Abstract—Multiyear ichthyoplankton surveys used to monitor larval fish seasonality, abundance, and assemblage structure can provide early indicators of regional ecosystem changes. Numerous ichthyoplankton surveys have been conducted in the northern Gulf of Mexico, but few have had high levels of temporal resolution and sample replication. In this study, ichthyoplankton samples were collected monthly (October 2004–October 2006) at a single station off the coast of Alabama as part of a long-term biological survey. Four seasonal periods were identified from observed and historic water temperatures, including a relatively long (June–October) "summer" period (water temperature >26°C). Fish egg abundance, total larval abundance, and larval taxonomic diversity were significantly related to water temperature (but not salinity), with peaks in the spring, spring–summer, and summer periods, respectively. Larvae collected during the survey represented 58 different families, of which engraulids, sciaenids, carangids, and clupeids were the most prominent. The most abundant taxa collected were unidentified engraulids (50%), sand seatrout (*Cynoscion arenarius,* 7.5%), Atlantic bumper (*Chloroscombrus chrysurus,* 5.4%), Atlantic croaker (*Micropogonias undulatus,* 4.4%), Gulf menhaden (*Brevoortia patronus,* 3.8%), and unidentified gobiids (3.6%). Larval concentrations for dominant taxa were highly variable between years, but the timing of seasonal occurrence for these taxa was relatively consistent. Documented increases in sea surface temperature on the Alabama shelf may have various implications for larval fish dynamics, as indicated by the presence of tropical larval forms (e.g., fistularids, labrids, scarids, and acanthurids) in our ichthyoplankton collections and in recent juvenile surveys of Alabama and northern Gulf of Mexico seagrass habitats.

Seasonal variability in ichthyoplankton abundance and assemblage composition in the northern Gulf of Mexico off Alabama

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Ichthyoplankton surveys provide fisheries-independent information that is inherently "ecosystem-based"; entire larval fish assemblages are collected (i.e., early stages of both exploited and unexploited finfish species) along with zooplankton predators and prey, and often with a suite of environmental observations (e.g., salinity, temperature). At the ecosystem level, information on larval assemblages can be used to detect changes in marine fish community composition and abundances over time (Sherman et al., 1984). Previous studies have indicated that larval assemblages are the result of convergent spawning strategies by multiple species taking advantage of favorable environmental conditions for larval fish survival (Doyle et al., 1993; Sherman et al., 1984). The composition of larval fish assemblages varies spatially and temporally because of the behaviors of the larvae (Gray and Miskiewicz, 2000; Hare and Govoni, 2005) and the spawning adults (Sherman et al., 1984; Hernández-Miranda et al., 2003), as well as oceanographic transport and mixing processes (Auth, 2008; Muhling et al., 2008). Variability in any of these factors, therefore, may result in a different structure of larval fish assemblages. Because larval fish survival is closely tied with primary and secondary productivity

in coastal oceans, changes in larval fish assemblage structure (over larger time scales) can be an early indicator of climate-related environmental shifts (Auth, 2008; Brodeur et al., 2008).

Despite the importance of the region to fisheries, seasonal variability in larval fish assemblages in the northern Gulf of Mexico has been examined in relatively few studies. Much of the previous ichthyoplankton research has focused on estuarine assemblages (Raynie and Shaw, 1994; Tolan et al., 1997) or on relatively short-term interactions between assemblages and specific oceanographic features, such as the Mississippi River plume (Sogard et al., 1987; Govoni et al., 1989) or the Loop Current (Richards et al., 1993). Other studies have used ichthyoplankton survey data from the National Marine Fisheries Service's (NMFS's) gulf-wide Southeast Monitoring and Assessment Program (SEAMAP), but these studies are typically focused on a single species (Scott et al., 1993; Lyczkowski-Shultz and Ingram, 2003; Lyczkowski-Shultz and Hanisko, 2007). Ditty et al. (1988) summarized the available ichthyoplankton literature at the time to provide information on larval fish seasonality for the entire northern Gulf of Mexico, and more
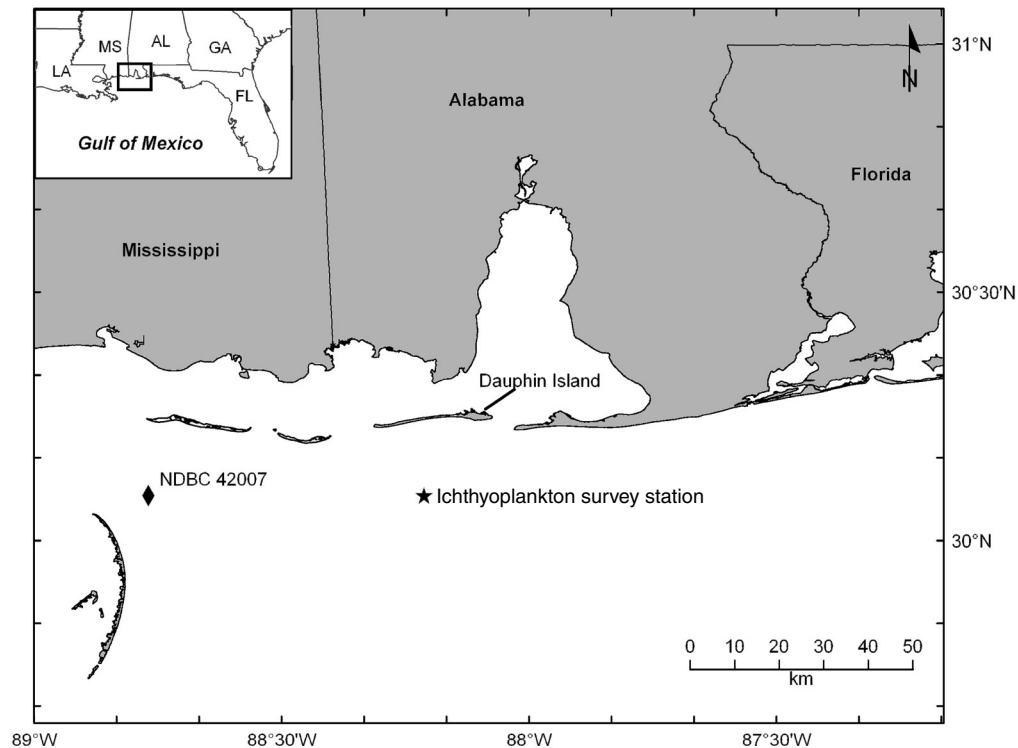
Figure 1

