Larval distribution patterns: Early signals for the collapse/recovery of Atlantic herring *Clupea harengus* in the Georges Bank area

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Abstract.–Changing temporal and spatial distribution patterns of Atlantic herring *Clupea harengus* larvae collected off southern New England over two decades provided early signals of large-scale changes in adult spawning biomass that are now a matter of record. Four contrasting spawning patterns were evident during the 20yr period. Each pattern covered successive multi-year intervals and reflected the corresponding status of the adult population. In 1971, spawning occurred throughout the Georges Bank/Nantucket Shoals/Massachusetts Bay study area. The principal spawning grounds of herring in the Gulf of Maine region were located on the Northeast Peak of Georges Bank. With the collapse of the Georges Bank fishery in 1976, spawning receded westward to Nantucket Shoals. By 1979, larvae occurred only in the Stellwagen Banks area of Massachusetts Bay, the smallest of the three subareas. After a 6yr hiatus, spawning beds on Nantucket Shoals were reoccupied in 1985. By 1988 spawning had advanced eastward to Cultivator Shoals on Georges Bank, but through 1990 we found no evidence of renewed spawning activity on the historically-prominent spawning beds on Northeast Peak. The rebuilding process was attributed to recolonization rather than resurgence.

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The Atlantic herring *Clupea harengus* has been a target species of broad-scale early-life-history research in the Gulf of Maine since 1956. The initial larval surveys were part of a collaborative study by U.S. and Canadian biologists to define the stock structure of herring in the Northwest Atlantic (Tibbo et al. 1958). This effort continued over two spawning seasons and was followed by annual observations on distribution patterns of herring larvae during 1962–70 (Boyar et al. 1973b). Thereafter, U.S. biologists participated in a multinational field program that represented the starting point of the Northeast Fisheries Science Center's (NEFSC) current database for larval herring. This study, sponsored by the International Commission for the Northwest Atlantic Fisheries (ICNAF), was initiated in 1971 to identify mechanisms that influence survival of larvae (Lough et al. 1985).

With the termination of ICNAF larval herring surveys in 1977, NEFSC began a comprehensive fisheries ecosystem study of the Northeast Shelf Ecosystem (Sherman 1986, Smith 1988). This program, known as Marine Resources Monitoring, Assessment and Prediction (MARMAP), included standardized year-round surveys of fish eggs and larvae to provide baselines against which shifts in species composition and diversity within the finfish community could be observed and evaluated. These surveys continued for 11 years, ending in December 1987.

In 1988, ecosystems research emphasis at NEFSC shifted away from year-round surveys of the entire Northeast Shelf Ecosystem and focused on the Georges Bank area during autumn and winter. The new initiative was designed to document the changing status of herring and investigate density-dependent population regulation between herring and sand lance *Ammodytes* spp., important coastal pelagic species in the western North Atlantic. When combined, the three multi-year research endeavors conducted since 1971 provide an uninterrupted 20yr database for larval herring in the Georges Bank/Nantucket Shoals/Massachusetts Bay area. During this period, dramatic changes occurred in the herring population.

Spawning biomass was relatively high at the onset of the ICNAF larval herring surveys in 1971, although in decline due to intense foreign fishing pressure that began in the mid 1960s. During the 1960s and continuing through the mid 1970s, biomass of herring on Georges Bank was estimated at 400,000–600,000 t. Annual catches ranged from 150,000 to 374,000 t. Dominating the population during the 1960s were three year-classes, 1956, 1960, 1961, and to a lesser extent 1966, although spawning success was poor in the closing years of the decade. Despite a strong 1970 year-class that entered the Georges Bank fishery in 1973, fishing pressure by the large international fleet was so intense that landings declined after 1971. From 1973 to 1975 the principal herring landings shifted from the bank to the vicinity of Great South Channel, just east of Nantucket Shoals. After 15yr of moderate-to-heavy exploitation, and several years of quota management under ICNAF, the Georges Bank herring fishery collapsed in 1976 (Anthony & Waring 1980).

This paper examines the 20yr larval database to look for early signals of the dramatic changes in adult biomass that have occurred since 1971. We evaluate the influence of transport mechanisms on the spatial and temporal distribution patterns of larvae to corroborate the herring stock hypothesis of Iles & Sinclair (1982) and Sinclair & Iles (1985). Finally, we search for supporting evidence that the late-1980s recovery of herring in the Georges Bank area resulted from population resurgence rather than recolonization, a conclusion of Stephenson & Kornfield (1990).

Methods

The 20yr time-series began during the final years of the international fishery. It included a 10yr period when essentially no fishing took place in the study area, and ended with the 1990 spawning season when a limited fishery was again underway. Without a directed fishery after 1976, this dataset, along with NEFSC semi-annual trawl surveys, provided the only source of information to evaluate the status of herring in the Georges Bank area for more than a decade.

