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The structure of the larval fish assemblage of Massachusetts Bay in 2008–2012 and 2015–2022

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Abstract—Ichthyoplankton samples were collected monthly at 2 stations in Massachusetts Bay from 2008 to 2012 and from 2015 to 2022 to characterize the larval fish assemblage for this area. The fauna was composed of 2 major assemblages that were 87% dissimilar from each other and associated with season and water temperature. A cold-water assemblage of low density (43.26 larvae/1000 m^3) occurred from November through May at mean water column temperatures between 4.1°C and 10.3°C, with sand lances (*Ammodytes* spp.) the dominant taxon as a group. A warm-water assemblage of higher density (432.58 larvae/1000 m^3) occurred from June through October at mean water column temperatures between 12.3°C and 16.1°C, with the silver hake (*Merluccius bilinearis*) the dominant taxon. Within the cold-water assemblage, statistically distinct groups occurred in November, December–March, and April–May. The Atlantic herring (*Clupea harengus*), sand lances, and the American plaice (*Hippoglossoides platessoides*) were the dominant taxa in those periods, respectively. Within the warmwater assemblage, statistically distinct groups occurred in June–August and September–October, with the cunner (*Tautogolabrus adspersus*) and true hakes as a group (*Urophycis* spp.) the dominant taxa in those periods, respectively. Water temperature explained 28% of the annual variation in the cold-water assemblage, and there was no significant relationship between temperature and annual variation in the warmwater assemblage. This larval fish characterization provides a baseline against which potential changes in the assemblages in this area can be measured.

Sampling the early life stages of fish can further our understanding of changes in variability in fish stock sizes and catch (Llopiz et al., 2014), as well as provide a characterization of baseline conditions for environmental assessments. Such data are often used to characterize areas that may be important in supporting fish stocks by providing habitats for fish eggs and larvae. Long-term datasets are preferable because data can be integrated over time and the influence of a few potentially anomalous years or seasons (i.e., interannual variability) can be minimized. Long-term monitoring programs also provide the data necessary for resource management and for descriptions of population abundance and community composition on both temporal and spatial scales (McClatchie et al., 2014). Data from a monitoring program with intensive temporal sampling can be used to accurately describe changes over time in the region sampled and provide an important benchmark against which potential changes can be measured.

Regional ichthyoplankton sampling in the continental shelf system of the northeastern United States has been conducted since the 1970s to understand broad-scale changes in the system's oceanography and plankton community. The Marine Resources Monitoring, Assessment, and Prediction Program and the Ecosystem Monitoring (EcoMon) program, both of the National Marine Fisheries Service, have provided valuable data on the seasonality and species composition of the larval fish assemblage on the northeastern U.S. shelf and in the Gulf of Maine. Using these data, Walsh et al. (2015) found that some fish larval distributions in the Gulf of Maine and Georges Bank shifted to offshore and shallower regions. Although these data are valuable in understanding the broad, long-term changes in the larval fish assemblage in this area, the spatiotemporal sampling frequencies of the surveys of these programs do not provide the fine-scale sampling frequency needed to understand local seasonal (or temporal) changes in the larval fish assemblage of Massachusetts Bay.

Sampling at a spatial scale finer than those of these programs has occurred in the larger Gulf of Maine system. Runge and Jones (2012) sampled 2 stations in Massachusetts Bay, 1 station

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in Ipswich Bay, and 4 nearby stations off the coasts of New Hampshire and southern Maine, usually 3 times per month in 2007 and 2008. The ichthyoplankton of Cape Cod Bay was monitored monthly from 1974 to 1976 as part of the Pilgrim Power Station monitoring program (Scherer, 1984). Chenoweth (1973), Townsend (1983, 1984), and Lazzari (2001) reported on the ichthyoplankton assemblages in inshore areas along the coast of Maine north and east of Massachusetts Bay. However, despite their finer scale, these examinations did not produce time series necessary to understand local seasonal changes in the larval fish assemblage of Massachusetts Bay.

We conducted ichthyoplankton monitoring monthly from 2008 to 2012 and from 2015 to 2022 to assess the potential effects of the operation of an offshore liquified natural gas regasification facility in Massachusetts Bay. Data from this program, collected over 13 years at a level of temporal detail not previously available, provide a description of the seasonality and structure of the larval fish assemblage in Massachusetts Bay at the start of the 21st century.

Materials and methods

Field procedures

Ichthyoplankton sampling was conducted in the central part of Massachusetts Bay about 22 km south of Gloucester, Massachusetts, and about 30 km east of Boston, Massachusetts, at 2 stations for 13 years from 2008 to 2012 and from 2015 to 2022 (Fig. 1, Suppl. Table 1). Massachusetts Bay is an embayment of the western Gulf of Maine, generally south of Gloucester and west of Stellwagen Bank. To the south, Massachusetts Bay merges into Cape Cod Bay. There is a weak counterclockwise flow in Massachusetts Bay with a residence time for surface water of 20–45 d (Geyer et al., 1992). The water column is usually stratified from April through October and well-mixed in the winter (Leo et al.[1]). The maximum depth in Massachusetts Bay is about 90 m in Stellwagen Basin.

From 2008 to 2012, sampling was typically conducted twice per month. From 2015 to 2022, sampling typically occurred twice per month in January, February, and December and once per month from March through November. On each sampling date, 3 samples were collected during both night and day; night was defined as more than 2 h after sunset to more than 2 h before sunrise and day was defined as more than 2 h after sunrise to more than 2 h before sunset. Generally, 6 samples were collected on each sampling date (3 samples in each of 2 periods). Each sample consisted of an oblique tow through the water column from near bottom to the surface with a target volume of 1000 m^3. The collection gear was a conical ring net equipped with a calibrated flowmeter. The net had a mesh size of 0.33 mm and a diameter of 1.0 m at the mouth, with a 4:1 ratio of length to mouth opening. Equipped with a swivel and a depressor hanging from the swivel, the net was towed off the stern quarter of the boat with a bridle in front of the net. Flowmeter readings before and after deployment were recorded to estimate the volume of water filtered by the net. Samples were preserved in 5%–10% buffered formalin for later identification of organisms. Coincident with ichthyoplankton sampling, water depth was recorded and temperature data were collected at depths of <0.5 m (surface), 0.5–2.5 m (near surface), 9.0–16.0 m (mid-depth), and 18.0–24.0 m (near bottom).

Laboratory procedures

All larvae were identified to the lowest practical taxon, usually to species, and enumerated. Primary references used for identifications were Jones et al. (1978), Elliott and Jimenez (1981), Richards (2005), and Fahay (2007). Because of morphometric similarities, some taxa were grouped to genus. Red hake (*Urophycis chuss*), white hake (*U. tenuis*), and spotted hake (*U. regia*) were grouped together as true hakes (*Urophycis* spp.). Similarly, American sand lance (*Ammodytes americanus*) and northern sand lance (*A. dubius*) were grouped as sand lances (*Ammodytes* spp.). Nomenclature followed Page et al. (2023), and a list of the taxa used, with common and scientific names and months of occurrence, is presented in Supplementary Table 2.

For taxa with clearly defined developmental stages, individuals were assigned to the appropriate life stage, such as egg, yolk-sac larvae, post-yolk-sac larvae, young of the year, and yearling or older. Yolk-sac and post-yolk-sac larvae were the focus of our analysis for this study and hereafter are referred to as *larvae*. Yolk-sac larvae ranged from hatchlings to individuals with a complete and functional digestive system. Post-yolk-sac larvae included individuals after the yolk sac stage up to transformation to the young-of-the-year form, which included a full complement of fin rays.

