

**Abstract**—Biweekly ichthyoplankton surveys were conducted in Penobscot Bay, Maine, during the spring and early summer of 1997 and 1998. Larvae from demersal eggs dominated the catch from late winter through spring, but not in early summer collections. Larval fish assemblages varied with temperature, and to a lesser extent, plankton volume, and salinity, among months. Temporal patterns of larval fish abundance corresponded with seasonality of reproduction. Larvae of taxa that spawn from late winter through early spring, such as sculpins (*Myoxocephalus* spp.), sand lance (*Ammodytes* sp.), and rock gunnel (*Pholis gunnellus*) were dominant in Penobscot Bay in March and April. Larvae of spring to early summer spawners such as winter flounder (*Pleuronectes americanus*) Atlantic seasnail (*Liparis atlanticus*), and radiated shanny (*Ulvaria subbifurcata*) were more abundant in May and June. Penobscot Bay appears to be a nursery for many fishes; therefore any degradation of water quality during the vernal period would have wide reaching effects on the nearshore fish community.

## Dynamics of larval fish abundance in Penobscot Bay, Maine

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For most fish, the greatest mortality occurs during early life stages (Hjort, 1914; Cushing, 1975; Leggett and DeBlois, 1994). Therefore, it is essential that fish eggs and larvae develop in favorable habitats that maximize the probability of survival. Bigelow (1926) recognized the significance of the coastal shelf for the production of fish larvae within the Gulf of Maine, noting that most larvae were found within the 200-m contour. He also observed that larval drift was generally to the southwest and that abundance increased progressively to the west with the result that few larvae were observed off eastern Maine and in the Bay of Fundy. Other surveys (Fish and Johnson, 1937; Marak, 1960; Marak and Colton, 1961; 1962) further defined the composition of the ichthyoplankton of the Gulf of Maine. Ichthyoplankton of inshore waters of the Gulf of Maine has been documented for the Damariscotta, Sheepscot, and Sullivan Harbor estuarine systems and nearby waters in the central area of the Maine coast (Graham and Boyar, 1965; Graham, 1972; Chenoweth, 1973; Hauser, 1973; Lee, 1975; Laroche, 1980; 1982; Shaw, 1981; Townsend, 1981; 1983; 1984). However, the ichthyoplankton of Penobscot Bay has not been studied despite the fact that it is the largest embayment in the region and that coastal environments, such as bays and estuaries, may constitute favorable habitats for the early life stages of a large number of marine fishes (Frank and Leggett, 1983).

This study describes the results of a two-year, spring survey of larval fishes in Penobscot Bay, Maine. The objectives of the study were 1) to describe the structure of the larval fish community, 2) to determine the temporal and spa-

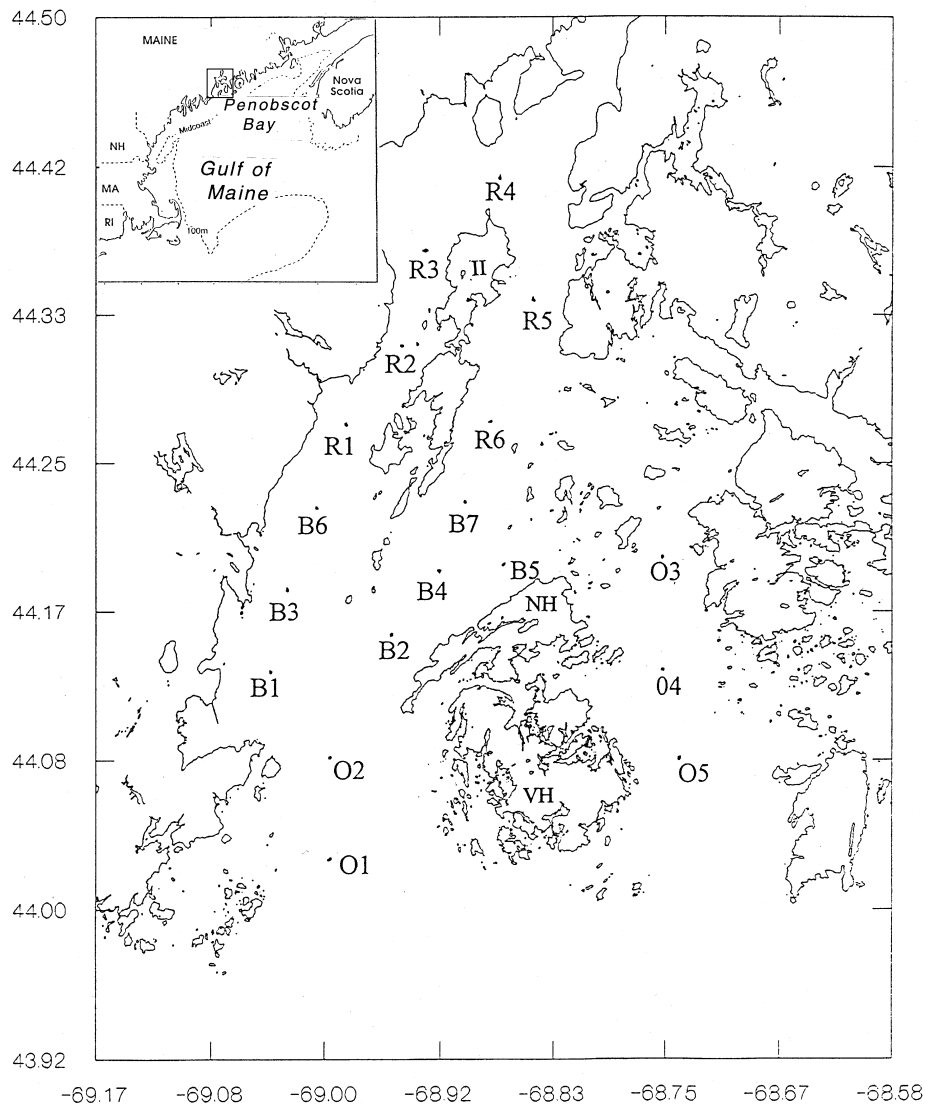
tial variation in species diversity and abundance, and 3) to relate these variations to differences in location and environmental variables.

### Materials and methods

#### Field methods

Penobscot Bay is a large (80-km) drowned river valley typical of the Maine coast. It has a drainage area of over 21,000 km<sup>2</sup> (Haefner, 1967). The study area is about 40 km long and varies in depth from 15 to 110 m. Sixteen ichthyoplankton stations (Fig. 1) were selected to encompass Penobscot Bay for the larval surveys. Six upper bay stations (R1–R6) were located in the northern estuarine portion of the bay between Isleboro Island and the mainland. Seven midbay stations (B1–B7) were located in the central portion of the bay. Three lower bay stations (O2–O4) were located in the southern estuarine portion of the bay adjacent to the islands of North Haven and Vinalhaven.

In 1997, seven, two- or three-day cruises (97I–97VII) were conducted bi-weekly from 4 April through 25 June 1997 to coincide with spring and summer spawning times for many fishes. Data collection involved towing a 1.0-m, 333-micron mesh plankton net equipped with a General Oceanics flowmeter during daylight hours (Fig. 1). The net was hauled for 20 minutes in stepped oblique fashion at the surface, at 10 m, and at 20 m, or to within 5 m of the bottom. At each station, a vertical profile of salinity and temperature was collected with a Seabird 19 CTD (conductivity, temperature, and depth) probe.



**Figure 1**

Map of stations sampled biweekly with a 1.0-m plankton net in Penobscot Bay, Maine, from 4 April to 25 June 1997 and from 18 March to 30 April 1998. II = Iselboro Island; NH = North Haven Island; and VH = Vinalhaven Island.

In 1998, four one- or two-day cruises (98I–98IV) were conducted biweekly from 18 March through 30 April 1998 and data collection was the same as in 1997 except that ten ichthyoplankton stations were sampled in the lower bay only. Eight of these stations were sampled in 1997 including five midbay stations (B1–B5) and three lower bay stations (O2–O4). Two additional lower bay stations, O1 and O5, were added in 1998. Larvae from both years were preserved in 5% formalin for later identification to the lowest taxon possible by the Atlantic Reference Center of the Huntsman Marine Biological Laboratory in St. Andrews, New Brunswick, and for quantitative determination of larval fish densities (number of larvae per filtered 100 m<sup>3</sup>). Fish larvae were measured for standard length, or in some cases notochord length, to the nearest mm.

