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## REVIEW

### Ecology of larval herring in relation to the oceanography of the Gulf of Maine

David W. Townsend

*Bigelow Laboratory for Ocean Sciences, McKown Point, W. Boothbay Harbor, ME 04575, USA*

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**Abstract.** The dynamics of larval herring in the north-eastern Gulf of Maine are reviewed with reference to the important physical and biological oceanographic processes of the region. Particular attention is given to the apparently conflicting hypotheses of larval drift from the tidally well-mixed spawning areas to nursery areas, and larval retention in spawning areas for a period of several months. Both processes have been reported for the eastern Maine–Grand Manan spawning area of the Gulf of Maine, but the relative importance of each to larval survival through the winter and recruitment to the juvenile stage is not clear. Both transport and retention are interpreted in light of oceanographic processes that might impart variability, especially between years, in the proportion of larvae transported away versus that retained. Results of recent survey cruises in the Gulf of Maine show both hypotheses to have merit. It is suggested that (i) interannual differences in slope water intrusions into the Gulf of Maine as they affect the residual circulation, (ii) the lunar periodicity in the intensity of tidal mixing in relation to hatching times, and (iii) the potential for variable spawning locations relative to the tidal fronts, may affect the distributions of herring larvae immediately after hatching in the fall, and may control the proportion of larvae that are advected away with the residual currents versus that retained in the vicinity of spawning. It is also suggested that those processes that affect larval distributions and survival in the fall are important in determining the overwintering distributions of larvae in the Gulf of Maine, where the subtle influences of variable food regimes and water temperatures could potentially exact large interannual differences in winter survival and recruitment to the juvenile stage.

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#### Introduction

The Atlantic herring (*Clupea harengus* L.) is one of the most important commercial species in the Gulf of Maine area and has been fished heavily for the past century. Populations in the Gulf of Maine, as well as world-wide, are noted for extreme year-to-year fluctuations in year class strength (Sindermann, 1979). As an example, Figure 1 shows the variability in recruitment to the Maine juvenile (sardine) fishery from 1947 to 1982 (Anthony and Fogarty, 1985). Strong recruitment, assuming that the catch of 1 year old herring is a proxy for recruitment success, is shown in Figure 1 as high abundance peaks, which are as much as 50 times as great as the lowest years. Highly variable landings are also exemplified by the George Bank fishery, which collapsed in 1977 after having once represented the largest herring population in the north-west Atlantic (Anthony and Waring, 1980); over the years 1977 and 1984 there was virtually no spawning activity recorded. There is evidence, however, that the Georges Bank stock may be staging a comeback. Renewed spawning activity has been reported since 1984 and substantial numbers of larvae are now being collected there (R.L. Stephenson, personal communication). The reappearance is believed to be a resurgence of remnants of the Georges Bank herring stock itself

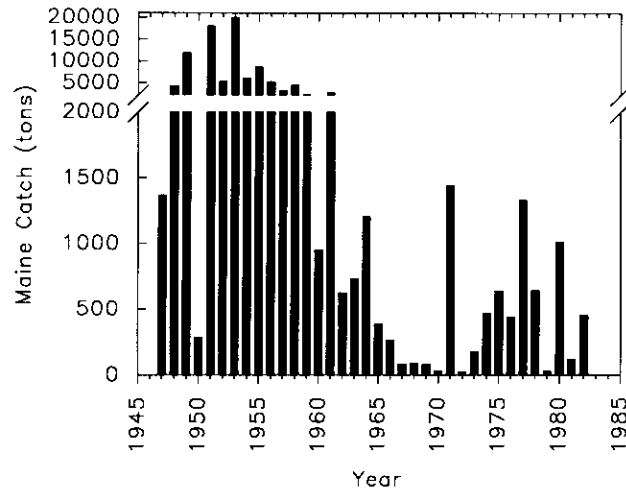


Fig. 1. Maine catch of 1 year old herring from 1947 to 1982 (from Anthony and Fogarty, 1985).

and not recolonization by neighboring stocks (Stephenson and Kornfield, 1990). The herring fishery in the Gulf of Maine proper, despite stock depletions over the same time period as that for Georges Bank, remains relatively viable, especially the juvenile fishery in Maine and New Brunswick (Anthony and Fogarty, 1985).

Because of their high economic value, the large interannual variability in their recruitment, and particular features of their life history (especially their long larval period), herring present more than just interesting challenges to fishery scientists and oceanographers trying to understand how various processes affect recruitment. Because recruitment is believed to be fixed during the first year of life (Anthony and Waring, 1980; Lough *et al.*, 1985) research on larval herring dynamics has occupied the continual attention of scientists for decades. For all this effort, we are little closer to a working understanding of how herring populations fluctuate in relation to natural environmental variability (Anthony and Fogarty, 1985). The purpose of this paper is to review, in an oceanographic context, the dynamics of larval herring of the north-eastern Gulf of Maine, drawing comparisons where appropriate to populations in the north-east Atlantic and North Sea, with the belief that new insights and more promising avenues of research might be identified.

### Herring life history

Part of the challenge to understanding how various oceanographic processes affect recruitment of herring lies in the species' somewhat unusual life history. Fall-spawning herring in the Gulf of Maine deposit demersal and adhesive eggs in shoal waters (10–60 m), which tend to be tidally well-mixed (Iles and Sinclair, 1982). The locations of the various spawning areas in the Gulf of Maine are shown in Figure 2, and include the once-prominent Georges Bank, Nantucket

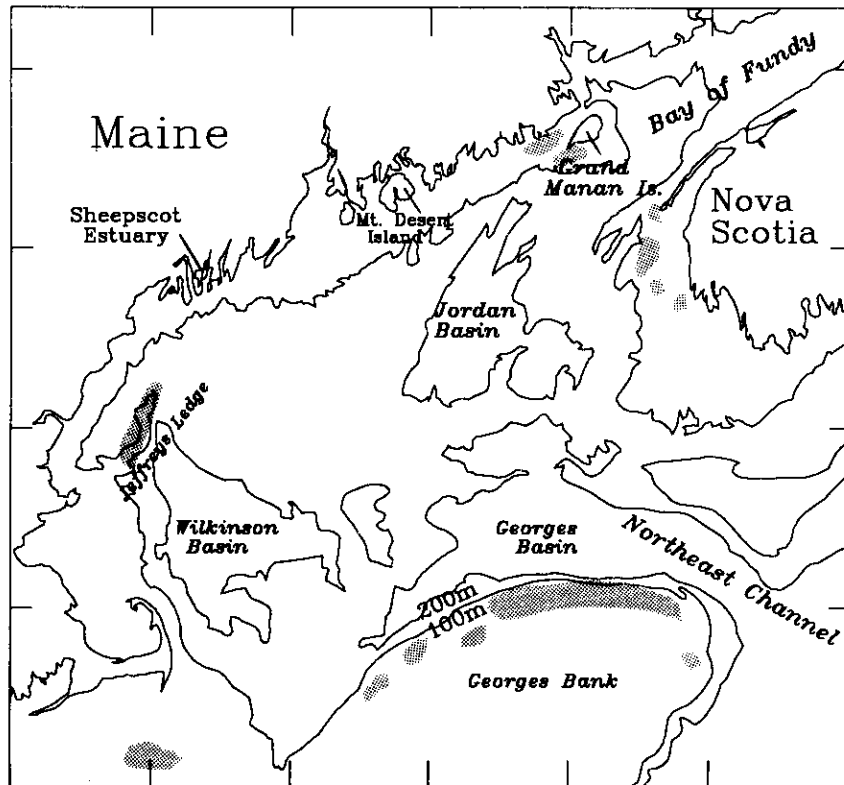


Fig. 2. Map of the Gulf of Maine area showing the major features referred to in the text. The 100 and 200 m depth contours are given. Approximate locations of herring spawning areas in the Gulf of Maine are indicated by the shaded areas (after Boyer *et al.*, 1973).

Shoals, the Nova Scotian Shelf, Jeffreys Ledge in the western Gulf, and the eastern Maine coast–Grand Manan Island area (which is the area we will focus on for most of this discussion). The spawning season in the Gulf of Maine lasts from August to December, with most spawning occurring from September to November (Bigelow and Schroeder, 1953). Spawning usually begins earlier in the eastern Gulf, in late August and early September, and a few weeks later in the western areas. The eggs incubate on the bottom for 1–3 weeks on average, as influenced by temperature (Boyar *et al.*, 1973; Sindermann, 1979). The newly hatched larvae rely on yolk reserves for up to 10 days, at which time they must begin exogenous feeding, principally upon the early development stages of copepods.

