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# Cross-Shore, Seasonal, and Depth-Related Structure of Ichthyoplankton Assemblages in Coastal Alabama

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ARTICLE

# Cross-Shore, Seasonal, and Depth-Related Structure of Ichthyoplankton Assemblages in Coastal Alabama

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*Abstract*

**Investigations of the spatial and temporal structure of larval fish assemblages are essential for a better understanding of the dynamics of fish populations and their resilience to environmental change. This study provides an original typology of the spatial, seasonal, and depth-related structure of ichthyoplankton assemblages collected along a 77-km cross-shore gradient in Alabama coastal waters. This typology is based on a depth-discrete ichthyoplankton survey conducted across multiple years at a high spatial and temporal resolution in the northern Gulf of Mexico. A total of 350,766 larvae were collected, among which >95% could be identified to families. The total density of fish larvae was significantly higher inshore, whereas the number of families increased offshore. Multivariate regression trees and Dufrêne–Legendre indices were used to identify seven assemblages dominated by different families of larvae. These assemblages were primarily structured by distance from the shore, followed by season and depth, and were associated with different water masses characterized by distinct temperature and salinity conditions. Families Clupeidae, Bregmacerotidae, Synodontidae, Scombridae, and Ophidiidae were typical offshore, whereas families Engraulidae, Gobiidae, and Gobiesocidae were typical inshore. These observed spatial distributions likely reflected interactions between adult spawning behaviors and oceanographic processes, in particular the influence of the Mobile River. Our results thus confirm existing lines of evidence suggesting that riverine influences play a major role in fish population dynamics along the Alabama inner shelf. For many families, the observed seasonal distributions were largely consistent with the results of previous studies conducted at smaller spatial resolution in the area. However, our large-scale, high-resolution, cross-shore design clearly improved the detection of seasonal variations for inshore and offshore taxa otherwise rarely collected.**

The survival rates of larval stages, which vary spatially and temporally, contribute to variable recruitment success and year-class strength in adult fish populations (Cushing 1996; Houde 1997). As a result, examination of the spatial and temporal patterns characterizing larval fish abundance and diversity provides essential information about the processes that ultimately determine adult population size and distribution (Fuiman and Werner 2002). The spatial and temporal distributions of larval fish assemblages are initially determined by adult spawning behaviors (Hernández-Miranda et al. 2003; Marancik et al. 2005). Assemblage dynamics are then modified over time, as larvae develop and respond to oceanographic processes and water column conditions (Auth and Brodeur 2006; Muhling and Beckley 2007). Therefore, changes in the dynamics of

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larval fish assemblages closely reflect changes in environmental conditions, making ichthyoplankton studies particularly relevant not only for understanding fish population dynamics, but also for addressing the impact of environmental changes on marine communities (Brodeur et al. 2008; Hsieh et al. 2009).

The spatial and temporal distribution of larval fish assemblages and their response to environmental factors have been studied in a variety of coastal locations from the Atlantic (e.g., Reiss and McConaugha 1999; Marancik et al. 2005), Pacific (e.g., Hernández-Miranda et al. 2003; Auth and Brodeur 2006), and Indian oceans (e.g., Munk et al. 2004), as well as in the southern Gulf of Mexico (e.g., Sanvicente-Añorve et al. 1998). This issue has received comparatively little attention in the northern Gulf of Mexico, where high coastal primary and secondary productivity sustains major commercial and recreational fisheries (Browder 1993). To date, most ichthyoplankton studies conducted in this region have focused on individual species (e.g., Scott et al. 1993; Lyczkowski-Shultz and Hanisko 2007; Johnson et al. 2009). Multispecies or assemblage studies from the region have typically been limited to small spatiotemporal scale and/or resolution (e.g., Sogard et al. 1987; Govoni et al. 1989; Grimes and Finucane 1991; Raynie and Shaw 1994; Rakocinski et al. 1996; Hernandez et al. 2003; Tolan 2008). Here we present an investigation of the cross-shelf spatial and temporal structure of larval fish assemblages off the coast of Alabama using a high spatial and temporal resolution survey design. The Alabama shelf is relatively small, bounded by the Mississippi River Delta to the west and the DeSoto Canyon to the east, and is greatly influenced by the Mobile River, which drains the fourth largest watershed in the United States and has the sixth largest freshwater discharge on the North American continent (Schroeder 1979). These properties provide a unique opportunity to examine the distribution of larval fish assemblages along a gradient of environmental conditions, ranging from highly productive estuarine waters to offshore oceanic waters.

The main objective of this study was to examine the cross-shore, seasonal, and depth-related structure of larval fish assemblages collected over 28 months along a transect extending 77 km in linear distance across the Alabama inner shelf. A secondary objective was to determine the ranges of ecological preferences displayed by various families of larvae in our region, based on their associations with differing water masses characterized by different physical properties (i.e., salinity, temperature, and depth).

## METHODS

*Field and laboratory procedures*.—Larval fish were collected monthly from March 2007 to December 2009 at five stations positioned along a cross-shore transect extending from inner Mobile Bay to an offshore station located 54 km south of Dauphin Island, Alabama (Figure 1). Collections were made during the day using a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS; Open Seas Instrumentation, Inc., Musquodoboit Harbor, Nova Scotia), with a 0.25-$m^2$ mouth opening fitted with eight 0.333-mm-mesh plankton nets. During each monthly survey, two depth-discrete samples (1–6 and 6–12 m) were collected at the nearshore stations MB and DI, three depth-discrete samples (1–3, 3–6, and 6–9 m) at station T10, six depth-discrete samples (1–3, 3–6, 6–9, 9–12, 12–15, and 15–18 m) at station T20, and seven depth-discrete samples (1–3, 3–6, 6–9, 9–12, 12–20, 20–30, and 30–33 m) at station T35. The term "depth" will refer hereafter to a vertical stratum of the water column (i.e., a depth-bin), whereas "stations" will refer to different locations along the cross-shore transect (i.e., distance from the shore). Three replicate tows were performed for each depth, station, and month, resulting in nominal totals of 6, 9, 18, and 21 samples per month at stations MB and DI, T10, T20, and T35, respectively. Deviations from this nominal design were due to adjustments caused by weather constraints or equipment issues. A total of 1,500 samples were included in the present analysis (Table 1).

Plankton net contents were rinsed with seawater, sieved, and preserved in 4% formalin for 48 h before being transferred to 70% ethanol. A conductivity–temperature–depth probe (CTD; SBE19, Sea-Bird Electronics, Inc., Bellevue, Washington) was integrated into the BIONESS and provided temperature (°C), salinity (practical salinity scale), and depth profiles for each plankton tow. A flowmeter (General Oceanics, Miami, Florida) mounted within the BIONESS frame estimated the volume of water filtered for each sample (in $m^3$). Fish larvae from plankton samples were sorted and identified at the Plankton Sorting and Identification Center (Szczecin, Poland) and at the Dauphin Island Sea Laboratory. Due to the lack of species-level descriptions for many larvae in our region and the large number of larvae collected (>350,000), analyses were conducted at the family level.

*Data analysis*.—Mean temperature and salinity observations (average of values measured at the opening and closing time of the nets for each bin; $n = 1{,}477$) were examined at each station each month to define the range of environmental conditions in which larval fish were collected. Larval fish abundances were standardized by the volume of water filtered, providing estimates of larval density (number/$m^3$) for each family in each sample. One-way analyses of variance (ANOVA) and Bonferroni–Dunn tests (Day and Quinn 1989; Zar 1999) were used to compare (1) the total density of fish larvae and the number of families (i.e., family richness) among stations ($df = 4$) and months ($df = 11$) and (2) monthly temperature and salinity values along the cross-shore transect ($df = 4$, except in February when only two stations were sampled, so $df = 1$; Table 1). The ANOVAs and Bonferroni–Dunn tests were performed using the Statview software (SAS, StatView version 5.0).