Location of the sampling station used during the October 2004–October 2006 ichthyo-plankton monitoring survey (star symbol) and the NOAA National Data Buoy Center oceanographic data buoy (NDBC 42007) used to determine the 10-year (1993–2003) mean monthly water temperature estimates for the region (diamond symbol).

recently, Lyczkowski-Shultz et al.[1] reported on larval fish seasonality and distribution for the northeastern Gulf of Mexico.

Although these latter studies provided information on multiple species, no analyses of larval fish assemblages and environmental variability were presented. Here we report on the seasonality and concentrations of larval fishes in relation to water temperature based on data collected during an intensive two year (October 2004–October 2006) ichthyoplankton survey conducted off the coast of Alabama. The objectives of this study were 1) to examine the seasonal variability in ichthyo-plankton diversity and taxon-specific abundances off the coast of Alabama; and 2) to examine variability in the relationship between larval fish assemblages and seasonal changes in water temperature. These objectives would contribute to our overall goal of understanding the oceanographic factors that maintain larval fish assemblages.

[1] Lyczkowski-Shultz, J., D. S. Hanisko, K. J. Sulak, and G. D. Dennis III.   2004.   Characterization of ichthyoplankton within the U.S. Geological Survey's northeastern Gulf of Mexico study area—based on analysis of Southeast Area Monitoring and Assessment Program (SEAMAP) sampling surveys, 1982–1999, 136 p.   NEGOM Ichthyoplankton Synopsis Final Report, U.S. Dep. Interior, U.S. Geological Survey, USGS SIR-2004-5059.

Materials and methods

Data collection

The sampling station was located on the inner continental shelf of the northern Gulf of Mexico, approximately 18 km south of Dauphin Island, Alabama, at a water depth of approximately 20 m (Fig. 1). Ichthyoplankton sampling was conducted during monthly day-time surveys (n=26) and quarterly diel surveys (n=8) from October 2004 to October 2006 (Table 1). All samples were collected with a Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS) (Open Seas Instrumentation, Inc., Musquodoboit Harbour, Nova Scotia, Canada), with a 0.25-m^2 mouth opening fitted with seven (during quarterly surveys) or eight (during monthly surveys) plankton nets. During monthly surveys, six depth-discrete samples (18–15 m, 15–12 m, 12–9 m, 9–6 m, 6–3 m, and 3–1 m) and one oblique sample (18–1 m) were collected during eight replicate tows at the study site with 202-μm mesh nets. An additional oblique sample was collected during each tow with a 333-μm mesh net for a nominal total of 64 samples per monthly cruise. All eight replicate tows were collected during daylight hours, generally during a single day. During the quarterly surveys, a set of six depth-discrete samples (same depth bins as monthly survey) and one

Table 1

Station data for ichthyoplankton samples collected during a larval fish monitoring survey at a site located approximately 18 km south of Dauphin Island, Alabama (October 2004–October 2006). Seasonal classification is based on historic (10-year average) and observed monthly mean temperatures for the region (see Fig. 2).

Year	Cruise date	Survey type	Seasonal classification	Number of samples
2004	22 Oct	monthly	Summer	54
2004	16–17 Nov	diel	Fall	41
2004	29 Nov	monthly	Fall	47
2004	08 Dec	monthly	Fall	47
2005	06–07 Jan	monthly	Winter	48
2005	18–21 Jan	diel	Winter	76
2005	16 Feb	monthly	Winter	50
2005	29 Mar	monthly	Spring	23
2005	05 Apr	monthly	Spring	18
2005	19 Apr	monthly	Spring	47
2005	09–13 May	diel	Spring	72
2005	17 May	monthly	Spring	48
2005	09 Jun	monthly	Summer	47
2005	13 Jul	monthly	Summer	48
2005	09 Aug	monthly	Summer	46
2005	14 Sep	monthly	Summer	48
2005	27–29 Sep	diel	Summer	72
2005	11 Oct	monthly	Summer	31
2005	09 Nov	monthly	Fall	32
2005	29 Nov–02 Dec	diel	Winter	71
2005	16 Dec	monthly	Winter	40
2006	12 Jan	monthly	Winter	44
2006	07–10 Feb	diel	Winter	60
2006	17 Feb	monthly	Winter	43
2006	16 Mar	monthly	Spring	39
2006	12–13 Apr	monthly	Spring	38
2006	01–04 May	diel	Spring	70
2006	17 May	monthly	Spring	43
2006	15 Jun	monthly	Summer	42
2006	05 Jul	monthly	Summer	46
2006	10 Aug	monthly	Summer	46
2006	08 Sep	monthly	Summer	46
2006	19–22 Sep	diel	Summer	66
2006	12 Oct	monthly	Summer	47

oblique sample were collected with 202-μm mesh nets at dawn, noon, dusk, and midnight (local time) over the course of three diel periods for a nominal total of 84 samples per quarterly cruise. Contents of nets were rinsed with seawater, sieved, and preserved in 4% formalin for 48 hours before being transferred to 70% ethanol. A conductivity-temperature-depth probe (CTD) (SBE19, Sea-Bird Electronics, Inc., Bellevue, WA) was integrated into the BIONESS system and provided temperature, salinity, and depth profiles for each plankton tow. A flowmeter (General Oceanics, Miami, FL) mounted within the BIONESS frame estimated the volume of water filtered for each sample. Filtered volume estimates for each sample were compared with measurements from a second, externally mounted flowmeter to estimate filtra-tion efficiency. In all, 1634 ichthyoplankton samples were processed and used in subsequent analyses. Although all fish larvae were collected from a single station, Alabama has a relatively short coastline (<85 km), thus the larval fishes collected likely represent the ichthyofauna of the entire Alabama inner shelf region.