Sampling designs

All three larval surveys used the 61cm bongo, fitted with 0.333 and 0.505mm mesh nets. Larval herring catches from the 0.505mm net were analyzed. Net mesh selection was based on recommendations in Smith & Richardson (1977) and on Colton et al. (1980) who found no significant difference in retention rates of herring larvae captured in the two mesh sizes.

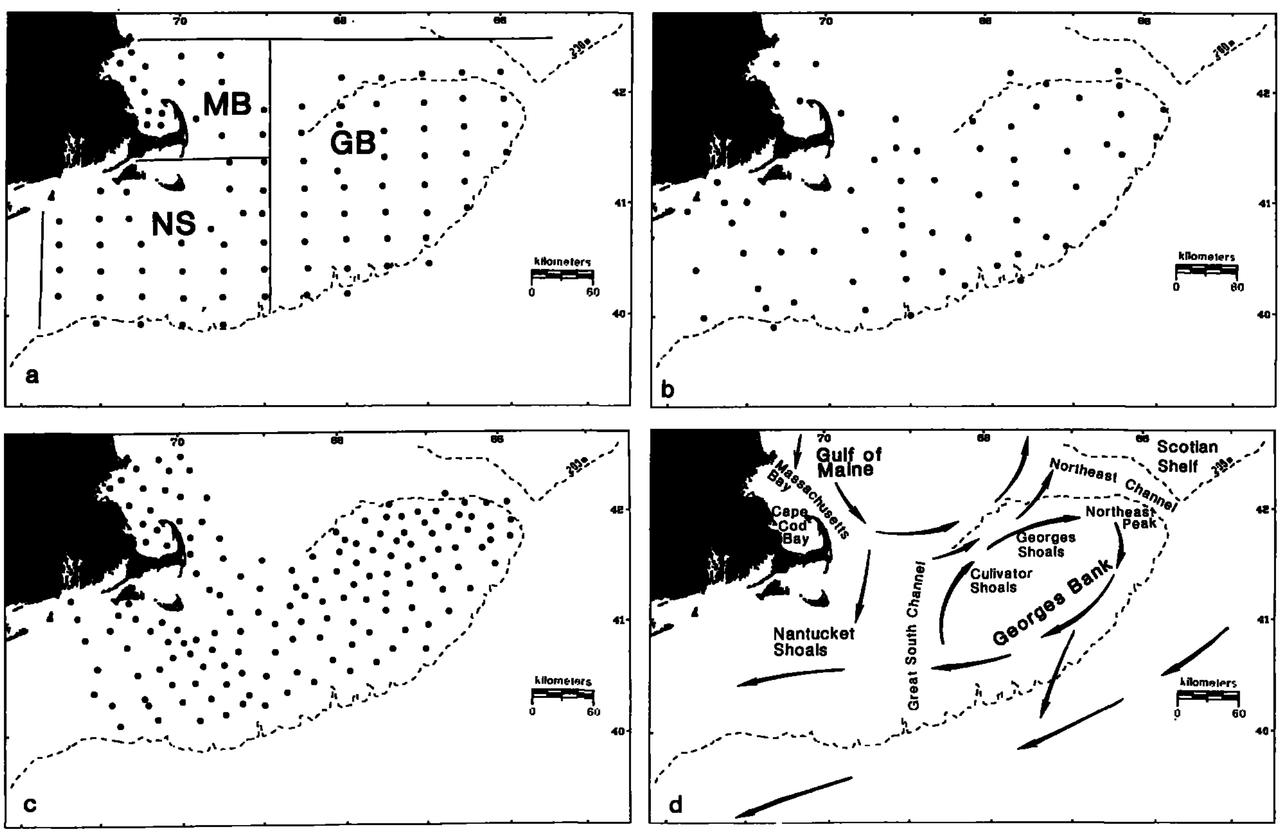

Figure 1
Station plan for **(a)** ICNAF larval herring surveys in the Georges Bank area, 1971–76, **(b)** MARMAP surveys in Georges Bank, 1977–87, and **(c)** studies of herring/sand lance interactions, 1988–90. **(d)** General surface circulation in the Georges Bank area (after Ingham 1982).

The ICNAF larval herring program included the entire Gulf of Maine region but concentrated on the Nantucket Shoals/Georges Bank area (Lough & Bolz 1979a, Lough et al. 1985). The 33 surveys conducted between 1971 and 1976 were used in our analysis. ICNAF participants deployed the bongo at 50 m/min to a maximum depth of 100 m and retrieved it in a smooth oblique profile at 10 m/min. Towing speed was 3.5 kn at stations spaced at 28–37 km intervals on a standard grid pattern (Fig. 1a). Additional stations in areas of high larval abundance were sampled after 1974. Lough & Bolz (1979b) provided a detailed account of sampling operations and cruises for the ICNAF time-series.

MARMAP surveys, conducted at monthly to bimonthly intervals, covered the continental shelf from Cape Hatteras, North Carolina to Cape Sable, Nova Scotia. Cruise activities were described by Sibunka & Silverman (1984, 1989). MARMAP surveys fished the 61cm bongo to a maximum depth of 200 m with payout at 50m/min and retrieval at 20 m/min. Ship speed varied between 1 and 2 kn to maintain a 45° angle in the towing wire. Station intervals ranged from 15 to 45 km (Fig. 1b).