The structure of larval assemblages was analyzed using a multivariate regression tree (MRT) approach. The MRT was chosen because it provides a hierarchical classification of the

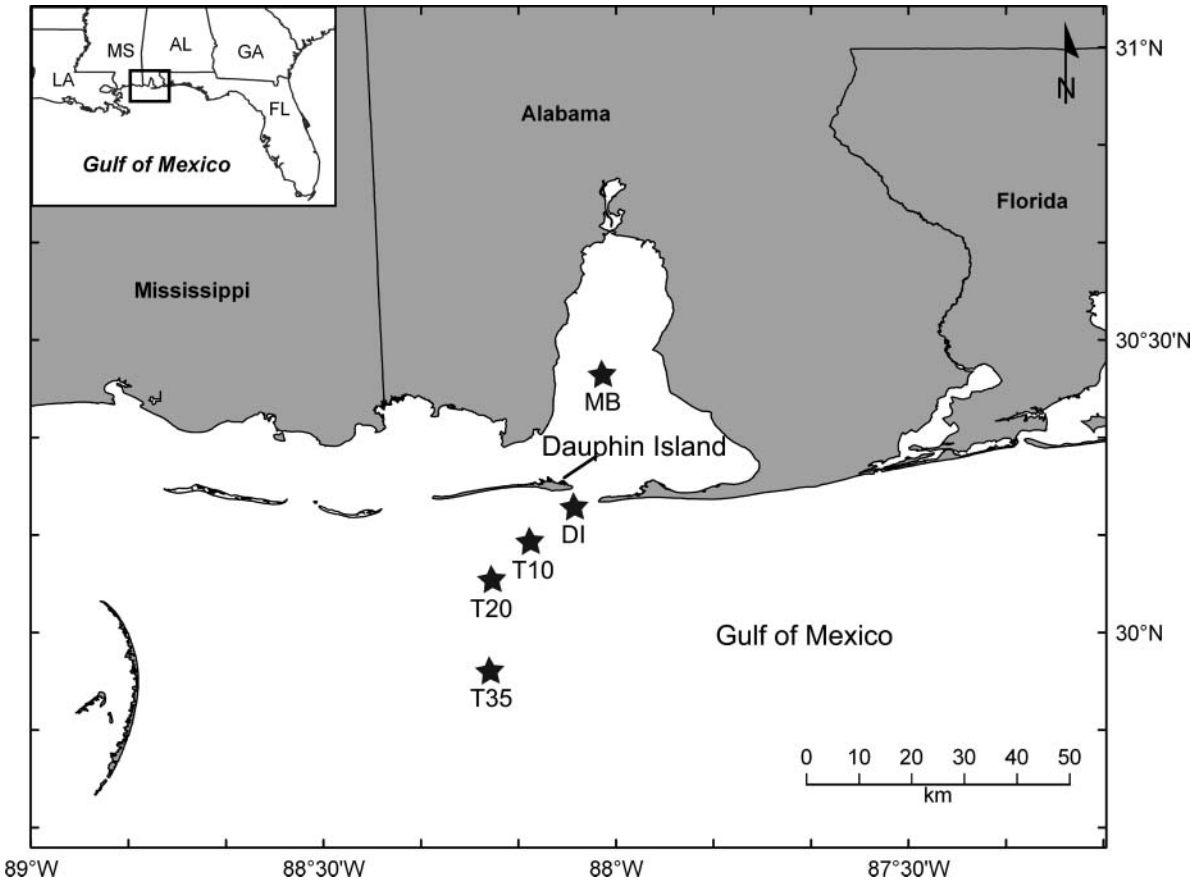


FIGURE 1. Locations of ichthyoplankton sampling stations off the coast of Alabama in the northern Gulf of Mexico.



effect of explanatory variables (represented as the nodes of the tree) on the faunal composition of samples (clustered at the branches). This method can be applied on imbalanced data sets and on continuous and/or qualitative explanatory variables that may be collinear (De'ath 2002). In our analyses, explanatory variables were represented by year, month, season, station, depth, temperature, and salinity. Faunal variables were represented by the densities (number/$m^3$) of fish larvae families in the samples.

A total of 18 MRT trials were conducted, corresponding to 18 different combinations of explanatory variables. Depth was defined as either a continuous variable corresponding to the average depth at which each sample was collected (i.e., the average depth at the opening and closing time of the nets for each depth bin) or as a categorical variable. In the latter case, two categories of depth were used to characterize the vertical strata of the water column at the inshore stations MB and DI: surface (<6 m depth) and bottom (>6 m depth). Three categories were used for the remaining stations: surface (<3 m at T10 and <6 m at T20 and T35), midwater (from 3 to 6 m at T10 and from 6 to 12 m at T20 and T35), and bottom (>6 m at T10 and >12 m at T20 and T35). Similarly, seasons were defined in two ways, either by calendar date (winter: December to February; spring: March to May; summer: June to August; and fall: September to November), or as a function of observed temperature variations, following Hernandez et al. (2010a). In the latter case, monthly patterns of temperature values were used to define four seasons. Months characterized by an average water temperature $\leq$17.5°C were classified as winter months, months characterized by an average water temperature >17.5°C and $\leq$24.8°C as spring months, months characterized by an average water temperature >24.8°C and $\leq$30.1°C as summer months, and months characterized by an average water temperature >17.5°C and $\leq$25.4°C as fall months (Table 1).

Extremely rare families were excluded from the faunal data, since their low and highly variable abundance and occurrence may confound the definition of larval assemblages associated with the explanatory variables (Pepin and Anderson 1997). Consequently, families contributing to <0.02% of the total abundance of larvae collected over the course of the survey were excluded (Table 2). Densities were $\log_e(x + 1)$ transformed in order to reduce the weight of the most abundant families (Zar 1999). Samples with no larvae were also removed because they do not contribute to our understanding of the ecological preferences of larval fish families. However, a trial analysis was also conducted using presence–absence data, allowing the

TABLE 1. Number of samples collected using 0.333-mm-mesh nets mounted in BIONESS at five stations along coastal Alabama from March 2007 to December 2009. Samples correspond to 3-m depth-discrete bins at stations T10, T20, and T35 and to 6-m depth-discrete bins at stations DI and MB. The locations of the sampling stations are depicted in Figure 1. For statistical analyses, each sampling period was assigned to a calendar- and temperature-related season.

