Estuaries Vol. 15, No. 3, p. 282-288 September 1992

# Spawning Origin of Small, Late-Hatched Atlantic Herring (*Clupea harengus*) Larvae in a Maine Estuary

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**ABSTRACT: Atlantic herring (*Clupea harengus*) larvae have been collected for resource monitoring purposes in the Sheepscot River in mid-coastal Maine during October–February, for the past 20 years. During this period, the larval population in the river has typically peaked in October–early November and has been composed of larvae derived from August–September spawning in eastern Maine and New Brunswick waters and from September–early October spawning along the central Maine coast. Larvae from eastern coastal spawning areas are transported to the river by the prevailing westerly coastal current. The appearance of small (≤15 mm SL) larvae in the river during December and January 1985–1989 suggested an additional time and area of origin. Aging procedures based on enumeration of daily otolith increments showed the majority of these small larvae were spawned from mid October to mid November when spawning usually occurs in western Maine coastal waters and in the vicinity of Jeffreys Ledge. Comparison of back-calculated hatching dates for small larvae collected in the river with wind direction and velocity data from mid October through November suggested that larvae were transported eastward against a weakened Gulf of Maine coastal current to the Sheepscot River by complex wind-driven surface currents that occur off the western Maine coast in the fall.**

## Introduction

Various studies indicate that Atlantic herring (*Clupea harengus*) in the Gulf of Maine begin spawning earlier in eastern Maine and New Brunswick waters than off the western Maine, New Hampshire, and Massachusetts coasts (Bigelow and Schroeder 1953; Graham et al. 1972a; Sinclair and Tremblay 1984). Spawning begins in coastal waters near Grand Manan Island, New Brunswick, and off eastern Maine as early as late July or early August and continues through late September (Stevenson 1989). Recently-hatched larvae from this spawning area drift westward with the prevailing coastal current (Graham et al. 1973; Townsend et al. 1986; Chenoweth et al. 1988). Sporadic spawning activity also has been reported at scattered locations along the central Maine coast (i.e., in outer Penobscot Bay) during September and October (Stevenson 1989). A second principal spawning area is located along the western Gulf of Maine coast south of Cape Elizabeth near Wood Island and offshore in the vicinity of Jeffreys Ledge. Herring spawn in September and October in this region of the gulf (Graham et al. 1972a, b; Boyar et al. 1973; Graham et al. 1973; Cooper et al. 1975). Boyar et al. (1973) also reported an inshore transport of larvae from spawning sites near the southern end of Jeffreys Ledge.

Other important herring spawning grounds in United States waters of the northwest Atlantic are located on Nantucket Shoals and Georges Bank, where spawning occurs during September–December (Caddy and Iles 1973; Graham and Chenoweth 1973; Pankratov and Sigaev 1973; Lough et al. 1981). It is unlikely that larvae from these spawning grounds contribute significantly to the coastal herring population north of Cape Cod. Herring also spawn in large numbers southwest of Nova Scotia, but larvae from that area are not believed to recruit to the Gulf of Maine coastal stock in significant numbers (Ridgway 1975). A recent paper (Campbell and Graham 1991) models the recruitment dynamics of herring larvae which originate in eastern Maine and New Brunswick waters during their westward transport along the Maine coast, but does not consider larvae from other spawning grounds.

Larval sampling at two inshore locations, the Sheepscot River and Sullivan Harbor (Fig. 1), along the Maine coast during the past 20 years (Graham and Venno 1968; Graham 1982; Stevenson et al. 1989) has revealed that larval abundance typically peaks in October–November and then declines rapidly. Based on estimated spawning dates of August to early October back-calculated from daily otolith increment data collected during 1980–1986 (Graham et al. 1984; Graham and Townsend 1985; Stevenson et al. 1989; Graham et al. 1990), these abundance peaks were the result of larvae that entered both locations from eastern waters. These