Plankton volume standardized by volume filtered was determined for each tow by displacement of the unidentified plankton.

### Data analysis

Larval fish abundance and environmental data were analyzed by using three multivariate techniques: principal components analysis (PCA), multivariate analysis of variance (MANOVA), and canonical correlation analysis (CCA). PCAs of the variance-covariance matrices derived from both environmental and larval abundance data were performed to reduce intercorrelated variables to a smaller number of uncorrelated variables. This procedure provided a concise description and comparison of complex spatial

and temporal patterns of the larval fish assemblage and environmental data (Gauch, 1982). Varimax rotation was performed on factors from the PCAs in both cases because rotated solutions tend to extract components that correlate highly with a smaller number of variables than unrotated PCAs (Stevens, 1986). This step aided in the interpretation of the factors. Rotated factor scores from the PCA were used as the dependent variables in the MANOVA because they were uncorrelated, thus satisfying the assumption of independence for parametric statistical tests.

Environmental data were log-transformed to satisfy assumptions of univariate normality and then summarized by PCA. The resulting factor scores were grouped by month, and means were compared by MANOVA to assess the null hypothesis that environmental variables did not differ among months. This analysis was followed by a Tukey-Kramer multiple range test to detect which monthly means differed. This test controls for increases in the type-I error rate associated with unequal sample sizes (Day and Quinn, 1989). Temporal changes in environmental variables were interpreted by evaluating product moment correlations of the environmental variables and factor scores from PCA. I considered only variables that were significantly correlated with an individual factor in interpreting that factor (significance levels were adjusted for multiple comparisons, where  $p' = 1 - (1 - p)^{1/k}$  and  $k$  equals the number of comparisons [Sokal and Rohlf, 1981]). The results of these analyses were used to discriminate among months.

The analysis of larval fish assemblage composition was similar to that performed for environmental data. However, fish taxa not present in 5% of the samples were eliminated to reduce the influence of rare taxa (taxa that were excluded were present in five of 102 samples in 1997 and two of 40 samples in 1998) as potential outliers (Gauch, 1982). A matrix of angularly transformed [arcsine of the square root of a proportion (Sokal and Rohlf, 1981)] relative abundances for the  $m = 12$  taxa in  $n = 102$  samples in 1997, and the  $m = 13$  taxa in  $n = 40$  samples in 1998 were constructed and summarized by PCA. Varimax rotated factor scores generated from PCA of the relative abundance matrix were compared among months by using MANOVA (unbalanced design). The null hypothesis was that mean factor scores (and taxonomic composition) did not change among months. This was followed by a Tukey-Kramer test of significantly affected factors to identify the extent to which monthly means differed.

Factor scores were then grouped by location and served as the dependent variables in MANOVA to test for differences in sample location (upper, mid, or lower bay). The null hypothesis was that mean factor scores (and taxonomic composition) did not change among locations. A Tukey-Kramer test was performed to identify location mean factor scores that differed significantly. Temporal and spatial changes in the taxonomic composition of larval fish assemblages were then interpreted by identifying which factors were affected by month and location treatments and by evaluating product-moment correlations of angularly transformed relative abundance data

**Table 1**

Mean ( $\pm$  standard error) environmental variables for the entire study period, reported by month for 1997 and 1998. Temperature ( $^{\circ}$ C) and salinity recorded as mean for top 20 m of the water column and volume displacement (Pvol) in mL of unidentified plankton per 100  $m^3$ .

| Month | Temperature | Salinity     | Depth (m)   | Pvol       |
|-------|-------------|--------------|-------------|------------|
| 1997  |             |              |             |            |
| April | 3.37 (0.13) | 30.56 (0.13) | 74.0 (9.4)  | 17.3 (1.7) |
| May   | 5.49 (0.12) | 30.24 (0.08) | 58.0 (11.8) | 4.2 (0.5)  |
| June  | 8.52 (0.22) | 30.44 (0.05) | 46.8 (8.2)  | 13.7 (2.1) |
| 1998  |             |              |             |            |
| March | 2.41 (0.01) | 29.90 (0.05) | 38.8 (18.8) | 34.4 (0.5) |
| April | 4.23 (0.14) | 30.14 (0.05) | 56.5 (10.7) | 25.5 (0.9) |

and significant PCA factor scores (i.e. "loadings" on factors significantly affected by time and location; Pielou, 1984). The relationships of the factor scores from PCA of the relative larval fish abundance matrix and the log-transformed environmental variables were examined by CCA.

Standard lengths, or notochord lengths, from 1997 and 1998 were compared among cruises (sample dates) for each species by using Kolmogorov-Smirnov two-sample tests. The null hypothesis was that size distribution did not differ significantly between sample dates.

## Results

A total of 102 plankton net samples and CTD measurements were collected during biweekly sampling between 4 April and 25 June 1997 in Penobscot Bay. Sixteen stations were sampled on five of the seven sampling trips; however, inclement weather (wind speeds  $>25$  knots) during the first week of April (4–7, 97I) and from late April to early May (29 April–1 May 97III) limited the number of stations that could be sampled during these trips to 10 and 12, respectively. The number of cubic meters of water filtered per 20-minute tow varied from 137.5 to 755.7  $m^3$  depending on station location and sample date. The total volume of filtered in 1997 was 44,622  $m^3$ .

In 1998, 40 plankton net samples and CTD measurements were collected during approximately biweekly sampling between 18 March and 30 April 1998. Ten stations were sampled on each of the four sampling trips. The number of cubic meters of water filtered during each 20-minute tow varied from 54.2 to 582.5  $m^3$  depending on station location and sample date. The total volume of water filtered in 1998 was 12,459  $m^3$ .

## Environmental data

Station depth ranged from 20 m at mean low water at the upper bay station R4 to 91 m at station O2 (Table 1).

Table 2

Correlations among environmental variables and factor scores from varimax-rotated PCA of the log-transformed environmental data. Underlined values significant at  $P = 0.05$ , adjusted for multiple comparisons such that  $P < 0.01$  for a significant correlation.

|             | Depth | Pvol         | Temp  | Salinity | Factor 1     | Factor 2     |
|-------------|-------|--------------|-------|----------|--------------|--------------|
| 1997        |       |              |       |          |              |              |
| Depth       | 1.00  |              |       |          | 0.08         | <u>0.98</u>  |
| Pvol        | 0.07  | 1.00         |       |          | <u>0.84</u>  | -0.06        |
| Temperature | -0.13 | <u>-0.35</u> | 1.00  |          | <u>-0.68</u> | -0.05        |
| Salinity    | 0.20  | <u>0.44</u>  | -0.24 | 1.00     | <u>0.71</u>  | 0.25         |
| 1998        |       |              |       |          |              |              |
| Depth       | 1.00  |              |       |          | 0.08         | <u>0.83</u>  |
| Pvol        | -0.08 | 1.00         |       |          | <u>-0.90</u> | 0.08         |
| Temperature | 0.18  | <u>-0.71</u> | 1.00  |          | <u>0.90</u>  | -0.09        |
| Salinity    | -0.16 | -0.29        | 0.21  | 1.00     | <u>0.42</u>  | <u>-0.68</u> |

Station mean water temperatures for the top 20 m of the water column in 1997 were variable and ranged from 2.3°C on 4 April to 10.8°C on 25 June. Station mean salinity ranged between 27.8 ppt on 30 April and 31.2 ppt on 16 April. Plankton volume ranged from 0.8 to 44.9 mL per 100 m<sup>3</sup> and generally was greatest during early April (97I) with a secondary peak in volume observed in late June (97VII). Greatest plankton volumes occurred at the lower bay stations. In 1998, mean water temperatures ranged from 2.4°C on 18 March to 5.3°C on 30 April. Mean salinity ranged between 29.6 ppt on 18 March and 30.6 ppt on 30 April. Station plankton volume in 1998 ranged from 6.1 to 280 mL per 100 m<sup>3</sup> and was greatest during late April (98IV) at the lower bay stations.

