on Georges Bank provides further evidence of their westerly displacement on Georges Bank (Fig. 9). At the outset of the spawning season in February, larvae 3.3 and 3.4 mm modal length occur only over the eastern part of Georges Bank, in Zones 4 and 5 respectively. By March, larvae occur in all 5 zones. Although abundance levels are low in March, 91 % of the larval population remains in Zones 4 and 5 where modal lengths are < 4.0 mm. This distribution pattern holds through April. Small larvae occur in all zones but 89 % of the population lies east of 68° W longitude, or in Zones 4 and 5.

By May, there is evidence of a westerly movement of larvae. The modal length of fish in Zones 2 and 3 increases significantly to 8.9 and 9.0 mm respectively, and these 2 zones now account for 40 % of the total catch. Small larvae continue to dominate in Zone 4, but the contribution to the overall catch from Zone 5 declines significantly. We attribute this decline to diminished spawning activity over the principal spawning grounds on the eastern part of the bank, and the westward displacement of spawning products which increases the relative abundance of large larvae on the western part of the bank. The distribution pattern observed in May continues into June. Recently hatched larvae with modal lengths < 4.0 mm occur in Zones 4 and 5 while predominantly older larvae with modal lengths ≥ 7.0 mm occupy Zones 2 and 3. By July, only remnants of the spawning season remain and their distribution is limited to Zones 2 and 3. The larvae that occur in Zone 1 during the course of the spawning season probably represent limited spawning that occurs on or around Nantucket Shoals.

DISCUSSION

Our findings on time of spawning and location of principal spawning grounds generally agree with those of Walford (1938), Bigelow & Schroeder (1953) and Colton (1965). Haddock eggs occur over all of Georges Bank from late winter through spring but spawning is centered over the eastern part of the bank from mid March through mid April. Our results differ from those of Walford (1938) in that we found no evidence of significant spawning in the vicinity of Great South Channel, nor did we find larvae abundant along the northern edge of Georges Bank. Finally, our