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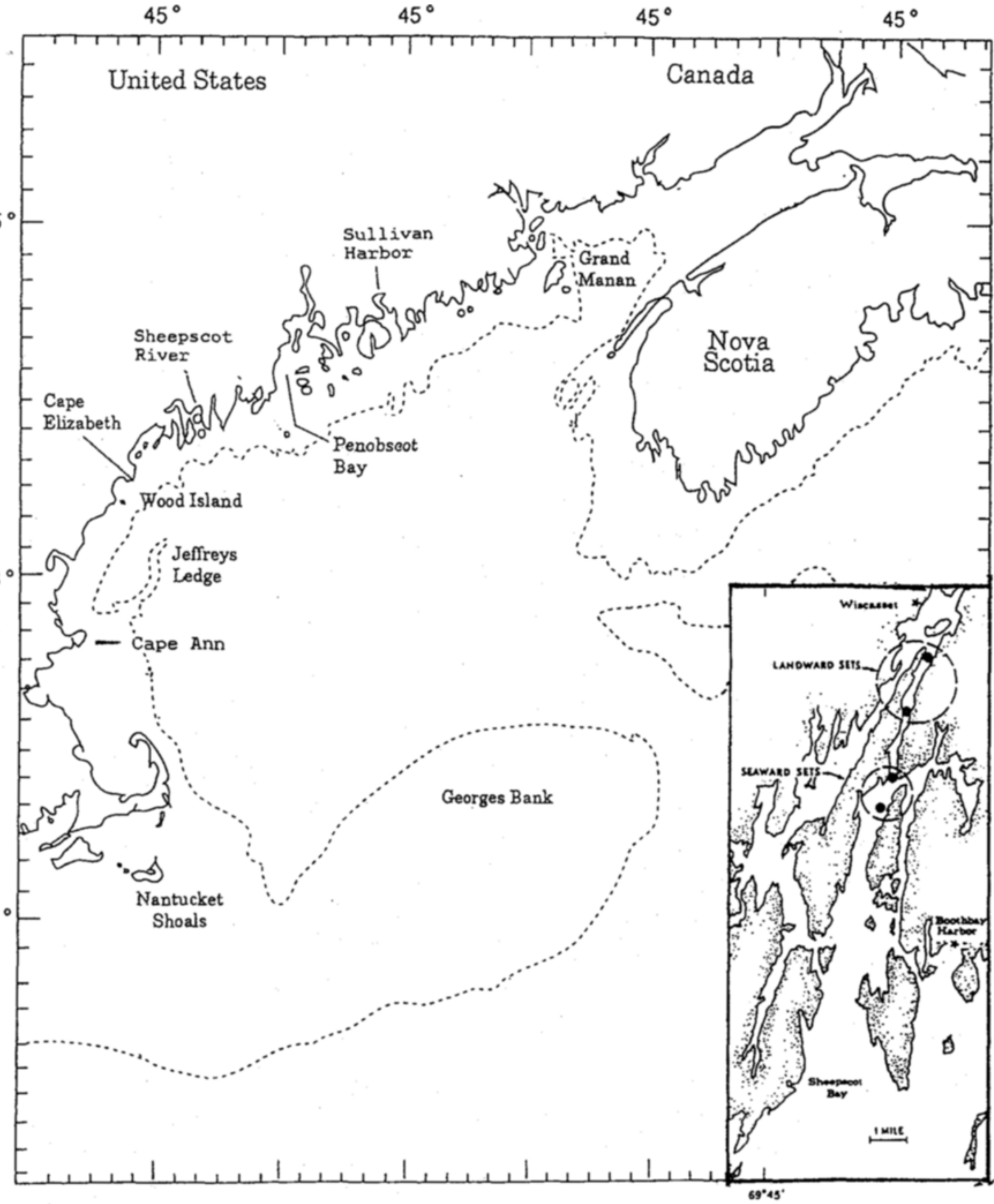


Fig. 1. The Gulf of Maine with the Sheepscot River (inset).

larvae must survive density-dependent fall mortality and density-independent winter mortality (Graham 1982; Townsend et al. 1986; Stevenson et al. 1989; Townsend et al. 1989) in order to metamorphose in spring. Small larvae collected in December and January during the late 1980's at the more westerly location, the Sheepscot River, appear to be derived from spawning over a later time period (October–December) and probably originate from spawning areas along the coasts of western Maine, New Hampshire, and Massachusetts.