For quality control, 10% of samples (randomly selected out of batches of 10 samples) were reexamined to ensure that a minimum of 95% of the ichthyoplankton individuals were removed. For taxonomic quality control, a randomly selected 10% of samples were reanalyzed by a senior taxonomist to ensure a minimum taxonomic efficiency of 95%. Data quality control followed procedures in Geoghegan (1996). Data were subject to univariate and multivariate error checking routines and then audited against original field and laboratory data sheets.

Data analysis

Temporal patterns in the overall composition of larval fish assemblages in the sampling area were examined through multivariate analyses performed by using functions

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[1] Leo, W., R. Geyer, and M. Mickelson. 2003. Physical and biological oceanography of Massachusetts Bay. *In* Briefing for OMSAP workshop on ambient monitoring revisions, June 18–19, 2003. Environ. Qual. Dep. Rep. 2003-ms-085, p. 4-1–4-21. Mass. Water Resources Auth., Boston, MA. [Available from website.]

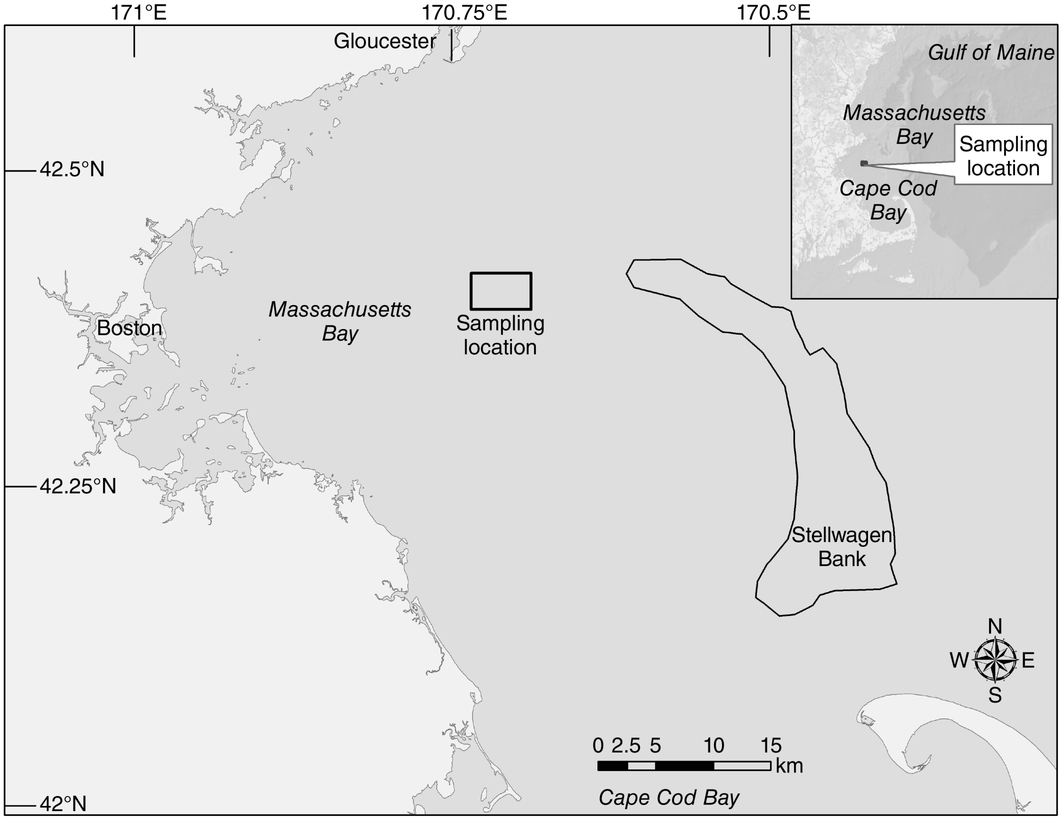

Figure 1

Map of Massachusetts Bay showing the location of ichthyoplankton sampling in 2008–2012 and 2015–2022. Fish larvae were sampled at 2 stations in an area about 22 km south of Gloucester, Massachusetts, and 30 km east of Boston, Massachusetts. Background mapping data are from Esri and MassGIS.

within the R package vegan (vers. 2.6-2; Oksanen et al., 2022) in R (vers. 4.2.1; R Core Team, 2022). The species-specific densities for larvae captured in each collection, measured as the number of larvae per 1000 m^3, were $\log_{10}(x+1)$ transformed to ensure that all taxa regardless of catch magnitude could contribute to similarity measures. Results are considered statistically significant if the P-value is less than 0.05. The average transformed density (geometric mean) for each month of each year of this study was determined, and these values were used to calculate a dissimilarity matrix by using the Bray–Curtis dissimilarity index (Bray and Curtis, 1957). Values of the Bray–Curtis index range from 0% for absolute similarity to 100% for absolute dissimilarity. We used Bray–Curtis index values to perform hierarchical clustering using the unweighted pair group method (Sokal and Michener, 1958) to visualize potential seasonal (across-months) groupings for each year in the study.

These multivariate analyses were originally performed for all years combined to visualize the integrated monthly patterns in the larval community. Then they were performed separately for each year to visualize if the monthly patterns found in the multiyear analyses also occurred in individual years. Using observed $\log_{10}$(density+1) values, each for a given species in a particular month and year of this study, we calculated means for each species in each month and year. These species-specific means for each month were averaged across all years to get species-specific grand means for each month, and these grand means were used to calculate Bray–Curtis indices between months. The hierarchical clustering described in the previous paragraph was used to reveal the levels of dissimilarity for larval fish assemblages characterized by the monthly grand means.

A similarity profile permutation test was used to determine the significant groups within the cluster dendrogram of the larval fish assemblages for each month (Clarke et al., 2008). At each dendrogram node (starting with the least similar), 1000 permutations of the samples were used to calculate similarities used to represent the distribution of the similarity profile under the hypothesis of no multivariate structure within the samples. If the null hypothesis was rejected ($P<0.01$, to account for multiple tests) for the actual observed similarity profile, the process was repeated at the next lower (more similar) node until the null hypothesis could not be rejected.

Logical contiguous groupings determined from the results of the annual cluster analyses were visualized by using nonmetric multidimensional scaling ordination to produce plots in which the distance between samples represented rank ordered similarities with closer proximity in the plot representing higher similarity. Stress metrics were used as a measure of adequacy of the representation of similarities in the ordination plot. Stress levels ≥0.1 and <0.2 provide an adequate representation but should be evaluated in conjunction with the dendrogram based on Bray–Curtis index values (Clarke and Warwick, 2001). Together, results from the cluster analysis and nonmetric multidimensional scaling ordination provide insight into the similarity among samples at the community level. Similarity percentage analysis (Clarke, 1993; Clarke and Warwick, 2001) was used to determine the contribution of each species to the average Bray–Curtis index between the major ichthyoplankton assemblages identified as groups in the dendrogram from cluster analysis. Larval densities were back-transformed to the arithmetic scale for presentation in tables as geometric mean densities of larvae for months and years, and group means were identified by numerical classification.

Mean temperatures in the upper 2.5 m of the water column (surface and near surface temperatures) were averaged with mid-depth and near-bottom temperatures to estimate water column temperature (hereafter referred to as *water temperature*). Monthly average water temperatures were calculated from values for each depth strata sampled each month. The overall mean water temperature (for all years combined) for a given month was calculated as the mean of the averages for that month. Mean monthly water temperatures were compared between the 2 sampling periods, 2008–2012 and 2015–2022, by using paired *t*-tests. Results of these 2-sample *t*-tests and correlations between water temperature and occurrence of larval taxa are considered statistically significant if the *P*-value is less than 0.05.