| | Season | | Station | | | | | |
|---|---|---|---|---|---|---|---|---|
| Month | Calendar | Temperature | MB | DI | T10 | T20 | T35 | Total |
| Mar 2007 | Spring | Winter | 0 | 4 | 9 | 18 | 0 | 31 |
| Apr 2007 | Spring | Spring | 12 | 12 | 9 | 18 | 14 | 65 |
| May 2007 | Spring | Spring | 0 | 0 | 0 | 18 | 28 | 46 |
| Jun 2007 | Summer | Summer | 8 | 8 | 6 | 18 | 21 | 61 |
| Jul 2007 | Summer | Summer | 6 | 6 | 9 | 18 | 21 | 60 |
| Aug 2007 | Summer | Summer | 6 | 4 | 9 | 18 | 21 | 58 |
| Nov 2007 | Fall | Fall | 6 | 6 | 8 | 18 | 21 | 59 |
| Dec 2007 | Winter | Fall | 6 | 6 | 9 | 18 | 21 | 60 |
| Jan 2008 | Winter | Winter | 6 | 6 | 9 | 18 | 21 | 60 |
| Feb 2008 | Winter | Winter | 0 | 0 | 0 | 18 | 22 | 40 |
| Mar 2008 | Spring | Spring | 6 | 6 | 9 | 18 | 21 | 60 |
| Apr 2008 | Spring | Spring | 6 | 6 | 9 | 18 | 21 | 60 |
| May 2008 | Spring | Spring | 6 | 6 | 10 | 12 | 21 | 55 |
| Sep 2008 | Fall | Summer | 6 | 6 | 6 | 18 | 21 | 57 |
| Oct 2008 | Fall | Fall | 12 | 12 | 18 | 36 | 42 | 120 |
| Nov 2008 | Fall | Fall | 6 | 6 | 9 | 18 | 14 | 53 |
| Dec 2008 | Winter | Winter | 6 | 6 | 6 | 12 | 0 | 30 |
| Jan 2009 | Winter | Winter | 6 | 6 | 9 | 18 | 14 | 53 |
| Mar 2009 | Spring | Spring | 6 | 6 | 9 | 12 | 21 | 54 |
| Apr 2009 | Spring | Spring | 6 | 6 | 9 | 18 | 7 | 46 |
| May 2009 | Spring | Spring | 6 | 6 | 9 | 17 | 13 | 51 |
| Jun 2009 | Summer | Spring | 6 | 6 | 9 | 17 | 14 | 52 |
| Jul 2009 | Summer | Summer | 6 | 6 | 9 | 18 | 14 | 53 |
| Aug 2009 | Summer | Summer | 6 | 4 | 9 | 18 | 15 | 52 |
| Sep 2009 | Fall | Summer | 6 | 6 | 6 | 18 | 14 | 50 |
| Oct 2009 | Fall | Summer | 5 | 6 | 9 | 18 | 14 | 52 |
| Nov 2009 | Fall | Fall | 0 | 0 | 0 | 17 | 14 | 31 |
| Dec 2009 | Winter | Fall | 0 | 0 | 0 | 18 | 13 | 31 |
| Total | | | 151 | 152 | 213 | 501 | 483 | 1,500 |



consideration of all families and samples (results not presented). Since the results obtained were largely the same, both in terms of assemblage structure and statistical score, only analyses based on density data are presented here. This procedure resulted in a total of 1,355 samples being included in the MRT matrix.

The ultimate goal of our MRT approach was to obtain the most concise, comprehensive picture of ichthyoplankton assemblages within the range of environmental conditions observed. The performance of the 18 MRT trials was thus assessed based on a trade-off among three criteria: (1) parsimony, (2) relevance, and (3) statistical score, following Questier et al. (2005) and Carassou et al. (2008). Parsimony means that the tree characterized by the minimum number of nodes and branches, and thus providing as concise a comprehensive picture of larval fish assemblages as possible, was preferred. Relevance was assessed by the ratio of the number of explanatory variables appearing at the nodes to the number of variables included in the analysis and by observing the position of the samples from each branch on the first plane of a principal components analysis (PCA). The tree preferred was the one in which as many as possible of the explanatory factors included in the analysis were represented and for which the samples from the different branches were well distinguishable on the PCA plane. Among the most parsimonious and relevant trees, the one showing the lowest relative error (RE), which corresponds to the amount of variation among the samples not described by the tree (De'ath 2002), was finally selected.

Once the final tree was selected, the Dufrêne–Legendre index (DL) was used to identify families which were characteristic of the samples constituting each branch (Dufrêne and Legendre 1997). This index corresponds to the product of the relative

abundance and the occurrence of families, namely,

$$DL_{ij} = A_{ij} \times O_{ij},$$

where $A_{ij}$ is the mean abundance of individuals of family $i$ across samples of branch $j$ relative to its mean abundance over all branches, and $O_{ij}$ is the mean frequency of occurrence of family $i$ across samples of branch $j$ relative to its mean frequency of occurrence over all branches (see Dufrêne and Legendre 1997 for more details). The value of DL varies from zero for families that do not occur in a branch to one for families only occurring in samples from a branch and not in any other sample (De'ath 2002). The statistical significance of the index was assessed by randomized permutations (Dufrêne and Legendre 1997). Finally, temperature and salinity values from the groups of samples constituting each branch were plotted in order to visualize the range of environmental conditions within which each assemblage defined by MRT occurred. The MRT and DL calculations were performed with R 2.10.1 using the "mvpart" and "labdsv" packages.

## RESULTS

### Environmental Conditions

Temperature values varied significantly among stations in all months ($P < 0.05$ in all cases) except September, when temperature was similar at the five stations ($P = 0.13$; (Figure 2a). Differences among stations remained low from March to October ($F < 10.0$ in all cases), with slightly warmer temperatures generally being observed in shallow inshore waters (Figure 2a). Conversely, a clear temperature front characterized the cross-shore transect from November to February, with warmer waters being observed at the offshore station T35 (Figure 2a). Temperature increased from January to August in the sampling area, with minimum and maximum values of 12.0°C and 31.7°C at station MB in January and August, respectively (Figure 2a). Salinity also varied significantly among stations in all months ($P < 0.01$ in all cases), with a clear salinity gradient ranging from low and variable values at inshore stations MB and DI to consistently high values at offshore stations T10, T20 and T35 (Figure 2b). Minimum and maximum salinities of 8.2 and 36.5 were recorded at station MB in March and station T35 in June, respectively (Figure 2b).

### Total Larval Fish Density and Richness

A total of 350,766 larvae were collected over the course of the survey, among which 334,178 (i.e., >95%) could be identified to the family level (Table 2). These larvae belonged to 17 orders and 70 families, of which 36 had a total abundance ≥0.02% of the total (Table 2). The total density of fish larvae varied significantly among stations ($F = 14.9$, $P < 0.01$), with minimum values observed at stations T10 and T20, followed by T35, DI, and MB (Figure 3a). The total density of fish larvae also varied significantly among months ($F = 9.0$, $P < 0.01$), with the lowest values being observed in January and the highest in October and August (Figure 3b). Family richness varied among stations ($F = 87.9$, $P < 0.01$) following an inverse gradient to that of total density, with minimum values at stations MB, DI, and T10 and the highest values at station T35 (Figure 3c). Monthly variations were also detected ($F = 46.9$, $P < 0.01$), with minimum richness in December and maximum in May (Figure 3d).

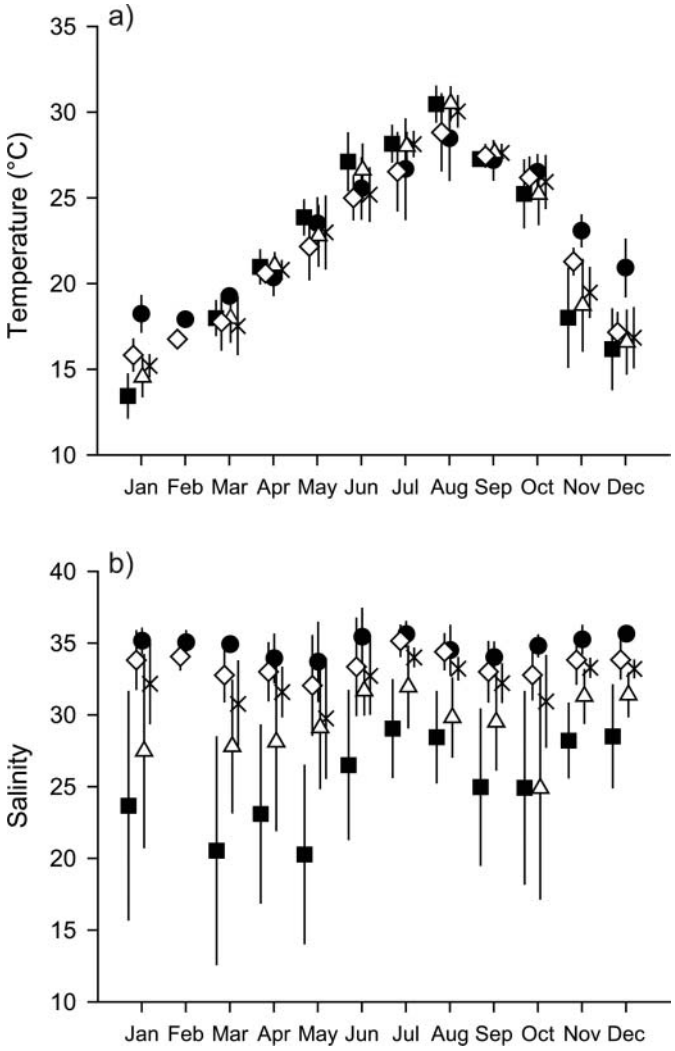


FIGURE 2. Variations in **(a)** temperature and **(b)** salinity across months at five stations positioned along a cross-shore transect in coastal Alabama. Stations are denoted as follows: squares = MB, triangles = DI, crosses = T10, diamonds = T20, and circles = T35 (see Figure 1). The symbols indicate mean values and the vertical lines denote standard errors. A total of 1,477 observations are included in each panel.