The herring recovery study initiated in 1988 employed MARMAP sampling methods. Cruises were conducted at about monthly intervals and occupied 151 stations in the Nantucket Shoals/Massachusetts Bay/Georges Bank study area (Fig. 1c).

Data analysis

We adjusted the number of larvae caught at each station in the time-series to reflect day/night/twilight catch differences (see Morse 1989). Larvae were partitioned into size-intervals to depict changes in distribution patterns over time. When the partitioned size-intervals of 4.0–7.9 mm, 8.0–12.9 mm, 13.0–17.9 mm, and >17.9 mm were corrected for shrinkage (see Theilacker 1980), they approximated age-groups of <2 wk, 2–5 wk, 5–8 wk, and >8 wk, respectively (Lough et al. 1982). Surveys were grouped by multi-year periods that represented time-intervals between the most apparent changes in spawning patterns during the 20 yr period. Figures showing mean numbers of larvae per 10 m^2 surface area were based on methods recommended for the delta distribution (Pennington 1983). Distributions of larvae grouped by age over time are discussed in relation to circulation patterns shown in Fig. 1 d.

Results

Changes in distribution and abundance of herring larvae during the 20 yr time-series reflected four contrasting spawning patterns that spanned successive multi-year intervals. Larvae were abundant on both Nantucket Shoals and Georges Bank, but not so in Massachusetts Bay, during 1971–75. Conversely, we found low to no measurable numbers of larvae on Nantucket Shoals and Georges Bank during 1976–84, a period when spawning activity increased in Massachusetts Bay. Spawning resumed on Nantucket Shoals in 1985. During 1985–87, larval abundance peaked in Massachusetts Bay but the center of spawning activity shifted to Nantucket Shoals.

Herring were again spawning on the western half of Georges Bank in 1988. The dramatic increase in spawning activity on Nantucket Shoals and renewed spawning on western Georges Bank during 1988–90 elevated larval abundance estimates to their highest levels during the closing years of the time-series (Fig. 2).

When the time-series began in 1971, Georges Bank had been the principal spawning grounds for herring

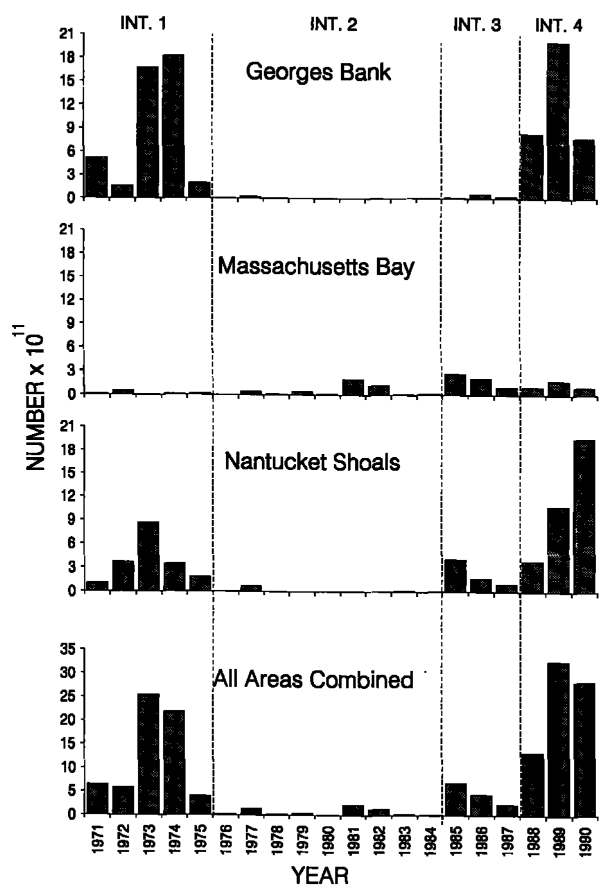

Figure 2
Changes in abundance of Atlantic herring *Clupea harengus* larvae by subarea during the 20yr time-series. Intervals (Int) represent multi-year periods that reflect the most apparent changes in spawning patterns.