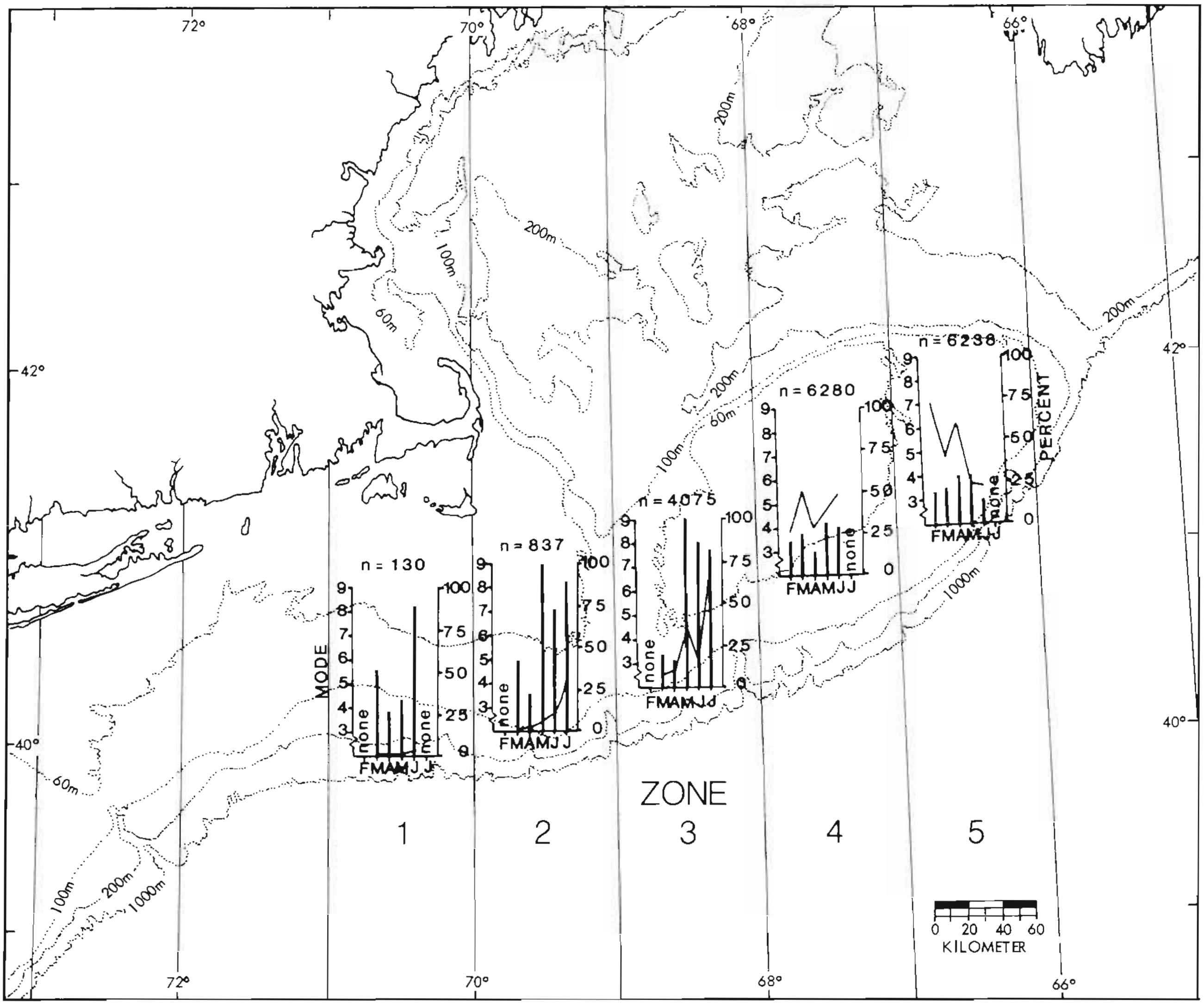

Fig. 9. Modal lengths (bars) in mm and % contribution (lines) of catch by month for haddock larvae in 5 longitudinal zones in the Nantucket Shoals/Georges Bank region as determined from MARMAP surveys, Feb through Jul 1977–82. n = total number of larvae taken in each zone

interpretation of larval drift on Georges Bank corresponds with what Walford (1938) found in 1931 but we see no evidence in our 6 yr data base of the offshore transport he reported for the 1932 spawning season. Walford's analytical approach cannot be faulted but it should be pointed out that his research was based on a single survey of the bank in 1932. His questionable interpretation of events surrounding this survey led him to conclude that the 1931 year class was larger than the 1932 year class. Subsequent research showed that 1932 produced the stronger of the 2 year classes, although neither was very good (Clark et al. 1982).

Chase (1955) investigated the possible effects of winds and the resulting wind driven currents on year class strength on Georges Bank haddock during 1928–1951. He reported a correlation of 0.77 between the predicted and actual year class strength as a function of the offshore wind component and concluded that wind velocity determined whether or not larvae remained on the bank. Subsequent attempts to duplicate Chase's methods were unsuccessful and it was later discovered that his analysis was flawed (Grosslein & Hennemuth 1973).

Colton (1959) reported taking dead larvae of shelf species in warm slope water south of Georges Bank but it was more than 2 decades after Walford's study that Colton & Temple (1961) next took up the challenge of investigating advective processes in the region. They examined observations on the spawning times and locations of Atlantic herring *Clupea harengus* and haddock, and circulation data from bottle returns and transponding buoys. They concluded that only during summer, when the gyral circulation pattern was most pronounced, were eggs and larvae retained on the bank. During other seasons surface water transport was largely seaward and significant egg and larval mortality resulted from advection off the shelf.

Bumpus (1976) examined drift patterns of Atlantic herring larvae during autumn over a 3 yr period. He found that the distribution of larvae expanded with time, and that advection was largely towards the west. Although Bumpus recognized the possibility that some larvae might drift off the southeast edge of Georges Bank, his data indicated that young herring were retained on the bank. Given that herring spawn during the autumn months, Bumpus' results tend to refute the conclusion of Colton & Temple (1961) regarding the seasonal influence of the gyre.

