# DYNAMICS OF LARVAL HERRING (CLUPEA HARENGUS L.) PRODUCTION IN TIDALLY MIXED WATERS OF THE EASTERN COASTAL GULF OF MAINE

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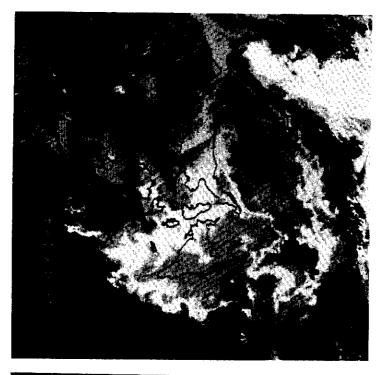
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## INTRODUCTION

The interactions of tidal mixing and plankton dynamics in shelf seas have been receiving increasing attention in recent years. It is now generally recognized that favorable conditions for phytoplankton growth, i.e., compromises between incident light levels, or upper mixed layer depth, and inorganic nutrient concentrations, are often achieved in shallow mixed areas and at fronts in deeper regions where thermally stratified and tidally mixed waters meet. Not surprisingly, it is becoming increasingly apparent that much of the overall biological productivity of the Gulf of Maine can be ascribed to such mixing processes (Yentsch and Garfield, 1981).

The importance of tidal mixing in the Gulf of Maine, where tides range from about 2 m in the west to >6 m in the east, has been recognized since the time of Henry Bigelow (1927), and is illustrated in Figures 1 and 2. Cooler surface water temperatures, which appear darker in satellite infrared images, usually represent those areas where tidal mixing is strong enough to overcome thermal stratifica-

Lecture Notes on Coastal and Estuarine Studies, Vol. 17 Tidal Mixing and Plankton Dynamics. Edited by J. Bowman, M. Yentsch and W.T. Peterson © Springer-Verlag Berlin Heidelberg 1986



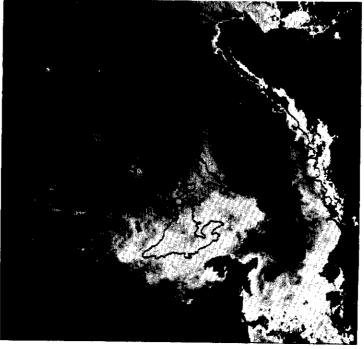
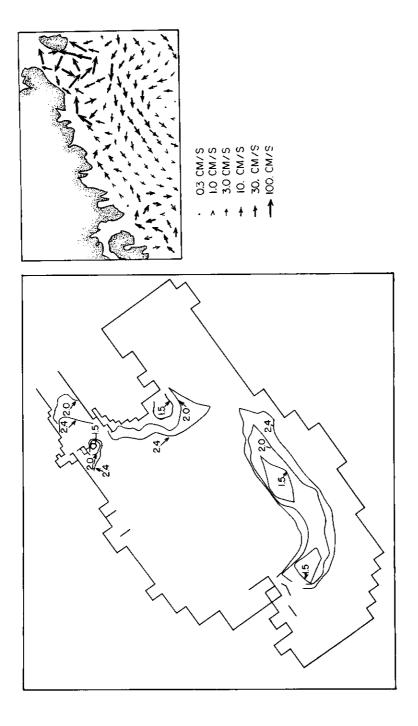


Figure 1. Composite satellite infrared image of the Gulf of Maine taken June 22 and 24, 1984. The panel on the right is a black and white photograph of a color enhancement and shows greater detail along the eastern Maine coast. The 200 m bottom contour is given.



Contours of  $\log (H/D)$  where H= water depth and D= the rate of tidal energy dissipation (from Garrett et al., 1978) for the Gulf of Maine-Georges Bank region, and model-produced residual currents driven by wind and tidal forcing (from Greenberg, 1983) off the coast of eastern Maine. Figure 2.