Preparation of environmental data

CTD data were processed using the manufacturer's software (SEASOFT, Seabird Electronics, Inc., Bellevue, WA) and averaged into 0.5-m bins. Seasonal patterns in water temperature were examined using depth-integrated monthly mean temperatures recorded during each sampling month. For historic comparisons, the 10-year

average for water temperature was calculated for each month with data from a coastal observing buoy (NOAA National Data Buoy Center Station 42007) located approximately 54 km west of our sampling station at a water depth of approximately 15 m (Fig. 1). Although the temperature values from the buoy were measured near the surface (0.6-m depth), these observations serve as good indicators of seasonal shifts in water-column thermal structure, as indicated by our own CTD comparisons of sea surface temperature and depth-integrated temperature (correlation coefficient, r^2=0.98; slope, m=0.90; P<0.0001). Together, these data were used to define ecologically relevant "seasons" (rather than calendar date) for multivariate analyses.

Preparation of ichthyoplankton data

Ichthyoplankton samples were sorted and larval fish were identified to the lowest possible taxonomic level at the Plankton Sorting and Identification Center (Szczecin, Poland) and at the Dauphin Island Sea Laboratory (Dauphin Island, Alabama). Many larval fishes were not identified to the species level, owing to the relatively small sizes of larvae collected in the 202-μm mesh nets and the overall diversity of larval forms present in the western central Atlantic region, which includes the Gulf of Mexico (Marancik et al., 2005). Most identifications were at the family level (52%), followed by species (22%), order (14%), and genus (7%) level identifications. Five percent of the larvae collected were damaged or unidentified.

Unidentified clupeiforms (engraulids and clupeids) were excluded from further analyses because their extreme concentrations and taxonomic ambiguity can often mask abundance and assemblage trends (Tolan et al., 1997; Hernandez et al., 2003). Order-level taxa and unidentified larvae were removed from consideration for similar reasons. Further taxonomic analyses, therefore, were limited to taxa that represented at least 1% of the total catch during any individual sampling event, where the proportion of the total catch for each taxonomic group was determined after removing unidentified larvae, order-level larvae, and all unidentified clupeiforms. Following Marancik et al. (2005), we further modified the data sets to exclude genus-level groupings in instances where many congeners could potentially mask any seasonal trends. The following genus-level groupings were retained because each represented relatively few congeners with likely similar early life histories in the northern Gulf of Mexico: *Auxis* spp. (*A. rochei* and *A. thazard*), *Centropristis* spp. (*C. philadelphica*, *C. ocyurus,* and *C. striata*), *Diplectrum* spp. (*D. bivattatum* and *D. formosum*), *Microdesmus* spp. (*M. lanceolatus* and *M. longipinnis*), and *Paralichthys* spp. (*P. albigutta*, *P. lethostigma,* and *P. squamilentus*). Similarly, all family-level groups were removed except Gerreidae (most likely *Eucinostomus gula* or *E. argentus*) and Labridae (most likely *Xyrichtys novacula*). In all, 30 taxa were considered for analyses (Table 2). Because the objective of this study was to examine the seasonal variability of

larval fish occurrence and relative larval fish concentrations and not size-selectivity or vertical distribution, our analyses included ichthyoplankton data collected from all surveys (monthly and quarterly diel), mesh sizes (202 μm and 333 μm), and depth bins. Depth stratification and gear selectivity will be addressed in separate analyses in forthcoming publications.

Analyses

All fish egg and larval fish abundances were standardized by the volume filtered to determine concentration estimates (no./m³). Taxonomic diversity was calculated for each sample by taking the exponential of Shannon entropy, exp(H), following the method of Jost (2006). Monthly mean observations of total fish eggs, total fish larvae, and taxonomic diversity were compared to mean temperature and salinity data by using least squares regressions. Two approaches were used to examine larval fish seasonality. First, monthly mean concentrations (no./100 m³) were calculated for the dominant taxa to examine monthly trends in abundance. Second, observed and historic water temperature observations were used to define distinct seasons for the sampling region. Seasonality in fish egg concentrations, total larval fish concentrations, and taxonomic diversity was examined (after log+1 transformation) by using one-way ANOVAs with season as a factor and Tukey's honesty significant difference (HSD) tests. Lastly, larval concentrations for dominant taxa were square-root transformed and analyzed by using Bray Curtis similarity and cluster analysis with the PRIMER statistical package (PRIMER, vers. 6, Plymouth Marine Laboratory, Plymouth, U.K.).

Results

Mean monthly water temperature varied seasonally over the two year period, with a low of 16.5°C (January 2005) and a high of 30.2°C (August 2006) (Fig. 2). The general pattern of our monthly temperature observations was similar (±2°C) to that of recent historical values (Fig. 3). Notable deviations were relatively cooler temperature observations in May during our study (mean differences of 3.2°C and 2.4°C during 2005 and 2006, respectively) and warmer temperatures in October (mean differences of 2.6°C and 3.0°C during 2005 and 2006, respectively) and December (mean difference of 3.0°C in 2004). Even with these disparities, both data sets were in agreement to define seasonal breaks in water temperature. (Fig. 3). Sampling periods with mean water temperature values <18°C were classified as winter, and those with mean water temperatures above 26°C were classified as summer. The transitional periods of spring and fall had mean water temperatures between 18°C and 26°C. In general, the observed seasonal pattern comprised three-month winter (December–February) and spring (March–May) seasons, a relatively long five-month summer period (July–October), and a relatively

Table 2

Seasonal (X) and peak (*) occurrence of the dominant larval fish taxa collected in plankton samples ($n=1634$) off the coast of Alabama from October 2004 to October 2006. Seasonal classification is based on historic (10-year average) and observed monthly mean temperatures for the region. (see Fig. 2).