The purpose of this study was to determine spawning dates and origins for small ($\leq 15$ mm SL) herring larvae collected in the Sheepscot River in December and January during the late 1980's and to examine a possible mechanism which would account for their transport from spawning grounds in western Maine, New Hampshire, and Massachusetts.

## Study Location

The Sheepscot River flows through a steep-walled, drowned river valley located along the west central coast of Maine (Fig. 1). The lower estuary (downstream of Wiscasset) is characterized by deeper water, a smaller tidal exchange ratio, higher and less variable salinity, and a narrower range of temperatures than the shallower upper estuary (Stickney 1959). Depth of the lower estuary ranges from 60 m at its seaward end to about 20 m at its upper end. Width ranges from 1,000 m to 300 m throughout the 9-km study area and tidal range is about 3 m. Pronounced vertical gradients in temperature and salinity existed prior to 1974, particularly during spring and summer (Stickney 1959). However, removal of a causeway in 1974 increased tidal flows by 50% and altered circulation and vertical stratification patterns, resulting in more homogeneous conditions throughout the lower estuary (McAlice and Jaeger 1983).

## Methods

Herring larvae were collected using stationary, vertically-deployed, buoyed and anchored nets (Graham and Venno 1968) set at four locations in the river. Four to six strings of four 0.5-m diameter plankton nets (0.50–0.75 mm mesh) were set at 1 m, 10 m, 15 m, and 1 m off the bottom every 2 wk from October through February during 1985–1990 for a total of 12–13 sampling dates per year. The nets were set to sample overnight for a full tidal cycle. Nets were suspended from wooden triangular vanes so as to orient them continuously to the tidal flow; a flow meter was suspended in the opening of each net to measure flow rates.

Cod-end samples were collected at dawn, placed on ice, and returned to the laboratory where the larval herring were removed and counted prior to freezing or preservation in 95% ethanol. Catch rates were calculated by dividing the total number of larvae collected in all the nets by the total volume of water strained by all nets on each sampling date. The total amount of water strained for all the nets on each sampling date was about 35–40 $\times$ $10^3$ $m^3$. The standard lengths of 100+ randomly selected larvae per sampling date were measured to the nearest mm using an ocular micrometer or mm ruler. Catch rates at length were determined by 1-mm increments for each sampling date by apportioning the total catch rate according to the proportion of larvae caught at each length for each year class.

Sagittal otoliths were removed and examined for daily growth increments. Larvae selected for otolith removal were chosen in order to obtain a representative size range of larvae collected on each sampling date. At least 50 pairs of otoliths per date were mounted on glass slides for microscopic examination and enumeration of growth increments. Unpolished otoliths were examined either at 400$\times$ magnification or under oil immersion at 1,000$\times$. Since we were interested in late hatching, only larvae $\leq$15 mm SL collected in December and January were examined. This maximum size defined approximately one-month-old larvae based on a daily growth rate of 0.2 mm (Lough et al. 1982; Graham and Townsend 1985) and assumed hatching at 7 mm.

Increment counts were converted to spawning dates by treating each increment as a daily growth ring and adding 23 d to the increment count to account for the time lag between spawning and formation of the first three growth rings. Daily ring formation was verified by Graham and Townsend (1985) who compared the growth rates for individual cohorts calculated from changes in modal length over time with the growth rates for the same larvae calculated on the assumption that otolith increments were formed daily. The 23-d conversion factor was based on a comparison of back-calculated dates of third increment formation and known spawning dates from egg bed surveys for two cohorts of larvae sampled in 1983 (Stevenson 1989; Graham and Sherman 1984). Similar results were found by Lough et al. (1982) who estimated the formation of the third increment averaged 22 d from hatching for larvae reared in the laboratory at 10°C. No attempt was made to check for resolution effects on increment counts (Campana et al. 1987), which may produce underestimated absolute age. However, close agreement between hatching dates and surveys of egg beds (Stevenson 1989) indicate that these ages were correctly estimated.