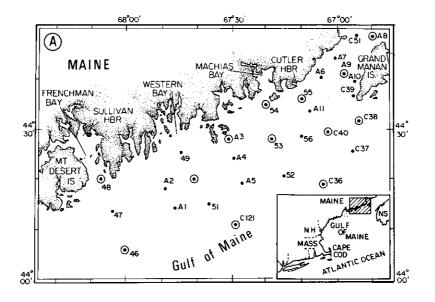
These shallower areas of the Gulf include the southwest Nova tion. Scotian shelf, Georges Bank, the Bay of Fundy and its approaches, and the coastal waters of New England. With a few exceptions, these areas of cool surface water temperatures coincide with the tidally mixed regions predicted by Garrett et al. (1978) using the Simpson and Hunter (1974) stratification parameter, a ratio between water column depth and tidal current speed. Since tides mix the water from the bottom up, it is assumed that for a given tidal current speed and value for bottom friction, mixing can be expected only out to a certain depth; for the Gulf of Maine mixing by tides can be expected only within the 50 to 60 m isobaths (Garrett et al., 1978; Yentsch and Garfield, 1981). It appears unlikely, then, that tidal mixing alone is responsible for maintaining the cooler surface water temperatures which extend beyond the 100 m isobath along the coast of Rather, Brooks (1985) has suggested that the cooler eastern Maine. waters along the Maine coast are advected from the tidally mixed waters in the east as part of a cyclonic gyre over Jordan Basin. He points out that, in keeping with accounts by earlier workers (Gran and Braarud, 1935; Graham, 1970), these coastal waters depart the coast east of Penobscot Bay producing the plume feature which extends into the Gulf. We show in the discussion which follows, that these mixing and advective processes may have significant consequences for fish larvae.

Important herring spawning grounds are located in the tidally mixed waters off the coast of eastern Maine and in the vicinity of Grand Manan Island (Bigelow and Schroeder, 1953; Iles and Sinclair, 1982; Graham, 1982). Recently, it has been suggested that tidally mixed areas in general serve as important herring spawning grounds and retention areas for the larvae, and that the geographic size of such areas determines the maximum size of a given adult spawning population (Iles and Sinclair, 1982). Our work concerns itself with the nature of larval herring production in the eastern coastal waters of Maine, and how the physical and biological features of these tidally mixed waters affect the distribution and abundance of herring larvae and their zooplankton food.

#### MATERIALS AND METHODS

Temperature, zooplankton and ichthyoplankton were sampled at the stations shown in Figure 3a on two cruises on the Canadian research vessel J.L. Hart during 4-7 Oct and 29 Nov-3 Dec 1982. Temperatures were measured with reversing thermometers. The zooplankton was sampled using an 80-cm diameter 80-um mesh net hauled vertically from near the bottom to the surface at about 1 m ·sec<sup>-1</sup>. A 61-cm bongo net (Posgay and Marak, 1981), fitted with 505-um mesh nets and digital flowmeters, was used to sample herring larvae. Samples were preserved in 5% buffered formalin. The bongo nets were towed in a double oblique manner to within 10-20 m of the bottom at a ship speed of 3.5 knots. A Boothbay Depressor trawl (Graham and Vaughan, 1966) was used at 14 of the 27 stations sampled on the 29 Nov-3 Dec cruise. It was used to test whether larger larvae might be caught more efficiently with the trawl; a comparison between the trawl and bongos showed no significant differences in the sizes of larvae caught with the two gears.

A second set of cruises followed in the fall of 1983 using the University of Maine's R/V Lee. On 13-15 Sept and 20-21 Sept, zooplankton and herring larvae were sampled at the stations shown in Figure 3b using the 80-cm 80-mm mesh net and 61-cm 505-mm mesh bongo net as described above. It was our intent in conducting two consecutive weekly surveys to document changes in the larval density pattern which would be indicative of transport along the coast from the spawning grounds in eastern Maine. For this reason samples were collected from Grand Manan Channel to Mt. Desert Island (Fig. 3). A small-scale survey of herring larvae was conducted on 27-28 September in the area shown in Figure 3b. The purpose of this was to determine larval distributions in the immediate vicinity of known egg beds in order to test whether or not small-scale larval density data could be used to locate egg beds and to examine dispersal of larvae from individual point sources rather than from an entire spawning ground. Sampling during the third survey was therefore concentrated in the Machias Bay area with stations located much closer together than in the other surveys.



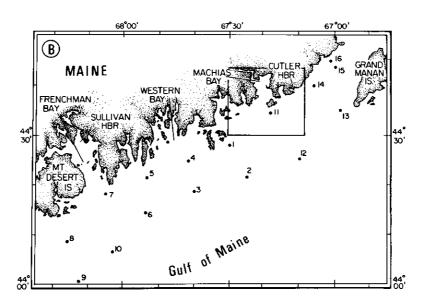


Figure 3. (A) Station locations for the 4-7 Oct and 29 Nov-3 Dec 1982 cruises. (0) = Sampling for zooplankton, herring larvae and hydrography; (•) = sampling for herring larvae and hydrography. Zooplankton were not sampled at stations 55 and A9 on the latter cruises. (B) Station locations for the 13-15 Sept and 20-21 Sept 1983 cruises. Herring larvae and zooplankton were sampled at each station; stations 13-16 were not sampled on the latter cruise. Station locations for the 27 Sept 1983 small scale herring larvae survey are shown by the enclosed box in B.