We compared environmental variables among months to aid in the characterization of Penobscot Bay. PCA of log-transformed variables identified two factors that explained 69% of the total variance in 1997 and 76% in 1998 (Table 2). Factor 1 was related to temperature, plankton volume, and salinity in 1997 and in 1998. Factor 2 was related to depth in both years. MANOVA of mean factor scores indicated significant differences by month in 1997 (Wilk's lambda=0.792,  $P < 0.001$ ) and 1998 (Wilk's lambda=0.778,  $P < 0.001$ ). Temperature was negatively correlated and plankton volume and salinity were positively correlated with PCA factor 1 in 1997 (Table 2). *Post hoc* comparisons of monthly scores for factor 1 indicated that the mean scores for April were different from those for May and June. In 1998, temperature was positively correlated and plankton volume negatively correlated with PCA factor 1 (Table 2) and *post hoc* comparisons indicated that the mean scores for March were different from those for April. Salinity was correlated with both PCA factor 1 (positively) and factor 2 (negatively) in 1998. Depth was positively correlated with factor 2 in both 1997 and 1998. *Post hoc* comparisons of monthly scores for PCA factor 2 indicated that the mean scores for April were different from those for May and June in 1997; the mean score for March was different from that for April in 1998.

### Fish larvae

Differences existed between the two years in the kinds of fish larvae found in Penobscot Bay. At least, 26 species (23 individuals [1.5%] not identified to species) belonging to 15 families were identified (Table 3). A total of 23 species (15 families) were found in 1997, and 16 species (9 families) in 1998; 13 species were common to both years. Differences in taxonomic composition were mainly due to the collection of rare specimens during the year, such as inquiline snailfish (*Liparis inquilinus*) in 1997 and pollock (*Pollachius virens*) in 1998. In addition, several species that were present in 1997, including American eel (*Anguilla rostrata*), capelin (*Mallotus villosus*), fourbeard rockling (*Enchelyopus cimbrius*), Atlantic tomcod (*Microgadus tomcod*), cunner (*Tautoglabrus adspersus*), Atlantic mackerel (*Scomber scombrus*), alligatorfish (*Aspidophoroides monopterygius*), windowpane flounder (*Scophthalmus aquosus*), and American plaice (*Hippoglossoides plattessoides*), did not occur in the 1998 collections. In contrast, pollock, snake blenny (*Lumpenus lampraetiformis*) and Arctic shanny (*Stichaeus punctatus*) were collected only in 1998. The assemblage of species was slightly more diversified in 1997 than in 1998 with Shannon-Wiener indices of  $H' = 3.1$  and 2.8, respectively. The three most abundant species in 1997 (*U. subbifurcata*, *Ammodytes* sp., *P. americanus*) constituted about 59% of all captures compared with 68% in 1998 (*M. octodecimspinosus*, *P. gunnellus*, *Ammodytes* sp.).

A total of 779 larvae of 23 species of fishes were collected during the seven cruises in 1997 (Table 3). The most commonly occurring larvae (>35% of the samples) were Atlantic seasnail (*Liparis atlanticus*), winter flounder (*Pleuronectes americanus*), radiated shanny (*Ulvaria subbifurcata*), sand lance (*Ammodytes* sp.), and *H. plattessoides*. Rare larvae (<1% of the samples) included Atlantic cod (*Gadus morhua*), Gulf seasnail (*Liparis coheni*), *L. inquilinus*, shorthorn sculpin (*Myoxocephalus scorpius*), and *S. aquosus*. The highest number of species (14) occurred dur-

**Table 3**

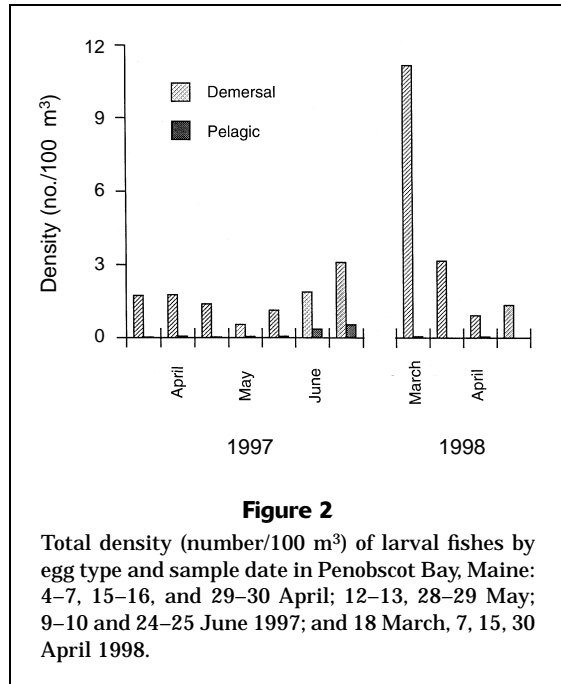
Egg type, total density (number/100 m<sup>3</sup>), and percent frequency of occurrence (FO) of larval fishes collected by 1.0 m plankton net from April to June 1997 (102 samples) and March to April 1998 (40 samples) in Penobscot Bay. D = demersal; P = pelagic.

| Family<br>Species                    | Egg type | 1997    |    | 1998    |    |
|--------------------------------------|----------|---------|----|---------|----|
|                                      |          | Density | FO | Density | FO |
| Anguillidae                          |          |         |    |         |    |
| <i>Anguilla rostrata</i>             | —        | 0.004   | 2  |         |    |
| Clupeidae                            |          |         |    |         |    |
| <i>Clupea harengus</i>               | D        | 0.009   | 4  | 0.072   | 15 |
| Osmeridae                            |          |         |    |         |    |
| <i>Mallotus villosus</i>             | D        | 0.022   | 5  |         |    |
| Gadidae                              |          |         |    |         |    |
| <i>Enchelyopus cimbrius</i>          | P        | 0.034   | 11 |         |    |
| <i>Gadus morhua</i>                  | P        | 0.002   | 1  | 0.022   | 5  |
| <i>Microgadus tomcod</i>             | D        | 0.007   | 2  |         |    |
| <i>Pollachius virens</i>             | P        |         |    | 0.007   | 3  |
| Labridae                             |          |         |    |         |    |
| <i>Tautoglabrus adspersus</i>        | P        |         |    | 0.007   | 3  |
| Stichaeidae                          |          |         |    |         |    |
| <i>Lumpenus lampraetiformis</i>      | D        |         |    | 0.086   | 23 |
| <i>Ulvaria subbifurcata</i>          | D        | 0.462   | 41 | 0.014   | 5  |
| <i>Stichaeus punctatus</i>           | D        |         |    | 0.014   | 3  |
| Pholidae                             |          |         |    |         |    |
| <i>Pholis gunnellus</i>              | D        | 0.099   | 27 | 1.428   | 75 |
| Cryptacanthodeidae                   |          |         |    |         |    |
| <i>Cryptacanthodes maculatus</i>     | D        | 0.054   | 12 | 0.294   | 33 |
| Ammodytidae                          |          |         |    |         |    |
| <i>Ammodytes</i> sp.                 | D        | 0.350   | 35 | 0.596   | 35 |
| Scombridae                           |          |         |    |         |    |
| <i>Scomber scombrus</i>              | P        | 0.016   | 4  |         |    |
| Cottidae                             |          |         |    |         |    |
| <i>Hemirhamphus americanus</i>       | D        | 0.064   | 21 | 0.215   | 43 |
| <i>Myoxocephalus aeneus</i>          | D        | 0.022   | 9  | 0.237   | 35 |
| <i>M. octodecimspinosus</i>          | D        | 0.034   | 9  | 1.550   | 40 |
| <i>M. scorpius</i>                   | D        | 0.004   | 1  | 0.366   | 33 |
| Agonidae                             |          |         |    |         |    |
| <i>Aspidophoroides monopterygius</i> | D        | 0.007   | 3  |         |    |
| Cyclopteridae                        |          |         |    |         |    |
| <i>Liparis atlanticus</i>            | D        | 0.182   | 51 | 0.043   | 13 |
| <i>L. coheni</i>                     | D        | 0.002   | 1  | 0.187   | 23 |
| <i>L. inquilinus</i>                 | D        | 0.002   | 1  |         |    |
| Bothidae                             |          |         |    |         |    |
| <i>Scophthalmus aquosus</i>          | D        | 0.002   | 1  |         |    |
| Pleuronectidae                       |          |         |    |         |    |
| <i>Hippoglossoides platessoides</i>  | P        | 0.094   | 30 |         |    |
| <i>Pleuronectes americanus</i>       | D        | 0.229   | 47 | 0.029   | 8  |

ing mid-April (97II). The most abundant larvae were *U. subbifurcata* (26% of total number), *Ammodytes* sp. (20%), *P. americanus* (13%), and *L. atlanticus* (10%). Total density of all larvae combined ranged from 0.6 larvae per 100 m<sup>3</sup> in mid-May (97IV) to 3.9 larvae per 100 m<sup>3</sup> in late June

(97VII). The high larval densities in late June were a result of the large number of *U. subbifurcata* collected at the three lower bay stations.