Larval herring are somewhat unusual in that they remain in the larval stage for an extended period of time and do not metamorphose into juveniles until the following spring, when they may be 5–8 months old, and from 30 to 55 mm in length (Boyar *et al.*, 1973; Ehrlich *et al.*, 1976; Doyle, 1977; Lough *et al.*, 1982). Processes affecting survival during this long larval period are uncertain, although

the larvae are believed to depend a great deal on being transported to productive inshore nursery grounds (Graham, 1972; Graham *et al.*, 1972, 1984, 1990; Stevenson *et al.*, 1989). Following metamorphosis in the spring, the young herring are known to school in large numbers in nearshore areas along the Maine coast throughout the summer before moving offshore as one-year-olds in the fall and winter (Speirs, 1977). Little is known about the movements of juvenile herring, but it is believed that 1 and 2 year old fish move into the inshore waters of Maine in the following spring where they recruit to the sardine fishery (NERFMC, 1978). Herring reach sexual maturity at ~4 years old.

### Larval herring dynamics

Studies directed at the larval stage of herring in the Gulf of Maine region have been conducted extensively since the early 1960s (reviewed by Anthony and Waring, 1980; Graham, 1982; Graham *et al.*, 1984; Lough *et al.*, 1985; Sinclair and Iles, 1985). Very briefly, the results of those studies suggest that following hatching, the larvae are dispersed and drift with the residual currents. On Georges Bank the larvae drift around the bank and to the south-west in a clockwise pattern, and on Nantucket Shoals they drift in a general south-west direction (Lough *et al.*, 1985). On the Scotian shelf, a large portion of the larvae remain aggregated on the shelf and at the entrance to the Bay of Fundy, while some move into the Bay (Stephenson and Power, 1989). Very little is known about the movements of larvae from the Jeffreys Ledge spawning group in the western Gulf of Maine.

Herring larvae from spawning units in the north-eastern Gulf, as well as along the Maine coast, have been thought, until recently (Townsend *et al.*, 1989; discussed below), to drift along the coast in a south-westerly direction, and to enter the numerous estuaries and bays where they overwinter. The abundances of larvae sampled inshore along the Maine coast have been sharply reduced since 1978 (Graham, 1982; Graham *et al.*, 1984). This period is coincident with the collapse of the Georges Bank stock (Sindermann, 1979), although the larvae sampled in the fall inshore along the Maine coast are believed to be produced from both local spawning units and the eastern Maine–Grand Manan spawning group (Graham, 1982) which apparently remain viable despite heavy fishing pressure (Graham *et al.*, 1984).

Herring recruitment appears to be determined in the first year of life, and may be set by the time the larvae metamorphose to the juvenile stage (Anthony and Waring, 1980; Lough *et al.*, 1985). It is important to note that, while most fishes in temperate and higher latitudes spawn in spring at a time of increasing plankton abundance and warming temperatures, fall-spawning herring do just the opposite, and must deal with extremely low winter temperatures and the lowest food abundances of the year. Thus, the processes operating during the fall and winter period following spawning and prior to metamorphosis to the juvenile stage in the spring are likely to be critical to the recruitment process.

Graham (1982) presented a conceptual model of larval herring recruitment based on 15 years of data on the dynamics of herring larvae on the Maine coast.

He suggested that the primary mechanism fixing the year-class strength of larvae just before their metamorphosis into juveniles in the spring was related to the distribution of larvae among the many inshore nursery areas in the fall shortly after hatching. He argued that density-dependent mortality operated to reduce the numbers of larvae in the inshore nursery areas in the fall, and that this was followed by a density-independent winter mortality. His model also pointed to the apparent increased recruitment that results in some years when aggregations of larvae enter the inshore nursery areas during the late winter months. Graham (1982) suggested that some of these late-arriving larvae may be the result of late spawning.

These processes were later developed into a numerical simulation model by Campbell and Graham (1991) that underscored the complexity of herring recruitment. They suggested that a number of interacting processes, including larval food supply, winter temperatures and longshore transport, may influence larval survival following hatching in the coastal, tidally mixed areas of the Gulf of Maine as the larvae face the overwintering period prior to metamorphosis to the juvenile stage the following spring. Of these, the period of larval drift between the spawning area and nursery grounds is perhaps the least understood, both in terms of its particular oceanographic processes, as well as in terms of its significance to the recruitment process.

#### **Larval drift versus retention**

Iles and Sinclair (1982) introduced what has perhaps been the most important and thought-provoking hypothesis of herring recruitment processes to be offered in a long time. They drew attention to the remarkable correlation between the locations of tidally well-mixed continental shelf waters, as predicted by the Simpson and Hunter (1974) vertical stratification parameter, and the spawning grounds of herring in both the eastern and western North Atlantic. They argued that the thermal fronts delimiting the tidally well-mixed areas acted as boundaries to herring larvae and that the larvae are retained in the mixed regime, thus helping to maintain stock discreteness. They went on to suggest that the geographic size of these areas determines the stock size.

Sinclair and Iles (1985) clarified points they raised in their 1982 paper and reported that maintenance of a reproductive unit is primarily why herring spawn in mixed areas, and that it is also why it is advantageous for the larvae to be retained within those areas for a number of months following hatching. That food resources, predation or low temperatures in such tidally mixed retention areas may be deleterious to larval survival was considered to be of secondary importance. In fact, they suggested that slowed growth resulting from low food concentrations in the retention areas helps to delay metamorphosis until the optimal time the following spring, as reported by Sinclair and Tremblay (1984). Sinclair and Iles (1985) went on to argue that herring migrate to juvenile nursery areas following metamorphosis, and not during a period of larval drift. In effect, they suggested that the proportion of larvae that may be advected away from the retention areas prior to metamorphosis is relatively insignificant compared with

juvenile migrations following metamorphosis. It is this point regarding the relative significance, or insignificance, of larval drift that is perhaps the most controversial of their contentions (Cushing, 1986). It can be argued quite convincingly that the retention hypothesis is, in general, valid in many instances; however, it must be interpreted in the light of other, highly variable oceanographic processes operating following hatching that create apparent contradictions to the retention scenario.

The larval retention hypothesis has yet to gain widespread acceptance, and work in both the Gulf of Maine area and the eastern North Atlantic has provided evidence of both scenarios: larval retention in the vicinity of spawning and larval transport to other nursery areas. The recent literature on the subject of larval herring drift is particularly rich in examples for the north-east Atlantic and North Sea, much of which documents transport of larvae to nursery areas far removed from the area of spawning, thus obfuscating the universal applicability of the Iles and Sinclair hypothesis.

Herring larvae in the north-east Atlantic and North Sea have been shown by a number of recent studies to exhibit a larval drift period and to utilize both inshore and offshore nursery areas (Corten, 1986; Heath and MacLachlan, 1987; Heath *et al.*, 1987, 1989; Heath and Rankine, 1988; Kiorboe *et al.*, 1988; Bartsch *et al.*, 1989; Munk and Christensen, 1990). Urho and Hilden (1990) reported that herring larvae off Helsinki in the Baltic Sea move inshore into shallow coastal waters shortly after spawning, as has been observed by Graham (1972, 1982) for the coastal Gulf of Maine. The drift of larvae to relatively distant nursery areas, however, is believed to be an important precondition for successful recruitment of herring in the North Sea (Corten, 1986). Corten (1986) reported that the abundance of herring larvae in the central and eastern North Sea nursery areas is significantly correlated with recruitment. Further, the relationship between observed larval distributions and hydrodynamic model simulations of larval drift has shown that the circulation pattern in the North Sea does not always conform to the long-term mean and may impart interannual variability in larval drift patterns and ultimately affect recruitment (Bartsch *et al.*, 1989). Bartsch *et al.* (1989) showed that anomalous atmospheric conditions during the winter of 1987–88 resulted in a reduced wind-driven circulation and transport of larvae away from the spawning areas, and they predicted poor recruitment. Heath and Richardson (1989) took the general argument even further and suggested that the spawning strategies of herring in offshore spawning areas of the North Sea may be adapted to result in a particular advective transport route for the larvae.

Heath and Rankine (1988) and Heath *et al.* (1987) found that the advection of herring larvae hatched on the west coast of Scotland could either be retained in the vicinity of spawning or advected into the North Sea, depending on the exact location of spawning in relation to the coastal current. Larvae hatched near the shore would be retained off Scotland for several months, while larvae hatched further offshore would be advected with the coastal current into the North Sea at rates up to  $36 \text{ km day}^{-1}$ . Even in areas where retention has been observed, there appear to be smaller-scale advective processes operating which may affect larval

survival. This was shown by Heath *et al.* (1989) who found that a relatively sluggish drift rate of 1–2 km day<sup>-1</sup> effectively retained larvae in the Moray Firth of Scotland, while slowly carrying them into waters with increasing concentrations of copepodid and adult stages of copepods, which serve as food items as the larvae develop. This observation is similar to those reported by Townsend *et al.* (1986) for the eastern Gulf of Maine herring-spawning area.

Heath and Rankine's (1988) observation of different larval transport patterns, which depend on the relative location of the spawning center to the core of the coastal current off Scotland, may be central to reconciling the apparent discrepancies observed in larval transport/retention in the Gulf of Maine, a problem that has its solution embedded in understanding the nature of the physical and biological oceanography of the Gulf of Maine.