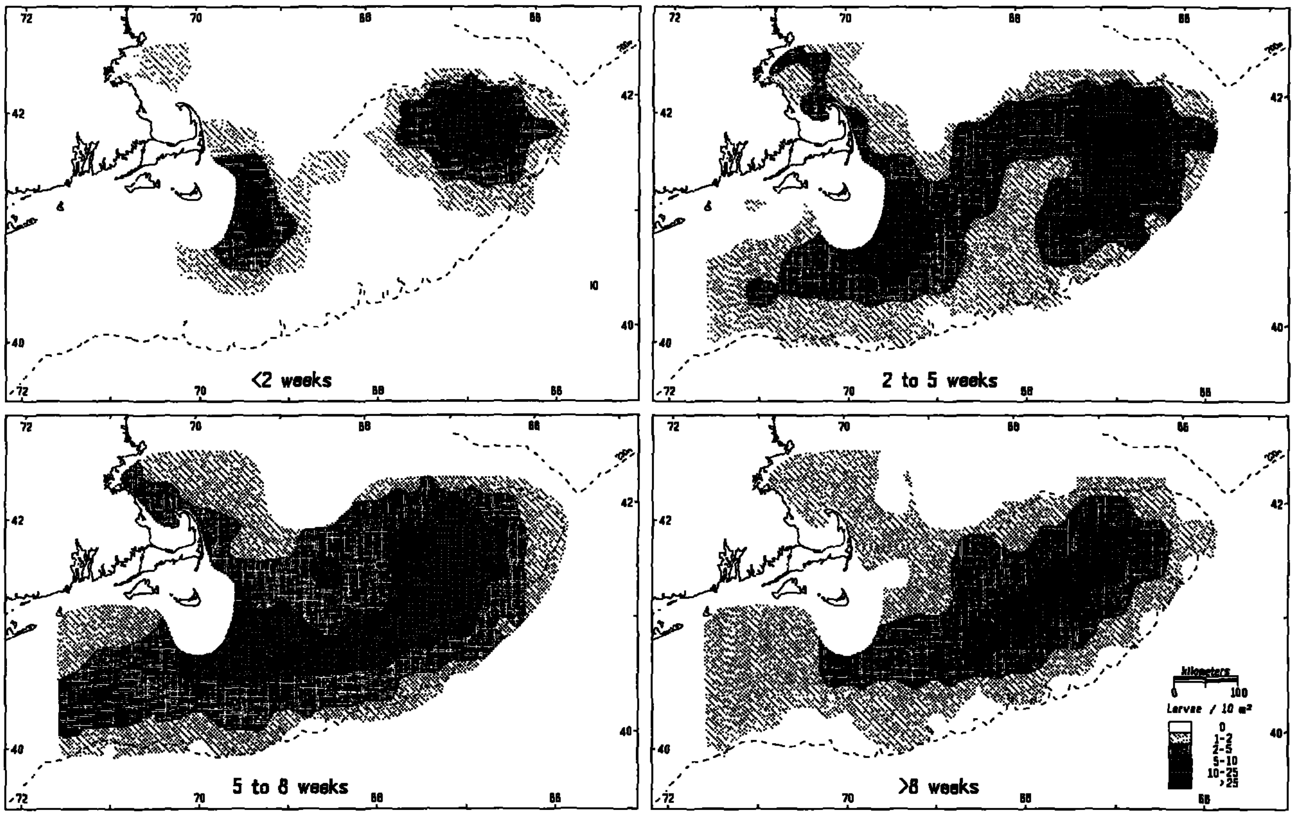

Figure 3
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1971–75.

in the western North Atlantic for at least 15yr (Tibbo et al. 1958, Boyar et al. 1973b, Anthony & Waring 1980, Lough et al. 1985, Grosslein 1987). The magnitude of spawning activity, as measured by the abundance of larvae, was low in 1971 and 1972 but increased sharply in 1973 and continued upward in 1974, the initial spawning years of the strong 1970 year-class. In 1975, larval abundance on Georges Bank declined dramatically and spawning activity on Nantucket Shoals equaled that on the bank. By 1976, when surveys showed only negligible spawning activity east of the 69° meridian, Georges Bank had lost its longstanding status as the principal spawning ground for herring in the western North Atlantic (Fig. 2).

ICNAF surveys of 1971–75 identified two geographically-separate spawning areas: one centered along the eastern edge of Nantucket Shoals, the other on northeastern Georges Bank (Fig. 3). Within 2–5 wk of hatching, larvae began to disperse and the two spawning centers were no longer discrete. At 5–8 wk after hatching, some larvae originating on the Northeast Peak were transported westward across the southern half of Georges Bank by anticyclonic currents. Together with larvae from Nantucket Shoals, their distribution extended over shelf waters from Cape Cod eastward and continued into adjacent slope waters. Although distributions of both Nantucket Shoals and Georges Bank larvae exhibited the influence of known circulation patterns within 5 wk of hatching (Fig. 1d), centers of abundance remained near their points of origin for at least 8 wk. Thereafter, a single center of abundance for larvae >8 wk old emerged over the shallow central part of Georges Bank (Fig. 3).