#### RESULTS

# Egg Bed Locations

Herring in the Gulf of Maine spawn in late summer and fall and lay demersal and adhesive eggs in small, discrete patches, generally in depths of 10-100 m, along the coast and on offshore shoals and ledges (Bigelow and Schroeder, 1953; Sindermann, 1979); spawning occurs earlier in eastern Maine waters than anywhere to the west (Graham, 1982; Kelly and Stevenson, in press). Egg bed sites in the study area were determined by interviewing local fishermen who have observed herring eggs adhering to lobster pots. These interviews revealed that herring generally spawn in a number of discrete locations in the Grand Manan Channel and in the coastal waters near Machias, Little Machias, and Little Kennebec Bays (Fig. 4). These findings confirm published reports based on larval abundance data (Graham, 1982) which show that eastern Maine is an important spawning ground. Spawning also takes place in the vicinity of Grand Manan Island (Iles and Sinclair, 1982), although the number of adult spawning herring in that area has apparently diminished in recent years.

Three egg beds were located by lobster fishermen in 1983 (Fig. 4). The first was located south of Great Head near Cutler Harbor; eggs were first noticed in this location on 23-24 August. Two additional sites were located east and west of Cross Island on 8 and 14 September. All three sites were near the 40 m contour. Since lobster fishermen haul their pots every 3-4 days, the dates when eggs were first observed should have roughly corresponded to spawning dates. No attempts were made to locate egg beds in the Cutler-Machias area in 1982 or in the Western Bay area in either 1982 or 1983.

# Hydrography

Our data support the general contention that the degree of vertical mixing along coastal Maine increases from west to east (Fig. 5, here using only the vertical distributions of temperature). This is in general agreement with Bigelow (1927) and the model predictions by Garrett et al. (1978) which showed greatest tidal mixing around Grand Manan Island.

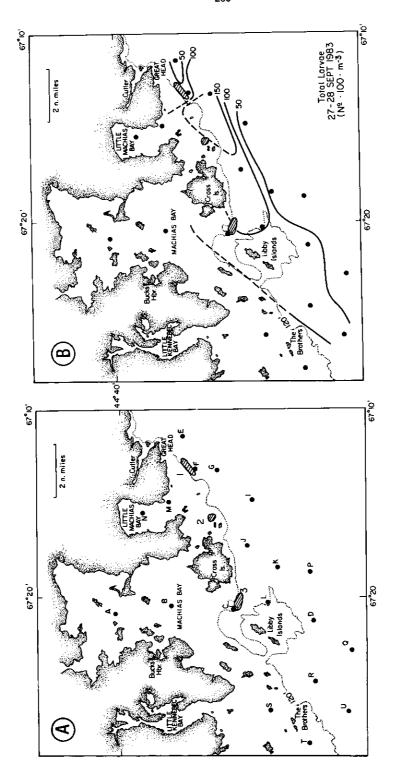
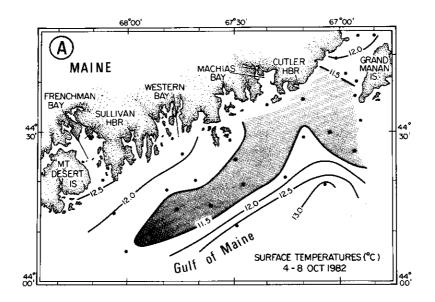


Figure 4. (A) Station locations for small scale survey of herring larvae 27-28 Sept 1983 and locations of egg beds (hatched). (B) Contours of densities of herring larvae (all sizes) for the 27-28 Sept survey given as a number of larvae per 100 m<sup>3</sup>.



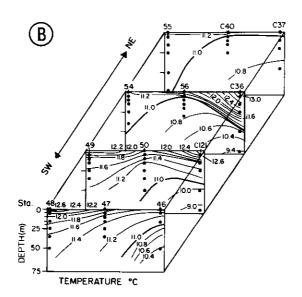


Figure 5. (A) Contours of surface temperatures (shaded area indicates surface temperatures <11.5°C) and, (B) vertical sections of temperatures for the stations indicated, during the 4-7 Oct 1982 cruise. All temperatures were fairly uniform (8.5-8.8°C) during the 29 Nov-3 Dec 1982 cruises and are not plotted.