### The Gulf of Maine

The oceanography of the Gulf of Maine is fairly well studied, though by no means fully understood. The residual circulation is strongly baroclinic, with cyclonic eddies over the central basins that reflect differences between fresher coastal waters and deeper, more dense waters offshore (Bigelow, 1927; Brooks, 1985). Relatively warm and salty North Atlantic slope water enters the Gulf of Maine along the bottom through the Northeast Channel between Georges and Browns Banks and generally spreads into the major basins throughout the Gulf (Figure 3). The topographic lows that result from these density differences produce a set of interacting cyclonic gyres over the basins, which also influence the coastal circulation (Brooks, 1985), and the transport of herring larvae (Townsend *et al.*, 1986, 1987). Because of the Coriolis effect, which results in the diversion of more slope water into the eastern Gulf, Jordan basin has a greater volume of slope water than Wilkinson Basin in the western Gulf. This produces a more energetic baroclinic circulation in the north-eastern part of the inner Gulf, which in turn influences the coastal currents, particularly the eastern Maine coastal current emanating from the vicinity of eastern Maine and Grand Manan Island, near the entrance to the Bay of Fundy, which is an important herring spawning ground (Figure 3; Townsend *et al.*, 1987; Brooks and Townsend, 1989).

Tidal mixing is an important physical process that exerts significant controls on biological production in the Gulf of Maine. Because the Gulf of Maine basin is in near-resonance with the M2 tide, the tides are amplified. Tidal amplitudes range from ~3 m in the western Gulf, to ~6 m in eastern Maine, and to ~15 m in the upper reaches of the Bay of Fundy. Tidal mixing of the water column results in a number of vertically well-mixed regions that persist throughout the warmer months (Bigelow, 1927; Yentsch and Garfield, 1981; Loder and Greenberg, 1986). These mixed regions are delineated by thermal fronts that separate the cold mixed waters from the warmer surface waters that result from thermal stratification further offshore. The areal distributions of these mixed regions of cold surface waters are not readily predictable from tidal or wind-mixing models and are significantly influenced by the strong residual advection

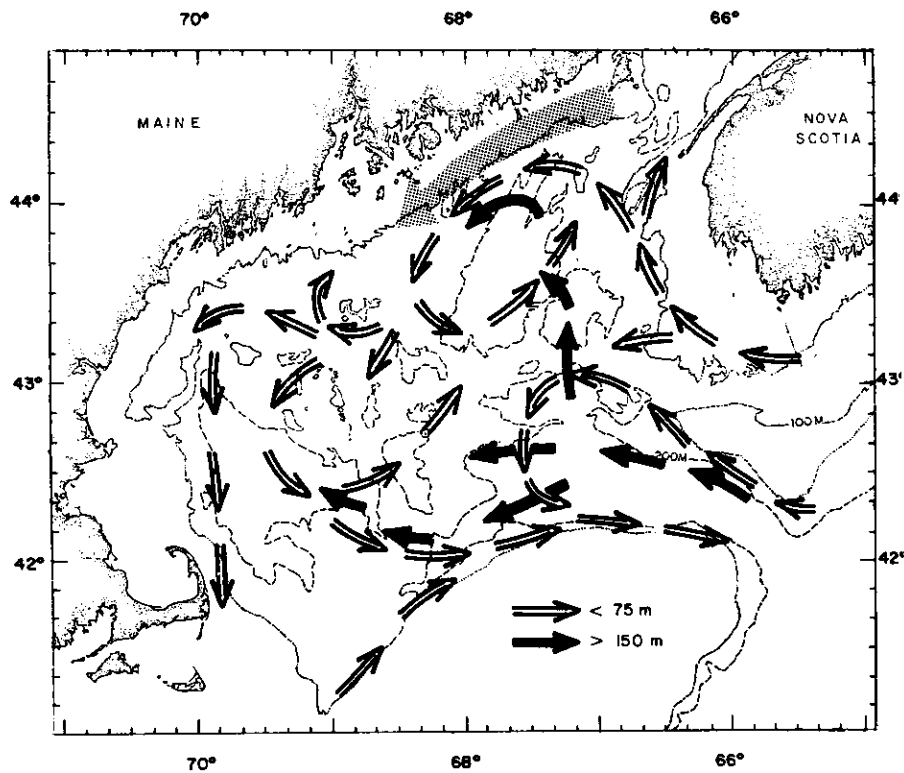


Fig. 3. Surface and deep water currents of the Gulf of Maine. The open arrows indicate surface currents (shallower than 75 m) and the solid arrows indicate the intrusion of slope water into the Gulf and the deep (>150 m) circulation (from Brooks, 1985). The location of the eastern Maine coastal current as discussed in the text is shown as a shaded arrow.

in the Gulf (Loder and Greenberg, 1986). This is the case for the eastern Maine–Grand Manan tidally mixed herring-spawning ground, where the cold tidally mixed waters are advected away from the areas of mixing by the residual circulation to produce the eastern Maine coastal current (Figure 3; Townsend *et al.*, 1986, 1987; Brooks and Townsend, 1989).

One of the more conspicuous cold water features in the Gulf of Maine region, clearly visible in satellite images of sea surface temperature (Figure 4), is a cold water plume that extends from the Grand Manan Island area along the Maine coast and offshore over the central portion of the Gulf (Townsend *et al.*, 1987). This feature is not predicted by models of local wind and tidal mixing (Loder and Greenberg, 1986) and appears to be the result of advection of the mixed waters from the eastern Maine–Grand Manan region (Loder and Greenberg, 1986; Townsend *et al.*, 1987; Brooks and Townsend, 1989). Townsend *et al.* (1987) have shown that these waters are rich in inorganic nutrients (surface nitrate concentrations  $>7 \mu\text{M}$ ), as a result of entraining upwelled waters from Jordan Basin that mix with the coastal, tidally mixed waters. This cold, nutrient-rich



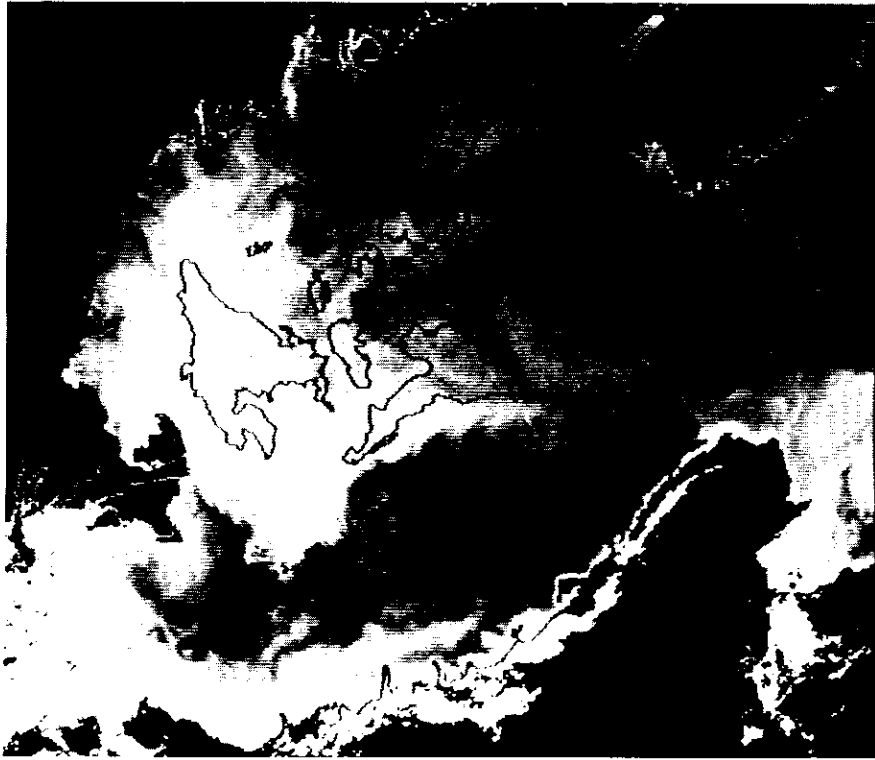


Fig. 4. AVHRR Satellite image of sea surface temperature in the Gulf of Maine on June 24, 1984. The 200 m bottom contour is given. The cooler waters normally indicative of the tidally mixed regions are presented as darker shades. The eastern Maine coastal current and offshore-directed plume system are clearly visible as cooler water not directly associated with tidal mixing (see text). The dark patches at the bottom of the image and around Cape Cod are clouds.

mixture flows to the south-west as the eastern Maine coastal current, which in turn is part of the northern extension of the Jordan Basin cyclonic gyre (Figure 3). Both the biological and physical aspects of this coastal current/plume system hold potentially important consequences for herring larvae emanating from the eastern Maine–Grand Manan spawning area.