More recently, Colton & Anderson (1983) related movements of satellite-tracked buoys to the distribution of larval Atlantic cod *Gadus morhua*, sand lance *Ammodytes* sp., hake *Urophycis* sp., silver hake *Merluccius bilinearis*, and redfish *Sebastes* sp. Buoy trajectories south and off the bank supported their hypothesis that significant losses of eggs and larvae could be tied to drift off the shelf. However, they were unable to establish a well-defined link between residual drift and the distribution and mortality of larvae for any of the above-listed species. They reluctantly concluded that the principal sources of early mortality were caused by factors other than transport off the shelf but lingering doubts led them to suggest that shortcomings in the data might have biased their results.

Finally, Cohen et al. (1983) examined 3 potential sources of haddock and silver hake egg and larval mortality: (1) entrainment of shelf water off the southern edge of Georges Bank by warm core rings; (2) wind-driven transport of shelf water off the bank; (3) the position of the shelf/slope front relative to the 200 m depth contour. Although they confessed to shortcomings in their data base, they found no relation between variations in mortality during the first year of life and the above environmental conditions.

Bigelow (1927) first described the anticyclonic gyre on Georges Bank. From the release of surface and bottom drift devices, Bumpus & Lauzier (1965) and Bumpus (1973, 1976) estimated that surface drift was on the order of 2 to 3 n miles d^{-1}. Bottom drift moved in the same direction as surface water but at a slower speed of less than 1 n mile d^{-1}. More recently, Butman et al. (1982) used surface and 10 m Langrangian and deeper-placed Eulerian current meters to study residual drift on Georges Bank. Their results show: (1) near surface drift of 3 to 4 n mile d^{-1}; (2) water over depths < 60 m may recirculate, i.e. the central core of the Georges Bank gyre may be partially closed; (3) surface water over the southern part of the bank may have an offshore component but mean subsurface flow is westward, and tends to parallel bottom contours; (4) flow along the southern flank diverges at Great South Channel with most continuing westward into the Middle Atlantic Bight and the remainder (< 30 %) turning northward toward the channel. Based on the conclusions of Butman et al. (1982), the 10 to 40 m depth distribution of most haddock larvae (Miller et al. 1965), and the distribution patterns of intermediate and large haddock larvae in Fig. 5, 6 & 7, we conclude that: (1) the westward displacement of larvae tends to parallel isobaths and, therefore, must be influenced largely by the gyre; (2) the displacement covers a maximum straight line distance of 140 n mile (252 km), thus our transport theory is consistent with mean current velocities presented by Butman et al. (1982) and growth rates of young haddock in Bolz & Lough (1983); (3) larvae associated with the outside of the Georges Bank gyre pass south of Great South Channel with most subsequently finding their way onto Nantucket Shoals; (4) larvae associated with the inside of the gyre are caught up in recirculating water and advected north along the eastern side of the channel, thus remaining on Georges Bank. Given the 78 m mean depth where haddock larvae $\geq$ 8.3 mm occur, and the large size and relative abundance of larvae in Zones 2 and 3 during May, June, and July (Fig. 9), it appears that most young haddock are associated with the inside of the gyre and, consequently, remain on Georges Bank.

Our results show limited westward displacement of haddock larvae during the March/April period but in May evidence of drift is obvious. We attribute this marked westward movement in May to a strengthening of the anticyclonic gyre, which reportedly occurs in association with spring warming (Butman et al. 1982). We suspect that when the gyre is weak during the March/April period larval transport is influenced largely by the strong semidiurnal rotary tidal currents that Bumpus (1976) described as a distinctive feature of Georges Bank. Limeburner & Beardsley (1982) reported that tidal currents had a dampening effect on advective processes on Nantucket Shoals. With no discernible evidence of larval drift during March and April, we assume they play the same role on Georges Bank.