The residual currents in these waters are quite complex. Bumpus and Lauzier (1965) showed using drift bottles that the general pattern of surface flow is from east to west along the coast, and that there may be an offshore component midway between Grand Manan Island and Mount Desert Island (Fig. 6). Greenberg's (1983) model-produced residual currents (Fig. 2), driven by tidal forcing and summer wind-stress (the latter from values given by Saunders (1977)) shows a series of complex eddies in the waters between Grand Manan Island and a point halfway to Mount Desert Island. These eddies could certainly provide a mechanism for retention of herring larvae as postulated by Iles and Sinclair (1982).

Our plots of the temperature structure (Fig. 5) suggest that the residual currents are probably more like those given by Bumpus and Lauzier (1965). Figure 5 shows that the cooler (<11.5°C) tidally mixed waters just to the west of Grand Manan flow to the west and then move more offshore as a tongue of cool surface water. Such a flow was first discussed by Gran and Braarud (1935) and the tongue feature shows up nicely in the enhanced satellite infrared image (Fig. 1). As discussed earlier, Brooks (1985) has shown that this coastal flow is not due principally to tides but has a strong baroclinic component and is part of a cyclonic gyre in the eastern Gulf. The distributions of herring larvae appear to be closely related to this coastal tongue.

## Larval Herring Distributions

The distributions of larvae deduced from our 4-7 Oct 1982 cruise show two centers of abundance (Fig. 7). Figure 7b shows an area off Western Bay with a high catch rate of young larvae (<10 mm) suggesting the close proximity of a discrete spawning site. Figures 7 c and d show another center of abundance of older larvae (>10 mm) off Machias Bay. A third, less dense, group of older larvae occurred just off Grand Manan Island.

Densities of larvae detected on our 29 Nov to 3 Dec cruise were considerably depleted by mortality and drift (Figs. 8 a-d). We were unable to demonstrate transport of the abundance centers of larvae, owing to the time elapsed between the two cruises (ca. 2 mo). However, a series of samples from Sullivan Harbor (Fig. 3) collected

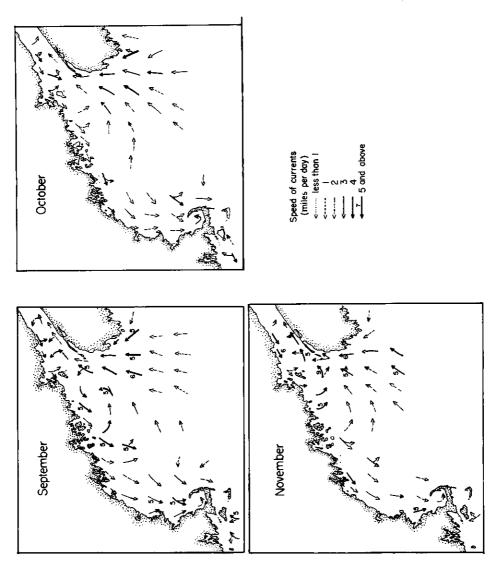


Figure 6. Inferred surface circulation from drift bottle returns (from Bumpus and Lauzier, 1965).

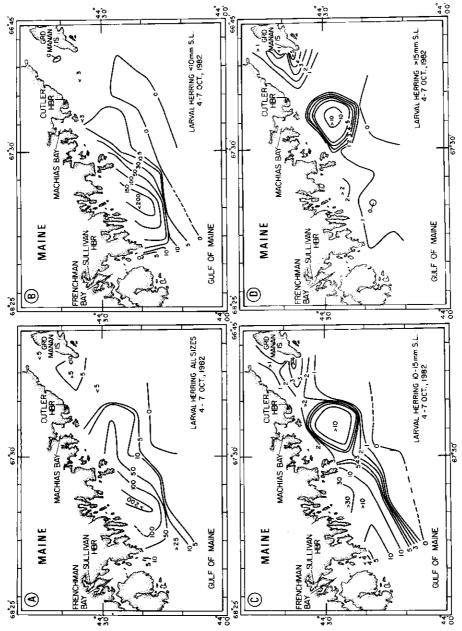


Figure 7. Distributions of herring larvae by size for the 4-7 Oct 1982 cruise. Contours are in numbers of larvae under a  $\rm m^2$  of sea surface.