Herring larvae hatching from the eastern Maine–Grand Manan spawning area (Figure 2), as well as from smaller spawning units along the coast, are believed to rely on the residual circulation, as well as selective tidal transport, to move along the coast of Maine and eventually enter the numerous inshore nursery areas in the estuaries and embayments (Graham *et al.*, 1972, 1990; Shaw, 1981; Graham and Townsend, 1985; Stevenson *et al.*, 1989). The larvae often accumulate in great numbers in these inshore areas in October and November, but shortly after the peak in abundance the numbers drop off to very low levels during winter (Figure 5). During the following March and April there is a second, sometimes even larger, peak in abundance of herring larvae inshore just prior to metamorphosis. These larvae are ~25–40 mm in length and appear to

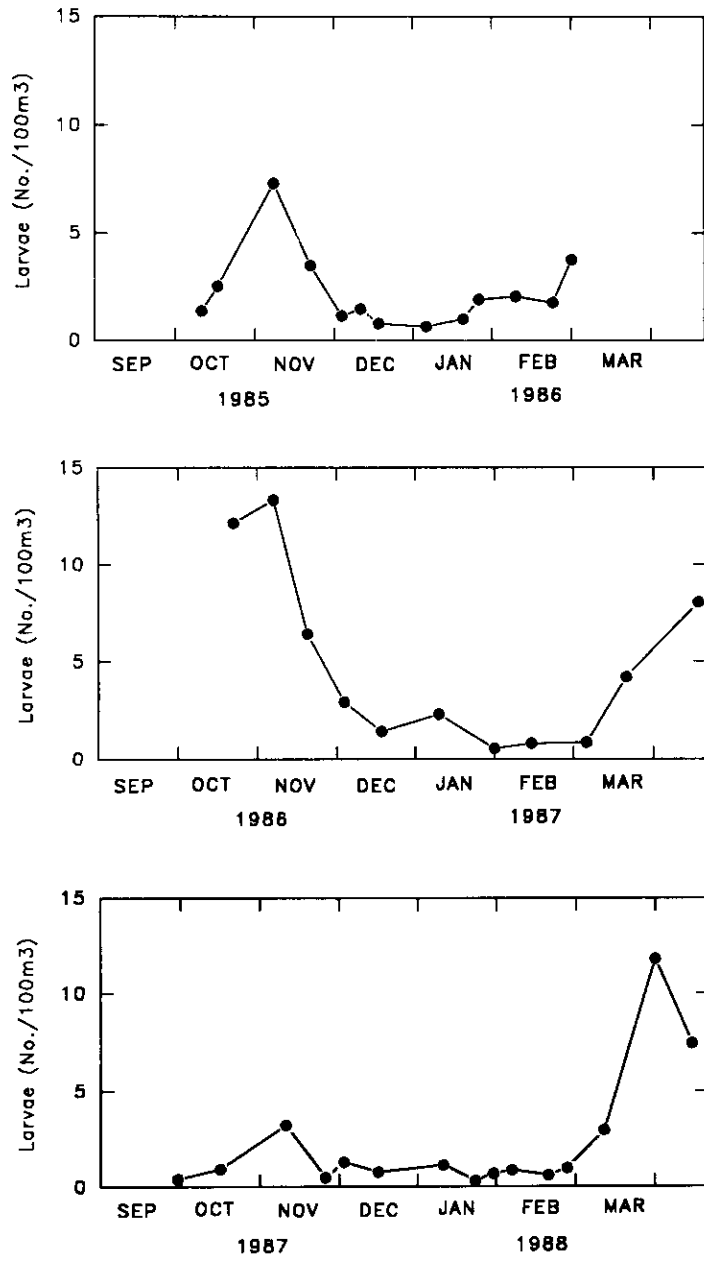
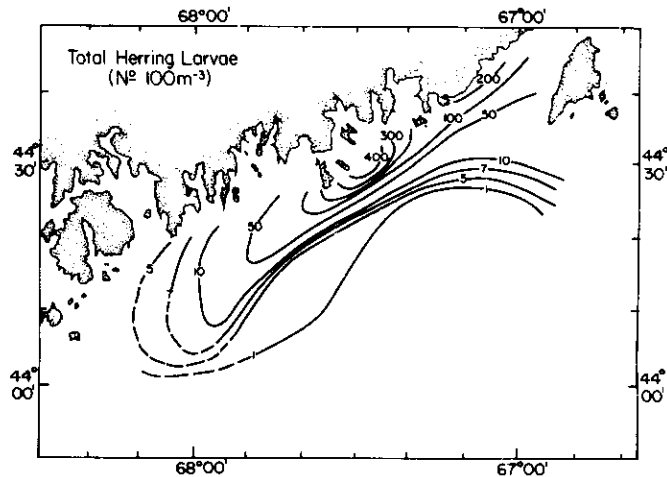


Fig. 5. Abundance of herring larvae in the Sheepscot River Estuary of Maine for 1986-88 (all data for 1985-86, and fall-winter data for 1986-87 and 1987-88 are from D.K.Stevenson, unpublished).

represent survivors from the previous autumn (Townsend and Graham, 1981; Townsend *et al.*, 1989). A similar bimodal abundance distribution in fall and spring is seen along the coast of Nova Scotia (Sameoto, 1972) and hence this does not appear to be a localized phenomenon. The exact nature of the origin of the second pulse of larvae and, in particular, their overwintering distributions during the mid-winter period of low abundance inshore, are uncertain (Townsend *et al.*, 1989).

Townsend *et al.* (1986, 1987) studied the relationships between herring larvae and the various oceanographic processes of the eastern Maine–Grand Manan spawning area (Figure 2), and reported that the larvae are advected to the southwest along with the coastal current system (Figure 6). They observed that the drift of larvae with this current resulted in their being presented a greater density of zooplankton food items at just the right time, as they become dependent on exogenous feeding following yolk sac absorption. The sequence of events that leads to this opportune feeding regime happens as the tidally mixed, nutrient-rich coastal water moves away from the area of mixing as part of the eastern Maine coastal current. With increasing distance away from the area of high energy and vertical mixing in the east, the water column begins to stratify. The increasing stratification leads to increasing phytoplankton production and biomass, followed closely by an increase in early developmental stages of copepods, which appear to propagate in response to the phytoplankton increases (Figure 7; Townsend *et al.*, 1987). The mean speed of the coastal current is  $\sim 17 \text{ km day}^{-1}$ , as measured by a current meter mooring deployed at the location shown in Figure 7; the current is unidirectional and does not reverse with the tide (Townsend *et al.*, 1987). This current transports larvae along with the developing planktonic food resources that peak at  $\sim 150 \text{ km}$  downstream 8–



**Fig. 6.** Contours of larval herring abundance along the eastern Maine coast on September 8–9, 1987 showing evidence of alongshore transport within the eastern Maine coastal current (from Townsend *et al.*, 1987).

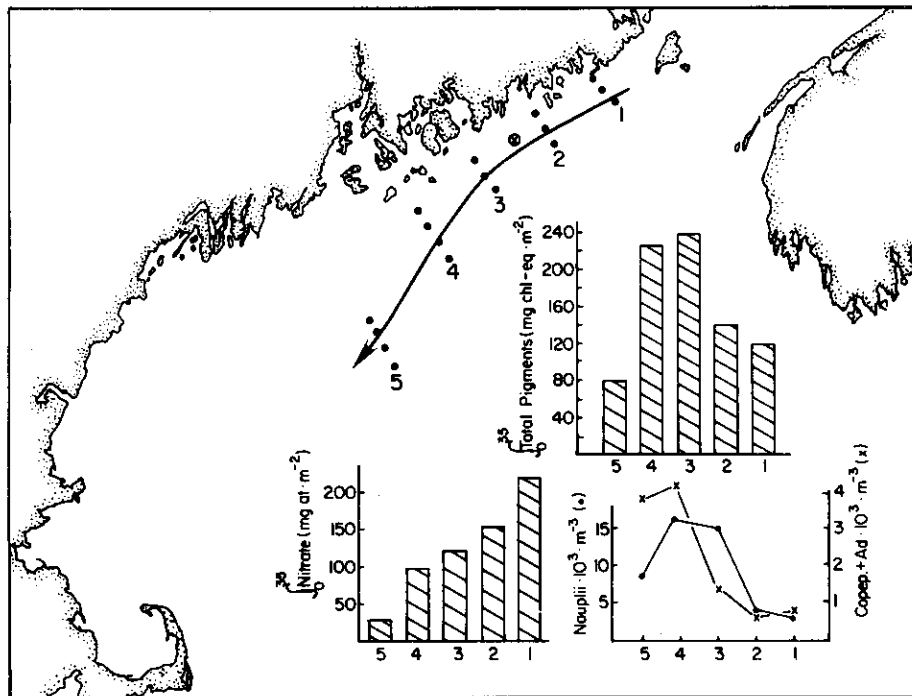


Fig. 7. Summary plot of the changes in nitrate, chlorophyll, and naupliar and copepodid stages of copepods along the eastern Maine coastal current/plume system for July 1985 (from Townsend *et al.*, 1987). The nitrate and chlorophyll histograms are the averages of the vertically integrated (to 35 m) values at the stations shown for each of the five transects. The arrow is a central streamline of the geostrophic current. The X indicates the position of a current meter mooring.