Family	Taxon	Season Winter	Spring	Summer	Fall
Elopidae	*Elops saurus*	*		X	X
Ophichthidae	*Myrophis punctatus*	X	X		*
Clupeidae	*Brevoortia patronus*	*	X	X	X
	Etrumeus teres	X	*		X
	Harengula jaguana		X	*	
	Opisthonema oglinum		*	X	
Serranidae	*Centropristis* spp.	X	X	*	
	Diplectrum spp.		X	*	
	Serraniculus pumilio		X	*	
Carangidae	*Chloroscombrus chrysurus*		X	*	
	Decapterus punctatus		X	*	
Lutjanidae	*Lutjanus campechanus*			*	
Gerreidae	Unidentified		X	*	
Sciaenidae	*Cynoscion arenarius*	X	X	*	
	Cynoscion nothus		X	*	X
	Larimus fasciatus	X	X	*	X
	Leiostomus xanthurus	X	X	X	*
	Micropogonias undulatus	X	X	*	X
	Sciaenops ocellatus			X	
Labridae	Unidentified		X	*	
Microdesmidae	*Microdesmus* spp.		X	*	
Scombridae	*Auxis* spp.		X	*	
	Euthynnus alletteratus		X	*	
	Scomberomorus maculatus		X	*	
Stromateidae	*Peprilus alepidotus*		X	*	
	Peprilus burti	X	X	*	X
Paralichthyidae	*Citharichthys spilopterus*	*	X	X	X
	Etropus crossotus		*	X	
	Paralichthys spp.	X	X	*	X
	Syacium papillosum		*	X	

short one-month fall period (November). In one instance, the interannual variability in water temperature at our sampling site allowed for the same month to be designated as a different season during different years (December was classified as "fall" in 2004 and "winter" in 2005) (Table 1).

No seasonal pattern in salinity was observed at the sampling station (Fig. 3). Salinity observations were generally lower and more variable during the first year of the study, with values fluctuating between 30.4 and 34.6 between October 2004 and September 2005. Salinity was generally higher and less variable between October 2005 and October 2006, with values ranging between 33.0 and 34.8.

A total of 504,478 fish eggs and 311,970 fish larvae were collected over the course of the survey. Total fish egg concentrations during the survey ranged from 0.16 to 48.3 eggs/m^3 (Fig. 3). Egg concentrations were sig-

nificantly higher in the spring than in other seasons ($F=271.3$, $P<0.0001$, spring>summer>fall>winter). Total fish larvae concentrations ranged from 0.15 to 35.0 larvae/m^3 (Fig. 3). Larval concentrations were significantly higher during summer and spring seasons ($F=206.1$, $P<0.0001$, spring=summer>fall>winter). The diversity of ichthyoplankton assemblages, $\exp(H)$, ranged from 1.32 to 9.48 and was also highest during the summer seasons ($F=299.3$, $P<0.0001$, summer>spring>fall>winter) (Fig. 3). Species diversity was significantly related to temperature as determined by a least squares regression ($F=34.7$, $P<0.001$, $r^2=0.60$). Although also significantly correlated, the relationships between temperature and fish egg concentrations ($F=4.4$, $P<0.05$, $r^2=0.16$) and total larval concentrations ($F=6.9$, $P<0.05$, $r^2=0.23$) were not as strong. No significant relationships were observed between salinity and fish eggs ($F=0.22$, $P=0.64$, $r^2=0.01$), total fish larvae ($F<0.01$, $P=0.94$,

$r^2<0.01$), and taxonomic diversity ($F=0.16$, $P=0.69$, $r^2=0.01$).

Excluding order-level larvae and unidentified larvae, unidentified engraulids dominated our collections and represented approximately 50% of the total (overall) catch (Table 3). Engraulid larvae were present year-round and likely comprised several commonly occurring species in the region, including *Anchoa hepsetus, A. nasuta, A. mitchilli*, and *Engraulis eurystole*. No attempt was made to examine these fishes beyond the family level because many were relatively small (<10 mm) and damaged, and engraulid identifications are problematic in our region (Farooqi et al., 2006a). Other taxa that represented over 1% of the overall catch included *Cynoscion arenarius* (7.5%), *Chloroscombrus chrysurus* (5.4%), *Micropogonias undulatus* (4.4%), *Brevoortia patronus* (3.8%), unidentified Gobiidae (3.6%), unidentified Sciaenidae (2.8%), unidentified Ophidiidae (2.5%), *Symphurus* spp. (2.1%), *Menticirrhus* spp. (1.2%), unidentified Clupeidae (1.2%), *Syacium* spp. (1.2%), and *Etropus crossotus* (1.0%).

Larval fish specimens collected during the survey represented 58 different families. Larvae belonging to 22 of these families could not be identified beyond the family level, usually because published descriptions of

representative species in our region are either lacking or are insufficient to discern between different species within the family (e.g., Gerreidae, Sparidae, Haemulidae, Echeneidae, Labridae, Scorpaenidae). Several families were well represented with numerous species or genera, including Ophichthidae (11 identified species), Sciaenidae (9 species), Carangidae (7 species), Myctophidae (6 genera), Paralichthyidae (5 genera), and Clupeidae (5 species). Overall, the dominant families collected during our survey (e.g., Engraulidae, Sciaenidae, Carangidae, and Clupeidae) are the same as those from previous surveys in the general vicinity (Table 3). In general, the taxonomic richness observed in our survey falls between that found in surveys of shorter duration and in limited spatial-scale surveys (e.g., Williams,1983; Rakocinski et al., 1996) and from SEAMAP surveys that encompass a larger area and longer (20 years) time scales (ENTRIX, 2006).