Distance-based redundancy analysis was employed to explore the relationship between water temperature and larval fish community composition (Legendre and Anderson, 1999). This examination acts as a version of principle component analysis in which Bray–Curtis dissimilarities are constrained by the linear relation to water temperature and provides a measure of the variation in larval fish community attributed to water temperature. A permutation test similar to an analysis of variance was used to determine the significance of the level of explained variation.

Results

Water temperature

Mean water temperature followed a monthly pattern in which it was highest in August and September and lowest in February and March (Table 1). The difference of 0.3°C in water temperatures between periods (2008–2012 and 2015–2022) is significant (P=0.036). There was no significant difference in mean water temperature for any month between 2008–2012 and 2015–2022, according to the results of the 2-sample *t*-tests. The maximum differences in mean monthly water temperatures occurred in January and July, when mean temperatures were 1.0°C and 0.8°C warmer in 2015–2022.

Table 1

Mean monthly water column temperatures in Massachusetts Bay during 2008–2012 and 2015–2022. Also provided are the *P*-values from the paired *t*-test used to compare mean temperatures between the 2 sampling periods. The significance level for this test is 0.05.

Month	Mean temperature (°C) 2008–2012	Mean temperature (°C) 2015–2022	Difference (°C)	*P*-value
January	4.9	6.0	1.0	0.17
February	3.8	4.3	0.4	0.36
March	4.2	4.2	0.0	0.94
April	6.4	6.5	0.1	0.84
May	8.9	9.2	0.2	0.78
June	12.5	12.2	–0.3	0.61
July	14.0	14.8	0.8	0.20
August	15.5	16.1	0.6	0.35
September	16.0	16.2	0.1	0.80
October	13.4	13.6	0.1	0.85
November	10.4	10.1	–0.3	0.63
December	8.0	8.3	0.3	0.60
All months	9.8	10.1	0.3	0.04

Larval fish assemblages

The 2 major larval assemblages apparent in the Bray–Curtis dendrogram are 87% dissimilar with all years combined (Table 2, Fig. 2). The density of the cold-water assemblage that occurred in November–May at mean monthly water temperatures from 4.1°C (in February) to 10.3°C (in November) (43.26 larvae/1000 m^3; Table 2) was lower than the density of the warmwater assemblage that occurred in June–October at mean monthly water temperatures from 12.3°C (in June) to 16.1°C (in September) (432.58 larvae/1000 m^3; Table 2). The cold-water assemblage was dominated by sand lances, Atlantic cod (*Gadus morhua*), and American plaice (*Hippoglossoides platessoides*). The warmwater assemblage was dominated by silver hake (*Merluccius bilinearis*), true hakes, and cunner (*Tautogolabrus adspersus*). None of the 5 most abundant taxa in either assemblage were among the 5 most abundant taxa in the other assemblage, confirming the degree of dissimilarity between assemblages.

Among the abundant taxa in the cold-water and warmwater assemblages, the silver hake (12%), true hakes (11%), and the cunner (8%) contributed most to the total dissimilarity (87%) between major assemblages (Table 2). These taxa were found almost exclusively in the

Table 2

Geometric mean density of fish larvae captured in the 2 major assemblages associated with season and water column temperature in Massachusetts Bay during 2008–2012 and 2015–2022. The cold-water assemblage occurred in November–May at mean temperatures of 4.1°C–10.3°C, and the warmwater assemblage occurred in June–October at mean temperatures of 12.3°C–16.1°C. Also provided for each taxon are the mean contribution to the Bray–Curtis dissimilarity index, the ratio of that mean contribution to the standard deviation of that mean, the contribution to total dissimilarity, and the *P*-value from the similarity percentage analysis. Values are provided for the abundant taxa that made statistically significant ($P<0.05$) contributions to the total dissimilarity between the 2 assemblages. Asterisks denote the 5 highest densities in each assemblage.

	Mean density (larvae/1000 m^3)					
Taxon	Cold-water assemblage	Warmwater assemblage	Mean contribution to dissimilarity	Ratio	Contribution to total dissimilarity (%)	*P*-value
American plaice	2.23*	3.64	0.03	1.06	3.90	1.00
Atlantic cod	7.75*	0.75	0.04	1.25	4.28	0.18
Atlantic herring	2.00*	1.29	0.03	0.94	3.89	1.00
Cunner	0.09	58.07*	0.07	1.28	7.98	0.01
Fourbeard rockling	0.72	42.20*	0.07	2.99	7.65	0.01
Pollock	3.33*	0.06	0.03	1.10	3.48	0.94
Sand lances	21.77*	0.00	0.06	1.26	7.20	0.69
Silver hake	0.08	184.78*	0.11	4.54	12.01	<0.01
True hakes	0.04	103.90*	0.10	2.39	11.08	<0.01
Yellowtail flounder	0.60	12.25*	0.05	1.58	5.17	0.05
All other taxa	4.65	25.64	–	–	–	–
Total (all taxa)	43.26	432.58	–	–	87.40	–

warmwater assemblage. The relatively high ratio of mean contribution to dissimilarity to the standard deviation of that mean indicates that these taxa were consistently influential in identifying assemblages.

The cold-water and warmwater assemblages were present in every year of the study (Fig. 3). The cold-water assemblage started to occur as early as October in 2008, 2012, and 2016 (at water temperatures of 12.6°C–15.2°C) and as late as December in 2009, 2011, 2015, and 2020–2022 (at water temperatures of 7.3°C–9.8°C). In 2020 and 2021, the cold-water assemblage may have begun to occur in November, but no sampling was done that month in either year. The warmwater assemblage started to occur as early as April in 2016 and 2018 (at water temperatures of 6.2°C–6.4°C) and as late as June in 2011, 2015, 2017, and 2020–2022 (at water temperatures of 9.3°C–13.6°C). In 2022, the warmwater assemblage may have begun to occur in May, but no sampling was done that month.

There were 5 statistically significant seasonal groups of fish larvae within the 2 major assemblages when all larval data were combined (Figs. 2 and 3). Three groups occurred within the cold-water assemblage: group 1 in November (at a water temperature of 10.3°C), group 2 in December–March (at water temperatures of 4.1°C–8.2°C), and group 3 in April and May (at water temperatures of 6.5°C–9.1°C). Group 1 was dominated by Atlantic herring (*Clupea harengus*) and occurred in the years 2015, 2017, and 2022, when larval Atlantic herring were present at high mean densities (45.32 larvae/1000 m^3; Table 3). Group 2 was dominated by sand lances and Atlantic cod and occurred in every year. A transitional group between the cold-water and warmwater assemblages, group 3 occurred in April and May in each of the years 2009–2011 and in 2018, when the American plaice was the dominant taxon.

Two high-density groups occurred within the warmwater assemblage: group 4 in June–August (at water temperatures of 12.3°C–15.9°C), with a density of 1448.29 larvae/1000 m^3, and group 5 in September and October (at water temperatures of 13.5–16.1°C), with a density of 177.63 larvae/1000 m^3 (Figs. 2 and 3, Table 3). Group 4 was dominated by cunner, silver hake, and true hakes and occurred every year. A transitional group between the warmwater and cold-water assemblages, group 5 occurred in 2009 and 2018. True hakes and silver hake were also dominant in group 5 but at lower densities than they were found in group 4.

Groups 2 and 4 (which occur in December–March and June–August, respectively) form the core of the major cold-water and warmwater assemblages because they were present in every year (Fig. 3). Cunner, silver hake, and true hakes contributed significantly and most to the 95% dissimilarity between these groups (Table 4). These taxa were the 3 most abundant in group 4 and occurred at lower densities in group 2 (Table 3).