10 days later. Larval condition factors increase to their maximum at this point (Townsend *et al.*, 1986). Townsend *et al.* (1986, 1987) argued that it was thus more advantageous for the larvae to drift with the residual coastal currents, which effectively bring them into contact with greater food supplies, than to be retained in the tidally mixed waters of the spawning areas which, because of light-limitation, exhibited relatively low plankton production. These findings contradict the Iles and Sinclair (1982) retention hypothesis, and are generally similar to those of Kiorboe *et al.* (1988) for a frontal region in the north-western North Sea.

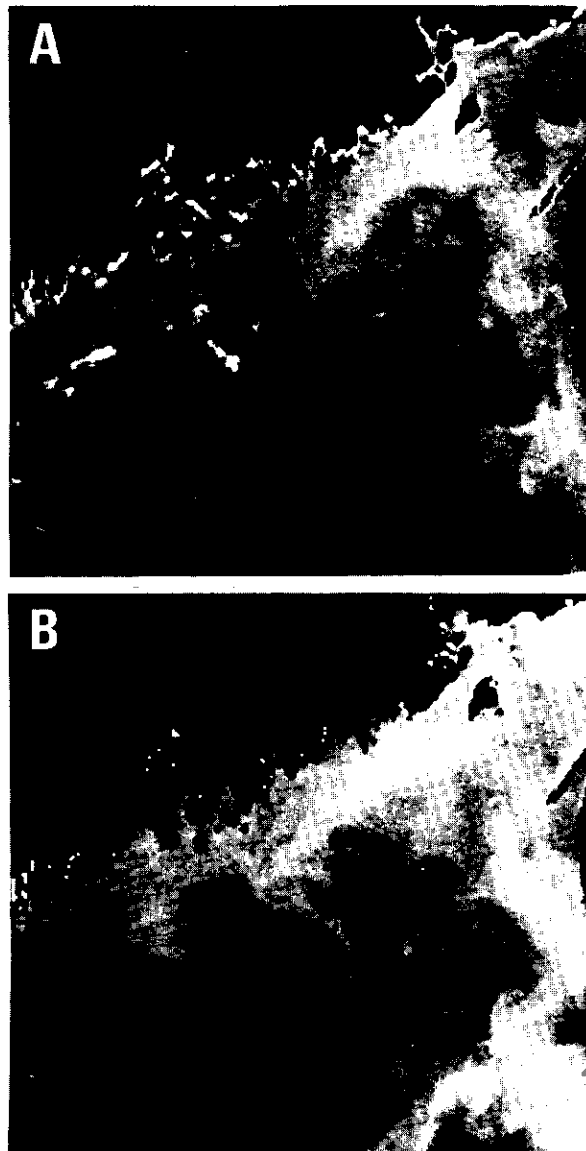
At a point downstream along the coast of Maine, part of the eastern Maine coastal current becomes a cold-water plume as it turns offshore to become, in turn, part of the Jordan basin cyclonic gyre system. These waters appear to carry at least some larvae offshore (Figure 6). Thus, the possibility exists for larvae to be carried along two drift routes: along the coast, where they are made available to the inshore nursery areas, or offshore over the central Gulf of Maine. The exact trajectory of the coastal current/plume system is quite variable, particularly in terms of the point where it leaves the coast as a cold-water plume.

Because the coastal current results primarily from the density contrast between tidally mixed coastal waters and more dense water of slope water origin in Jordan Basin, the baroclinicity, or intensity of the geostrophic current that results, is a direct function of the relative volume of slope water in the basin, which in turn is highly variable. Thus, the fate of herring larvae transported within this current is also potentially variable.

It has been shown that the intrusions of slope water into the Gulf of Maine occur in pulse-like events which may be related to storms (Ramp *et al.*, 1985) or the interactions of Gulf Stream warm-core eddies with the shelf edge in the vicinity of the Northeast Channel (Townsend and Spinrad, 1986; Brooks, 1987). One effect of variability in slope water intrusion events is the increase or decrease in the volume of dense slope water in Jordan Basin, and thus in sea surface slope between coastal waters and offshore waters in the basin. This translates into variable baroclinicity which can, during periods of greater slope water volume in Jordan Basin, spin up the cyclonic circulation over the basin and thus entrain more coastal water and redirect the coastal current/plume system offshore (Brooks and Townsend, 1989; Figure 8). This phenomenon has been hypothesized to result in a greater proportion of herring larvae emanating from the eastern Maine–Grand Manan spawning group overwintering offshore in the Gulf rather than in the inshore nursery areas (Townsend *et al.*, 1989).

Townsend *et al.* (1989) used a technique of larval otolith analysis, using the ratios of strontium to calcium as an analogue of environmental temperatures experienced by individual larvae, to infer the overwintering distributions of herring larvae that survive to spring and which are sampled inshore in the Sheepscot estuary of Maine as part of the springtime peak in larval abundance there (Figure 3). By profiling the Sr/Ca concentration ratios from the core of the otolith to the outer edge, they were able to reconstruct the temperature histories of individual larvae from hatching to the time of capture. They hypothesized that larvae that had been carried offshore in the fall with the coastal current/plume system would have spent the winter offshore in the Gulf of Maine, and would not have experienced water temperatures as low as those larvae that may have overwintered in the estuary, where temperatures approach the freezing point in winter. Based on Sr/Ca analyses of larvae from the spring abundance peak in the Sheepscot estuary, they concluded that those larvae had occupied warmer offshore waters during the winter rather than the much colder (by 2–4°C) inshore and estuarine waters. They went on to suggest that it is deleterious for larvae to be transported into the estuaries and inshore areas in the fall, where winter mortalities allowed few to survive to the spring, and that good recruitment might result in years when a significantly greater proportion of larvae are transported offshore for the winter. The importance of low winter temperatures was suggested by Graham *et al.* (1990) as potentially important to survival. In order for larvae to be carried offshore with the cold water plume, however, they would first have to escape the tidally mixed spawning areas where Iles and Sinclair (1982) argue they are retained.

Chance interactions of larvae from the eastern Maine–Grand Manan spawning group with the frontal region at the edge of the tidally mixed area



**Fig. 8.** AVHRR satellite images of sea surface temperature for (A) July 29, 1987 and (B) August 19, 1987 (from Brooks and Townsend, 1989). The lighter shades indicate cooler temperatures. In the July 29 image, the cold waters from the tidally mixed eastern Maine–Grand Manan area flow eastward and then turn offshore over Jordan Basin before reaching Mount Desert Island. In the August image taken 3 weeks later, the coastal current flows more to the west and along the coast before turning offshore at a point west of Mount Desert Island. A filament of cold water extends over Jordan Basin and is a remnant of the earlier departing coastal current in (A). The earlier departure of the cold water from the coast was the result of a slope water intrusion event in Jordan Basin in July which intensified the Jordan Basin gyre and entrained the eastern Maine coastal current, thus pulling coastal water offshore. The subsequent spreading of the slope water during the following 3 week period allowed relaxation of the baroclinicity, thus resulting in an extended alongshore flow (Brooks and Townsend, 1989).

could result in some larvae being advected away from the mixed area. This would be analogous to the findings of Heath and Rankine (1988), in that larvae hatching nearer the frontal region between mixed and thermally stratified waters, which is where the geostrophic flow along the front would be greatest, would be subject to greater alongshore transport in the coastal current, and thus would be more likely to be entrained in the plume of coastal water advected offshore. Brooks and Townsend (1989), for example, showed maximum geostrophic velocities within this front, as compared with conditions on either side. It could be speculated that the chances of significant alongshore transport of those larvae hatching nearer the coast, on the other hand, might be less likely, and a greater proportion of larvae hatching nearer the shore would then result in greater retention of larvae within the mixed region.

The variability in trajectory of the coastal current/plume system also could result in important interannual variability in both the relative and absolute numbers of larvae that overwinter offshore in the Gulf of Maine. Apart from the relative location of spawning to the tidal front (or core of the coastal current), Townsend *et al.* (1989) suggested that it is possible that episodes of slope water intrusions into the Gulf of Maine will increase the baroclinicity of the eastern Maine coastal current, which is the northern limb of the Jordan Basin cyclonic gyre, thus causing a more energetic coastal current, as well as a more tightly turning circulation around the topographic low over Jordan Basin, as was demonstrated by Brooks and Townsend (1989). This could transport more coastal water, and herring larvae, out over the central Gulf when these episodes of slope water intrusions coincide with the period of larval drift shortly after spawning. Should Townsend *et al.* (1989) be correct in concluding that larvae transported offshore under such circumstances are more likely to survive the winter, we would expect enhanced larval survival and perhaps a strong year class.