Seasonal patterns were observed for most of the dominant taxa collected (Fig. 4). *Lutjanus campechanus* and *Chloroscombrus chrysurus* were collected only during the summer periods (June–October). Similarly, *Sciaenops ocellatus* larvae were collected only during late summer (September–October). In contrast, *Citharichthys spilopterus* was collected in almost every sampling event, indicating year-round spawning or extended pelagic larval durations. Although several species had winter peaks, none were present exclusively during winter months. *Brevoortia patronus* and *Paralichthys* spp., for example, peaked in concentration during November–December, but were also collected in fall–spring. Similar patterns were observed for *Elops saurus* and *Micropogonias undulatus* (late summer–winter) and *Peprilus burti* and *Leiostomus xanthurus* (late summer–spring). *Etrumeus teres* differed in that larvae were collected during winter–spring periods. Most of the dominant taxa, however, were collected primarily during the late spring–late summer months (May–October), such as *Myrophis punctatus, Harengula jaguana, Opisthonema oglinum, Centropristis* spp., *Diplectrum* spp., *Serraniculus pumilio, Decapterus punctatus, Auxis* spp., *Euthynnus alletteratus, Scomberomorus maculatus, Peprilus alepidotus, Syacium* spp., gerreids, and microdesmids. The remaining taxa (*Cynoscion arenarius, C. nothus, Larimus fasciatus*, labrids, and *Etropus crossotus*) were collected during the same period, but inclusive of the early spring months (March–April).

Larval concentrations among the dominant taxa varied widely throughout the survey period (Fig. 4). Several taxa were present in low numbers throughout the survey. For example, mean densities of *E. saurus, O. oglinum, Diplectrum* spp., *S.*
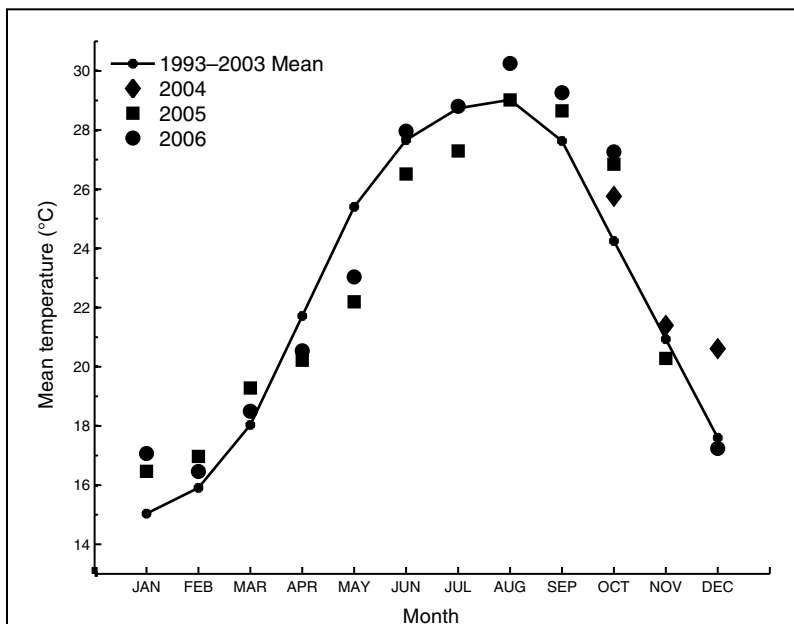

Figure 2

Mean monthly temperature observations (depth-integrated) at the ichthyoplankton sampling station and the 10-year average temperature (1993–2003). Sampling station means are derived from temperature profile observations recorded by the Bedford Institute of Oceanography Net Environmental Sampling System (BIONESS). The 10-year mean was determined from near-surface (0.6 m depth) temperature observations (T_s) recorded by an oceanographic buoy located approximately 54 km west of the sampling station. The plotted depth-integrated temperature estimates (T_i) were calculated through the relation ship $T_i = 0.90*T_s + 2.37$.

pumilio, L. campechanus, Gerreidae, *S. ocellatus,* Labridae, *Auxis* spp., *E. alletteratus, P. burti, C. spilopterus, Paralichthys* spp., and *Syacium* spp. did not exceed 10 larvae/100 m³ during any sampling event. Other taxa were characterized by relatively high concentrations, either during a single sampling event (e.g., *E. teres, C. chrysurus, C. arenarius, L. xanthurus, Microdesmus* spp., *S. maculatus, P. alepidotus*) or during a single year (e.g., *H. jaguana*). The remaining taxa (*M. punctatus, B. patronus, Centropristis* spp., *D. punctatus, C. nothus, L. fasciatus, M. undulatus, E. crossotus*) were present during multiple years in relatively similar concentrations.

Results from the cluster analysis were largely in agreement with the observed seasonal patterns previously defined by water temperature (Fig. 5). Taxonomic assemblages from fall and winter periods were clustered separately from spring and summer periods. All summer months (June–October) were clustered together with the exception of August 2005 and October 2004. Larval collections in August 2005 were characterized by atypically high concentrations of a few species, most notably *C. chrysurus* and *C. arenarius,* which were present in concentrations exceeding >500 larvae/100 m³ (Fig. 4), resulting in relatively low species diversity (Fig. 2) for the summer period. The October 2004 sampling event was included in the summer period, although the mean temperature was marginally below the 26°C criterion for the summer period (Fig. 3) and indicative of a seasonal transitional period. Similarly, the assemblages from the May sampling events were relatively distinct from the earlier spring period sampling events (March and April).