In 1998, 726 larvae of 16 species of fishes (Table 3) were collected over the four sampling cruises. The most common



larvae (>35% of the samples) were rock gunnel (*Pholis gunnellus*), sea raven (*Hemitripterus americanus*), long-horn sculpin (*Myoxocephalus octodecimspinosus*), grubby (*M. aeneus*), and *Ammodytes* sp., whereas *P. virens* and *S. punctatus* were the least common (<3%). *Myoxocephalus octodecimspinosus* (30% of total number), *P. gunnellus* (27%), and *Ammodytes* sp. (11%) were the most abundant larvae collected. The greatest number of species (12) were found during mid-March (98I). Densities of all larvae combined declined from 11.4 larvae per 100 m<sup>3</sup> in mid-March (98I) to about one larva per 100 m<sup>3</sup> in mid-April (98III). The high larval densities in mid-March resulted from the high numbers of *M. octodecimspinosus* and *P. gunnellus* larvae collected at that time.

Larvae originating from demersal eggs dominated the catches in both years (Table 3). In terms of abundance, most larvae collected in 1997 came from demersal eggs (70%) that dominated the catch at all stations. Larvae from demersal eggs composed most of the catch (>90%) until mid (79%) and late June (60%) when the number of larvae originating from pelagic eggs increased (Fig. 2). Overall, five of 23 species (22%) of larvae came from pelagic eggs in 1997, but by late June (97VII), four of the eight species (50%) collected hatched from pelagic eggs. Larvae from demersal eggs dominated the catches in 1998 to an even greater extent than in 1997 (Fig. 2). Two of the 16 species (13%) and four larvae (0.04%) collected in 1998 originated from pelagic eggs (three specimens of *G. morhua* and one of *P. virens*). *Ulvaria subbifurcata* were the most abundant larvae in 1997 with densities up to 9.1 per 100 m<sup>3</sup> at the lower bay stations, whereas in 1998, *M. octodecimspinosus* and *P. gunnellus* were the most abundant larvae, with station densities up to 12.9 and 6.1 larvae per 100 m<sup>3</sup>, respectively. Densities of sand lance (*Ammodytes* sp.) were highest (4 per 100 m<sup>3</sup>) at the upper bay

and midbay stations in 1997 and 1998, respectively. *Pleuronectes americanus* were more abundant in 1997 with densities up to 1.7 larvae per 100 m<sup>3</sup> at the midbay stations (B2, B3, B4). Larvae from pelagic eggs were rare in both years.

Several species appeared in plankton samples from most sampling dates in 1997 (Table 4). One species, *H. platte-soides* was taken during all seven cruises but was absent from the 1998 collections. *Ammodytes* sp. occurred from early April (97I) through late May (97V) in 1997 and from mid-March (98I), early April (98II), and late April (98IV) in 1998. *Pleuronectes americanus* and *L. atlanticus* were present from mid-April (97II) to late June (97VII) and *H. americanus* and *P. gunnellus* were found from early April (97I) to mid June (97VI). Four of the five species of fish larvae originating from pelagic eggs were taken during only one cruise. In 1998, three species, *P. gunnellus*, *H. americanus* and *M. aeneus*, were collected on all four cruises. Atlantic herring (*Clupea harengus*) and wrymouth (*Cryptacanthodes maculatus*) occurred from mid-March (98I) through mid April (98III). *Myoxocephalus octodecimspinosus*, *M. scorpius*, and *L. coheni* were taken only during the first two cruises.

Size of the most abundant species changed little over the survey time period (Table 4). For example, winter flounder larvae were 2–4 mm during mid April (97II) and 3–7 mm during late June (97VII) indicating successive spawning events or no observed growth. The length-frequency distributions of most larvae were not significantly different among sample dates (Kolmogorov-Smirnov two sample test,  $P > 0.05$ ). However, the proportion of larger larvae increased over time for three taxa collected over a two month period in 1997 (i.e. *Ammodytes* sp., *P. gunnellus*, *H. platte-soides*, Table 4). Few species showed a change in length frequency distribution during the shorter 1998 survey (Kolmogorov-Smirnov two sample test,  $P > 0.05$ ).

Temporal changes in the abundance of fish larvae were observed in both years. Two peaks in mean density of larval fish were observed among all locations in 1997, whereas only a single peak was seen during the shorter 1998 survey. In 1997, the mean density was initially about 1.9 larvae per 100 m<sup>3</sup> in early (97I) and mid-April (97II), then declined to 0.6 larvae per 100 m<sup>3</sup> by mid May (97IV). Larval density increased to 1.2 larvae per 100 m<sup>3</sup> by late May (97V) and peaked at 3.9 larvae per 100 m<sup>3</sup> in late June (97VII). Most of the initial reduction in density was due to fewer *Ammodytes* sp., *C. maculatus*, and *H. americanus* in the collections, whereas the June increase was due to *U. subbifurcata*, and to a lesser extent to *E. cimbrius* and *P. americanus*. Densities of fish larvae in 1998 declined from a peak of 11.4 larvae per 100 m<sup>3</sup> in mid-March (98I) to about 1 larva per 100 m<sup>3</sup> in mid-April (98III), before increasing to 1.4 larvae per 100 m<sup>3</sup> on late April. Fewer *Ammodytes* sp., *C. maculatus*, *L. coheni*, the three *Myoxocephalus* sp., and *P. gunnellus* accounted for the initial reduction. The increase during the latter part of the 1998 survey was due to greater numbers of *L. atlanticus*, *P. americanus*, and *U. subbifurcata* larvae in collections.

Relative abundance patterns of 12 of the most abundant taxa (by the 5% criterion) in 1997 and 13 taxa in 1998

**Table 4**

Length-frequency distributions of the more abundant larval fishes collected in Penobscot Bay in 1997 and 1998; and results of the Kolmogorov-Smirnov two-sample test ( $P < 0.05$ ).