Although larvae of shelf species occur in slope waters off northeastern United States (Colton 1959, Smith et al. 1983), their occurrences are scattered and do not suggest that significant numbers are swept off the shelf. Warm core rings have been speculatively identified as a mechanism for pulling larvae off the shelf but the magnitude of loss from ring-caused advection has yet to be demonstrated, and there is no evidence herein that rings influence the distribution of haddock larvae on Georges Bank. During the February to June (30 mo) period covered in this study, an average of 1.8 rings mo^{-1} occurred in slope waters south of Georges Bank. Only in February and March 1978, and February 1979, or in 3 of the 30 mo, were rings absent from slope waters adjacent to the bank (Mizenko & Chamberlin 1979, Celone & Chamberlin 1980, Fitzgerald & Chamberlin 1981, 1982). Despite this high frequency of ring occurrence and the erer-changing position of the shelf/slope front (Ingham et al. 1982), we caught young haddock along the southern flank of Georges Bank at only 12 of 97 stations where depths exceeded 100 m; at 1 of 26 stations beyond the shelf break, or depths > 200 m; and at none of the 10 stations over depths > 1,000 m. The multi-year composites of larval occurrences by size depict the broadest possible monthly distribution patterns. Yet the results are remarkably cohesive for all 3 size categories and provide convincing evidence that transport mechanisms are perennially consistent. They show that haddock larvae spawned on Georges Bank remain there largely over 40 to 100 m depths.

Our findings agree with those from other distribution studies of haddock eggs and larvae. O'Boyle et al. (1984) reported that the larvae remained largely over the spawning banks on the Scotian Shelf. They speculated that bank retention during early development was gyre-associated and that it plays an important role in the maintenance of stock integrity, a proposal put forth earlier for Atlantic herring *Clupea harengus* by Iles & Sinclair (1982). A similar static drift pattern has been reported in the eastern North Atlantic. Saville (1956) found no evidence of significant drift of young haddock near the Faroe Islands, an observation he too attributed to an unsubstantiated eddy system thought to be the dominant circulation feature around the islands. On the basis of their results, O'Boyle et al. (1984) suggested that the widely-held spawning-to-nursery ground drift concept described by Harden Jones (1968) should be modified to include the possibility that gyre-influenced spawning products can share a common spawning/nursery area. We concur. Our survey results of coastal waters off northeastern United States indicate that haddock spawn at geographically isolated spawning sites and that spawning products from the various sites do not intermix. Larvae originating on Georges Bank are transported in a westerly direction but they remain largely on the bank, which provides both spawning and nursery grounds.

LITERATURE CITED

Armstrong, R. S. (1983). Variations in the shelf water front position in 1982 from Georges Bank to Cape Romain. North Atlantic Fisheries Organisation (NAFO) SCR Doc. 83/VI/12, p. 1–8

Bailey, K. M. (1981). Larval transport and recruitment of Pacific hake, *Merluccius productus*. Mar. Ecol. Prog. Ser. 6: 1–9

Berrien, P. (1983). Silver hake, *Merluccius bilinearis*, egg census and adult population estimate for 1978 in waters off eastern United States. Coun. Meet. int. Coun. Explor. Sea C.M.-ICES/G:46, p. 1–17

Berrien, P. L., Naplin, N. A., Pennington, M. R. (1981). Atlantic mackerel, *Scomber scombrus*, egg production and spawning population estimate for 1977 in the Gulf of Maine, Georges Bank, and Middle Atlantic Bight. In: Lasker, R., Sherman, K. (ed.) The early life history of fish: recent studies. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178: 279–288

Bigelow, H. B. (1927). Physical oceanography of the Gulf of Maine. Bull., U.S. Bur. Fish. 40 (2): 511–1027

Bigelow, H. B., Schroeder, W. C. (1953). Fishes of the Gulf of Maine. Fish. Bull. U.S. 53: 1–577

Bolz, G. R., Lough, R. G. (1983). Growth of larval cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, on Georges Bank, spring 1981. Fish. Bull. U.S. 81 (4): 827–836