Chenoweth *et al.* (1988) conducted an intensive time series of larval herring surveys in the eastern Maine–Grand Manan spawning area in order to examine the retention hypothesis. They found that a significant portion of the larval population may be retained in the vicinity of the spawning grounds until late October, at which time, because of the seasonal cooling of the surface waters, the frontal boundary between the tidally mixed and stratified areas breaks down. They suggested that the larvae can then disperse. This observation is in keeping with the Iles and Sinclair (1982) retention hypothesis. Chenoweth *et al.* (1988) modified the retention hypothesis somewhat by showing that larval retention in the eastern Gulf of Maine spawning ground is incomplete; some of the larvae are retained while others (approximately half) appear to be advected to the west as was suggested by Townsend *et al.* (1986). It was not clear in the study by Chenoweth *et al.* (1988) whether the larvae transported away were those more closely associated with the frontal region, where advection along the front would be strongest. The model results of Campbell and Graham (1991) pointed to the likely importance of wind events in breaking up the hydrographic structure surrounding the tidally mixed spawning areas, resulting in the release of larvae. Regardless, it would appear that the origins of larvae that comprise the spring

abundance peak inshore on the Maine coast may be from either those larvae released in late fall from the retention areas, or larvae that had escaped earlier and had overwintered offshore in the Gulf of Maine.

Stephenson and Power (1988) have shown that herring larvae of the southwest Nova Scotian Shelf spawning stock (Figure 2) are retained within the mixed waters bounded by thermal fronts for a period of several months, despite a residual flow to the north. They observed that the larvae vertically migrated on what may have been either a semi-diel or tidal frequency. The result of controlling their vertical position in the water column was to interact with the reversing tidal currents and minimize their drift to the north, as part of the residual current system which flows at  $\sim 18 \text{ km day}^{-1}$ . In a later paper (Stephenson and Power, 1989) they reported that the edge of the larval herring patch on the Scotian Shelf corresponded only loosely to the frontal boundary between tidally mixed waters on the shelf and thermally stratified waters offshore, and that the position of the patch edge varied over a 3 week sampling period in October and November. This is an important point that again relates to the observation of Heath and Rankine (1988) which relates larval transport to the relative proximity of the larval hatching site and the core of the coastal current off Scotland. Because the maximum residual current speeds will be in the front itself, where the sea surface slope will be greatest, larvae that leak from the tidally mixed shelf waters into the front, which Stephenson and Power (1989) report, could result in a greater northerly transport than might be the case on the shelf, and thus could explain the drift of some larvae into the Bay of Fundy. There is no doubt that the majority of herring larvae on the Scotian shelf are in fact retained there for several months, in keeping with the Iles and Sinclair (1982) hypothesis. It leaves open the question, however, of whether the larvae spend the winter months retained on the shelf.

#### **Overwintering distributions**

Until recently, there have been virtually no field studies of the overwintering distributions (in January) of herring larvae in the Gulf of Maine that could shed light on the relative proportion of larvae that may be transported to inshore nursery areas, such as along the coast of Maine, to nursery areas offshore in the Gulf, similar to that reported for the North Sea (Heath and Richardson, 1989), or whether the majority of larvae are retained for the winter in the vicinity of spawning. Of the several larval herring survey cruises that have been conducted during early December and mid-February, most of the larvae in the Gulf of Maine tended to be distributed along the coast (Lough and Bolz, 1979). The discussion that follows is based on two cruises designed to test the larval drift versus retention question as it relates to the overwintering distributions of herring larvae in the Gulf of Maine.

The first of two larval herring survey cruises was conducted during October of 1989 to determine the relationship between the larval distributions  $\sim 1$  month after spawning in the eastern Maine–Grand Manan area (Figure 9), and the important oceanographic features, especially the trajectory of the coastal



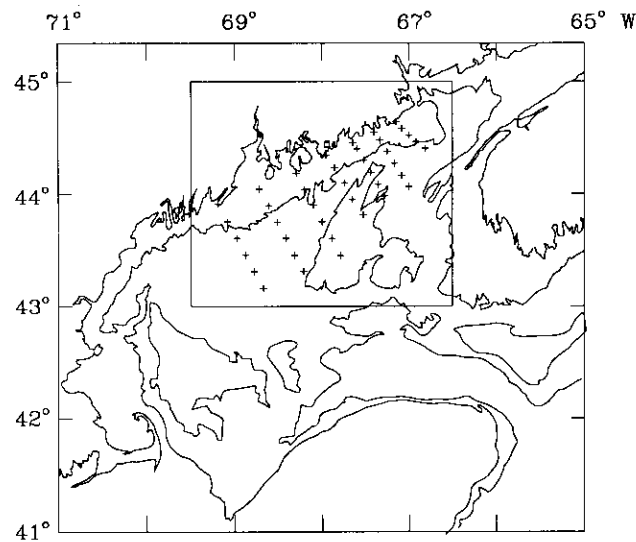
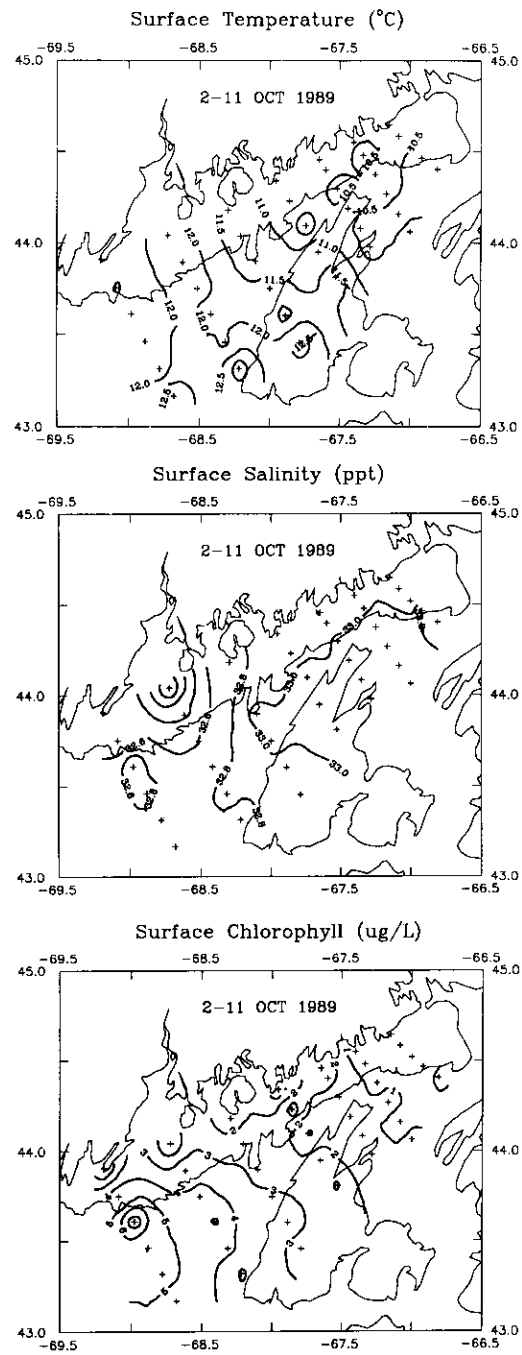


Fig. 9. Station locations in relation to Gulf of Maine region for the R/V *Cape Hatteras* cruise, October 2–12, 1989.

current plume system and phytoplankton biomass (Townsend *et al.*, 1989). The results are presented in Figures 10 and 11. The cold water of the coastal current/plume system along the eastern Maine coast is not well represented by contours of ship-board measures of surface temperatures (Figure 10), since the water column has already begun its autumnal cooling. It can still be seen that the coldest waters, however, are associated with the area of mixing to the northeast. The streamlines of dynamic height representing the geostrophic current field (Figure 11) correspond closely to the surface salinity distributions, which show fresher waters closer to the coast (Figure 10). The areal distribution of phytoplankton chlorophyll fits the scenario described earlier for these waters (Townsend *et al.*, 1986, 1987), with increasing concentrations downstream from the area of mixing (Figure 10). The majority of herring larvae of all sizes, shown in Figure 11, is essentially confined to the coast and roughly the vicinity of spawning. This distribution is greatly influenced by recently hatched larvae, however, and subtracting out larvae smaller than 16 mm total length shows that there is evidence that the older larvae have been transported offshore (Figure 11). Figure 11 shows that the contours of dynamic topography, which depict the geostrophic flow, explain quite well the distribution of cold water seen in the satellite image of sea surface temperature in Figure 12, which presumably emanates from the eastern Maine coast, and that the distribution of larvae offshore of Penobscot Bay in the central Gulf of Maine coincides with the core of the plume system (Figures 11 and 12). These results thus support earlier work showing that some larvae are advected with the coastal current/plume system to waters richer in plankton biomass and that some larvae are transported further offshore.