The nonmetric multidimensional scaling plot confirms the strong seasonal pattern evident in the Bray–Curtis dendrogram (Fig. 4). Group 1 (which occurs in November) appears at the bottom center of the nonmetric multidimensional scaling plot, and the months cycle counterclockwise around the plot, emphasizing the seasonal component of the larval assemblages. Some overlap in the nonmetric multidimensional scaling plot occurs among groups

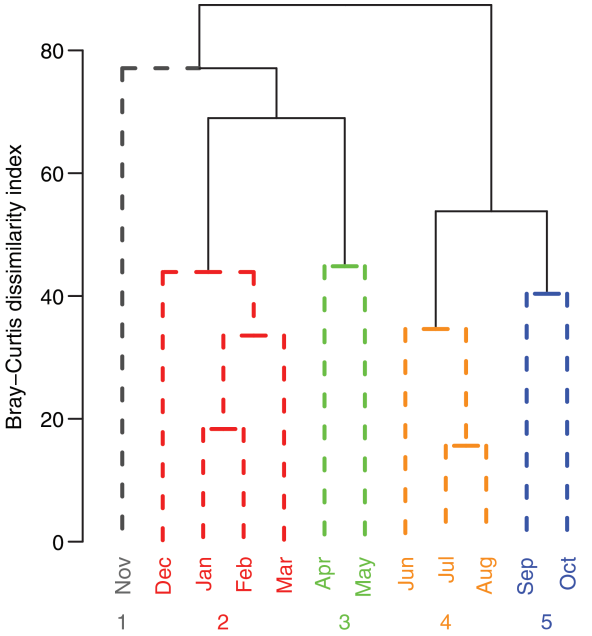

Figure 2

Dendrogram of the 5 statistically distinct seasonal groups of larval fish within the 2 major assemblages in Massachusetts Bay during 2008–2012 and 2015–2022, identified through cluster analysis with Bray–Curtis dissimilarity index values. Solid lines designate statistically distinct groups, and dashed lines indicate groups that are not statistically distinct. Numerals at the bottom of the figure indicate the groups, which are based on temporal changes in the cold-water assemblage (groups 1–3) and warmwater assemblage (groups 4 and 5). The cold-water assemblage occurred in November–May at mean temperatures of 4.1°C–10.3°C, and the warmwater assemblage occurred in June–October at mean temperatures of 12.3°C–16.1°C. Mean monthly densities for taxa were used to calculate Bray–Curtis dissimilarity index values.

identified in the Bray–Curtis dendrogram (Fig. 2). The least amount of overlap between adjacent groups occurs between groups 1 and 2, confirming the 73% Bray–Curtis dissimilarity between these groups (Fig. 2). Similarly, the overlap between adjacent groups 3 and 4, which form a boundary between the major cold-water and warmwater assemblages, is minimal (72% dissimilarity). Groups 1 and 5 also had minimal overlap (65% dissimilarity), and these groups are boundaries between the warmwater and cold-water assemblages.

The results of distance-based redundancy analysis indicate that the variation in composition of the cold-water assemblage (which occurs in November–May) was significantly, but weakly, correlated with mean water temperature (coefficient of correlation=0.28, P=0.011). No significant correlation was found between water temperature and the variation in composition of the warmwater assemblage (which occurs in June–October). The silver hake, Atlantic herring, and witch flounder (*Glyptocephalus cynoglossus*) were the taxa with the highest significant positive correlation between mean density and mean water temperature (Table 5, Figs. 5 and 6). However, the 10 years with no catch of witch flounder and the 3 years of relatively large catches of witch flounder strongly influenced the positive relationship for this taxon. Densities of Atlantic wolffish (*Anarhichas lupus*), wrymouth (*Cryptacanthodes maculatus*), and snakeblenny (*Lumpenus lampretaeformis*) were negatively correlated with water temperature (Table 5, Fig. 6). However, as with witch flounder, the relationship between density of Atlantic wolffish and water temperature was strongly influenced by 10 years with no catch and 3 years with relatively higher densities.

Discussion

We detected seasonal patterns in the local larval fish assemblage in central Massachusetts Bay by sampling ichthyoplankton at a high frequency over 13 years. Frequent sampling within a small area is useful in efforts to describe phenological changes (Staudinger et al., 2019) because potential spatial variability is minimized. The focus on the central location within Massachusetts Bay resulted in data that can be used for characterization not just of the larval fish assemblage in the sampling area but of the assemblage in the entire Massachusetts Bay.

Our data are in general agreement with the EcoMon program data collected in Massachusetts Bay during our study period (NEFSC[2]). A total of 36 ichthyoplankton samples were collected during 7 months in Massachusetts Bay as part of the EcoMon program in 2008–2012 and 2015–2022. No samples were collected in Massachusetts Bay as part of the EcoMon program in January, March, July, September, and December. The 3 most abundant taxa in the EcoMon data were among the 5 most abundant taxa in our study in 4 of the 5 seasonal groups defined in this study (those that occur in November, December–March, April–May, and June–August) (Table 6). The rank order of the 3 most abundant taxa were identical between the programs in 2 of the 5 groups (those that occur in December–March and April–May). Only in September and October was one of the most abundant taxa, the Atlantic menhaden (*Brevoortia tyrannus*), in the EcoMon program data not among the top 5 taxa in our study; however, only 2 samples were collected during September and October as part of the EcoMon program.

The agreement between our data and data from earlier work elsewhere in the southern Gulf of Maine and Massachusetts Bay is also a strong indication that our data are representative of the larger Massachusetts Bay.