### Structure of Larval Fish Assemblages

The relative error (RE) from the 18 MRT trials ranged from 0.619 to 0.788, corresponding to 21.2–38.1% of the explained variability in assemblage structure (i.e., [1 – RE] × 100). The inclusion of depth as a continuous or categorical variable

TABLE 2. Total number of fish larvae collected in BIONESS samples at five stations positioned along a cross-shore transect in coastal Alabama from March 2007 to December 2009. The proportion of each family within all identified larvae is indicated in the last column. Families retained for analysis are indicated by asterisks (i.e., when %Total ≥ 0.02). Orders and families are ranked in alphabetical order.

| Order and family | Code | MB | DI | T10 | T20 | T35 | Total | %Total |
|---|---|---|---|---|---|---|---|---|
| Anguilliformes | | | | | | | | |
| Anguillidae | Angu | | | | | 2 | 2 | <0.01 |
| Congridae | Cong | | | 6 | 6 | 226 | 238 | 0.07* |
| Muraenidae | Mura | | | | 2 | 4 | 6 | <0.01 |
| Nettastomatidae | Nett | | | | 2 | 26 | 28 | 0.01 |
| Ophichthidae | Ophi | 8 | 8 | 28 | 168 | 312 | 524 | 0.16* |
| Atheriniformes | | | | | | | | |
| Atherinidae | Athe | 16 | | | | 18 | 34 | 0.01 |
| Aulopiformes | | | | | | | | |
| Paralepididae | Para | | | | | 52 | 52 | <0.02 |
| Synodontidae | Syno | 6 | 22 | 62 | 748 | 1,396 | 2,234 | 0.67* |
| Beloniformes | | | | | | | | |
| Hemiramphidae | Hemi | | | | | 20 | 20 | 0.01 |
| Beryciformes | | | | | | | | |
| Holocentridae | Holo | | | | | 6 | 6 | <0.01 |
| Clupeiformes | | | | | | | | |
| Clupeidae | Clup | 306 | 584 | 1,036 | 3,508 | 20,396 | 25,830 | 7.73* |
| Engraulidae | Engr | 42,304 | 25,506 | 14,642 | 12,714 | 12,264 | 107,430 | 32.15* |
| Elopiformes | | | | | | | | |
| Elopidae | Elop | | 2 | | | 2 | 4 | <0.01 |
| Gadiformes | | | | | | | | |
| Bregmacerotidae | Breg | 4 | 4 | 24 | 1,248 | 2,056 | 3,336 | 1.00* |
| Phycidae | Phyc | | | | | 4 | 4 | <0.01 |
| Mugiliformes | | | | | | | | |
| Mugilidae | Mugi | | | | | 460 | 460 | 0.14* |
| Myctophiformes | | | | | | | | |
| Myctophidae | Myct | | | 2 | 10 | 1,258 | 1,270 | 0.38* |
| Ophidiiformes | | | | | | | | |
| Carapidae | Cara | | | | | 4 | 4 | <0.01 |
| Ophidiidae | Ophd | 10 | 22 | 186 | 1,490 | 3,270 | 4,978 | 1.49* |
| Perciformes | | | | | | | | |
| Acanthuridae | Acan | 2 | | | | 2 | 4 | <0.01 |
| Acropomatidae | Acro | | | | | 12 | 12 | <0.01 |
| Apogonidae | Apog | | | | | 2 | 2 | <0.01 |
| Ariommatidae | Ario | | | | | 16 | 16 | <0.01 |
| Blenniidae | Blen | 42 | 40 | 70 | 80 | 236 | 468 | 0.14* |
| Bramidae | Bram | | | | | 2 | 2 | <0.01 |
| Callionymidae | Call | | | 4 | 114 | 286 | 404 | 0.12* |
| Carangidae | Carg | 58 | 200 | 2,482 | 1,632 | 2,232 | 6,604 | 1.98* |
| Chaetodontidae | Chae | | | | | 2 | 2 | <0.01 |
| Coryphaenidae | Cory | | | | | 4 | 4 | <0.01 |
| Echeneidae | Eche | | | | | 6 | 6 | <0.01 |
| Ephippidae | Ephi | | 4 | 14 | 2 | | 20 | 0.01 |
| Gempylidae | Gemp | | | | 2 | 2 | 4 | <0.01 |
| Gerreidae | Gerr | | 2 | | 58 | 86 | 146 | 0.04* |
| Gobiesocidae | Gobs | 142 | 52 | 20 | 8 | 2 | 224 | 0.07* |
| Gobiidae | Gobi | 2,476 | 2,610 | 52 | 774 | 2,136 | 8,048 | 2.41* |

TABLE 2. Continued.