Herring larvae in all four age-groups occurred largely in coastal waters immediately adjacent to Cape Cod during the 1976–84 time-interval, a distribution pattern that differed significantly from those observed during the first 5yr of the time-series (Fig. 4). We found no larvae <2 wk old on Georges Bank in 1977. In 1978, only a few larvae in the youngest grouping were caught over the once-productive Northeast Peak. For the next decade, we caught no recently-hatched larvae anywhere on Georges Bank. Larvae <2 wk old were essentially absent on Nantucket Shoals during the 1976–84 time-interval as well. The center of larval abundance in each of the four groupings occurred in Massachusetts

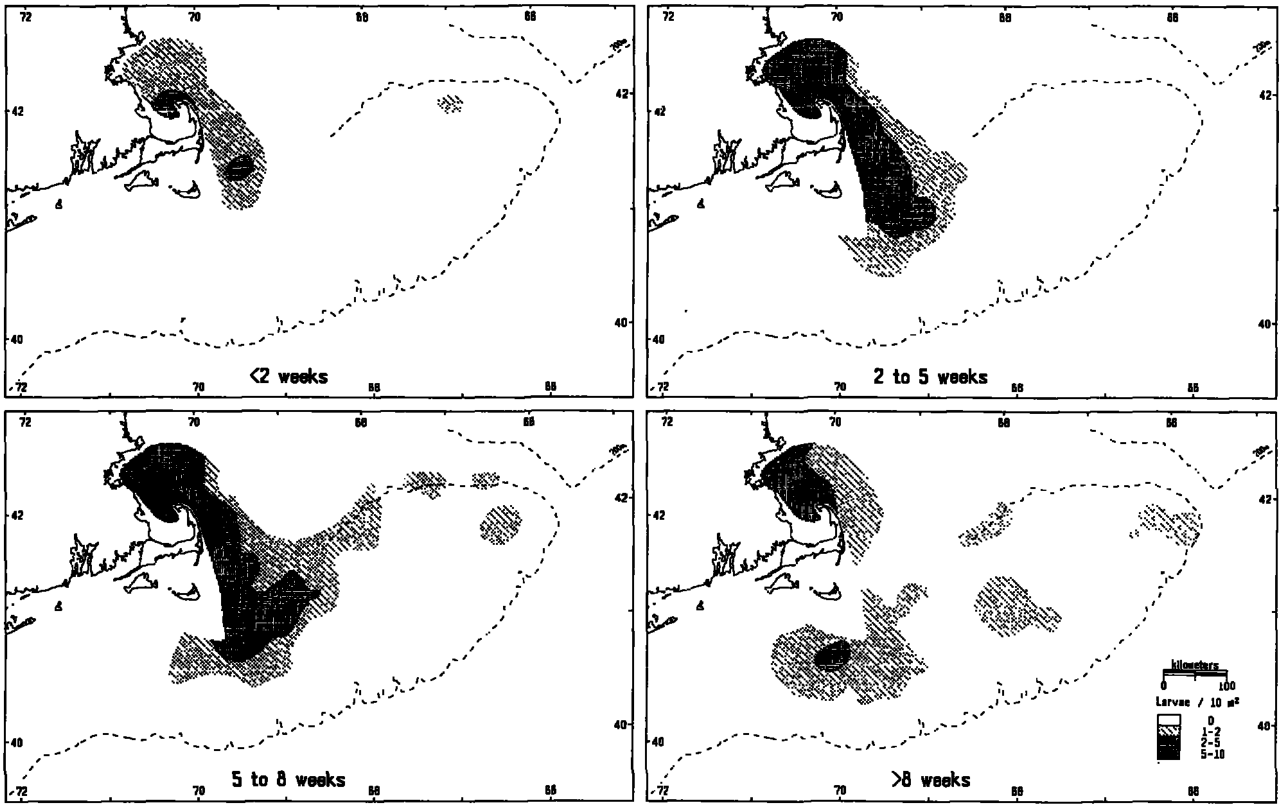

Figure 4
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1976–84.

and Cape Cod bays. As during the 1971–75 interval, larvae partitioned by age exhibited the influence of transport, especially in 1981 and 1982 when distribution patterns expanded from Massachusetts Bay to Nantucket Shoals. Averaging catches over a 9 yr period did not mask the effects of larval transport during the 1981 and 1982 spawning seasons (Fig. 4).

Further change marked the ensuing 3 yr period (1985–87), providing the first evidence that the herring population in the study area was beginning to recover. Spawning beds on Nantucket Shoals were reactivated in 1985, and the center of larval abundance shifted from Massachusetts Bay to Nantucket Shoals (Fig. 5). The influences of advective processes on the distribution of larvae were evident within a month after hatching. Nantucket Shoals larvae 2–5 wk old were transported by the Georges Bank gyre eastward across the northern part of the bank as far as the 68° meridian. The distribution pattern of 5–8 wk old larvae resembled that of 2–5 wk old fish, but exhibited the influence of further drift away from the Nantucket Shoals spawning beds. Larvae >8 wk old were caught in Massachusetts Bay and from Nantucket Shoals eastward onto Georges Bank. As in the 1976–84 period, no recently-hatched larvae occurred over the traditional spawning beds on eastern Georges Bank through 1987 (Fig. 5).