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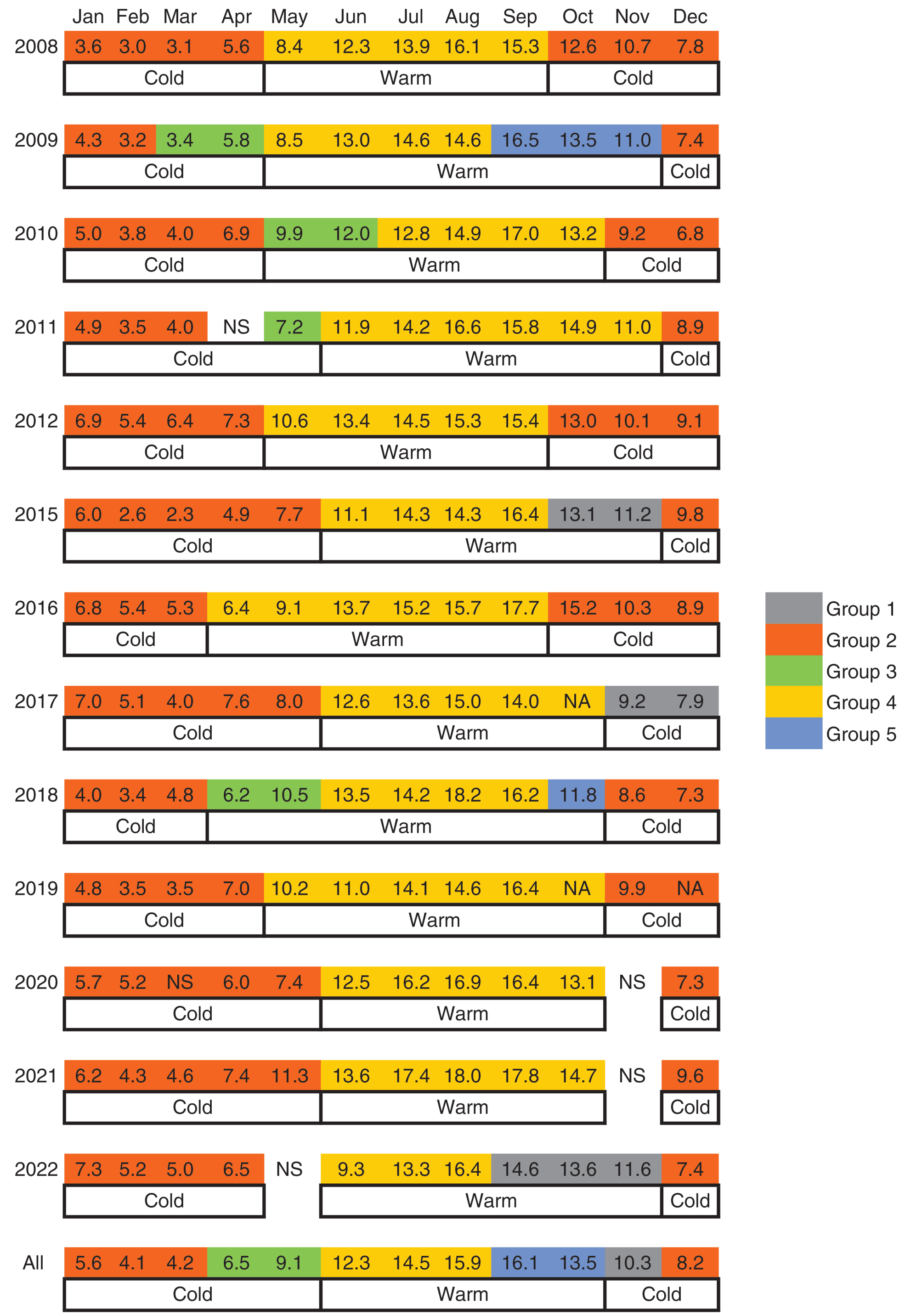
[2] NEFSC (Northeast Fisheries Science Center). 2019. Zooplankton and ichthyoplankton abundance and distribution in the North Atlantic collected by the Ecosystem Monitoring (EcoMon) Project from 1977-02-13 to 2021-11-15 (NCEI Accession 0187513). NOAA Natl. Centers Environ. Inf. [Dataset.] [Available from website, accessed October 2024.]



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2008	🟧 3.6	🟧 3.0	🟧 3.1	🟧 5.6	🟨 8.4	🟨 12.3	🟨 13.9	🟨 16.1	🟨 15.3	🟧 12.6	🟧 10.7	🟧 7.8
	Cold				Warm					Cold		
2009	🟧 4.3	🟧 3.2	🟩 3.4	🟩 5.8	🟨 8.5	🟨 13.0	🟨 14.6	🟨 14.6	🟦 16.5	🟦 13.5	🟦 11.0	🟧 7.4
	Cold				Warm							Cold
2010	🟧 5.0	🟧 3.8	🟧 4.0	🟧 6.9	🟩 9.9	🟩 12.0	🟨 12.8	🟨 14.9	🟨 17.0	🟨 13.2	🟧 9.2	🟧 6.8
	Cold				Warm						Cold	
2011	🟧 4.9	🟧 3.5	🟧 4.0	NS	🟩 7.2	🟨 11.9	🟨 14.2	🟨 16.6	🟨 15.8	🟨 14.9	🟨 11.0	🟧 8.9
	Cold					Warm						Cold
2012	🟧 6.9	🟧 5.4	🟧 6.4	🟧 7.3	🟨 10.6	🟨 13.4	🟨 14.5	🟨 15.3	🟨 15.4	🟧 13.0	🟧 10.1	🟧 9.1
	Cold				Warm					Cold		
2015	🟧 6.0	🟧 2.6	🟧 2.3	🟧 4.9	🟧 7.7	🟨 11.1	🟨 14.3	🟨 14.3	🟨 16.4	⬜ 13.1	⬜ 11.2	🟧 9.8
	Cold					Warm						Cold
2016	🟧 6.8	🟧 5.4	🟧 5.3	🟨 6.4	🟨 9.1	🟨 13.7	🟨 15.2	🟨 15.7	🟨 17.7	🟧 15.2	🟧 10.3	🟧 8.9
	Cold			Warm						Cold		
2017	🟧 7.0	🟧 5.1	🟧 4.0	🟧 7.6	🟧 8.0	🟨 12.6	🟨 13.6	🟨 15.0	🟨 14.0	🟨 NA	⬜ 9.2	⬜ 7.9
	Cold					Warm					Cold	
2018	🟧 4.0	🟧 3.4	🟧 4.8	🟩 6.2	🟩 10.5	🟨 13.5	🟨 14.2	🟨 18.2	🟨 16.2	🟦 11.8	🟧 8.6	🟧 7.3
	Cold			Warm							Cold	
2019	🟧 4.8	🟧 3.5	🟧 3.5	🟧 7.0	🟨 10.2	🟨 11.0	🟨 14.1	🟨 14.6	🟨 16.4	🟨 NA	🟧 9.9	🟧 NA
	Cold				Warm						Cold	
2020	🟧 5.7	🟧 5.2	🟧 NS	🟧 6.0	🟧 7.4	🟨 12.5	🟨 16.2	🟨 16.9	🟨 16.4	🟨 13.1	NS	🟧 7.3
	Cold					Warm						Cold
2021	🟧 6.2	🟧 4.3	🟧 4.6	🟧 7.4	🟧 11.3	🟨 13.6	🟨 17.4	🟨 18.0	🟨 17.8	🟨 14.7	NS	🟧 9.6
	Cold					Warm						Cold
2022	🟧 7.3	🟧 5.2	🟧 5.0	🟧 6.5	NS	🟨 9.3	🟨 13.3	🟨 16.4	⬜ 14.6	⬜ 13.6	⬜ 11.6	🟧 7.4
	Cold					Warm						Cold
All	🟧 5.6	🟧 4.1	🟧 4.2	🟩 6.5	🟩 9.1	🟨 12.3	🟨 14.5	🟨 15.9	🟦 16.1	🟦 13.5	⬜ 10.3	🟧 8.2
	Cold					Warm					Cold	

⬜ Group 1
🟧 Group 2
🟩 Group 3
🟨 Group 4
🟦 Group 5

Figure 3

The 5 statistically distinct groups identified through cluster analysis with Bray–Curtis dissimilarity index values for the larval fish assemblage in Massachusetts Bay in 2008–2012 and 2015–2022, with mean monthly water column temperatures in degrees Celsius. Groups 1–3 were discerned within the cold-water assemblage, which occurred in November–May, and groups 4 and 5 were found within the warmwater assemblage, which occurred in June–October. NS=not sampled; NA=not available because water column temperatures were not collected.

Table 3

Geometric mean density for 5 statistically distinct groups of fish larvae captured in Massachusetts Bay during 2008–2012 and 2015–2022. The groups occurred in different seasons: group 1 in November, group 2 in December–March, group 3 in April and May, group 4 in June–August, and group 5 in September and October. Asterisks denote the 5 highest densities in each group.