| Year and species                  | Cruise | <i>n</i> | Notochord or standard length (mm) |   |    |    |    |    |    |    |    |    |     | Mean | KS test |          |          |
|-----------------------------------|--------|----------|-----------------------------------|---|----|----|----|----|----|----|----|----|-----|------|---------|----------|----------|
|                                   |        |          | 1                                 | 2 | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | >10 |      |         |          |          |
| 1997                              |        |          |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
| <i>U. subbifurcata</i>            | I      | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | II     | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | III    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | IV     | 8        |                                   |   |    |    |    |    | 2  | 6  |    |    |     |      |         | 6.8      | VII>VI   |
|                                   | V      | 21       |                                   |   |    |    | 1  | 9  | 11 |    |    |    |     |      |         | 6.5      |          |
|                                   | VI     | 54       |                                   |   |    |    | 4  | 31 | 17 | 2  |    |    |     |      |         | 6.3      |          |
|                                   | VII    | 119      |                                   |   |    |    | 25 | 44 | 28 | 10 | 8  | 3  | 1   |      |         | 6.5      |          |
| <i>P. gunnellus</i> <sup>1</sup>  | I      | 20       |                                   |   | 2  | 8  | 7  | 2  | 1  |    |    |    |     |      |         | 14.6     | III>I,II |
|                                   | II     | 14       |                                   |   | 2  | 1  | 3  | 1  | 2  | 1  | 2  | 2  |     |      |         | 16.5     |          |
|                                   | III    | 6        |                                   |   |    | 1  |    |    |    |    |    | 1  | 4   |      | 20.3    |          |          |
|                                   | IV     | 1        |                                   |   |    |    |    |    |    |    |    |    | 1   |      | 25.0    |          |          |
|                                   | V      | 1        |                                   |   |    | 1  |    |    |    |    |    |    |     |      | 14.0    |          |          |
|                                   | VI     | 1        |                                   |   | 1  |    |    |    |    |    |    |    |     |      | 13.0    |          |          |
|                                   | VII    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
| <i>C. maculatus</i> <sup>1</sup>  | I      | 12       |                                   |   |    |    |    |    |    | 2  | 1  | 4  | 5   |      | 20.4    | ns       |          |
|                                   | II     | 10       |                                   |   |    |    |    |    |    |    |    | 3  | 7   |      | 22.1    |          |          |
|                                   | III    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | IV     | 1        |                                   |   |    |    |    |    |    |    |    |    | 1   |      | 38.0    |          |          |
|                                   | V      | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | VI     | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | VII    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
| <i>Ammodytes</i> sp.              | I      | 7        |                                   |   |    |    |    | 1  |    | 2  | 2  |    | 2   |      | 9.0     | V>II,III |          |
|                                   | II     | 94       |                                   |   |    | 1  | 4  | 12 | 15 | 11 | 18 | 16 | 17  |      | 8.6     |          |          |
|                                   | III    | 44       |                                   |   |    |    | 1  | 1  | 4  | 8  | 10 | 7  | 13  |      | 9.7     |          |          |
|                                   | IV     | 4        |                                   |   |    |    |    |    | 1  | 1  |    |    | 2   |      | 12.0    |          |          |
|                                   | V      | 2        |                                   |   |    |    |    |    |    |    |    |    | 2   |      | 36.5    |          |          |
|                                   | VI     | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | VII    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
| <i>H. americanus</i> <sup>1</sup> | I      | 10       |                                   |   | 2  | 6  | 1  | 1  |    |    |    |    |     |      | 14.1    | IV>I,II  |          |
|                                   | II     | 11       |                                   |   | 1  | 2  | 3  | 2  |    | 1  | 2  |    |     |      | 15.8    |          |          |
|                                   | III    | 3        |                                   |   | 1  |    |    |    |    |    |    | 1  | 1   |      | 18.3    |          |          |
|                                   | IV     | 3        |                                   |   |    |    |    |    |    |    |    |    | 3   |      | 21.7    |          |          |
|                                   | V      | 1        |                                   |   |    |    |    |    |    |    |    |    | 1   |      | 23.0    |          |          |
|                                   | VI     | 1        |                                   |   |    | 1  |    |    |    |    |    |    |     |      | 14.0    |          |          |
|                                   | VII    | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
| <i>L. atlanticus</i>              | I      | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | II     | 3        |                                   |   |    | 1  | 2  |    |    |    |    |    |     |      | 4.7     | II>VI    |          |
|                                   | III    | 11       |                                   |   |    | 7  | 3  | 1  |    |    |    |    |     |      | 4.5     |          |          |
|                                   | IV     | 10       |                                   |   | 3  | 7  |    |    |    |    |    |    |     |      | 3.7     |          |          |
|                                   | V      | 18       |                                   |   | 8  | 8  | 2  |    |    |    |    |    |     |      | 3.7     |          |          |
|                                   | VI     | 17       |                                   |   | 10 | 5  | 2  |    |    |    |    |    |     |      | 3.5     |          |          |
|                                   | VII    | 21       |                                   | 1 | 9  | 8  | 2  |    | 1  |    |    |    |     |      | 3.7     |          |          |
| <i>P. americanus</i>              | I      | 0        |                                   |   |    |    |    |    |    |    |    |    |     |      |         |          |          |
|                                   | II     | 1        |                                   | 1 |    |    |    |    |    |    |    |    |     |      | 2.0     | VII>IV   |          |
|                                   | III    | 18       |                                   | 1 | 11 | 6  |    |    |    |    |    |    |     |      | 3.3     |          |          |
|                                   | IV     | 24       |                                   | 1 | 9  | 14 |    |    |    |    |    |    |     |      | 3.5     |          |          |

continued

Table 4 (continued)

| Year and species                  | Cruise | n   | Notochord or standard length (mm) |    |    |    |    |    |    |    |    |    |     | Mean | KS test |        |
|-----------------------------------|--------|-----|-----------------------------------|----|----|----|----|----|----|----|----|----|-----|------|---------|--------|
|                                   |        |     | 1                                 | 2  | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | >10 |      |         |        |
| <i>P. americanus</i> (cont.)      | V      | 16  |                                   | 1  | 7  | 5  | 3  |    |    |    |    |    |     |      | 3.6     |        |
|                                   | VI     | 17  |                                   |    | 6  | 8  | 1  | 2  |    |    |    |    |     |      | 3.9     |        |
|                                   | VII    | 24  |                                   |    | 7  | 7  | 3  | 5  | 2  |    |    |    |     |      | 4.5     |        |
| <i>H. platessoides</i>            | I      | 1   |                                   |    |    |    | 1  |    |    |    |    |    |     |      | 5.0     | VII>VI |
|                                   | II     | 4   |                                   |    |    | 2  | 1  | 1  |    |    |    |    |     | 4.8  |         |        |
|                                   | III    | 2   |                                   |    |    | 1  |    | 1  |    |    |    |    |     | 5.0  |         |        |
|                                   | IV     | 3   |                                   |    | 1  | 1  |    |    | 1  |    |    |    |     | 4.7  |         |        |
|                                   | V      | 4   |                                   |    |    | 2  | 1  |    | 1  |    |    |    |     | 5.0  |         |        |
|                                   | VI     | 17  |                                   | 1  | 3  | 3  | 9  |    |    | 1  |    |    |     | 4.5  |         |        |
|                                   | VII    | 10  |                                   |    |    | 2  | 1  | 2  | 4  |    | 1  |    |     | 6.2  |         |        |
| 1998                              |        |     |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
| <i>P. gunnellus</i> <sup>1</sup>  | I      | 134 | 2                                 | 16 | 46 | 37 | 18 | 9  | 5  | 1  |    |    |     |      | 13.8    | ns     |
|                                   | II     | 47  | 1                                 | 12 | 14 | 8  | 7  | 1  | 1  | 2  | 1  |    |     |      | 13.7    |        |
|                                   | III    | 12  |                                   | 3  | 2  | 3  | 1  | 1  | 2  |    |    |    |     |      | 14.1    |        |
|                                   | IV     | 3   |                                   |    | 1  | 1  |    |    | 1  |    |    |    |     |      | 14.7    |        |
| <i>C. maculatus</i> <sup>1</sup>  | I      | 18  |                                   |    |    |    |    |    |    | 3  | 6  | 5  | 4   |      | 19.6    | ns     |
|                                   | II     | 12  |                                   |    |    |    |    |    |    |    | 4  | 6  | 2   |      | 20.0    |        |
|                                   | III    | 10  |                                   |    |    |    |    |    |    | 1  | 3  | 6  |     |      | 19.5    |        |
|                                   | IV     | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
| <i>Ammodytes</i> sp.              | I      | 72  |                                   |    |    |    | 5  | 16 | 22 | 15 | 4  | 4  | 6   |      | 7.7     | ns     |
|                                   | II     | 9   |                                   |    |    |    |    | 3  |    | 1  | 1  | 2  | 2   |      | 8.9     |        |
|                                   | III    | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
|                                   | IV     | 1   |                                   |    |    |    |    |    |    |    |    | 1  |     |      | 10.0    |        |
| <i>H. americanus</i> <sup>1</sup> | I      | 8   |                                   | 1  |    | 4  | 1  | 1  | 1  |    |    |    |     |      | 14.5    | III>I  |
|                                   | II     | 15  |                                   |    | 1  |    | 3  | 3  | 4  | 1  | 2  | 1  |     |      | 16.7    |        |
|                                   | III    | 5   |                                   |    |    |    |    |    | 3  | 1  |    | 1  |     |      | 17.8    |        |
|                                   | IV     | 2   |                                   |    |    |    |    |    |    |    |    |    | 2   |      | 23.0    |        |
| <i>L. coheni</i>                  | I      | 19  |                                   |    |    |    | 4  | 3  | 4  | 1  | 1  | 6  |     |      | 7.5     | II>I   |
|                                   | II     | 7   |                                   |    |    |    |    |    |    | 1  |    |    | 6   |      | 11.0    |        |
|                                   | IV     | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
|                                   | V      | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
|                                   |        |     |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
| <i>M. aeneus</i>                  | I      | 22  |                                   |    |    |    | 2  | 15 | 5  |    |    |    |     |      | 6.1     | ns     |
|                                   | II     | 9   |                                   |    |    |    | 4  | 4  |    |    | 1  |    |     |      | 5.9     |        |
|                                   | III    | 2   |                                   |    |    |    |    | 1  | 1  |    |    |    |     |      | 6.5     |        |
|                                   | V      | 2   |                                   |    |    |    | 1  | 1  |    |    |    |    |     |      | 5.5     |        |
| <i>M. octodecimspinosus</i>       | I      | 200 |                                   |    |    |    |    | 1  | 12 | 46 | 45 | 40 | 56  |      | 9.6     | II>I   |
|                                   | II     | 16  |                                   |    |    |    |    |    | 2  | 1  | 2  |    | 11  |      | 10.4    |        |
|                                   | III    | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
|                                   | IV     | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
| <i>M. scorpius</i>                | I      | 38  |                                   |    |    |    |    | 1  |    | 1  |    | 6  | 30  |      | 11.5    | II>I   |
|                                   | II     | 13  |                                   |    |    |    |    |    |    |    |    |    | 13  |      | 14.0    |        |
|                                   | VI     | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |
|                                   | VII    | 0   |                                   |    |    |    |    |    |    |    |    |    |     |      |         |        |