Bolz, G. R., Lough, R. G. (1984). Retention of ichthyoplankton in the Georges Bank region during the autumn-winter seasons 1971–77. J. Northw. Atl. Fish. Sci. 5: 33–45

Bumpus, D. F. (1973). A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6: 111–157

Bumpus, D. F. (1976). Review of the physical oceanography of Georges Bank. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Bull. 12: 119–134

Bumpus, D. F., Lauzier, L. M. (1965). Surface circulation on the continental shelf of eastern North America between Newfoundland and Florida. Am. Geogr. Soc., Ser. Atlas Mar. Environ. Folio 7, p. 1–8

Butman, B., Beardsley, R. C., Magnell, B., Vermersch, J. A., Schlitz, R. J., Limeburner, R., Noble, M. A. (1982). The mean circulation on Georges Bank. J. phys. Oceanogr. 12: 569–591

Celone, P., Chamberlin, J. L. (1980). Anticyclonic warm core Gulf Stream eddies off northeastern United States during 1978. ICES Annls. Biol. 35: 50–55

Chase, J. (1955). Winds and temperature in relation to the brood strength of Georges Bank haddock. J. du Cons. 21: 17–24

Clark, S. H., Overholtz, W J., Hennemuth, R. C. (1982). Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. 3: 1–27

Cohen, E. B., Mountain, D. G., Smith, W. G. (1983). Physical processes and year class strength of silver hake and haddock on Georges Bank. NEFC, Woods Hole, MA, Lab. Ref. No. 83-06, p. 1–18

Colton, J B., Jr. (1959). A field observation of mortality of marine fish larvae due to warming. Limnol. Oceanogr. 4: 219–222

Colton, J. B., Jr. (1965). The distribution and behavior of pelagic and early demersal stages of haddock in relation to sampling technique. International Commission for the Northwest Atlantic Fisheries (ICNAF) Spec. Publ. 6: 317–334

Colton, J. B., Jr., Anderson, J. L. (1983). Residual drift and residence time of Georges Bank surface waters with reference to the distribution, transport, and survival of larval fishes. NOAA Tech. Memo. NMFS-F/NEC-24, p. 1–44

Colton, J. B., Jr., Temple, R. F. (1961). The enigma of Georges Bank spawning. Limnol. Oceanogr 6 (3): 280–291

Fitzgerald, J., Chamberlin, J. L. (1981). Anticyclonic warm core Gulf Stream eddies off the northeastern United States during 1979. ICES Annls Biol. 36: 44–51

Fitzgerald, J., Chamberlin, J. L. (1982). Anticyclonic warm core Gulf Stream eddies off the northeastern United States during 1980. ICES Annls Biol. 37

Grosslein, M. (1969). Groundfish survey program of BCF Woods Hole. Comm. Fish. Rev. 31 (8–9): 22–35

Grosslein, M., Hennemuth, R. (1973). Spawning stock and other factors related to recruitment of haddock on Georges Bank. Rapp. P.-v. Réun. Cons. int. Explor. Mer 164: 77–88

Harden Jones, J. R. (1968). Fish migrations. Arnold, London

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-v. Réun. Cons. int. Explor. Mer 20: 1–228

Hopkins, T. S., Garfield, N., III. (1981). Physical origins of Georges Bank water. J. mar. Res. 39: 465–500

Iles, T. D., Sinclair, M. (1982). Atlantic herring: stock discreteness and abundance. Science 215: 627–633

Ingham, M., Armstrong, R., Chamberlin, J., Cook, S., Mountain, D., Schlitz, R., Thomas, J., Bisagni, J., Paul, P., Warsh, C. (1982). Summary of the physical oceanographic processes and features pertinent to pollution distribution in the coastal and offshore waters of the northeastern United States, Virginia to Maine. NOAA Tech. Memo. NMFS-F/NEC-17. p. 1–60

Limeburner, R., Beardsley, R. C. (1982). The seasonal hydrography and circulation over Nantucket Shoals. J. mar. Res. 40 (Suppl.): 371–406