	Seasonal group density (larvae/1000 m^3)				
Taxon	1	2	3	4	5
American plaice	0.00	0.22	36.88*	11.18	0.09
Atlantic cod	1.93*	12.23*	4.28*	1.53	0.00
Atlantic menhaden	0.75*	0.07	0.03	10.06	3.93
Atlantic herring	45.32*	2.02*	0.06	<0.01	6.89*
Cunner	0.00	0.00	0.37	767.90*	0.26
Fourbeard rockling	0.77*	0.03	3.92	93.10*	12.44*
Haddock	0.00	0.37	4.44*	0.05	0.00
Longhorn sculpin	0.00	1.09*	0.46	0.00	0.00
Pollock	0.37	8.57*	0.39	0.05	0.07
Sand lances	0.00	73.34*	4.49*	0.00	0.00
Silver hake	1.31*	<0.01	0.04	356.79*	68.51*
True hakes	0.34	0.02	0.00	129.55*	74.55*
Windowpane	0.00	0.01	0.03	0.89	4.23*
Winter flounder	0.00	0.15	10.80*	0.90	0.00
Yellowtail flounder	0.00	0.00	4.17	45.90*	0.99
All other taxa	0.62	1.19	3.36	30.38	5.67
Total (all taxa)	51.41	99.32	73.72	1448.29	177.63

In addition, our data agree with those of Jury et al.[3], who compiled temporal and spatial distribution data on 58 invertebrate and fish species found in embayments and estuaries of Massachusetts, New Hampshire, and Maine, including in Massachusetts Bay. Each of the dominant taxa in our study (Table 3) were considered either "highly abundant" or "abundant" in Massachusetts Bay by Jury et al.[3] during the months they were dominant in our study.

Our data are also in agreement with those of Runge and Jones (2012), who sampled 2 stations in Massachusetts Bay and found that Atlantic herring, pollock (*Pollachius virens*), and sand lances were abundant in the winter months, similar to the composition of the cold-water assemblage defined in our study (Table 2). They also identified cunner, silver hake, red hake, American plaice, and daubed shanny (*Leptoclinus maculatus*) as dominant in the summer months, similar to the composition of the warmwater assemblage defined in our study, with some exceptions: the fourbeard rockling (*Enchelyopus cimbrius*) and yellowtail flounder (*Myzopsetta ferruginea*) were among the 5 most abundant warmwater taxa in our data, and we collected no daubed shanny.

In Cape Cod Bay, to the south of our sampling area, Scherer (1984) found that larval densities were highest from June through September, when fourbeard rockling, Atlantic mackerel (*Scomber scombrus*), true hakes, and cunner larvae were most abundant. The seasonality and composition of high larval densities in Cape Cod Bay from June through September is similar to the high-density warmwater assemblage that occurs from June through October and was identified in our study (Table 2), except that Atlantic mackerel were not abundant in our data. The spawning stock biomass of Atlantic mackerel is currently greatly reduced from the levels of the 1970s when Scherer (1984) sampled Cape Cod Bay, and this difference in spawning stock biomass likely explains the low levels of larval Atlantic mackerel in our data (NEFSC[4]). Each of the 5 most abundant taxa in our cold-water assemblage (November–May) was at its highest abundance in Cape Cod Bay from November through May (Scherer, 1984).

Mean water temperature increased by 0.3°C between the periods 2008–2012 and 2015–2022. Significant increases in surface water temperature in the Gulf of Maine and Northwest Atlantic Ocean have been widely reported (Mills et al., 2013; Pershing et al., 2015, 2021; Gonçalez Neto et al., 2021; Mills et al., 2024). In each of these studies, a longer time series of sea-surface temperatures was used, and linear models were sometimes used to illustrate increases in water temperature. The lack of sampling in 2013 and 2014 in our study prevented the use of methods for time-series analysis. The warmest mean water temperatures in our study were recorded in 2012, 2016, 2017, 2010, 2020, and 2021, and those years were among those with the greatest deviation from mean sea-surface temperatures reported by Mills et al. (2024) for the period 1982–2021. Our inclusion of colder mid-depth and near-bottom temperatures below the thermocline in the summer may have tempered an increase that would have been larger if we had used only sea-surface temperatures, although increases in bottom water temperatures have been reported from additional studies (Record et al., 2019; Friedland et al., 2020).

In our study, mean water temperature explained 28% of the variability in the composition of the cold-water larval assemblage but did not significantly explain the variability in the warmwater assemblage. Our data indicate that, in the cold-water assemblage, abundance of some of the taxa that range far to the north of Massachusetts Bay, such as the Atlantic wolffish, snakeblenny, and wrymouth, were negatively correlated with temperature. These 3 taxa can

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[3] Jury, S. H., J. D. Field, S. L. Stone, D. M. Nelson, and M. E. Monaco. 1994. Distribution and abundance of fishes and invertebrates in North Atlantic estuaries. Estuar. Living Mar. Resources Progam, ELMR Rep. 13, 221 p. Strateg. Environ. Assess. Div., Natl. Ocean Serv., NOAA, Silver Spring, MD. [Available from website.]

[4] NEFSC (Northeast Fisheries Science Center). 2022. Management track assessment June 2021. Northeast Fish. Sci. Cent. Ref. Doc. 22-10, 79 p. [Available from website.]

Table 4

Geometric mean density, mean contribution to the Bray–Curtis dissimilarity index, ratio of that mean contribution to the standard deviation of that mean, and contribution to total dissimilarity for abundant taxa that made statistically significant ($P<0.05$) contributions to total dissimilarity (95%) between 2 statistically distinct groups of fish larvae collected in Massachusetts Bay during 2008–2012 and 2015–2022. One group occurred in December–March, and the other occurred in June–August. The *P*-values are from the similarity percentage analysis.

	Density (larvae/1000 m^3)					
Taxon	December–March	June–August	Mean contribution to dissimilarity	Ratio	Contribution to total dissimilarity (%)	*P*-value
Cunner	0.00	767.90	0.11	6.83	12.08	<0.01
Fourbeard rockling	12.23	93.10	0.08	7.41	8.27	0.01
Silver hake	<0.01	356.79	0.10	4.47	10.68	0.01
True hakes	0.02	129.55	0.08	1.99	8.77	0.05
Yellowtail flounder	0.00	45.90	0.07	4.17	7.05	0.01

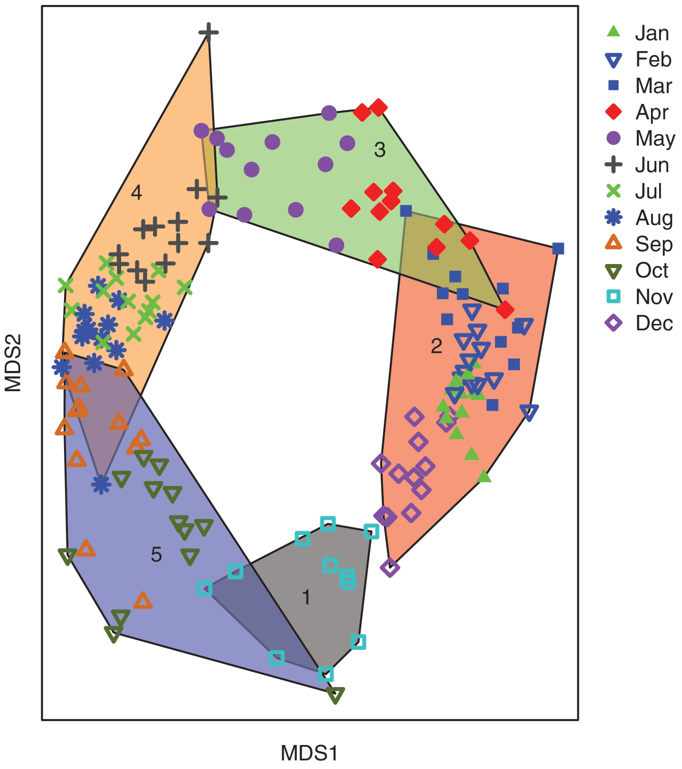

Figure 4

Nonmetric multidimensional scaling (MDS) plot of 5 statistically distinct seasonal groups within the larval fish assemblage of Massachusetts Bay in 2008–2012 and 2015–2022, identified through cluster analysis with Bray–Curtis dissimilarity index values. Each symbol represents a month-year combination. Polygons delineate and numerals indicate the groups, which are also illustrated in the dendrogram in Figure 2. The groups occurred in different seasons: group 1 in November, group 2 in December–March, group 3 in April and May, group 4 in June–August, and group 5 in September and October. The calculated stress level is 0.11.