<sup>1</sup> scale + 10 mm.

were examined in detail (Table 5). Relative abundances of fishes changed over the course of the study in both 1997 and 1998 (Fig. 3). Three factors (species assemblages) were retained from the PCA of the relative abundance matrices

in each year. In 1997, MANOVA and *post hoc* comparisons of mean factor scores indicated a significant temporal effect on factors 1 and 2 (Wilk's lambda=0.198,  $P<0.0001$ ). Values for taxa that were most abundant in June (*E. cim-*



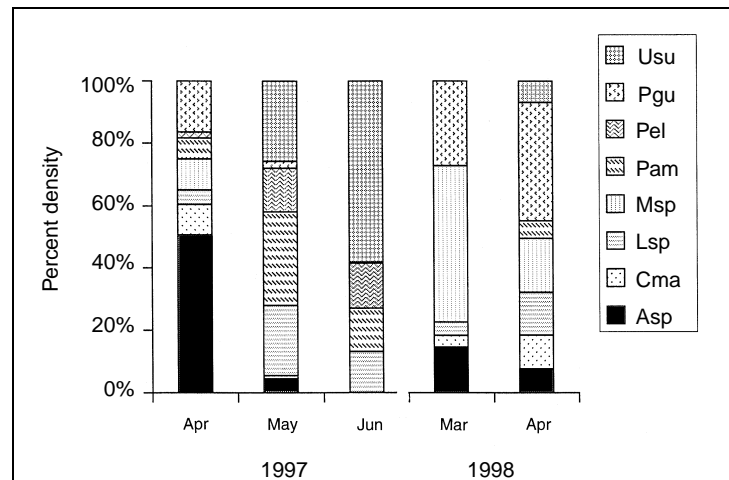
**Table 5**

Product-moment correlations between principal component scores and the angularly transformed relative abundances of larval fishes. Underlined values significant at  $P < 0.05$ , adjusted for multiple comparisons such that  $P < 0.004$  for a significant correlation. Rotated factor 1 explained 36% of the total variance, factor 2 explained 20%, and factor 3 explained 15% in 1997, and rotated factor 1 explained 35% of the total variance, factor 2 explained 28%, and factor 3 explained 11% in 1998.

| Taxon                               | 1997        |             |              | 1998        |             |             |
|-------------------------------------|-------------|-------------|--------------|-------------|-------------|-------------|
|                                     | Factor 1    | Factor 2    | Factor 3     | Factor 1    | Factor 2    | Factor 3    |
| <i>Clupea harengus</i>              |             |             |              | 0.05        | <u>0.51</u> | -0.04       |
| <i>Mallotus villosus</i>            | 0.02        | -0.16       | 0.08         |             |             |             |
| <i>Enchelyopus cimbrius</i>         | <u>0.44</u> | -0.14       | 0.11         |             |             |             |
| <i>Lumpenus lampraetiformis</i>     |             |             |              | -0.07       | 0.34        | 0.02        |
| <i>Ulvaria subbifurcata</i>         | <u>0.97</u> | -0.22       | 0.10         | -0.11       | -0.11       | 0.05        |
| <i>Pholis gunnellus</i>             | -0.22       | <u>0.46</u> | <u>-0.41</u> | <u>0.67</u> | 0.40        | <u>0.58</u> |
| <i>Cryptacanthodes maculatus</i>    | -0.14       | 0.23        | <u>-0.39</u> | <u>0.63</u> | -0.01       | 0.11        |
| <i>Ammodytes</i> sp.                | -0.17       | <u>0.98</u> | 0.05         | 0.06        | <u>0.92</u> | 0.31        |
| <i>Hemitripterus americanus</i>     | -0.15       | <u>0.37</u> | -0.27        | 0.13        | 0.02        | <u>0.73</u> |
| <i>Myoxocephalus aeneus</i>         | -0.12       | <u>0.31</u> | -0.13        | 0.41        | <u>0.58</u> | 0.35        |
| <i>M. octodecimspinosus</i>         | -0.14       | 0.07        | <u>-0.41</u> | <u>0.80</u> | <u>0.58</u> | -0.07       |
| <i>M. scorpius</i>                  |             |             |              | <u>0.56</u> | <u>0.66</u> | 0.17        |
| <i>Liparis atlanticus</i>           | <u>0.39</u> | -0.13       | <u>0.55</u>  | -0.42       | 0.16        | -0.05       |
| <i>L. coheni</i>                    |             |             |              | <u>0.67</u> | 0.10        | 0.40        |
| <i>Pleuronectes americanus</i>      | 0.06        | -0.23       | <u>0.89</u>  | -0.20       | -0.09       | -0.13       |
| <i>Hippoglossoides platessoides</i> | <u>0.48</u> | -0.07       | 0.27         |             |             |             |

*brius*, *H. plattesoides*, *U. subbifurcata*) were uniformly positively correlated with factor 1. Species that were most abundant earlier in the year (*Ammodytes* sp., *H. americanus*, *M. aeneus*, *P. gunnellus*) were positively correlated with factor 2. Values for several species (*C. maculatus*, *M. octodecimspinosus*, and *P. americanus*) were not significantly correlated to either factor 1 or 2, but were correlated to factor 3. In 1998, MANOVA and *post hoc* comparisons of mean factor scores indicated a significant temporal effect on factors 1 and 2 (Wilk's lambda=0.341,  $P < 0.0001$ ). Values for taxa that were more abundant in March (*Ammodytes* sp., *C. maculatus*, *C. harengus*, *L. coheni*, *M. aeneus*, *M. octodecimspinosus*, *M. scorpius*) were uniformly positively correlated with factor 1 or factor 2, or with both factors. Values for *H. americanus* were not significantly correlated to either factor 1 or 2, but were highly correlated to factor 3 as their relative abundances increased in April.

Assemblage composition was similar among sampling locations as indicated by MANOVA of mean factor scores in 1997 and 1998. In 1997, MANOVA (Wilk's lambda=0.985,  $P > 0.10$ ) indicated that means for lower bay, midbay and upper bay sites were not significantly different from each other for any factor. Similarly, MANOVA (Wilk's lambda=0.831,  $P > 0.08$ ) indicated that means for lower estuary and bay sites were not significantly different for any factor in 1998.

**Figure 3**

Percent density (number/100 m<sup>3</sup>) by month of the dominant larval fishes collected with 1.0-m plankton net in Penobscot Bay, Maine, from April to June 1997 and from March to April, 1998. Asp = *Ammodytes* sp., Cma = *Cryptacanthodes maculatus*, Lsp = *Liparis* spp., Msp = *Myoxocephalus* spp., Pam = *Pleuronectes americanus*, Pel = pelagic spp., Pgu = *Pholis gunnellus*, Usu = *Ulvaria subbifurcata*.

CCA revealed significant overall association between factor scores from the PCA of the relative fish abundances and environmental variables in 1997 (Wilk's lambda=0.17,

$P < 0.0001$ ) and 1998 (Wilk's  $\lambda = 0.21$ ,  $P < 0.0001$ ). In 1997, the first canonical correlation (Table 6) indicated that the relative abundance of larval fishes with high positive loading on factor 1 (*E. cimbrius*, *H. plattesoides*, and *U. subbifurcata*) exhibited a positive association with temperature. These taxa also exhibited a weaker negative association with plankton volume and salinity. Fish taxa that loaded positively on factor 2 were negatively associated with temperature and positively associated with plankton volume and salinity. These species included *Ammodytes* sp., *H. americanus*, *M. aeneus*, and *P. gunnellus*. Fish taxa that loaded positively on factor 3 (*L. atlanticus* and *P. americanus*) were positively associated with temperature and were present in every month sampled. In 1998, the first canonical correlation (Table 6) indicated that the relative abundance of larval fishes with high positive loading on factor 1 (*C. maculatus*, *L. coheni*, and *P. gunnellus*) and factor 2 (*Ammodytes* sp., *C. harengus*, and *M. aeneus*) all exhibited a negative association with temperature and a positive association with plankton volume. There was no correlation between factor 3 scores and environmental data for the first canonical correlation (Table 6).