Discussion

Although numerous ichthyoplankton surveys have been conducted in the northern Gulf of Mexico, most have been conducted off the coasts of Texas, Louisiana, and Florida (Ditty et al., 1988), and few have been conducted with a high level of temporal resolution and sample replication. The Alabama shelf region, although
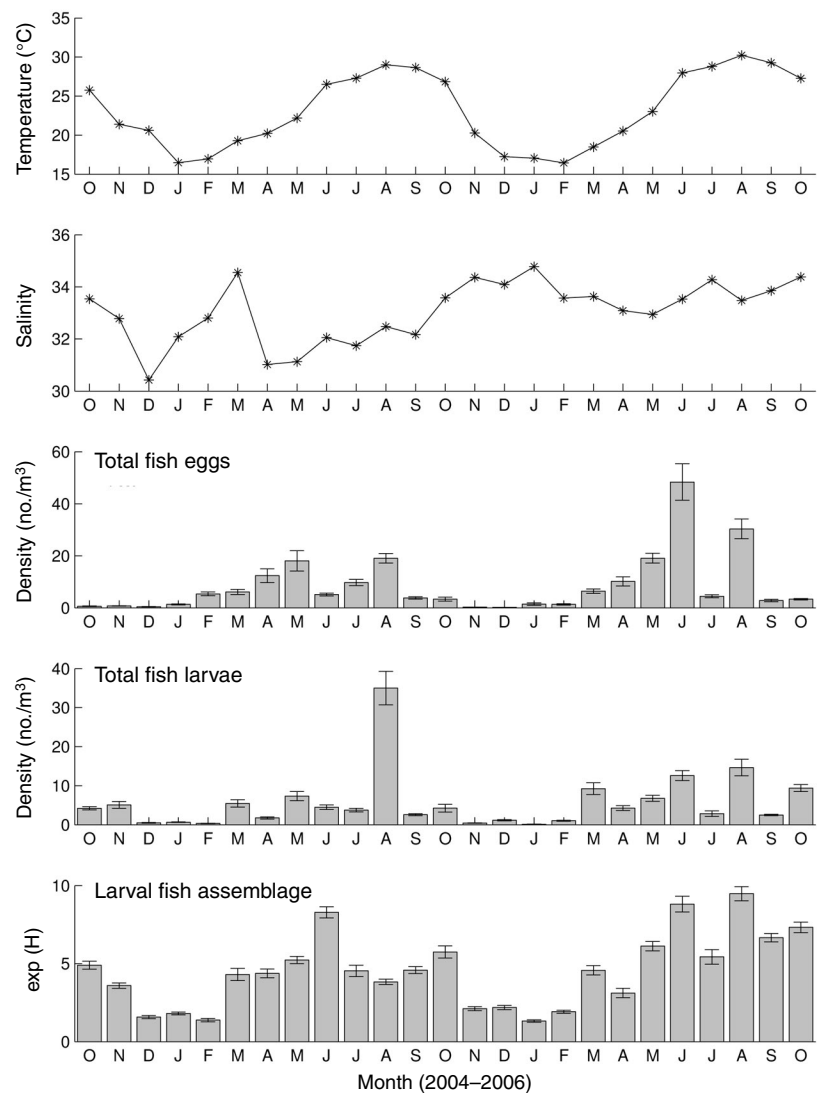

Figure 3

Mean temperature and salinity, fish egg and larval fish concentrations, and diversity indices for larval fish assemblages for October 2004–October 2006. Temperature and salinity are depth-integrated mean values for each month. Egg and larval fish concentrations are standardized by volume of water filtered (error bars denote ±1 standard error). Calculation of diversity follows Jost (2006) and depicts the exponential function of Shannon entropy, *H* (error bars denote ±1 standard error).

relatively small, is unique in that it is bounded by two major topographic features (Mississippi River Delta to the west and DeSoto Canyon to the east) that potentially inhibit alongshore transport of larvae (Johnson et al., 2009). In addition, the Alabama continental shelf receives freshwater outflow from the Mobile River system, which drains the fourth largest watershed in the United States and has the sixth largest freshwater discharge on the North American continent (Park et al., 2007). As a result, the inner shelf environment off Alabama is a highly productive region that supports valuable

Table 3

Summary (90% cumulative percentage and abundance ranking) of the dominant family groups collected during the 2004–2006 ichthyoplankton survey in the northern Gulf of Mexico off the coast of Alabama and from other ichthyoplankton surveys in the general vicinity.