The reoccupation of spawning beds on the western half of Georges Bank and the increasing abundance of larvae on Nantucket Shoals during 1988–90 provided further signals of the changing status of herring in the study area (Fig. 6). Although the principal spawning grounds remained on Nantucket Shoals, the appearance of recently-hatched larvae on Georges and Cultivator shoals in all 3 yr provided the first evidence in a decade of spawning east of the 68° meridian on Georges Bank. Within 5 wk of hatching, larvae were dispersed over all but the eastern tip of the bank. By the time larvae reached 8 wk of age, they occurred throughout the study area (Fig. 6). As with the reactivation of Nantucket Shoals spawning beds in 1985, 3 yr lapsed from the time we first observed larval transport onto Georges Bank until we found evidence of spawning on the bank. Although the recovery of herring in the Georges Bank region was clearly underway during the closing years of the 1980s, we found no evidence in

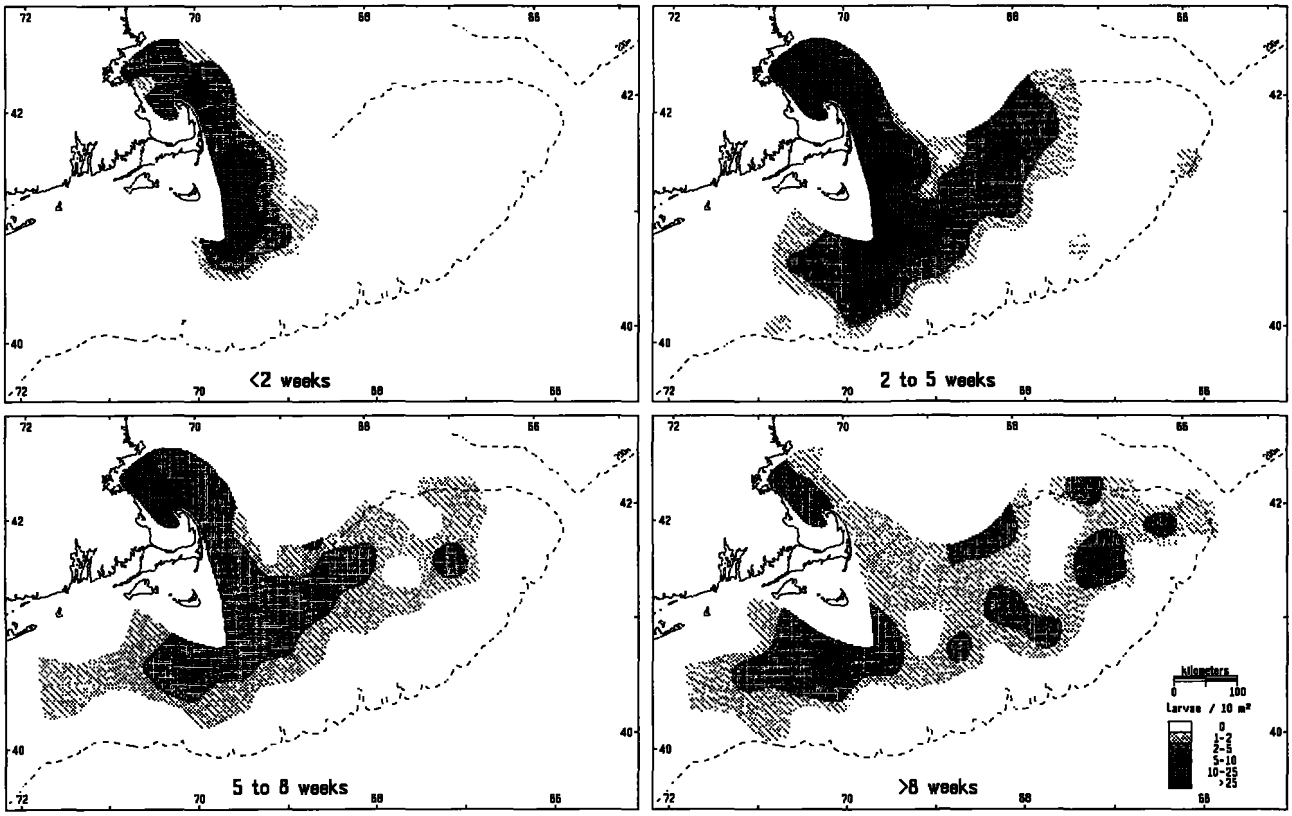

Figure 5
Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1985–87.

larval distribution patterns through the 1990 spawning season that the historically prominent spawning beds on eastern Georges Bank had been reoccupied.

Discussion

The literature contains conflicting descriptions of the herring population structure in the western North Atlantic. Iles & Sinclair (1982) hypothesized that the number of Atlantic herring spawning stocks in the Gulf of Maine region is determined by the number of geographically-stable larval retention areas. They recognized four stocks: southwest Nova Scotia, Grand Manan, Georges Bank, and Nantucket Shoals. Sinclair & Iles (1985) revised the stock structure to include Jeffreys Ledge, coastal Gulf of Maine, and Scots Bay. Both Iles & Sinclair (1982) and Sinclair & Iles (1985) further hypothesized that (1) stocks are segregated only during autumn when herring return to their respective spawning grounds, (2) larvae of different stocks do not intermix for several months after hatching, the period when imprinting occurs, and (3) hydrographic conditions create retention areas by isolating larvae in vertically-mixed areas surrounded by stratified waters. Their retention hypothesis recognized that the geographic extent of the retention areas could vary annually and that some horizontal displacement could occur during larval development.