## Discussion

### Species composition

Ichthyoplankton typical of the Gulf of Maine and the Northwest Atlantic was observed in Penobscot Bay: liparids, sculpins (*Myoxocephalus* spp.), *Ammodytes* sp., *P. gunnellus*, *U. subbifurcata*, and *P. americanus*. The dominant species are similar to those previously reported for areas of the Maine coast, including the Sheepscot estuary (Graham and Boyar, 1965; Hauser, 1973; Shaw, 1981), the central Maine coast and estuaries (Chenoweth, 1973), the Damariscotta River estuary (Lee, 1975; Laroche, 1980; 1982; Townsend, 1981; 1984), and Sullivan Harbor (Townsend,

1984). Of the twenty-two species collected in the Damariscotta estuary and 21 species collected in Sullivan Harbor (Townsend, 1984), 17 and 18 of these species, respectively, occurred in Penobscot Bay. The dominant species in these two systems was *P. gunnellus* along with the three species of *Myoxocephalus* and a stichaeid, *Lumpenus lampraetiformis* (Townsend, 1984). Twenty-two kinds of boreal larvae with centers of abundance north of the mid-Atlantic coast were found in the Damariscotta and Sheepscot estuaries and along the central coast of Maine (Chenoweth, 1973), and 18 of these taxa were also found in Penobscot Bay. *Pholis gunnellus*, *Liparis* sp., *C. maculatus*, *L. lampraetiformis*, and Cottidae accounted for 91% of the total catch; the number of larvae declined sharply in spring with the end of the larval stage of these dominant species before reaching a low point in July and August (Chenoweth, 1973). The ichthyoplankton of the St. Lawrence estuary, principally osmerids, gadids, cottids, cyclopterids and pleuronectids, consisted of 25 species (Able, 1978) and 15 of these also occurred in Penobscot Bay.

### Significance of demersal eggs

The ichthyoplankton community of Penobscot Bay is dominated by larvae that hatch from demersal eggs within the estuary, whereas larvae that hatched from pelagic eggs are rare. This finding was first noted for the Mystic River estuary (Pearcy and Richards, 1962) and subsequently for the Sheepscot and Damariscotta estuaries (Chenoweth, 1973). Able (1978) observed that the St. Lawrence estuary was almost exclusively inhabited by larvae that hatched from demersal eggs, primarily cottids, stichaeids, *P. americanus*, and *C. harengus* and that the larvae from pelagic eggs were merely strays from more offshore waters. In all of these areas, larvae that hatched from demersal eggs dominated the catch within the estuary, whereas larvae that hatched from pelagic eggs were more common at the mouth of the estuary or adjacent ocean.

**Table 6**

Canonical correlation coefficients for relative larval fish abundance factor scores and environmental variables in 1997 and 1998. Underlined values significant at  $P = 0.05$ , adjusted for multiple comparisons such that  $P < 0.004$  for a significant correlation.

| Variables                      | 1997                      |                                      | 1998                      |                                      |
|--------------------------------|---------------------------|--------------------------------------|---------------------------|--------------------------------------|
|                                | Standardized coefficients | Correlation with canonical variables | Standardized coefficients | Correlation with canonical variables |
| Larval fish relative abundance |                           |                                      |                           |                                      |
| Factor 1                       | 0.63                      | <u>0.66</u>                          | -0.66                     | <u>-0.65</u>                         |
| Factor 2                       | -0.58                     | <u>-0.61</u>                         | -0.74                     | <u>-0.74</u>                         |
| Factor 3                       | 0.46                      | <u>0.49</u>                          | -0.16                     | -0.09                                |
| Environment                    |                           |                                      |                           |                                      |
| Depth                          | -0.06                     | -0.19                                | 0.24                      | 0.36                                 |
| Plankton                       | -0.02                     | <u>-0.37</u>                         | -0.28                     | <u>-0.82</u>                         |
| Temperature                    | 1.00                      | <u>1.00</u>                          | 0.66                      | <u>0.94</u>                          |
| Salinity                       | 0.07                      | <u>-0.21</u>                         | 0.19                      | 0.37                                 |

The dominant fishes in Penobscot Bay lay demersal and adhesive eggs (Bigelow and Schroeder, 1953). Fourteen of 16 species (87%) of larvae collected in Penobscot Bay in 1998 and 17 of 22 (78%) of the larvae collected in 1997 hatched from demersal eggs. Twenty-two species of larvae were taken in the central coastal area of Maine and a comparatively large number of pelagic-egg species (41%) compared with demersal-egg species, as might be expected in an area strongly influenced by coastal water (Chenoweth, 1973). In upper Sheepscot Bay, 42 species of fish larvae were taken (Shaw, 1981), but this relatively high number reflects the long time series (nine years) of this survey and the inclusion of several coastal species that were rare in the total catch. Even so, these catches were dominated by demersal egg-laying species (76%). In the Damariscotta estuary and Sullivan Harbor, only one of 22 species (<5%) taken as larvae came from pelagic eggs (Townsend, 1981; 1984). The ichthyoplankton of the St. Lawrence estuary were almost exclusively forms from demersal eggs (Able, 1978) and only seven of 25 (28%) larval forms collected came from pelagic eggs. However, pelagic eggs did occur in the St. Lawrence estuary, but these were usually nonresident species, such as *S. scombrus* and *G. morhua*, whose larvae were virtually absent from the upper bay. *Gadus morhua* were very rare in Penobscot Bay and the Sheepscot estuary (Chenoweth, 1973; Shaw, 1981) and were absent from the Damariscotta estuary and Sullivan Harbor (Townsend, 1984). Typically, the abundance of larvae from demersal eggs peaked in the winter–spring period whereas larvae from pelagic eggs peaked in the summer (Chenoweth, 1973).

Egg type has major implications on larval fish ecology. Coastal shelf spawners, such as *G. morhua*, *E. cimbrius*, *H. plattesoides*, and *T. adspersus* lay pelagic eggs that may be dispersed over a wide area by the counterclockwise current flow in the Gulf of Maine (Sherman et al., 1984). Nearshore spawners, such as *P. americanus*, *P. gunnellus*, *Myoxocephalus* spp., *U. subbifurcata*, and *C. harengus* lay demersal eggs and depend on protected areas of the coastline for nursery areas. Larvae that hatch from demersal eggs are less likely to be transported out of their nearshore nursery grounds, rather they are entrained in the landward moving bottom layer (Pearcy and Richards, 1962; Norcross and Shaw, 1984).

### Variation in distribution and abundance

Larval fish assemblage composition in Penobscot Bay varied considerably over time but not among sampling locations. Interannual and monthly differences in both species composition and abundance of ichthyoplankton in the bay appeared to be associated with differences in environmental conditions, particularly with temperature. Temporal patterns of larval fish abundance corresponded with seasonality of reproduction (Bigelow and Schroeder, 1953). Larvae that hatched from demersal eggs from late winter through early spring, such as *Myoxocephalus* spp., *Ammodytes* sp., and *Pholis gunnellus*, were abundant in Penobscot Bay in March and April and gradually their numbers in plankton samples declined. Such a spawning pattern

suggests that adults use the bay and nearshore areas for an extended period of time. Larvae of taxa that hatch later in spring such as *P. americanus*, *L. atlanticus* and *U. subbifurcata*, were abundant in Penobscot Bay in May and June.