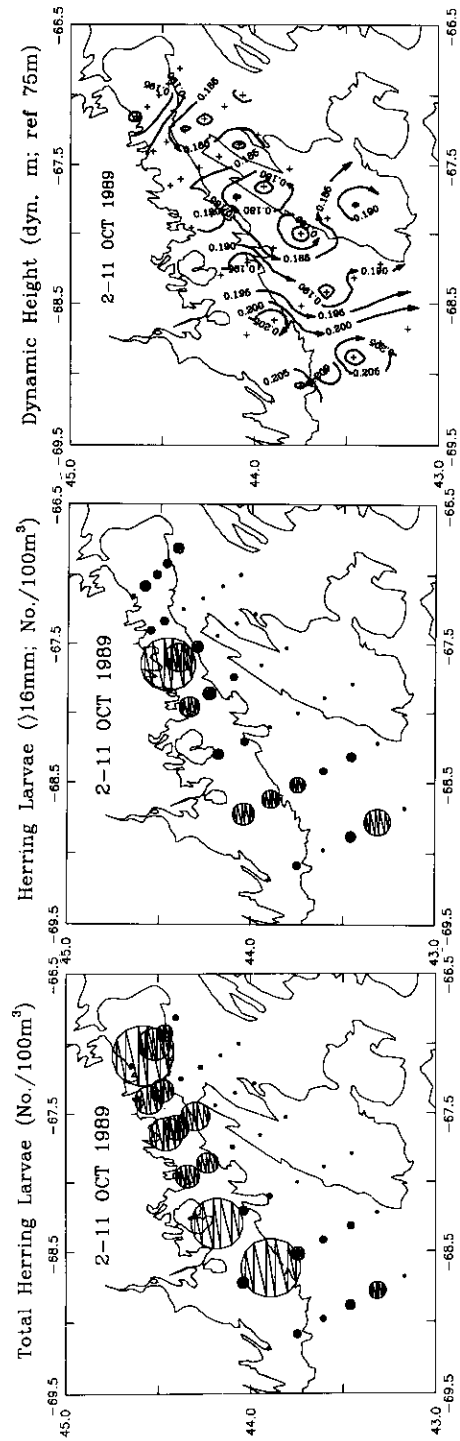


**Fig. 10.** Results of R/V *Cape Hatteras* cruise, October 2–12, 1989. **Top panel**, surface temperature (at 2 m); **middle panel**, surface salinity (at 2 m); **bottom panel**, surface concentrations of chlorophyll *a* (at 2 m).

The second cruise was conducted during January of 1990 and was aimed primarily at determining the Gulf-wide distribution of larvae during the mid-winter period. The results are given in Figure 13. It is clear from Figure 13 that the majority of the herring larvae are still in the vicinity of the spawning grounds, both in the eastern Maine–Grand Manan area and the Scotian Shelf area. This pattern is in agreement with the retention hypothesis and provides further evidence that retention is apparently still operating well into the winter, which is after the time we would have expected the thermal fronts to have broken down (Chenoweth *et al.*, 1988). Even in January, however, the coastal waters in the mixed regions of Grand Manan and the Nova Scotian shelf are still colder than the waters offshore, though the fronts may be less sharply defined (Figure 13). Interestingly, most of the larvae on the Nova Scotian Shelf were relatively small (~15 mm total length), which would suggest either a very slow growth rate, or that these fish were hatched in late November or December. Subtracting those larvae smaller than 25 mm total length shows the distributions of only the older larvae hatched earlier in the fall (Figure 13). This shows that indeed there are larger larvae from earlier hatchings that apparently have been advected into the offshore Gulf of Maine. The depth-integrated abundance of the larger larvae beyond the 100 m depth contour is ~50% of that for the larger larvae shoreward of the 100 m depth contour. Thus, it would appear that roughly two-thirds of the larvae from the hatchings earlier in the fall are still retained within the tidally mixed areas, while the other third has been advected to the offshore Gulf of Maine. The estimated abundance of herring larvae in the relatively restricted areas of the inshore nursery areas, i.e. the estuaries and embayments, are on the order of 1% of that seen in the coastal and offshore survey area in Figure 13.

These winter 1990 cruise results, coupled with the evidence of offshore transport provided by the fall 1989 cruise results, would seem to support earlier contentions that a significant number of herring larvae do overwinter offshore in the Gulf of Maine rather than in the inshore nursery areas (Townsend *et al.*, 1989). It is also possible that significant concentrations overwinter along the coast inshore of the 100 m isobath, as suggested by Campbell and Graham (1991). The results also show quite convincingly that still more larvae are retained in the tidally mixed spawning areas. As already discussed, Townsend *et al.* (1989) concluded, based on Sr/Ca otolith analyses, that the herring larvae they sampled in the Sheepscot estuary of Maine during the spring had overwintered offshore and not in the much colder estuaries. Their analyses do not rule out the possibility that larvae retained in the eastern Maine–Grand Manan area, or even on the Nova Scotian Shelf, could have contributed to the springtime inshore samples, since the winter temperatures in these eastern Maine coastal waters (Figure 13) are roughly similar (between 3 and 4°C) to water temperatures offshore (4–5°C). Such an influx of larvae into the inshore areas on the Maine coast during the spring would assume the dispersion from the retention areas of late-larvae that are near metamorphosis, as was suggested by Sinclair and Iles (1985).

The winter survey results also show that larvae from the Jeffreys Ledge



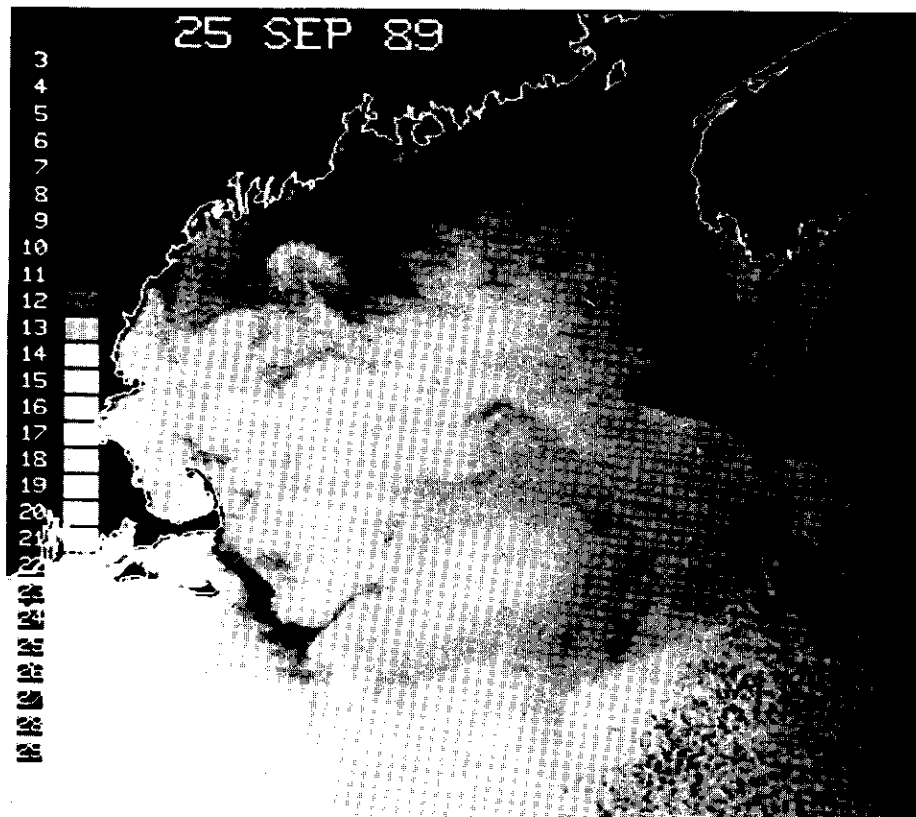
**Fig. 11.** Results of R/V *Cape Hatteras* cruise, October 2-12, 1989. **Left panel**, numbers of herring larvae  $100\text{ m}^{-3}$  of all sizes; **middle panel**, numbers of herring larvae  $100\text{ m}^{-3}$   $> 16$  mm total length. The diameters of the circles are proportional to the square roots of the larval densities, where the largest circle corresponds to  $500\text{ larvae } 100\text{ m}^{-3}$ . Larvae were collected using a 60 cm Bongo net equipped with a 350  $\mu\text{m}$  mesh nets and digital flow meters. A single double-oblique tow was made to a depth of  $\sim 40$  m at each of the stations shown in Figure 9. The **right panel** gives contours of dynamic height in dynamic meters, calculated with a reference depth of 75 m, which depict the residual geostrophic current streamlines.

spawning group could also contribute to the larvae seen in the inshore areas in spring. The distribution of larvae shown in Figure 13 could be interpreted as three centers of larval abundance: (i) the Nova Scotian Shelf; (ii) the eastern Maine–Grand Manan area, with a trail of larvae extending out into the Gulf as part of the plume system; and (iii) the Jeffreys Ledge area in the western Gulf.