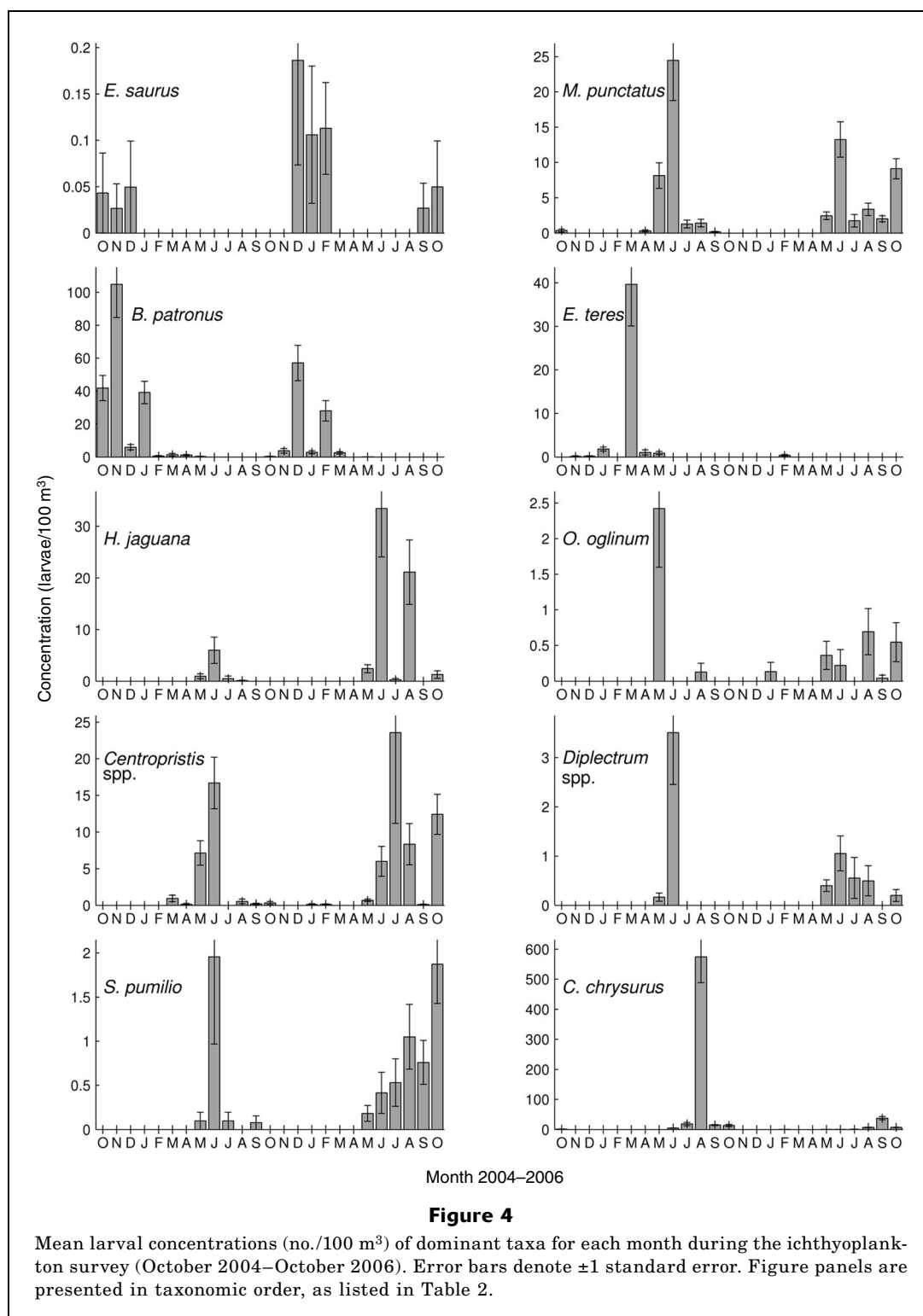| Family	This study % (Rank)	ENTRIX (2006)[1] % (Rank)	Rakocinski et al. (1996)[2] % (Rank)	Williams (1983)[3] % (Rank)
Engraulidae	50.5 (1)	32.3 (1)	82.0 (1)	69.3 (1)
Sciaenidae	15.9 (2)	10.2 (3)	4.0 (3)	14.0 (2)
Carangidae	5.4 (3)	2.7 (8)	5.0 (2)	2.8 (4)
Clupeidae	5.0 (4)	15.5 (2)		4.3 (3)
Paralichthyidae	3.9 (5)	8.5 (4)		
Gobiidae	3.6 (6)	4.1 (6)		
Ophidiidae	2.5 (7)	3.6 (7)		
Cynoglossidae	2.1 (8)	5.6 (5)		
Synodontidae	0.9 (9)	1.9 (9)		
Triglidae	0.8 (10)	0.8 (13)		
Serranidae		1.9 (10)		
Bregmacerotidae		1.6 (11)		
Labridae		1.0 (12)		
Callionymidae		0.7 (14)		
Stromateidae		0.4 (15)		
Scombridae		0.3 (16)		
Lutjanidae		0.2 (17)		
Congridae		0.2 (18)		
Ophichthidae		0.2 (19)		
Tetraodontidae		0.2 (20)		
Cumulative %	90.6	91.9	91.0	90.4

[1] Samples (oblique) were collected as part of the SEAMAP ichthyoplankton survey (Rester el al., 2000) during the months of June–November from 1982 to 2002 by using a 61-cm bongo net fitted with 333-μm mesh. Sample stations were limited to the Mississippi and Alabama inner-shelf region.

[2] Samples (upper and lower water column) were collected monthly from November 1979 to October 1980 in Mississippi Sound by using a 1-m diameter opening-closing conical-ring plankton net with 335-μm mesh.

[3] Samples (surface and demersal) were collected monthly from March 1979 to February 1980 in lower Mobile Bay by using a 1×0.5-m rectangular opening plankton net with 505-μm mesh.

fisheries resources (Shipp, 1992). The establishment of our survey is the first to specifically target larval fish assemblages in Alabama shelf waters and is the only survey from the northern Gulf of Mexico to combine frequent sampling effort (monthly) with high temporal replication (64+ samples/month) for a relatively long duration (25 months). Few ichthyoplankton surveys have been conducted near our sampling location, including a one-year survey of lower Mobile Bay (Williams, 1983), a one year survey of Mississippi Sound (Rakocinski et al., 1996), and a summary of SEAMAP ichthyoplankton data collected on the Mississippi and Alabama shelf during 1982–2002 (ENTRIX, 2006). The fisheries-independent data collected during our survey, therefore, provide a baseline for future comparisons with respect to variability in local oceanographic and climatic features (e.g., warming water temperatures), water and land usage (e.g., Mobile Bay nutrient loading and water outflow), and habitat modifications (e.g., artificial reef programs).