We examined the number of days of southerly winds and mean wind velocities for October 15 through November of 1985–1989, that is, during the period when the majority of larvae spawned southwest of the Sheepscot River would be hatching and subject to wind-driven surface currents and Ekman transport. National Climatic Center wind direction and velocity data from the Portland International Jetport (located approximately 10 km inland) were used to determine the number of days the wind blew from the southeast-southwest (120°–240°) and the mean velocity (m $s^{-1}$). Graham (1970) found little difference in average prevailing winds at the Portland Jetport from those usually encoun-

TABLE 1. Mean catch of small (≤15 mm SL) herring larvae (larvae 100 m$^{-3}$) collected in December and January, the number of days of southerly winds, mean velocity and the wind-velocity index for the period from October 15 through November 1985–1989.

| Year Class | Mean Catch December | Mean Catch January | Number of Days | Mean Velocity (m s$^{-1}$) | Index |
|---|---|---|---|---|---|
| 1989 | 0.43 | 0.13 | 20 | 3.9 | 78.0 |
| 1988 | 1.72 | 0.43 | 22 | 4.6 | 101.2 |
| 1987 | 0.67 | 0.15 | 22 | 3.7 | 81.4 |
| 1986 | 0.08 | 0.01 | 16 | 3.5 | 56.0 |
| 1985 | 0.48 | 0.07 | 13 | 3.8 | 49.4 |

tered offshore. A simple southerly wind-velocity index was prepared by multiplying the number of days of southerly winds by the mean wind speed during the same days (Table 1). The SYSTAT statistical software (Wilkinson 1986) was used to generate regressions of the December mean catch (DMC) and the January mean catch (JMC) of larvae as functions of the wind-velocity index, and the January mean catch as a function of the December mean catch.

## Results

Small larvae (≤15 mm SL) were collected in December and January of all five years (Table 1). The mean catch of larvae in December ranged from 0.08 larvae 100 m$^{-3}$ in 1986 to 1.72 larvae 100 m$^{-3}$ in 1988. Small larvae comprised about 10–60% of the total larval catch for any single December sampling date during 1985–1989. The catch exceeded 0.50 larvae 100 m$^{-3}$ in December 1987 and 1988. Small larvae were less abundant in January, but some were collected in every year. January mean catch rates ranged from 0.01 larvae 100 m$^{-3}$ in 1986 to 0.43 larvae 100 m$^{-3}$ in 1988 and were highly correlated ($r^2 = 0.97$, $p < 0.01$) with December mean catch rates.

Daily otolith ring counts were obtained from 227 small larvae belonging to the 1985–1988 year classes (Table 2). The majority of the otoliths (84%) were from small larvae collected in December. The number of otoliths read per year class ranged from

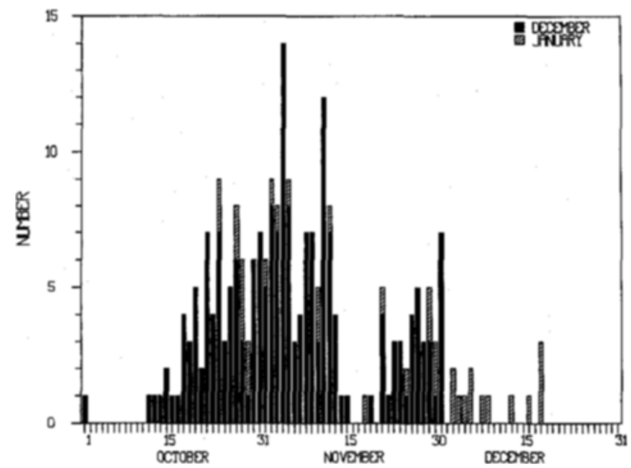


Fig. 2. Frequency distribution of estimated spawning dates for the 227 small (≤15 mm SL) Atlantic herring larvae aged using daily growth rings of sagittal otoliths for the 1985–1988 year classes.