Table 5

Taxa with a significant ($P<0.05$) correlation between geometric mean density and mean water column temperature for the cold-water assemblage in Massachusetts Bay during 2008–2012 and 2015–2022. The cold-water assemblage occurred in November–May at mean temperatures of 4.1°C–10.3°C. *r*=coefficient of correlation.

Taxon	*r*	*P*-value
Atlantic herring	0.66	0.02
Atlantic wolffish	−0.85	<0.01
Fourbeard rockling	0.58	0.04
Silver hake	0.65	0.02
Snakeblenny	−0.76	<0.01
True hakes	0.56	0.05
Witch flounder	0.61	0.03
Wrymouth	−0.72	0.01
Yellowtail flounder	0.60	0.03

be considered northern fish because they occur as far north as Davis Strait, between western Greenland and Baffin Island (Atlantic wolffish: Rountree, 2002; snakeblenny: Collette, 2002a), and Labrador (wrymouth: Collette, 2002b). Abundance of these cold-water taxa may decrease if water temperatures in the cold-water season continue to rise. The thermal habitat of each of these 3 taxa is projected with medium-to-low uncertainty to decrease in waters of the northeastern United States or eastern Canada under predicted greenhouse gas scenarios (Morley et al., 2018). Abundances of snakeblenny and wrymouth were low in the 2 warmest years of 2012 and 2016, although these species were found in samples in

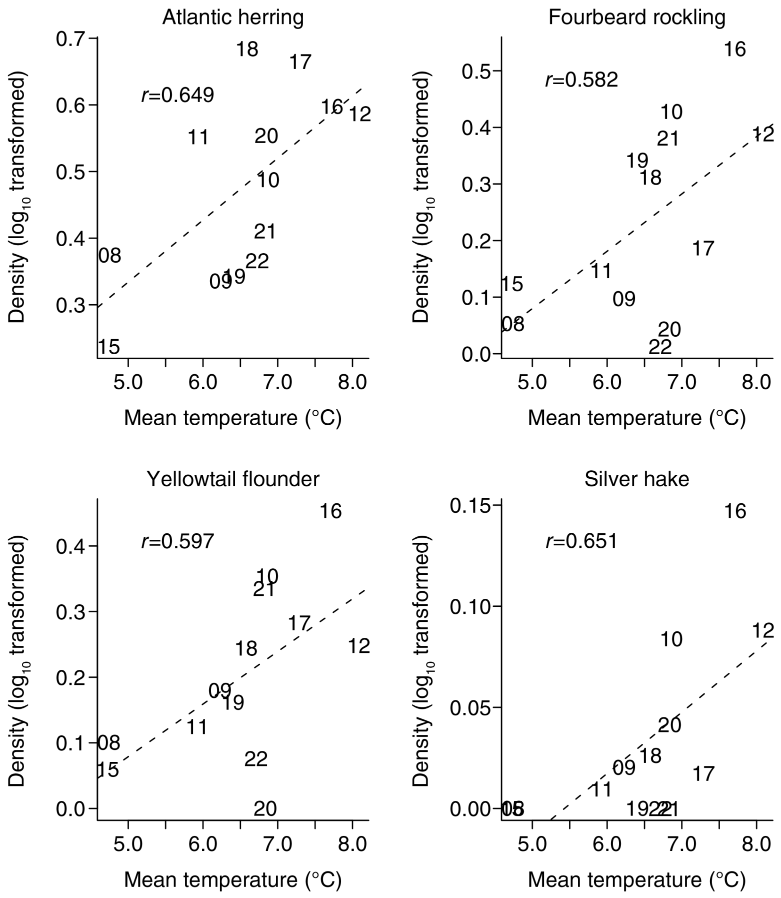

Figure 5

Significant ($P<0.05$) relationships between $\log_{10}(x+1)$-transformed density of fish larvae and mean water column temperature for Atlantic herring (*Clupea harengus*), fourbeard rockling (*Enchelyopus cimbrius*), yellowtail flounder (*Myzopsetta ferruginea*), and silver hake (*Merluccius bilinearis*) captured in the cold-water assemblage in Massachusetts Bay during 2008–2012 and 2015–2022. The cold-water assemblage occurred in November–May at mean temperatures of 4.1°C–10.3°C. The coefficient of correlation (r) for each trend line (dashed line) is given in each graph. Numerals in the graphs indicate years of occurrence. Densities of larvae in raw data from ichthyoplankton sampling are recorded as number of larvae per 1000 m^3.

most years. Atlantic wolffish occurred only in the coldest years of 2008, 2015, and 2011; however, the occurrence of this taxon is too limited to draw a strong conclusion.

Larval abundances of 5 taxa (the Atlantic herring, fourbeard rockling, silver hake, witch flounder, and yellowtail flounder) in the cold-water assemblage were positively correlated with increasing mean water temperature. The center of distribution of larvae of these taxa, except for Atlantic herring and witch flounder, moved significantly northward between the period 1977–1987 and the period 1999–2008 along the northeast U.S. continental shelf (Walsh et al., 2015). Furthermore, the distribution of adults of the fourbeard rockling, silver hake, and yellowtail flounder also moved north along the northeast U.S. continental shelf between the period 1970–2009 and the period 2010–2019 (Mills et al., 2024), potentially contributing to the increase in abundance of larvae with the rise in temperature observed in our study area. The positive relationship with increasing water temperatures during the cold-water period may indicate that these taxa will become more abundant in our study area during cold-water seasons as water temperatures continue to rise. Witch flounder were not abundant in any year in our study area, and the low density of this taxon observed in our study (Fig. 6) does not support major inferences.

A single variable, whether environmental or biological, is not likely to entirely explain the spatial and temporal occurrence of larvae. The incorporation of environmental