| Order and family | Code | MB | DI | T10 | T20 | T35 | Total | %Total |
|---|---|---|---|---|---|---|---|---|
| Haemulidae | Haem | 4 | 22 | 6 | 36 | 30 | 98 | 0.03* |
| Labridae | Labr | | | 2 | 116 | 296 | 414 | 0.12* |
| Lutjanidae | Lutj | | | 4 | 62 | 842 | 908 | 0.27* |
| Malacanthidae | Mala | | | | | 4 | 4 | <0.01 |
| Microdesmidae | Micr | 6 | | 4 | 42 | 322 | 374 | 0.11* |
| Mullidae | Mull | | | | | 24 | 24 | 0.01 |
| Nomeidae | Nome | | | | 2 | 16 | 18 | 0.01 |
| Opistognathidae | Opis | | | | 2 | 26 | 28 | 0.01 |
| Percophidae | Perc | | | | | 106 | 106 | 0.03* |
| Pomacentridae | Poma | | | | | 6 | 6 | <0.01 |
| Pomatomidae | Pomt | | | | | 6 | 6 | <0.01 |
| Priacanthidae | Pria | | | | | 10 | 10 | <0.01 |
| Scaridae | Scar | 2 | | | 4 | 10 | 16 | <0.01 |
| Sciaenidae | Scia | 18,062 | 19,726 | 14,940 | 41,180 | 45,888 | 139,796 | 41.83* |
| Scombridae | Scom | | 4 | 120 | 440 | 600 | 1,164 | 0.35* |
| Serranidae | Serr | | 2 | 26 | 380 | 1,182 | 1,590 | 0.48* |
| Sparidae | Spar | 6 | | 2 | 10 | 706 | 724 | 0.22* |
| Sphyraenidae | Sphy | | | 4 | 4 | 230 | 238 | 0.07* |
| Stromateidae | Stro | 4 | 18 | 138 | 836 | 2,536 | 3,532 | 1.06* |
| Trichiuridae | Tric | | | 8 | 104 | 636 | 748 | 0.22* |
| Uranoscopidae | Uran | | | | 2 | 12 | 14 | <0.01 |
| Pleuronectiformes | | | | | | | | |
| Achiridae | Achi | 76 | 64 | 12 | 4 | 4 | 160 | 0.05* |
| Bothidae | Both | 6 | 2 | 2 | 12 | 252 | 274 | 0.08* |
| Cynoglossidae | Cyno | 54 | 16 | 1,164 | 2,206 | 1,662 | 5,102 | 1.53* |
| Paralichthyidae | Parl | 74 | 70 | 334 | 5,338 | 6,566 | 12,382 | 3.71* |
| Scorpaeniformes | | | | | | | | |
| Scorpaenidae | Scor | | | 4 | 14 | 58 | 76 | 0.02* |
| Triglidae | Trig | 76 | 104 | 406 | 1,688 | 1,142 | 3,416 | 1.02* |
| Stomiiformes | | | | | | | | |
| Gonostomatidae | Gono | | | | 4 | 66 | 70 | 0.02* |
| Phosichthyidae | Phos | | | | | 26 | 26 | 0.01 |
| Stomiidae | Stom | | | | | 4 | 4 | <0.01 |
| Syngnathiformes | | | | | | | | |
| Centriscidae | Cent | | | | | 4 | 4 | <0.01 |
| Syngnathidae | Syng | 36 | 34 | 62 | 72 | 20 | 224 | 0.07* |
| Tetraodontiformes | | | | | | | | |
| Balistidae | Bali | | | | | 2 | 2 | <0.01 |
| Monacanthidae | Mona | | | | 14 | 32 | 46 | 0.01 |
| Tetraodontidae | Tetr | 4 | 2 | 10 | 64 | 68 | 148 | 0.04* |
| Total number of larvae identified to families | | 63,784 | 49,120 | 35,876 | 75,202 | 110,196 | 334,178 | |
| Damaged | | 50 | 168 | 36 | 234 | 334 | 822 | |
| Unidentified | | 3,298 | 2,186 | 736 | 3,696 | 5,850 | 15,766 | |
| Total | | 67,132 | 51,474 | 36,648 | 79,132 | 116,380 | 350,766 | |

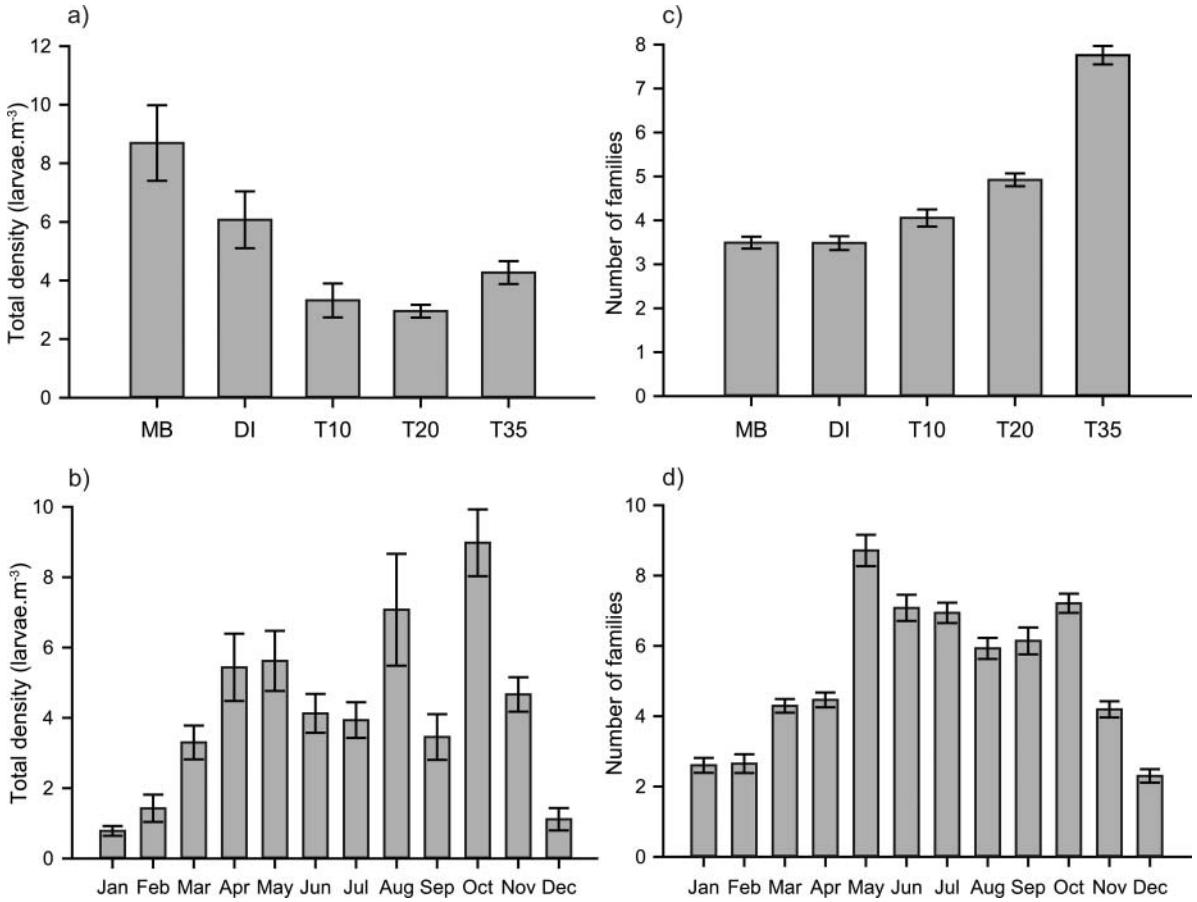


FIGURE 3. Total density of fish larvae by **(a)** station and **(b)** month and diversity of families (i.e., richness) by **(c)** station and **(d)** month in Alabama coastal waters between March 2007 and December 2009. The bars indicate mean values and the vertical lines denote standard errors. The locations of the sampling stations are depicted in Figure 1.



provided very similar results (Table 3). However, the use of categories generally provided more parsimonious and relevant trees (Table 3). The inclusion of year did not provide much improvement to the scores of the analyses. Moreover, even when included in the analyses, year rarely appeared in the resulting trees, showing that it had only a minor influence in structuring larval fish assemblages over the course of the survey (Table 3). The inclusion of temperature and/or salinity, although slightly increasing the amount of explained variability, produced complex trees (from 8 to 16 nodes and 9 to 17 branches) that were difficult to interpret, poorly relevant (poor discrimination of samples from the different branches on the PCA plane), and highly redundant (i.e., temperature and/or salinity appeared several times on different nodes defined by close threshold values) (Table 3). The MRT trials conducted using months, seasons defined by calendar dates, and seasons defined by temperature values were largely overlapping in terms of relevance and statistical performance (Table 3). However, MRT conducted using season defined by calendar dates provided the two most parsimonious trees (trees 1 and 2; Table 3). Tree 2 was finally retained since it appeared more relevant (all of the explanatory factors included were represented at the nodes, and the samples from the different branches were easily distinguished on the PCA plane), and it provided a better statistical score (RE = 0.778, corresponding to 22.2% of the explained variability in assemblage structure) (Table 3).