14 for the 1986 year class to 103 for the 1988 year class. No otoliths were read for the 1989 year class. Estimated spawning dates for small larvae collected in December ranged from October 1 to November 20, while January larvae were spawned from October 24 to December 18 (Table 2, Fig. 2). Eighty larvae (35%) were spawned in October, 127 (56%) in November, and 20 (9%) in December. The majority (80%) were spawned from October 12 through November 22.

Our assumption is that the majority of small larvae collected in December and January were hatched and released into the water column between mid October and late November since hatching occurred in about 8–9 d at 10°C (Cooper et al. 1975). Winds blew from the southeast to southwest (120°–240°) for 13 d to 22 d during the 47-d period from October 15 through November of 1985–1989 (Table 1). Mean velocities ranged from 3.5 m s$^{-1}$ in 1986 to 4.6 m s$^{-1}$ in 1988. The mean number of small larvae collected in the Sheepscot River during December and January were highly correlated ($r^2 = 0.69$, $p = 0.08$ and $r^2 = 0.80$, $p < 0.05$, respectively) with the wind-velocity index during the study period (Table 1, Fig.

TABLE 2. Estimated spawning date of small (≤15 mm SL) Atlantic herring larvae collected in December and January in the Sheepscot River from 1985 through 1988.

| Year Class | Date of Collection | Number | Spawning Date |
|---|---|---|---|
| 1988 | December 1–January 27 | 103 | October 22–December 18 |
| 1987 | December 1–January 19 | 71 | October 18–December 6 |
| 1986 | December 2–January 20 | 14 | October 1–December 18 |
| 1985 | December 2–January 16 | 39 | October 12–December 6 |

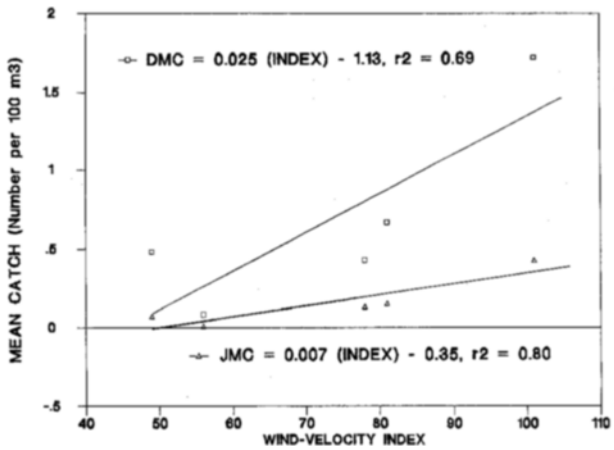


Fig. 3. Regressions of December mean catch (# 100 $m^{-3}$, DMC) and January mean catch (JMC) with the wind-velocity index for the period from October 15 through November 1985–1989.

3). However, only the January correlation coefficient was significant.

## Discussion

These results suggest that some Atlantic herring larvae spawned in western Maine, New Hampshire, and Massachusetts coastal waters in late October and November are transported to the Sheepscot River by wind-driven surface currents. Larvae hatching in the western gulf would have to be transported northeast against the prevailing cyclonic surface circulation pattern (Bigelow 1927; Graham 1970) to reach the river. This cyclonic surface circulation is from east to west along the coast (Bigelow 1927; Graham 1970) and set in motion by river runoff. It turns offshore near Casco Bay where a clockwise eddy develops near shore (Bigelow 1927; Bumpus 1960). Recent summer circulation surveys found the coastal current now begins to turn offshore east of Penobscot Bay and induces a clockwise gyre off of Penobscot Bay (Brooks 1985). Graham (1970) concluded that the current patterns near the coast were very complex, particularly in the west, with shoreward intrusions of water extending from well offshore. As a result, the drift patterns of larval Atlantic herring from spawning areas in coastal waters of the western Gulf of Maine are not as well understood as along the eastern and central Maine coast (Graham et al. 1972a; Graham 1982; Townsend et al. 1986; Chenoweth et al. 1988).