Grosslein (1987) reviewed the stock structure of herring in the Gulf of Maine region using the collective evidence from prior studies. He concluded that the population was composed of three major stocks: Georges Bank, western Nova Scotia, and the Gulf of Maine, with lesser spawning occurring elsewhere around the gulf. Grosslein indicated, however, that this breakdown was speculative and that direct attempts to differentiate between stocks through larval surveys, tagging studies, meristic and morphometric characters, biochemical methods, and parasitology produced inconclusive results.

Smith & Jamieson (1986) argued that no scientific basis existed for the stock concepts of Atlantic herring in either the eastern or western North Atlantic. They viewed the breakdown of herring stocks as transient subdivisions having no taxonomic or evolutionary

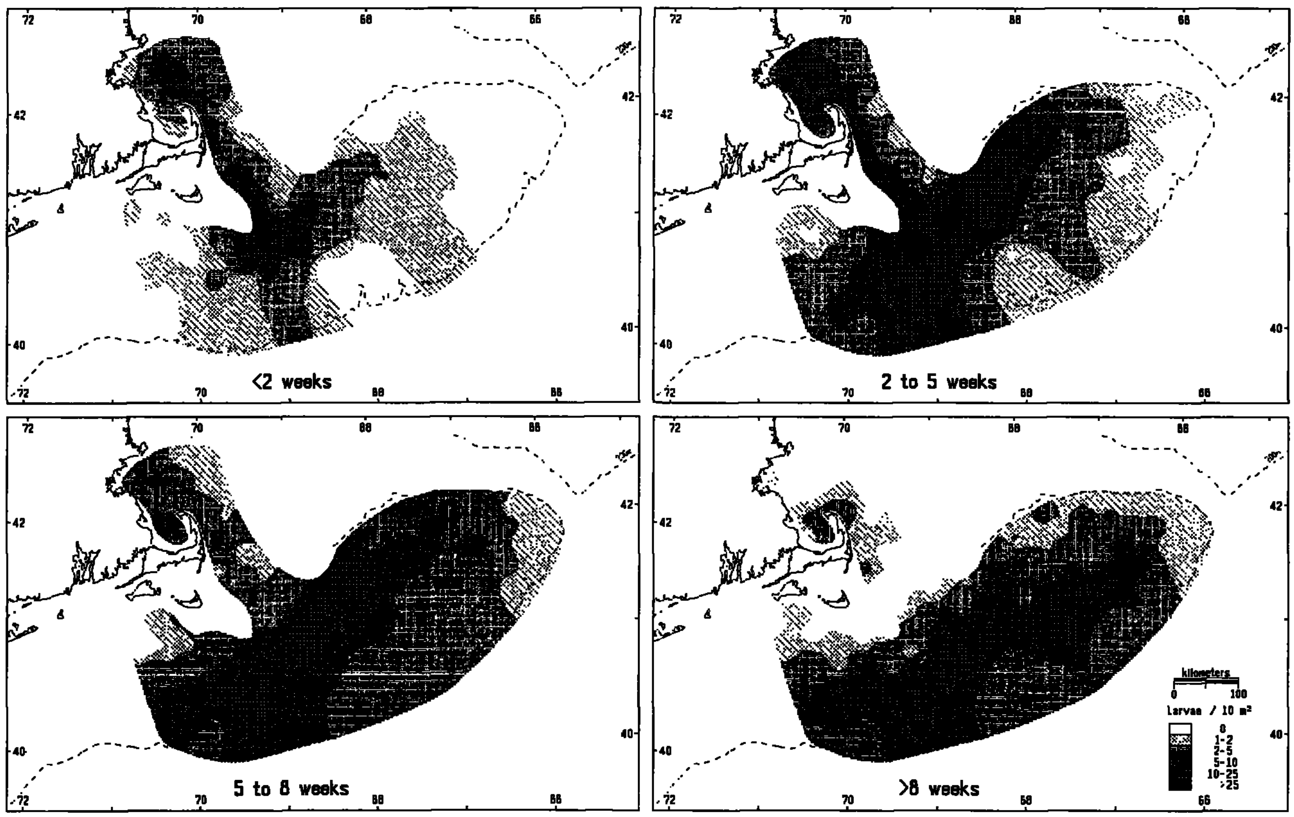

Figure 6

Composite representation of the distribution of Atlantic herring *Clupea harengus* larvae by age in the Georges Bank area, 1988–90.

status. Cushing (1986) also took exception to the retention hypothesis as applied by Iles & Sinclair (1982) to the North Sea area. Cushing (1986) noted that herring do not always spawn in transition zones around the British Isles and, where they do, the fronts brake down within a month after hatching. He further dismissed the retention concept by demonstrating that postlarval metamorphosis takes place near the nursery grounds after prolonged larval drift.