The selected tree (Figure 4) suggested that larval fish assemblages were hierarchically structured by (1) station (i.e., distance from the shore), (2) season (as defined by calendar dates), and (3) depth (i.e., vertical stratum of the water column). The tree was made of seven branches, thus defining seven assemblages (I–VII; Figure 4). Assemblages I–IV were all typical of offshore stations T10, T20, and T35 but of different seasons and depths (Figure 4). Assemblage I was found in winter and was characterized by high abundances and occurrences of clupeid and sparid larvae (DL = 0.37 and 0.11, respectively; $P < 0.05$; Table 4; Figure 4). Assemblage II was found in spring and summer at the bottom of the water column and was characterized by the families Bregmacerotidae, Synodontidae, Paralichthyidae, Serranidae, and Trichiuridae (DL > 0.10, $P < 0.05$; Table 4; Figure 4). Assemblage III was also typical of spring and summer, but at the surface and midwater column, and was characterized by the families Scombridae, Cynoglossidae,

TABLE 3. Multivariate regression trees coupling the $\log_e(x + 1)$ transformed densities of 36 fish larvae families and 18 different combinations of explanatory factors in Alabama coastal waters. Trees are ranked in increasing order of (1) parsimony (number of nodes and branches), (2) relevance (ratio of the number of explanatory factors appearing in the tree relative to the number of factors included), and (3) statistical score (relative error [RE]). Other factors are defined as follows: season (dates) = season defined by calendar dates; season (temp) = season defined based on temperature variations; depth (cont.) = depth defined as a continuous variable; and depth (cat.) = depth defined as a categorical variable. The symbol "X" indicates environmental factors included in each analysis, and "(X)" indicates factors that were included in the analyses but that are not represented in the resulting tree (i.e., no effect in structuring larval fish assemblage).

| | Selection criteria | | | | Explanatory factors | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tree code | Nodes | Branches | Ratio no. factors | RE | Year | Month | Season (dates) | Season (temp) | Station | Depth (cont.) | Depth (cat.) | Temperature | Salinity |
| 1 | 5 | 6 | 3/4 | 0.788 | (X) | | X | | X | | X | | |
| 2 | 6 | 7 | 3/3 | 0.778 | | | X | | X | | X | | |
| 3 | 7 | 8 | 3/3 | 0.731 | | X | | | X | | X | | |
| 4 | 7 | 8 | 3/3 | 0.763 | | | | X | X | | X | | |
| 5 | 7 | 8 | 3/4 | 0.731 | (X) | X | | | X | | X | | |
| 6 | 7 | 8 | 3/4 | 0.763 | (X) | | | X | X | | X | | |
| 7 | 8 | 9 | 3/3 | 0.718 | | X | | | X | X | | | |
| 8 | 8 | 9 | 3/4 | 0.718 | (X) | X | | | X | X | | | |
| 9 | 8 | 9 | 4/4 | 0.750 | | | | X | X | | X | | X |
| 10 | 10 | 11 | 5/5 | 0.694 | | | | X | X | | X | X | X |
| 11 | 10 | 11 | 5/5 | 0.728 | X | | | X | X | | X | | X |
| 12 | 12 | 13 | 6/6 | 0.673 | X | | | X | X | | X | X | X |
| 13 | 12 | 13 | 5/6 | 0.665 | X | | X | | X | | (X) | X | X |
| 14 | 12 | 13 | 4/5 | 0.672 | | | X | | X | | (X) | X | X |
| 15 | 14 | 15 | 5/6 | 0.639 | (X) | X | | | X | | X | X | X |
| 16 | 16 | 17 | 5/5 | 0.619 | | X | | | X | | X | X | X |
| 17 | 16 | 17 | 5/5 | 0.624 | | X | | | X | X | | X | X |
| 18 | 16 | 17 | 5/6 | 0.624 | (X) | X | | | X | X | | X | X |



Synodontidae, Carangidae, Engraulidae, Paralichthyidae, and Microdesmidae (DL > 0.10, $P < 0.05$; Table 4; Figure 4). Assemblage IV was found exclusively in fall and was associated with high abundances and occurrences of ophidiid, sciaenid, stromateid, paralichthyid, carangid, triglid, callionymid, lutjanid, and cynoglossid larvae (DL > 0.10, $P < 0.05$; Table 4; Figure 4).

Assemblages V–VII were typical of inshore stations MB and DI (Figure 4). Assemblage V was found in fall and winter and characterized by high abundances and occurrences of sciaenid larvae (DL = 0.17, $P < 0.05$; Table 4; Figure 4). Assemblage VI was found in spring and summer at the surface of the water column and was characterized by the families Engraulidae, Gobiidae, Gobiesocidae, Achiridae, and Sciaenidae (DL > 0.10, $P < 0.05$; Table 4; Figure 4). Finally, assemblage VII was also found in spring and summer but at the bottom of the water column and was characterized by the families Gobiidae, Engraulidae, and Sciaenidae (DL > 0.10, $P < 0.05$; Table 4; Figure 4).

Some families presented a restricted seasonal and habitat range, such as the Achiridae in assemblage VI and the Clupeidae and Sparidae in assemblage I. Other families had a more widespread distribution, i.e., they were found in high abundance and occurrence in several assemblages but presented different DL values in each of these groups. For example, gobies were characteristic of assemblages VI and VII, with DL values of 0.18 and 0.30, respectively ($P < 0.05$; Table 4; Figure 4). This family was thus typical of inshore stations during spring and summer (i.e., the conditions associated with both assemblages), but it was more abundant and frequent at the bottom (assemblage VII) than at the surface of the water column (assemblage VI; Table 4; Figure 4). Similarly, the family Paralichthyidae was typically associated with assemblages II, III, and IV, with DL values of 0.12, 0.11, and 0.18, respectively ($P < 0.05$; Table 4; Figure 4). This family was thus consistently found offshore but with higher abundance and occurrence during fall (assemblage IV; Figure 4). Synodontids, carangids, cynoglossids, engraulids, and sciaenids were also associated with several assemblages. Their respective affinities for different assemblages and associated habitats and seasons can be classified in decreasing order of the corresponding DL values (Table 4).

The assemblages identified by MRT were clearly associated with distinct water column conditions (Figure 4). Overall, inshore larval fish assemblages were found in low and highly variable salinity values (V to VII; Figure 4). Conversely, offshore assemblages were consistently associated with high salinities (I to IV; Figure 4). A single assemblage was characteristic of fall and winter inshore (V) and associated with relatively cool