Lough, G. (1984). Larval fish trophodynamic studies on Georges Bank: sampling strategy and initial results. Flodevigen rapportser 1: 395–434

Miller, D., Colton, J. B., Jr., Marak, R. R. (1965). A study of the vertical distribution of larval haddock. J. du Cons. 28 (1): 37–49

Mizenko, D., Chamberlin, J. L. (1979). Gulf Stream anticyclonic eddies (warm core rings) off the northeastern United States in 1977. ICES Annls Biol. 34: 39–44

Morse, W. (1982). Spawning stock biomass estimates of sand lance, *Ammodytes* sp., off northeastern United States, determined from MARMAP surveys, 1974–80. Coun. Meet. int. Coun. Explor. Sea C.M.-ICES/G:59, p. 1–11

O'Boyle, R. N., Sinclair, M., Conover, R. J., Mann, K. H., Kohler, A. C. (1984). Temporal and spatial distribution of ichthyoplankton communities of the Scotian Shelf in relation to biological, hydrological and physiogeographic features. Rapp. P.-v. Réun. Cons. int. Explor Mer 183: 27–40

Overholtz, W. J., Clark, S. H., White, D. (1983). A review of the status of the Georges Bank and Gulf of Maine haddock stocks for 1983. Woods Hole Lab. Ref. Doc. 83-23, NOAA, NMFS, p. 1–33

Parrish, R. H., Nelson, C. S., Bakun, A. (1981). Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr 1 (2): 175–203

Poulsen, E. (1930). On the fluctuations in the abundance of cod fry in the Kattegatt and the Belt Sea. Rapp. P.-v. Réun. Cons. Perm. int. Explor. Mer 65: 26–30

Rollefsen, G. (1930). Observations on cod eggs. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 65: 31–34

Saville, A. (1956). Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. Mar. Res. Scot. 4: 1–27

Sherman, K. (1980). MARMAP, a fisheries ecosystem study in the NW Atlantic: Fluctuations in ichthyoplankton-zooplankton components and their potential for impact on the system. In: Diemer, F. P., Vernberg, F. J., Mirkes, D. Z. (ed.) Advance concepts in ocean measurements for marine biology. Belle W. Baruch Institute for Marine Biology and Coastal Research, Univ. South Carolina Press, Berkeley, p. 9–37

Sherman, K., Lasker, R., Richards, W., Kendall, A. (1983). Ichthyoplankton and fish recruitment studies in large marine ecosystems. Mar. Fish. Rev. 45 (10–12): 1–25

Sherman, K., Smith, W., Morse, W., Berman, M., Green, J., Ejsymont, L. (1984). Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses in zooplankton off the northeastern United States. Mar. Ecol. Prog. Ser. 18: 1–19

Smith, P. E., Richardson, S. (1977). Standard techniques for pelagic fish eggs and larval surveys. FAO Fish. Tech. Pap. 175: 1–100

Smith, W., Berrien, P., McMillan, D., Wells, A. (1981). The distribution, abundance and production of Atlantic cod and haddock larvae off northeastern United States in 1978–79 and 1979–80. Coun. Meet. int. Coun. Explor. Sea C.M.-ICES/G:52, p. 1–16

Smith, W., Morse, W., Wells, A., McMillan, D. (1983). Fish eggs and larvae. In: Pearce, J., Miller, D., Berman, C. (ed.) 106-mile Site characterization update. NOAA Tech. Memo. NMFS-F/NEC-26, 7-1 to 7-47

Smith, W., Pennington, M., Berrien, P., Sibunka, J. (1979). Annual changes in the distribution and abundance of Atlantic cod and haddock larvae off the northeastern United States between 1973–74 and 1977–78. Coun. Meet. int. Coun. Explor. Sea C.M.-ICES/G:47, p. 1–19

Walford, L. A. (1938). Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. Bull. U.S. Bur. Fish. 49: 1–73

Wiebe, P. H. (1982). Rings of the Gulf Stream. Sci. Am. 246 (3): 60–70

This paper was submitted to the editor; it was accepted for printing on April 7, 1985