### Discussion

The issue of larval retention versus larval transport from spawning area to nursery area in the Gulf of Maine is not easily resolved, especially given the various accounts of both processes for the same spawning areas. This is the case for the eastern Maine–Grand Manan spawning area, but if the oceanography of the region is considered we can gain some insights into the causes of the apparent discrepancies. We might conclude from the two survey cruises in 1989 and 1990 that both retention and transport occur. A large proportion of herring larvae are retained in the tidally mixed spawning area, even into January, and a significant proportion of larvae drift away in a westerly direction along the coast of Maine, where some in turn are advected out over the open Gulf of Maine. That both retention and transport processes operate in the eastern Maine–Grand Manan region might be due to the particular locations of spawning relative to the frontal region, which is the area of maximum geostrophic flow, as was alluded to in the North Sea by Heath and Rankine (1988). For example, data presented in Chenoweth *et al.* (1988) showed a westward drift, from the eastern Maine–Grand Manan area, of a patch of herring larvae that was quite closely associated with the frontal region where it comes closest to the Maine coast. This was at a point roughly halfway between Grand Manan Island and Mount Desert Island (see Figure 2), where the 100 m isobath is closest to shore (Figures 4 and 5 in Chenoweth *et al.*, 1988). A similar advective process could explain the retention of herring larvae nearest the coast on the Nova Scotian Shelf, as presented in Stephenson and Power (1989), while larvae in the northward-flowing frontal region further offshore might have been advected to the north toward the Bay of Fundy (their Figs 3 and 4).

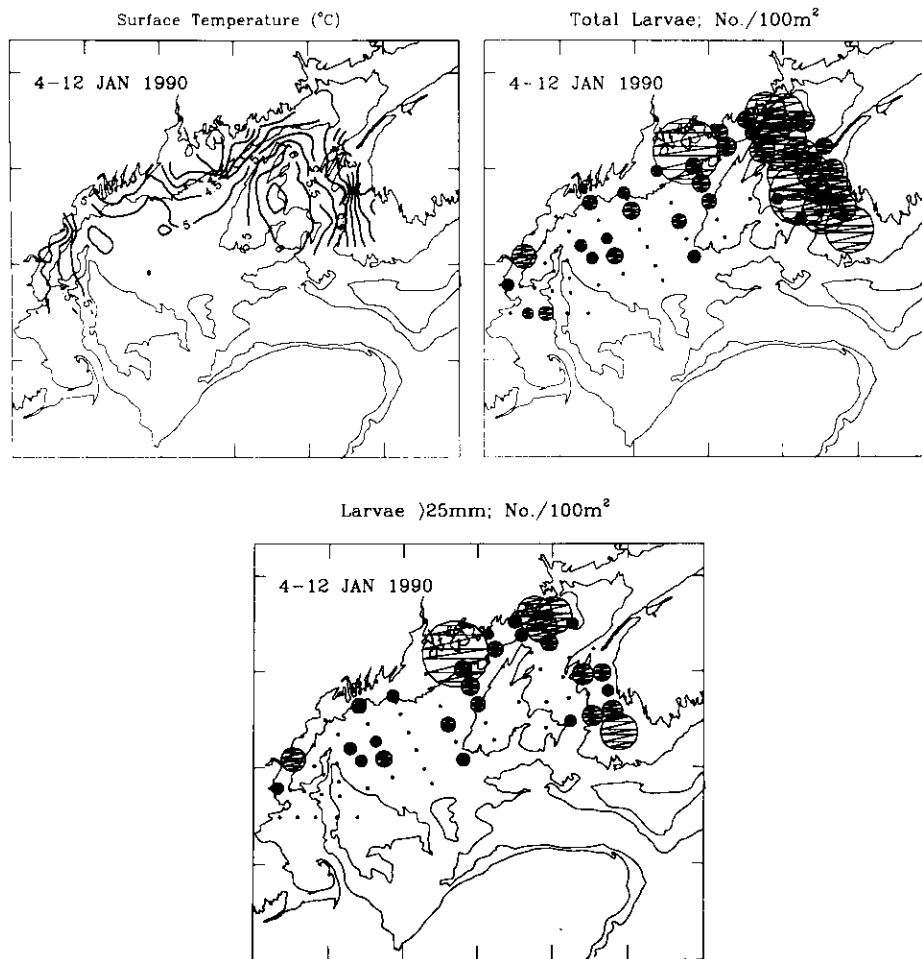
It is possible that the relative proportion of larvae that is advected away from the eastern Maine–Grand Manan spawning area differs between years. Should either the exact locations of spawning vary between years in relation to the position of the tidal front, we might expect to see corresponding interannual differences in the proportions of herring larvae retained in the area or transported away. It is possible that in some years larvae hatch closer to the frontal region, which would facilitate their being entrained in the eastern Maine coastal current. In addition, and perhaps more significantly, the position of the tidal front itself varies in its onshore–offshore position depending on the lunar tidal phase. Loder and Greenberg (1986) showed that monthly and fortnightly variations in the intensity of tidal mixing could advance and retreat the position of the tidal front by as much as several kilometers in the onshore–offshore direction, depending on the bottom slope. This lunar period, in concert with variable egg bed locations, could produce a periodic release of larval cohorts



**Fig. 12.** AVHRR satellite image of sea surface temperature taken on September 25, 1989, ~10 days before the October cruise, showing cooler waters as darker shades of gray. The cool filament of the eastern Maine coastal current–plume system, which extends offshore from the central Maine coast, corresponds well with the distributions of the larger, older larvae offshore shown in the middle panel of Figure 11. Also, the position of the cooler waters in the plume correspond well with the inferred geostrophic current streamlines, given in Figure 11 as contours of dynamic height. Note the relatively warm surface water temperatures on Georges Bank at this late summer date, despite the vigorous tidal mixing there, as opposed to the Scotian Shelf and the north-eastern Gulf, which maintain cool surface temperatures via local upwelling and mixing of deeper waters.

from the spawning areas, which have been reported to arrive along the coast of Maine (Graham and Townsend, 1985). Thus it is possible that these two processes, variable egg-bed locations and variations in tidal mixing on a lunar cycle, could interact to affect the relative proportion of larvae retained versus transported.

Further variability in larval transport could be explained by the above processes interacting with the episodic nature of slope water intrusions into the Gulf of Maine and the corresponding changes in the coastal current plume system (Brooks and Townsend, 1989). A significant proportion of the larvae that are advected along the Maine coast in the coastal current could be advected offshore over the central Gulf, should they be present in the water column when



**Fig. 13.** Results of R/V *Endeavor* cruise, January 4–12, 1990. **Top left panel**, surface temperature (at 2 m); **top right panel**, abundances of herring larvae (number  $100\text{ m}^{-2}$  sea surface area) of all sizes; **bottom panel**, abundances of only those larvae  $>25$  mm total length. The diameters of the circles are proportional to the square roots of the abundances, where the largest circle corresponds to  $500\text{ larvae m}^{-2}$ . Larvae were collected using a 1 m square Tucker Trawl, equipped with  $505\text{ }\mu\text{m}$  mesh nets and digital flowmeters. A single double-oblique tow was made at each station to within 5–15 m of the bottom, as indicated by a maximum depth recorder.

a slope water intrusion event intensifies the coastal current and diverts coastal water into the Jordan Basin Gyre. Those larvae would then likely spend the winter months in the offshore Gulf, which is the scenario offered by Townsend *et al.* (1989) as having been the case for larvae sampled in the Sheepscot estuary in spring.

The fate of larvae from the Jeffreys Ledge area is virtually unknown, although it would appear that they remain in the general western Gulf of Maine area into

the winter, as we observed in our January survey. These larvae may be significant to the recruitment of pre-juvenile fish that enter the Maine coastal and inshore waters in spring, and certainly need to be studied further.

Apart from the issue of larval retention or transport, fall-spawned herring larvae face relatively harsh conditions during the winter prior to their metamorphosis to juveniles in spring (Graham *et al.*, 1990; Campbell and Graham, 1991). Relatively slight changes in survival during this period can be amplified into much larger changes in survival to the juvenile stage (Houde, 1987). Water temperatures vary by as much as 5°C between inshore coastal waters along the coastal areas of both Maine and Nova Scotia and the offshore waters in winter. Growth rates could thus be dependent on where the larvae overwinter. Feeding conditions are also quite different among the various overwintering areas in the region, as pointed out by Townsend *et al.* (1986, 1987) and Chenoweth *et al.* (1988). Larval feeding conditions would generally be better initially for those larvae that are transported along with the coastal current/plume system, since this system is quite productive and important to the biological productivity of the Gulf of Maine in general (Townsend *et al.*, 1987). Although planktonic production of larval herring food items in the tidally mixed retention areas are in general lower than in other areas, microscale turbulence could possibly compensate, by making more items available to the larvae despite lower absolute concentrations (Murphy, 1961; Rothschild and Osborn, 1988). Larvae that spend the winter months in the offshore waters of the Gulf of Maine could derive some benefit should they reside near the bottom, where the waters are the warmest in the Gulf of Maine in winter (Bigelow, 1927) and where zooplankton populations associated with the bottom nepheloid layer could enhance their feeding environment (Townsend *et al.*, 1991).

As is nearly always the case in any attempt to assess the relative state of our understanding of a complicated problem, we must admit that more research is needed. Although not a particularly gratifying overall conclusion, this admission is fitting to our understanding of the dynamics of herring larvae in the Gulf of Maine. But perhaps by keeping the local oceanographic processes clearly in mind in designing future experiments, we may be able to focus more accurately on some of the processes and problems discussed in this review and begin to capture the nature of recruitment variability in herring populations.

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