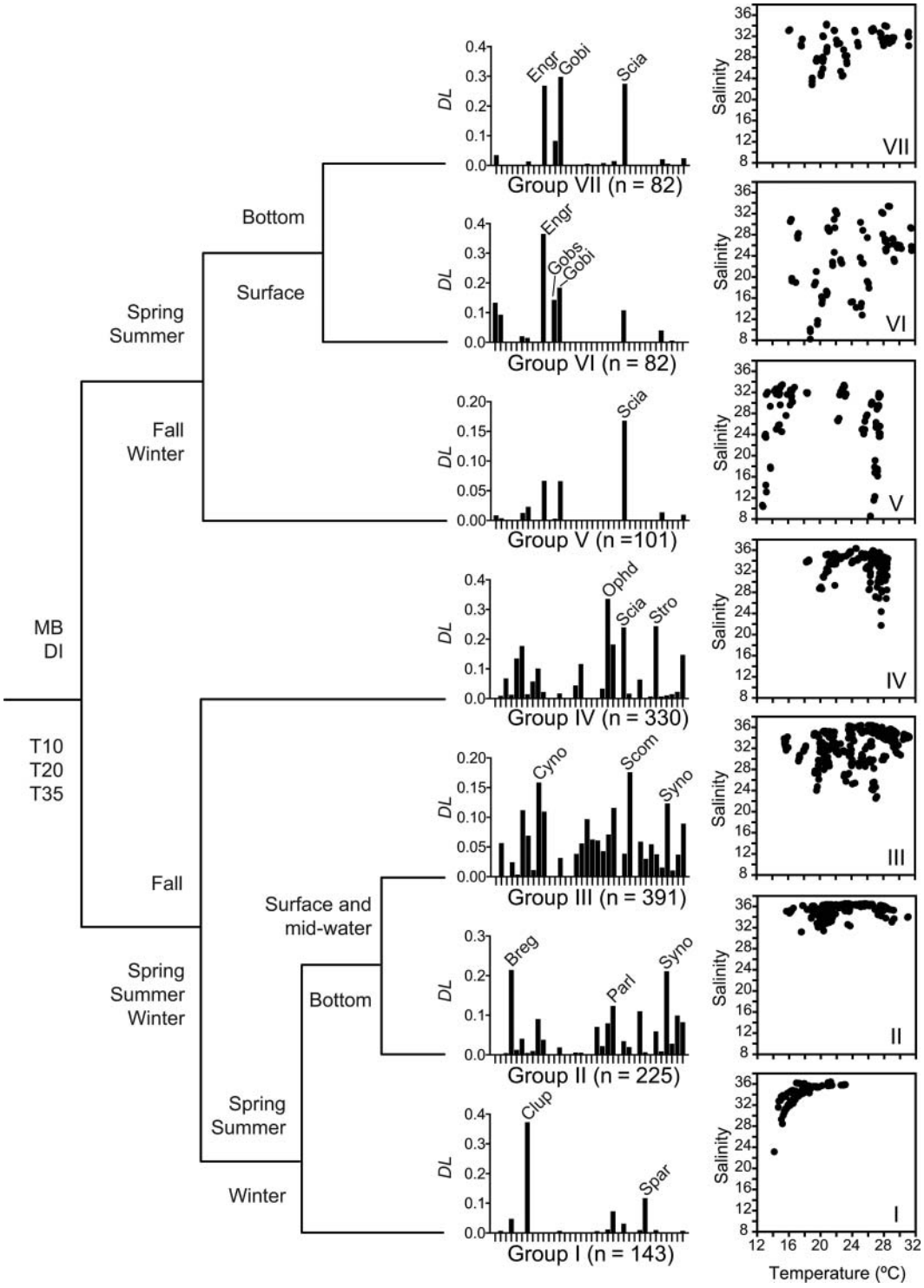


FIGURE 4. Multivariate regression tree synthesizing the structure of larval fish assemblages (the $\log_e[x + 1]$ transformed densities of 36 families; Table 2) as a function of sampling station (i.e., distance from shore), season (as defined by dates), and depth (vertical strata of the water column, expressed by categories). This tree corresponds to test 2 in Table 3 (RE = 0.778). Each node is associated with a particular explanatory variable, the values of which vary in different directions. The order in which the variables appear on the tree corresponds to the weights these variables have on the structure of the assemblages, with one assemblage = one group. The locations of the sampling stations (first node) are depicted in Figure 1. The histograms represent the Dufrêne–Legendre indices (DLs) obtained for each of the 36 fish larvae families in each assemblage, the families being ordered alphabetically from left to right. For clarity, only families with the highest DL are labeled, but see Table 4 for the full list of families included and the corresponding DL values and their significance. Family codes are given in Table 2. Each group has been assigned a Roman numeral from I to VII, and the number of samples constituting each group is also indicated ($n$). The plots at the right of the graph represent temperature ($x$-axis) and salinity ($y$-axis) in the samples constituting groups I to VII.

TABLE 4. Values of Dufrêne–Legendre indices characterizing the relative abundance and occurrence of 36 fish larvae families in seven assemblages observed at different stations, seasons, and depths in Alabama coastal waters. Assemblages were identified using the multivariate regression trees depicted in Figure 4. Blank cells indicate values of 0; the symbol " × " indicates values <0.01.

| | Assemblage | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Family | I | II | III | IV | V | VI | VII | *P*-value |
| Achiridae | | | × | × | 0.01 | 0.13 | 0.03 | 0.01 |
| Blenniidae | × | × | 0.06 | 0.01 | × | 0.09 | × | 0.01 |
| Bothidae | × | × | × | 0.06 | × | | × | 0.01 |
| Bregmacerotidae | 0.04 | 0.21 | 0.02 | 0.01 | × | | × | 0.01 |
| Callionymidae | | 0.01 | × | 0.13 | | | | 0.01 |
| Carangidae | × | 0.04 | 0.11 | 0.17 | 0.01 | 0.02 | × | 0.01 |
| Clupeidae | 0.37 | × | 0.07 | 0.01 | 0.02 | 0.01 | 0.01 | 0.01 |
| Congridae | × | 0.01 | 0.01 | 0.05 | | | | 0.01 |
| Cynoglossidae | × | 0.09 | 0.16 | 0.10 | × | × | × | 0.01 |
| Engraulidae | × | 0.04 | 0.11 | 0.02 | 0.07 | 0.36 | 0.27 | 0.01 |
| Gerreidae | | × | 0.02 | × | | | × | 0.07 |
| Gobiesocidae | | × | × | × | × | 0.14 | 0.08 | 0.01 |
| Gobiidae | × | 0.02 | 0.03 | 0.01 | 0.06 | 0.18 | 0.30 | 0.01 |
| Gonostomatidae | × | 0.01 | 0.01 | 0.01 | | | | 0.30 |
| Haemulidae | × | 0.01 | 0.01 | × | | 0.01 | 0.02 | 0.23 |
| Labridae | | × | 0.04 | 0.04 | | | | 0.03 |
| Lutjanidae | | × | 0.05 | 0.11 | | | | 0.01 |
| Microdesmidae | × | × | 0.10 | × | | | × | 0.01 |
| Mugilidae | | × | 0.06 | × | | | | 0.01 |
| Myctophidae | × | 0.07 | 0.06 | × | | | | 0.01 |
| Ophichthyidae | × | 0.02 | 0.04 | 0.03 | × | × | 0.01 | 0.02 |
| Ophidiidae | 0.01 | 0.08 | 0.07 | 0.33 | × | × | × | 0.01 |
| Paralichthyidae | 0.07 | 0.12 | 0.11 | 0.18 | × | × | 0.01 | 0.01 |
| Percophidae | | × | | | | | | 0.52 |
| Sciaenidae | 0.03 | 0.03 | 0.04 | 0.24 | 0.17 | 0.11 | 0.27 | 0.01 |
| Scombridae | | 0.02 | 0.17 | 0.01 | | × | | 0.01 |
| Scorpaenidae | | 0.01 | 0.01 | 0.01 | | | | 0.24 |
| Serranidae | 0.01 | 0.11 | 0.06 | 0.06 | | × | | 0.01 |
| Sparidae | 0.11 | × | 0.03 | × | × | × | | 0.01 |
| Sphyraenidae | | × | 0.05 | × | | | | 0.01 |
| Stromateidae | 0.01 | 0.06 | 0.04 | 0.24 | × | × | × | 0.01 |
| Syngnathidae | × | 0.01 | 0.01 | × | 0.01 | 0.04 | 0.02 | 0.03 |
| Synodontidae | × | 0.21 | 0.12 | 0.01 | | × | × | 0.01 |
| Tetraodontidae | | 0.03 | 0.01 | 0.01 | | × | × | 0.06 |
| Trichiuridae | × | 0.10 | 0.04 | 0.02 | | | | 0.01 |
| Triglidae | × | 0.08 | 0.09 | 0.14 | 0.01 | × | 0.02 | 0.01 |



temperatures, while two separate offshore assemblages were associated with warm waters in fall (IV) and cool waters in winter (I) (Figure 4).