These results suggest that temperature is the principal factor controlling the temporal occurrence of fish larvae in Penobscot Bay. Temperature is a primary factor associated with the occurrence and distribution of young stages of fish inhabiting temperate and cold oceans (Obenchain, 1981; Frank and Leggett, 1982; Laprise and Pepin, 1995). This association may be critical in ecosystems characterized by a short growing season (Conover, 1992). However, the influence of temperature on larval occurrence no doubt resulted from species-specific responses of spawning adults. The late winter–early spring species, such as *Myoxocephalus* spp., *Ammodytes* sp., and *Pholis gunnellus*, had a negative association with temperature, whereas late-spring spawners, such as *P. americanus*, *L. atlanticus*, and *U. subbifurcata*, had a positive association. The synchronous emergence of the larvae of several species of fishes in the planktonic environment may be a strategy to further reduce predation (Frank and Leggett, 1983) regardless of temperature. The association observed in this study between salinity and ichthyoplankton may be artificial. Although the influences of temperature and salinity could not be separated, it seems unlikely that the minute differences in salinity observed between samples would greatly affect marine animals.

Penobscot Bay plays an important role in the early life history of fish inhabiting the central coast of Maine by offering favorable habitat for ichthyoplankton. A hydrographic front off of Penobscot Bay separates the coastline into two different hydrographic regimes (Bigelow, 1927). West of Penobscot Bay, a combination of increased runoff and reduced tidal mixing, favors more rapid development of vertical stratification in spring and summer. East of Penobscot Bay, tidal mixing is enhanced and the development of vertical stratification is much reduced throughout the summer months. Vertical stability of the water column is controlled more by salinity stratification than by temperature, and peaks of stability are the result of influxes of low-salinity surface waters (Townsend, 1984). Therefore, the peak in abundance of both phytoplankton and zooplankton occurs earlier in the western Gulf of Maine and gradually spreads to the east with the onset of vertical stratification during spring and summer (Bigelow, 1927).

Marine fishes may be categorized as those that use the estuaries, such as Penobscot Bay, as primary spawning and nursery areas and those that do not. Winter–early-spring spawning species (*P. gunnellus*, *Ammodytes* sp., *H. americanus*, *Myoxocephalus* spp.) belong to the first group of resident demersal fishes whose larvae hatch from demersal eggs and use the bays and estuaries as nursery areas. Typically, these larvae disappear from collections in April and May. Two species that spawn in late spring, *P. americanus* and *U. subbifurcata*, also use Penobscot Bay as a spawning and nursery habitat and have areas of greatest larval abundance in the midbay and lower bay, respectively. The larvae of *E. cimbrius*, *G. morhua*, *T. adspersus*, *S. scombrus* and *H. plattesoides*, although present,

were not abundant in spring and early summer; therefore Penobscot Bay does not appear to be a primary nursery area for these species. Possibly the numbers of spawning adults of these species are low in the bay or the pelagic eggs that they produce are dispersed before hatching, or both the number of spawning adults are low and the pelagic eggs they produce are dispersed before hatching. Penobscot Bay appears to act as a nursery for many fishes; therefore degradation of water quality during the vernal period would have wide reaching effects on the nearshore fish community.

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## Literature cited

- Able, K. W.  
1978. Ichthyoplankton of the St. Lawrence estuary: composition, distribution and abundance. *J. Fish. Res. Board Can.* 35:1518–1531.
- Bigelow, H. B.  
1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, vol. XL, 1924, part II, 509 p.  
1927. Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.* 40:511–1027.
- Bigelow, H. B., and W. C. Schroeder.  
1953. Fishes of the Gulf of Maine. *U.S. Fish and Wildl. Serv. Fish. Bull.* 53(74), 477 p.
- Chenoweth, S. B.  
1973. Fish larvae of the estuaries and Coast of central Maine. *Fish. Bull.* 71(1):105–113.
- Conover, D. O.  
1992. Seasonality and the scheduling of life history at different latitudes. *J. Fish Biol.* 41 (suppl. B):161–178.
- Cushing, D. H.  
1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge, England, 278 p.
- Day, R. W., and G. P. Quinn.  
1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59:433–463.
- Fish, C. J., and M. W. Johnson.  
1937. The biology of the zooplankton in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *J. Biol. Board Can.* 3:189–322.
- Frank, K. T., and W. C. Leggett.  
1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator-prey complex associated with larval capelin (*Mallotus villosus*). *Can. J. Fish. Aquat. Sci.* 39:991–1003.  
1983. Multispecies larval fish associations: accident or adaptation? *Can. J. Fish. Aquat. Sci.* 40:754–762.
- Gauch, H. G.  
1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge, England, 298 p.
- Graham, J. J.  
1972. Retention of larval herring within the Sheepscot estuary of Maine. *Fish. Bull.* 70 (2):299–305.
- Graham, J. J., and H. C. Boyar.  
1965. Ecology of herring larvae in the coastal waters of Maine. International Commission for the Northwest Atlantic Fisheries (ICNAF) Spec. Publ. 6:625–634.
- Haefner, P. A.  
1967. Hydrography of the Penobscot Bay (Maine) estuary. *J. Fish. Res. Board Can.* 24:1553–1571.
- Hauser, W. J.  
1973. Larval fish ecology of the Sheepscot River-Montsweag Bay estuary, Maine. PhD. diss., Univ. Maine, Orono, ME, 79 p.
- Hjort, T. J.  
1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Rapp. P.-V. Cons. Perm. Int. Explor. Mer* 20, 228 p.
- Laprise, R., and P. Pepin.  
1995. Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically dynamic coastal environment. *Mar. Ecol. Prog. Ser.* 122:73–92.
- Laroche, J. L.  
1980. Larval and juvenile abundance, distribution, and larval food habits of the larvae of five species of sculpins (Family: Cottidae) in the Damariscotta River estuary, Maine. PhD. diss., Univ. Maine, Orono, ME, 169 p.  
1982. Trophic patterns among larvae of five species of sculpins (Family: Cottidae) in a Maine estuary. *Fish. Bull.* 80:827–840.
- Lee, W. Y.  
1975. Succession and some aspects of population dynamics of copepods in the Damariscotta River estuary, Maine. PhD. diss., Univ. Maine, Orono, ME, 181 p.
- Leggett, W. C., and E. Deblois.  
1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg larval stages? *Neth. J. Sea Res.* 32:119–134.
- Marak, R. R.  
1960. Food habits of larval cod, haddock and coalfish in the Gulf of Maine and Georges Bank area. *J. Cons. Int. Explor. Mer* 25:147–157.
- Marak, R. R., and J. B. Colton Jr.  
1961. Distribution of fish eggs and larvae, temperature and salinity in the Georges Bank, Gulf of Maine area, 1953. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish.* 398, 61 p.  
1962. Distribution of fish eggs and larvae, temperature and salinity in the Georges Bank, Gulf of Maine area, 1956. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish.* 411, 66 p.
- Norcross, B. L., and R. F. Shaw  
1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Trans. Am. Fish. Soc.* 113(2):153–165.
- Obenchain, C. L.  
1981. A study of the larval fish community in the New York Bight, July 1974 to June 1976. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 178:217–219.
- Pearcy, W. G., and S. W. Richards.  
1962. Distribution and ecology of fishes of the Mystic River, Connecticut. *Ecology* 43(2):248–259.
- Pielou, E. C.  
1984. The interpretation of ecological data. John Wiley and Sons, New York, NY, 286 p.

Shaw, R.

1981. Seasonal species composition, diversity, spatial distributions and tidal retention and transport of ichthyoplankton in the Sheepscot River-Back River-Montsweag Bay estuary system, Maine. PhD. diss., Univ. Maine, Orono ME, 285 p.

Sherman, K.W., W. Smith, W. Morse, and M. Berman.

1984. Spawning strategies of fishes in relation to circulation, phytoplankton production and pulses in zooplankton off the northeast United States. *Mar. Ecol. Prog. Ser.* 18:1-19.

Sokal, R.R., and F. J. Rohlf.

1981. *Biometry*. W. H. Freeman and Company, New York, NY, 859 p.

Stevens, J.

1986. *Applied multivariate statistics for the social sciences*. Lawrence Erlbaum and Associates, Hillsdale, NJ, 341 p.

Townsend, D.W.

1981. Comparative ecology and population dynamics of larval fishes and zooplankton in two hydrographically different areas on the Maine coast. PhD. diss., Univ. Maine, Orono, ME, 282 p.

1983. The relations between larval fishes and zooplankton in two inshore areas of the Gulf of Maine. *J. Plankton Res.* 5(2):145-173.

1984. Comparison of inshore zooplankton and ichthyoplankton in the Gulf of Maine. *Mar. Ecol. Prog. Ser.* 15: 79-90.