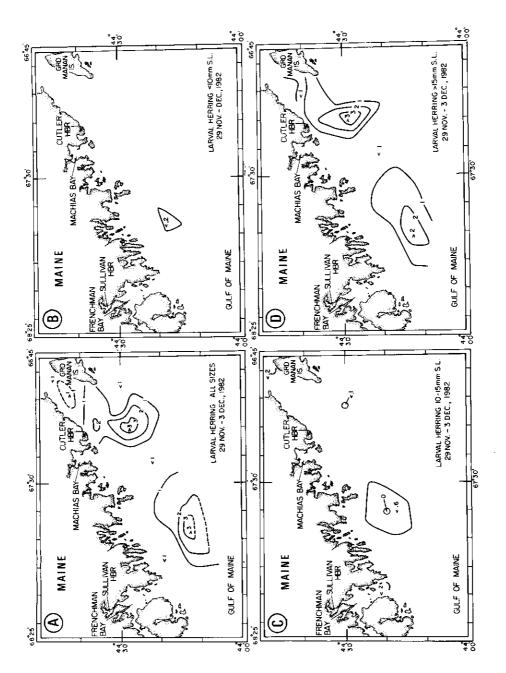


Figure 8. Distributions of herring larvae by size for the 29 Nov-3 Dec 1982 cruise. Contours are in numbers of larvae under a m<sup>2</sup> of sea surface.

each year by one of us (Graham) showed that larvae began to arrive in this inshore area in October, culminating in a small abundance peak (ca.  $1.5 \cdot 100 \, \text{m}^{-3}$ ) in November. This also points out the fact that larval transport may include both active and passive components, since we have already noted that the coastal current turns offshore east of this inshore nursery area.

Our 1983 cruises were spaced one week apart, and afforded us the opportunity to examine more closely the advective transport and dispersion of larvae (Figs. 9 and 10). As we found in 1982, there were two centers of abundance of larvae, one off Machias Bay, representing recently hatched larvae, and a second center off Western Bay. This second center was comprised of larvae somewhat older (one to two weeks older) than the first, and may represent an aggregation rather than a spawning site. Transport of larvae to the west and somewhat offshore was evident between the two cruises. Such transport is in keeping with the residual current pattern discussed earlier. dispersion and transport of larvae from the Machias Bay spawning area is reflected in the more even distribution of larvae shown by the second cruise (Fig. 10a). The results of the small scale sampling conducted on 27-28 Sept show more clearly the dispersion and transport of larvae to the west from the egg beds (Fig. 4). Given an incubation time of 10-15 days (Bigelow and Schroeder, 1953) and the fact that the majority of larvae collected in the 27-28 Sept. survey were still <10 mm, it seems probable that at least some of these larvae had hatched from the Cross Island egg beds. evident from the results of this survey that larvae were initially being dispersed primarily along the coast, perhaps as part of the coastal tongue discussed above, rather than immediately into the bays and inlets (Fig. 4).

# Zooplankton Distributions

The distributions of zooplankton on each cruise in 1982 and 1983 all showed the same general pattern: an increase in abundance from east to west (Figs. 11 and 12). On the 4-7 Oct 1982 cruise the abundances of naupliar and post naupliar stages of copepods increased from a low in Grand Manan channel to a high in the offing of Frenchman Bay (Fig. 11a and b). The same pattern held on the 29 Nov-3 Dec