The most reasonable origin for the small larvae seems to be either spawning near Wood Island or Jeffreys Ledge. Herring larvae are located in the upper water column immediately over spawning areas (Graham and Chenoweth 1973; Lough 1975) and while Stephenson and Powers (1988) found that small herring larvae (<9–14 mm) undergo semidiel vertical migrations, the maximum density was recorded at 5 m with the mean center of mass at 8.7 m, indicating larvae were abundant in surface waters. Since larvae are then dispersed by nontidal surface and near surface currents (Tibbo 1958; Graham et al. 1973; Townsend et al. 1986; Chenoweth et al. 1988), wind would be a major force affecting their dispersal. Movement of larvae northeastward seems possible given that the Gulf of Maine cyclonic surface circulation weakens in the summer as river runoff slows (Bigelow 1927) and may be modified by wind or river runoff at any time during the year (Bumpus 1960). Graham (1970) also noted that winds, dynamic topography at the surface and bottom topography directed surface drift shoreward within the central and western portions of the coast.

Further evidence of a weakened gyre along the western Maine coast was reported in the fall 1979 (Parker and Garfield 1981) when surface currents were observed moving in a northeasterly direction from as far south as Cape Ann. These surface currents were probably wind-driven since winds blew from the south to west-southwest (150°–250°) for 5 d of the 8 d of this cruise. Under these conditions, wind-driven surface currents presumably could transport recently hatched herring larvae to the Sheepscot River from as far south as Jeffreys Ledge. Boyar et al. (1973) studied the dispersal of recently hatched herring larvae from egg beds at the southern end of Jeffreys Ledge in the fall 1972 and concluded that most larvae were transported shoreward, although there was evidence that larvae were dispersed in all directions. Graham and Sherman (1985) collected herring larvae produced during a single hatching episode in both the Sheepscot and Saco rivers and suggested that a complex system of coastal eddies could transport recently hatched larvae eastward as well as westward from their source. Movement of small larvae into the Sheepscot River in December and January is not limited to the late 1980's and may be relatively common since it also occurred during 1974–1976 (Graham 1982) and 1980 (Graham and Townsend 1985).

Other possible sources of small, late-hatched larvae in the Sheepscot River in December and January are nearby spawning sites (i.e., sites located along the central Maine coast) and more distant areas such as Georges Bank. Consistent spawning has been reported at a few locations in outer Penobscot Bay and periodically in the Boothbay region (Graham 1982), but takes place in September, not late October and November (Stevenson 1989). With the apparent recovery of the Georges Bank herring stock (Stephenson and Kornfield 1990), it is possible that spawning on Georges Bank may contribute larvae to the coastal Gulf of Maine herring stocks. This subject has generated considerable debate in the past (Tibbo 1958; Bumpus 1960; Colton and Temple 1961). Recently, the model proposed by Campbell and Graham (1991) concluded that any previous recruitment of Georges Bank herring to the coastal stock occurred after metamorphosis.

Since the Sheepscot River receives herring larvae from the eastern and western coastal spawning grounds, future studies of larval recruitment to the coastal stock should include the entire western coast of the Gulf of Maine, regardless of state and international boundaries. Larvae from western coastal spawning areas may contribute significantly to the juvenile population in the mid-coast region since larvae produced later in the year experience mortality over a reduced time period. Additionally, larvae that arrive from eastern spawning areas in large numbers early in the fall are subjected to severe density-dependent mortality in October and November (Graham 1982). Future research will be directed at more fully examining the contribution of larvae from central and western coastal areas to recruitment in the Gulf of Maine stock.

## Acknowledgments

We wish to thank E. Brewer and K. Sherman for field assistance and S. Chenoweth, D. Libby, and D. Townsend for their comments on an earlier draft.

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*Received for consideration, February 26, 1991*
*Accepted for publication, October 8, 1991*