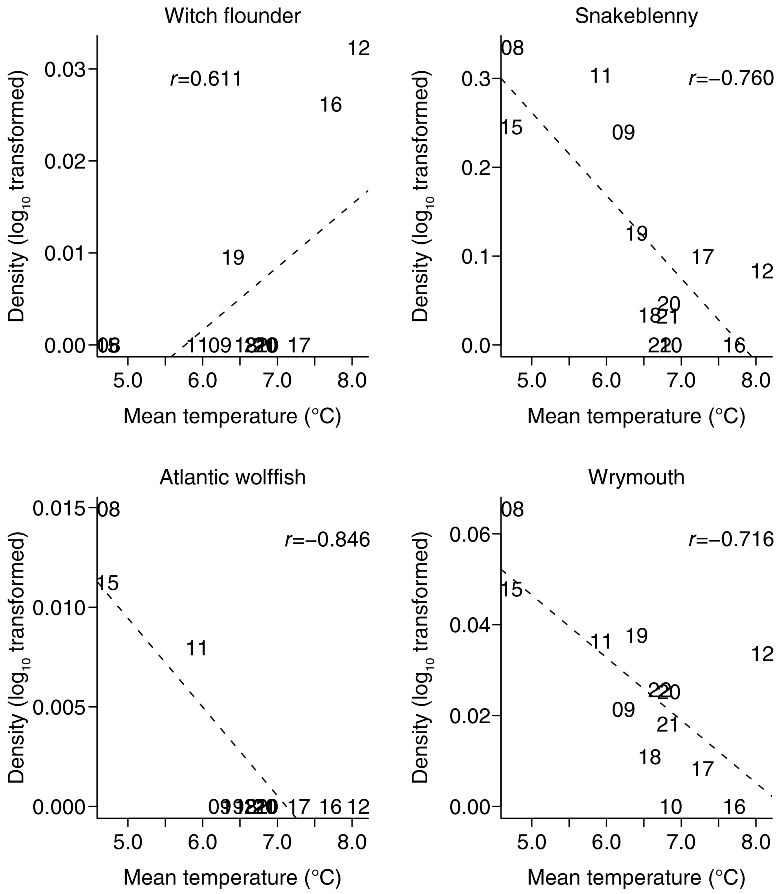

Figure 6

Significant ($P<0.05$) relationships between $\log_{10}(x+1)$-transformed density of fish larvae and mean water column temperature for witch flounder (*Glyptocephalus cynoglossus*), snakeblenny (*Lumpenus lampretaeformis*), Atlantic wolffish (*Anarhichas lupus*), and wrymouth (*Cryptacanthodes maculatus*) captured in the cold-water assemblage in Massachusetts Bay during 2008–2012 and 2015–2022. The cold-water assemblage occurred in November–May at mean temperatures of 4.1°C–10.3°C. The coefficient of correlation (r) for each trend line (dashed line) is given in each graph. Numerals in the graphs indicate years of occurrence. Densities of larvae in raw data from ichthyoplankton sampling are recorded as number of larvae per 1000 m^3.

variables, such as water temperature, can improve the performance of fishery models, but several factors can limit their usefulness (Keyl and Wolff, 2008). The spawning stock of adults and environmental factors, such as circulation patterns that retain or advect propagules, can be important to the occurrence and abundance of fish larvae in a particular location. Churchill et al. (2011) found that spring-spawned larval Atlantic cod were retained in the western Gulf of Maine and transported to areas favorable to juvenile development during periods of winds favorable for downwelling. However, Hare et al. (2015) incorporated updated estimates of spawning stock biomass and recruitment into the model of Churchill et al. (2011) and found a decreased correlation between recruitment and wind direction, indicating that the influence of environmental variables on ecosystem processes can vary.

The phenology of fish larvae in the Gulf of Maine is changing in “complex and inconsistent ways” (Staudinger et al., 2019). Patterns in the occurrence of fish larvae outlined by Walsh et al. (2015) partially support the expectation that changes in fish larval phenology along the northeastern coast of the United States between the periods 1977–1987 and 1999–2008 could be attributed to changes in water temperature. The season of occurrence changed for about half of the 45 larval taxa examined by Walsh et al. (2015). Among larvae that had a change in occurrence, those common in the summer and fall shifted their occurrence most often to later in the season, and

Table 6

Comparison of the rank order of density of taxa collected in 5 statistically distinct seasonal groups within the larval fish assemblage in Massachusetts Bay during 2008–2012 and 2015–2022, between the sampling of the Ecosystem Monitoring (EcoMon) program and the sampling of this study. Density was measured as number of larvae per 10 m^2 in the EcoMon program and as number of larvae per 1000 m^3 in this study.

	Seasonal group									
	November		December–March		April and May		June–August		September and October	
Taxon	EcoMon	This Study	EcoMon	This Study	EcoMon	This Study	EcoMon	This Study	EcoMon	This Study
Atlantic herring	1	1							1	4
Atlantic cod	2	2	3	2						
Atlantic menhaden									2	
American plaice					3	1				
Cunner							1	1		
Fourbeard rockling	3	4					2	4		
Pollock			2	3						
Sand lances			1	1	1	3				
True hakes									3	1
Winter flounder					2	2				
Yellowtail Flounder							3	5		

those common in the winter and spring shifted most often to earlier in the season. In addition, sometimes organisms made "wrong-way migrations" to less-than-favorable habitat in response to larval transport (Fuchs et al., 2020) and possibly to increasing population size (Mills et al., 2024).

This study resulted in the first quantitative description of the larval fish assemblage of Massachusetts Bay and the influence of water temperature on this assemblage. Our data have the potential to aid identification of larval taxa that might be susceptible to climate change by using the projections and criteria of Hare et al. (2016). It is expected that the density of larvae of at least 4 commercially important fish taxa among the 5 most abundant taxa that we identified in the cold-water assemblage (the Atlantic herring, Atlantic cod, pollock, and American plaice) will be negatively affected by continued warming in Massachusetts Bay. Among the 5 most abundant taxa of larvae in the warmwater assemblage, at least 3 commercially important taxa (the white hake, silver hake, and yellowtail flounder) are expected to be negatively affected by increasing temperatures in Massachusetts Bay.

Conclusions

The time-integrated description of the structure of the ichthyoplankton assemblage in Massachusetts Bay in the early 21st century, based on our 13-year dataset, serves as an important baseline against which future changes in the assemblage may be compared. We identified 2 major larval fish assemblages that were 87% different from each other, a low-density cold-water assemblage present from November through May and a warmwater assemblage present at a higher density from June through October. Within the cold-water assemblage, 3 groups were found to occur at different times of year or seasons: November, December–March, and April–May. Within the warmwater assemblage, 2 groups were present at different seasons: June–August and September–October.

Water temperature explained 28% of the interannual variability in the cold-water assemblage but did not significantly explain any variability in the warmwater assemblage. However, it is apparent from our study and others that temperature alone does not control the composition and phenology of larval communities and that other factors, such as hydrography and local environmental conditions, can be important (Starko et al., 2024; Weisberg et al., 2024). The interaction between larvae and additional factors, such as hydrography, spawning stock, and changes in population size (Hare et al., 2015; Staudinger et al., 2019, Mills et al., 2024), warrant further investigation into their influences on ichthyoplankton assemblages.

Resumen

Se colectaron muestras de ictioplancton mensualmente en 2 estaciones de la bahía de Massachusetts de 2008 a 2012 y de 2015 a 2022 para caracterizar el ensamble de peces larvarios de esta zona. La fauna se componía de 2 conjuntos principales que eran un 87% diferentes entre sí y estaban asociados con la estación y la temperatura del agua. Un grupo de agua fría de baja densidad (43.26 larvas/1000 m^3) apareció de noviembre a mayo a temperaturas medias de la columna de agua entre 4.1°C y 10.3°C, con lanzón (*Ammodytes* spp.) como taxón dominante. Entre junio y octubre se observo un ensamblaje de aguas cálidas de mayor densidad (432.58 larvas/1000 m^3) con temperaturas medias de la columna de agua entre 12.3°C y 16.1°C, siendo la merluza plateada (*Merluccius bilinearis*) el taxón dominante. Dentro del conjunto de especies de aguas frías, se observaron grupos estadísticamente diferentes en noviembre, diciembre–marzo y abril–mayo. El arenque Atlántico (*Clupea harengus*), los lanzones y el lenguado americano (*Hippoglossoides platessoides*) fueron los taxones dominantes en esos periodos, respectivamente. Dentro del ensamble de aguas cálidas, se produjeron grupos de especies estadísticamente diferenciados en junio-agosto y septiembre-octubre, siendo el salmonete (*Tautogolabrus adspersus*) y el grupo de merluzas (*Urophycis* spp.) los taxones dominantes en esos periodos, respectivamente. La temperatura del agua explica el 28% de la variación anual del esnamble de aguas frías, y no existe una relación significativa entre la temperatura y la variación anual del ensamble de aguas cálidas. Esta caracterización de larvas de peces proporciona una línea base con la que se pueden medir los cambios potenciales en los ensambles de esta área.

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