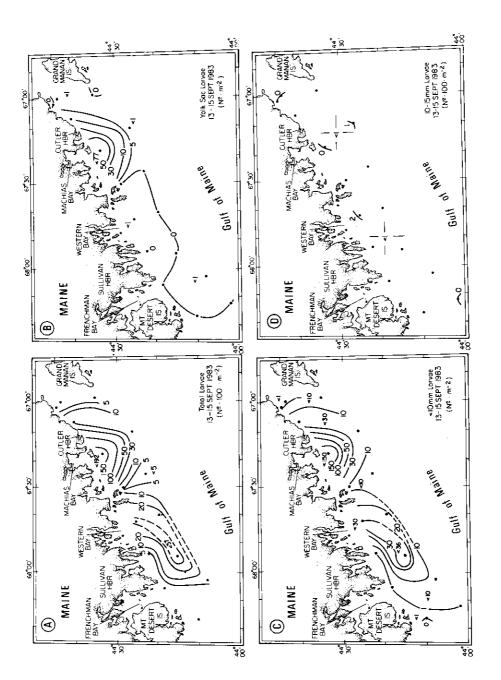
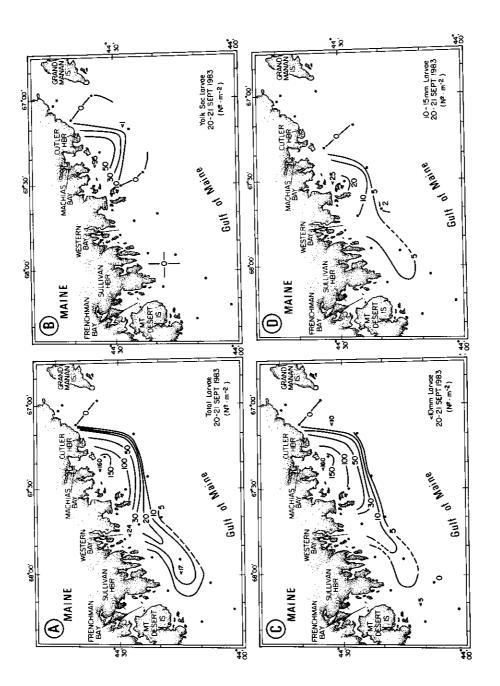
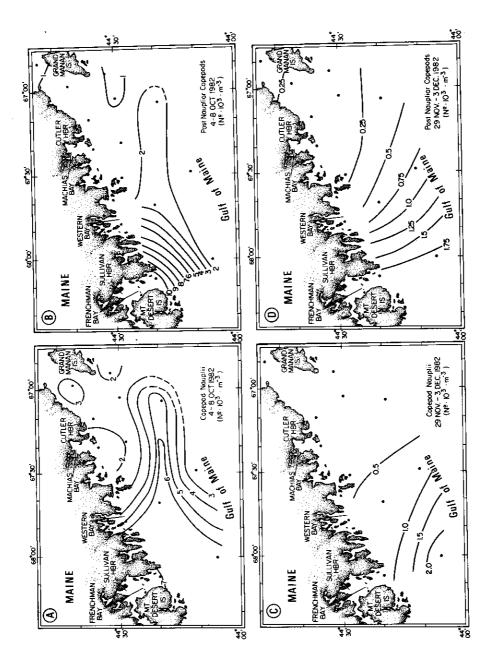


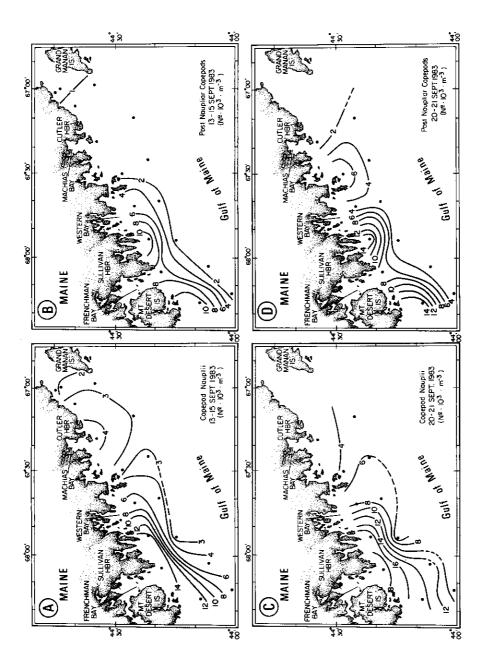
Figure 9. Distributions of herring larvae by size for the 13-15 Sept 1983 cruise. Contours are in numbers of larvae under a m<sup>2</sup> of sea surface.



Contours are Distributions of herring larvae by size for the 20-21 Sept 1983 cruise. in numbers of larvae under a  $\rm m^2$  of sea surface. Figure 10.



Distributions of naupliar and post-naupliar copepods for the two 1982 cruises. Contours are in thousands of animals per  $\mathrm{m}^3$ . Figure 11.

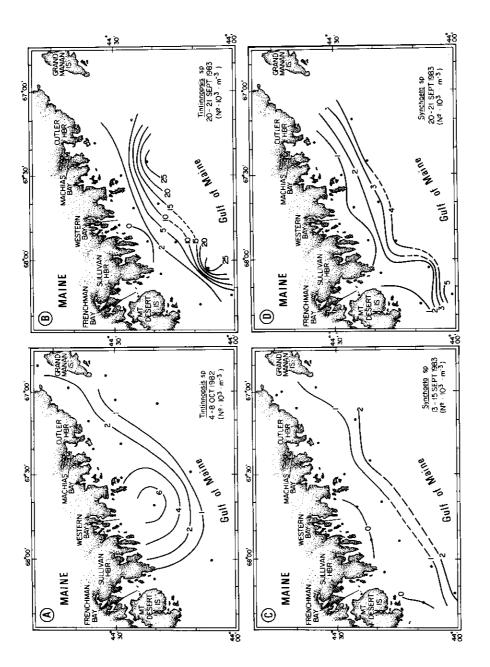


Distribution of naupliar and post-naupliar copepods for the two 1983 cruises. Contours are in thousands of animals per m<sup>3</sup>. Figure 12.