## DISCUSSION

Our MRT approach was successful in hierarchically organizing the spatial and temporal components of variability in larval fish abundance and diversity. The results emphasize the importance of cross-shore location in structuring assemblages on the Alabama shelf. Larval fish assemblages varied seasonally and as a function of depth, but inshore and offshore assemblages remained clearly separated regardless of the season and depth considered. The combined effects of adult spawning behavior and the later responses of larvae to local oceanographic conditions (and the influence of the Mobile River in particular) may explain this strong and consistent cross-shelf structure in ichthyoplankton assemblages. The discharge from the Mobile River indeed contributes to strong contrasts between inshore

and offshore water masses along the Alabama inner shelf (Dzwonkowski et al. 2011), as reflected by the strong cross-shore variations in temperature and salinity observed in this study. The seven larval fish assemblages distinguished by our MRT analyses were clearly related to these cross-shore variations in temperature and salinity (Figure 4). Coastal ichthyoplankton assemblages in the nearby Mississippi Sound have also been shown to respond to salinity variations arising from Mobile Bay discharge (Rakocinski et al. 1996). Similarly, variations in river discharge were identified as a major driver of interannual variability in juvenile fish abundances in our study region (Carassou et al. 2011). Our results thus confirm existing lines of evidence suggesting that riverine influences play a major role in fish population dynamics along the Alabama inner shelf. This is consistent with observations from other coastal locations from the East and West Coasts of the United States (Kimmerer et al. 2001; Martino and Houde 2010) and the southern Gulf of Mexico (Sanvicente-Añorve et al. 2000).

Consistent with observations from the U.S. southeast continental shelf (Marancik et al. 2005), the coasts of Oregon (Auth and Brodeur 2006), and the southern Gulf of Mexico (Sanvicente-Añorve et al. 1998), the spatial distribution patterns observed in this study also reflect adult spawning behavior. For example, larvae of Engraulidae, Gobiidae, and Gobiesocidae were typically collected within Mobile Bay and at the nearshore stations (Table 4; Figure 4). Larvae of these three families are also abundant in the protected estuarine waters of nearby Mississippi Sound, where bay anchovy *Anchoa mitchilli*, for example, comprised 81% of all ichthyoplankton collected (Rakocinski et al. 1996). In the northern Gulf of Mexico, engraulids such as the bay anchovy are extremely abundant in nearshore waters as adults, where they are known to spawn (Hoese and Moore 1998). Gobiids and gobiesocids lay demersal eggs on a variety of benthic substrates near the coast (Richards 2006). Our results suggest that larvae are then retained in nearshore habitats.

The spawning behavior of adults may also explain the offshore distribution of larvae from the families Clupeidae, Bregmacerotidae, Synodontidae, Scombridae, and Ophidiidae (Table 4; Figure 4), which were also abundantly collected in the offshore Gulf of Mexico Loop Current (Richards et al. 1993). Most species from these families release pelagic eggs in open waters offshore, and for some species larvae are then transported to coastal environments via currents (Rakocinski et al. 1996; Richards 2006; Able and Fahay 2010). Gulf menhaden *Brevoortia patronus*, the dominant clupeid in the region, spawns offshore during winter months, and the larvae are then transported to estuarine nursery habitats (Hoese and Moore 1998). Little is known about the spawning and early life history of Bregmacerotidae in the northern Gulf of Mexico, but most of the species occurring in the northern Gulf are primarily found in the mid or outer shelf as adults (Richards 2006; Hernandez et al. 2010b).

The MRT statistical scores obtained when we were using seasons defined by calendar date versus water temperature were very similar (RE comprised between 0.665 and 0.788, and between 0.673 and 0.763, respectively; Table 3). This result indicates that, at the spatial and temporal scales at which our study was conducted, calendar dates were sufficient for obtaining an accurate and comprehensive picture of the seasonal structure of ichthyoplankton assemblages. Therefore, larval seasonal patterns did not vary much over the 28 months during which sampling occurred, suggesting invariant spawning over the study period. Temperature-defined seasons might have performed better for a longer time series, where potential variations in the spawning periods of adults could result in a higher variability in the monthly patterns of larval occurrences. Nevertheless, the seasonal structure of ichthyoplankton assemblages revealed using calendar-defined seasons in our study is largely consistent with the seasonal patterns previously reported in the same area using temperature-defined seasons (Hernandez et al. 2010a).

The seasonal distribution of larval fishes observed in our study (during 2007–2009) is also largely consistent with previous observations (during 2004–2006) based on samples collected from a single station corresponding to our station T20 (Hernandez et al. 2010a, 2010b). The lowest larval densities and taxonomic richness were consistently observed during winter periods, with clupeids and sparids dominating the collections (Table 4; Figure 4; Hernandez et al. 2010a, 2010b). Dominant spring and summer taxa were also similar to observations from Hernandez et al. (2010a, 2010b) and included synodontids, scombrids, and engraulids, while ophidiid and stromateid larvae appeared to be typical of the fall season. In some instances, however, seasonal differences were observed between our study and those of Hernandez et al. (2010a, 2010b), a likely result of the larger spatial scale of our study. For example, gobiid larvae were found to be abundant in spring and summer in the present study, whereas Hernandez et al. (2010b) reported low numbers of gobiid larvae all year round at T20, with a peak in October. Their density estimates of gobiid larvae, which (as revealed by the present study; Figure 4) are characteristic of inshore waters, may thus have been underestimated during spring and summer. This example highlights the advantages of a large-scale and high-resolution cross-shore sampling design, which enhances the probability of collecting larvae from inshore or offshore taxa that are otherwise rarely collected.

Although many ichthyoplankton assemblage studies are based on family-level analyses (e.g., Thorrold and Williams 1996; Sponaugle et al. 2003; Munk et al. 2004; Sampey et al. 2004), this approach is not without its limitations. In some instances, our family-level MRT approach performed well in describing the distributions of larval fishes that were largely restricted in their habitat (e.g., Bregmacerotidae, Gobiesocidae, Scombridae) or seasonal (e.g., Callionymidae, Lutjanidae, Synodontidae) ranges (Table 4; Figure 4). For these families, our results suggest that the species within each family are similar in their response to habitat and seasonal factors in our region (e.g., bregmacerotid species in our region are largely

restricted to offshore waters) and thus family-level analyses may be adequate for these groups. For other families, however, the relatively low taxonomic resolution of our analysis may have confounded their distribution patterns. This is reflected by the relatively low amount of variability explained by the selected tree (22.2%), although such statistical scores are typical for data sets describing patchily distributed communities, including larval and juvenile fish abundances (Sampey et al. 2004; DeVantier et al. 2006; Cappo et al. 2007; Carassou et al. 2008). Larval sciaenids and paralichthyids, for example, were abundant in a variety of water masses and throughout different seasons (Table 4; Figure 4). Therefore, the multiple associations obtained for these families may be indicative of important differences in the ecological affinities of the multiple species being combined. In these instances, the value of our family-level approach is that it identified families that likely need to be examined at higher taxonomic resolution (e.g., the genus or species level).

The families Sciaenidae and Paralichthyidae are among the most diverse in the Alabama shelf region, with approximately 16 and 19 species, respectively (Richards 2006), among which 9 species and 5 genera, respectively, were observed as larvae in the area (Hernandez et al. 2010b). Sciaenids are thus an ideal group for examining species-specific ecological preferences and early life histories. This group of diverse species supports important fisheries in the northern Gulf of Mexico, including Alabama waters (Browder 1993), and adequate morphological descriptions of sciaenid larvae are available for most species in the region (Richards 2006). Thus, our future work will include species-level identifications of sciaenids (based on both morphometric and molecular techniques), followed by a similar hierarchical approach to explore the spatial and temporal distributional patterns of these larvae in the northern Gulf of Mexico.

To conclude, our results showed that the larval fish assemblages from Alabama coastal waters were primarily structured by the distance from the shore, likely due to strong contrasts in physical characteristics (e.g., salinity) between inshore and offshore water masses generated by the Mobile River delta. These results emphasize the importance of riverine processes as a major determinant of fish population dynamics in the north-central Gulf of Mexico, as has been suggested by Govoni (1997) and Grimes (2001) in the Mississippi River delta.

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