Our analysis of the 20 yr larval time-series supports that segment of the literature showing herring larvae vulnerable to advection after hatching (e.g., Cushing 1986, Bartsch et al. 1989, Heath & Walker 1987). Although transport in our dataset is not extensive, it is not restricted to the retention areas described by Sinclair & Iles (1985). Larvae drift from Massachusetts Bay southward to Nantucket Shoals, and the anticyclonic gyre on Georges Bank mixes larvae originating there with those spawned on the shoals. The direction of transport generally corresponds with reported circulation, a pattern consistent with that of Parrish et al. (1981). Mixing of larvae from the three subareas occurs within weeks after hatching, or earlier in the life cycle than proposed by Sinclair & Tremblay (1984) and Sinclair & Iles (1985).

Drift trajectories of herring larvae from other studies in the Gulf of Maine region agree with our findings in that they correspond to dominant circulation patterns described by Ingham (1982) and Butman & Beardsley (1987). Graham et al. (1972) and Graham (1982) recognized that some herring larvae spawned off eastern Maine drifted westward to mix with larvae originating in central and western Maine waters. Townsend et al. (1986) provided further evidence that herring larvae off Maine are advected from east to west. Although Chenoweth et al. (1989) noted that residual currents do not demonstrate a persistent flow in any direction off eastern Maine, they too observed a westward displacement of herring larvae. Finally, Boyar et al. (1973a) showed herring larvae spawned on Jeffreys Ledge, another of the retention areas of Sinclair & Iles (1985), drifting into Massachusetts Bay where they could mix with larvae originating on and around Stellwagen Bank. Given these reports of drift and mixing in western Gulf of Maine waters near our study area and the demonstrated dispersion and mixing of early-stage larvae reported here, we see no compelling argument for the separation of herring stocks through larval retention in the western Gulf of Maine and Georges Bank areas.

We consistently found sufficient larval drift and mixing to question the stock structure of Sinclair & Iles (1985) in the Georges Bank region. However, Figs. 3–6 lend some support to the retention hypothesis by showing that a significant portion of the larvae up to 8wk old remained near their points of origin. Campana et al. (1989a, 1989b) reported similar results for haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* larvae, respectively, on Browns Bank. Some larvae of the two species were transported shoreward while others remained near the spawning grounds longer than known water residence time. Both of the 1989 studies concluded that the instability of the Browns Bank gyre accounted for the dichotomous distribution patterns. They interpreted the onshore drift as an all-or-none situation for individual larvae. Some readily exited the influence of a weakly established gyre, while most were retained during periods of pronounced gyral circulation. In our view, their theory provides a more plausible explanation for the shifting distribution patterns of herring larvae around Georges Bank, an area also influenced by gyral circulation, than the stock hypothesis proposed by Iles & Sinclair (1982).

Stephenson & Kornfield (1990) attributed the increasing biomass of herring on Georges Bank during the late 1980s to the resurgence of residual fish rather than to recolonization by fish from surrounding areas. Based largely on a 4 yr dataset that excluded Nantucket Shoals and Massachusetts Bay, they concluded that (1) adult herring caught on Georges Bank differed in age composition from herring on Jeffreys Ledge and southwestern Nova Scotia, (2) some of the Georges Bank herring exhibited different isoenzyme characteristics than neighboring herring, and (3) the return of herring to Georges Bank took longer than they expected through recolonization.

In our view, the change in spawning sites on Georges Bank during the 20 yr time-series, coupled with the recession and subsequent expansion of the spawning range over time, makes a convincing case for recolonization rather than resurgence. Larval distribution patterns on Georges Bank during the closing years of the time-series differed markedly from those observed at the outset of the program. Whereas recently-hatched larvae were concentrated on Northeast Peak during the initial survey years, their distribution on the bank progressed eastward only as far as Georges Shoals during the final years of survey activity. If, as proposed by Stephenson & Kornfield (1990), resurgence of residual fish accounted for the recovery of spawning herring on the bank, we would expect little or no change in the location of spawning centers over time. Instead, our 20 yr time-series shows dramatic change.

When the herring population in the study area declined in the early 1970s, its spawning range receded from Georges Bank to Massachusetts Bay. As the population began to grow in the 1980s, the spawning range expanded, initially from Massachusetts Bay to Nantucket Shoals, then from the shoals to Georges Bank. Whether the recovery resulted from an expanding adult population, from fortuitous transport and survival of larvae, or from a combination of the two, is not clear. However, it is worth noting that the reoccupation of spawning beds on both Nantucket Shoals and Georges Bank occurred 3–4 yr after we first observed evidence of larval drift towards these two subareas. This time period, perhaps coincidently, represents the age-at-maturity for Atlantic herring.

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