1982 cruise, but the overall densities were much reduced during this early winter sampling period (Fig. 11c and d) In September of 1983 the densities of copepod nauplii were greater than during October the previous year, yet the same pattern of highest densities off Frenchman Bay was again evident (Fig. 12a and c). The distributions of post naupliar copepods during the September 1983 cruises also displayed an increase in abundance from east to west, but did not show highest densities immediately off Frenchman Bay as did the nauplii (Fig. 11b and d). Rather, the densities of copepodid and adult stages increased from offshore to inshore where there were two areas of high concentration on either side of Frenchman Bay. The dominant species of copepods during each of the cruises included Pseudocalanus sp., Acartia longiremis, Microsetella norvegica, Oithona sp. and Centropages spp. A tintinnid Tintinnopsis sp. was also abundant on the 4-7 Oct 1982 cruise (Fig. 13), and had a maximum density (789·m<sup>-3</sup>) at station 50 (Fig. 3). It was much less abundant on the second cruise that year (<200 · m - 3 at 10 of the 11 stations). Tintinnopsis sp. was abundant on the second cruise in 1983 (20-21 Sept) but only at the offshore stations, reaching 28286·m<sup>-3</sup> at station 10 (Fig. 13), while densities were less than  $500 \cdot m^{-3}$  at all stations during the first cruise (13-15 Sept). A rotifer Synchaeta sp. was also more abundant on this second cruise and showed the same pattern as Tintinnopsis sp. in being more abundant at the offshore stations (Fig. 13).

# Larval Feeding and Condition Factors

The distribution of zooplankton appears to be advantageous to those fish larvae which are transported to the west. After having hatched in the east, off Machias Bay, the larvae are transported into waters richer in zooplanktonic food. This may represent mixing with waters already high in zooplankton abundances or that the zooplankton propagate while being transported in the same water mass as the larvae. Even for those larvae which are transported offshore, the higher densities of <u>Tintinnopsis</u> and <u>Synchaeta</u> could serve as forage. Our preliminary examinations of larval gut contents from the 1982 cruises showed that <u>Tintinnopsis</u> was fed upon, although to a lesser extent than copepod nauplii and copepodites. The young larvae sampled in 1983 had a very low (ca. 10%) incidence of food in the gut, and we were unable to assess food preferences. However, we did evaluate relative condition factors (post yolk sac) of those larvae

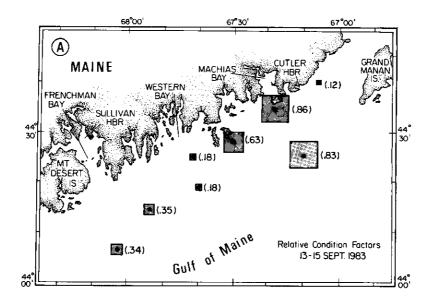


Contours are in thousands of sp. and Synchaeta sp. Tintinnopsis Distributions of animals per m<sup>3</sup>. Figure 13.

sampled in 1983 using the method given in Townsend (1983) in order to evaluate the relative physiological well-being of the larvae. Stated briefly, the condition factor incorporated the allometric equation W  $= aL^b$  where W = dry weight of a larva, L = total length and a and b are constants. All the data for that year were used to solve the allometric equation for the exponent, b, by using a geometric mean functional regression (Ricker, 1973). The condition factor for a larva is then  $K = W/L^b$ . These results are given in Figure 14, and demonstrate that recently hatched larvae sampled in the immediate vicinity of the egg beds had the highest condition factors, which we assume reflected good health after recently hatching and being in the transition period between relying on yolk sac reserves and exogenous feeding. As these larvae presumably are transported toward the west the condition factors drop considerably, but increase somewhat as they enter the zooplankton-richer waters to the west. relative condition factors are highest in the hatching area and in the area to the west which has greater concentrations of potential food organisms.

#### DISCUSSION

The results which we present here represent only the beginnings of an ongoing research effort to understand the dynamics of larval herring production in the eastern coastal Gulf of Maine, but already an interesting paradigm is emerging. The conceptual model presented by Iles and Sinclair (1982) suggests that Atlantic herring spawning sites are situated in tidally mixed waters to assure, among other reasons, the retention of larvae within the spawning area. assumed that it would then follow, and the empirical evidence bore this out, that the size of a given adult herring spawning stock would be dictated by the size of the tidally mixed larval retention area. Our data from coastal waters do not fit this general pattern. Rather than retention within tidally mixed waters in the east, which represent only a relatively small geographic area (Fig. 2), we observed that the larvae were being transported to the west and into waters progressively more stratified. This apparently involved either selective tidal transport by the larvae or passive drift in the nontidal residual flow, which is to be expected of recently mixed waters. Such a flow to the west and offshore was illustrated by our observations of water temperatures and larval distributions, and



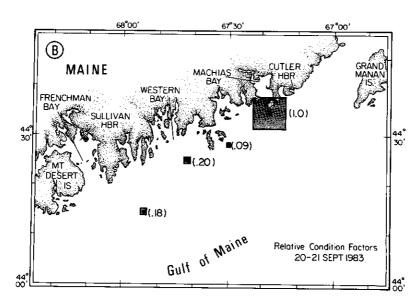


Figure 14. Relative condition factors for herring larvae collected 13-15 and 20-21 Sept 1983. The linear dimensions of each box are relative to the condition factor measured at that station (given in parentheses).

generally agrees with the patterns reported by Gran and Braarud (1935), Bumpus and Lauzier (1965), Graham (1970), and Brooks (1985). Further, we believe that it is more advantageous to the survival of the larvae to be transported away from the spawning site; the waters in the vicinity of the spawning site are low in potential zooplankton forage, but to the west food supplies are greater. For those larvae which are transported to western inshore areas, such as Frenchman Bay and Sullivan Harbor, an increased supply of zooplankton would then be available. Even for those larvae which are transported more offshore, there may be greater densities of food resources, in the form of tintinnids and rotifers, than available within the spawning area. Also, spawning in tidally well mixed waters, such as the eastern coastal Gulf of Maine where tidal excursions extend several kilometers, would result in effective dispersal and reduction of larval densities after hatching from the demersal eggs, consistent with the hypothesis that larval fish survival is density dependent (Shepherd and Cushing, 1980).

Since the demise of the Georges Bank herring spawning group (Anthony and Waring, 1980), one would expect there to be greater pressure on the remaining Gulf of Maine spawning populations to maintain the production of larvae necessary to support the fishery. Should Iles and Sinclair be correct in their assessment of the limitations imposed by the areal extent of the tidally mixed spawning areas, only a relatively small spawning stock could be supported by these waters. We suggest that the larval populations leave their restrictive "retention area/spawning site" less densely aggregated, as a result of tidal dispersion, and enter a transport system which provides additional nursery grounds.

In the case of the eastern coastal Gulf of Maine spawning area, it appears that the larvae are released "upstream" from food rich waters such as has been reported for tropical coral reef fishes (Johannes, 1978), and that the period of larval drift which ensues represents an important stage in their life history. It would appear that the herring larvae are drifting to the west along with recently mixed waters high in phytoplankton abundances (Yentsch and Garfield, 1981) and are ready to prey upon the early developing stages of zooplankton, which are drifting in the same water mass along with the larvae and which most likely propagate in response to the vertical mixing and increase in primary production.

Admittedly, the data we present are incomplete in that they deal only with the zooplankton and herring larvae, but we feel we have constructed a working hypothesis which can be tested. We will need to verify in the future our assumption that the injection of inorganic nutrients is enhanced by the intense vertical mixing in the waters of eastern Maine and those surrounding Grand Manan Island, and that these waters nurture a developing phytoplankton and zooplankton population as this water mass is advected downstream and to the west. This research is presently underway.

### ACKNOWLEDGEMENTS

We wish to thank Dr. T.D. Iles and the Department of Fisheries and Oceans for shiptime on the <u>J.L. Hart.</u> We thank also Keith Sherman, Ken Abott, David Hodges, Kevin Kelly, Andrea Swiecicki, Maureen Maritato, Michael Dunn and Kerry Lyons for their valuable assistance. The satellite image analysis in Figure 1 was performed by the University of Rhode Island's Oceanographic Remote Sensing Laboratory. Image processing software was developed and has been maintained by O. Brown, R. Evans, J. Brown and A. Li at the University of Miami. This work was funded by grants from NOAA Sea Grant and the State of Maine. This is Bigelow Laboratory for Ocean Sciences contribution number 84013.

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