A comparison of results among multiple ichthyoplankton surveys is complicated because the motives for surveys often differ, resulting in survey-specific protocols and sampling biases. For example, the summary of larval fish seasonality reported by Ditty et al. (1988) for the northern Gulf of Mexico included over 30 separate surveys covering a wide range of spatial extent (Gulf-wide to individual bays and passes), sampling depths (neuston to 200 m), mesh sizes (0.086–1.05 mm), gear types (eight different samplers), sampling frequency (biweekly to quarterly), and survey duration (weeks to years). In addition, the taxonomic level to which ichthyoplankton are identified and at which they are reported varies with larval fish size, condition after capture, and availability of adequate descriptions. Our decision to use a 202-μm mesh size (as opposed to more standard sizes, e.g., $\geq$333 μm) is the factor that most likely biases our survey results when compared with previous studies. The effect of mesh size on the reten-

Figure 4

Mean larval concentrations (no./100 m³) of dominant taxa for each month during the ichthyoplankton survey (October 2004–October 2006). Error bars denote ±1 standard error. Figure panels are presented in taxonomic order, as listed in Table 2.

tion of larvae has been documented in numerous studies, with the general conclusion that larger mesh sizes may efficiently collect the late larval stages but underestimate the smaller size classes because of extrusion (Houde and Lovdal, 1984; Leslie and Timmins, 1989). Conversely, smaller mesh nets may collect smaller size classes of larvae, but are prone to clogging, thus reducing their effectiveness in sampling ichthyoplankton, particularly late-stage fish larvae (Smith et al., 1968; Tranter and Smith, 1968). In our study the smaller mesh size enabled us to achieve better estimates of fish egg and preflexion larval fish concentrations, which

Figure 4 (continued)
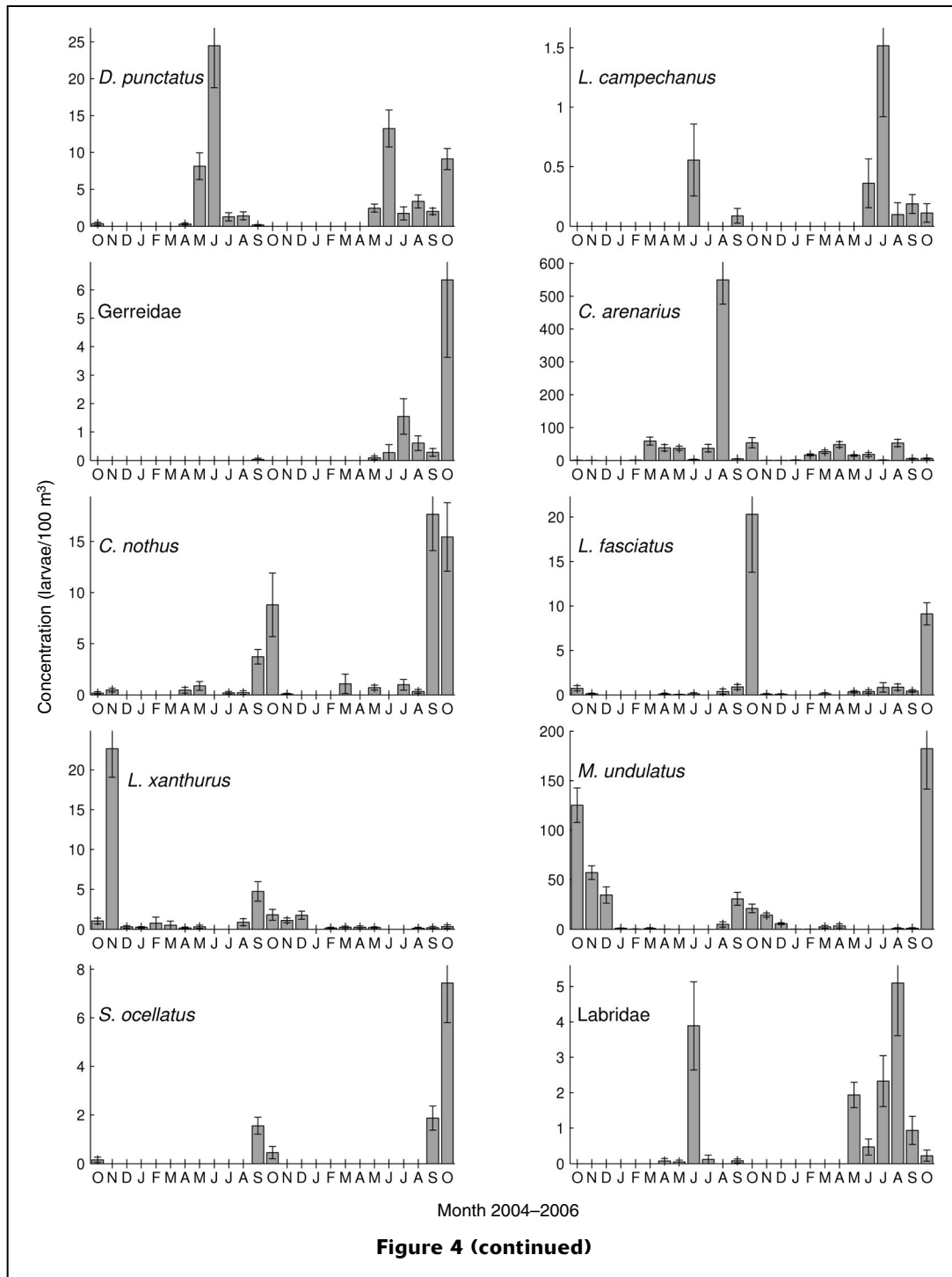
are indicative of nearby adult spawning activity. The tradeoff, however, was that many of the larvae were too small to identify to the genus or species level. As a result, most fish larvae collected in this survey were identified to the order and family level only (14% and 52%, respectively).
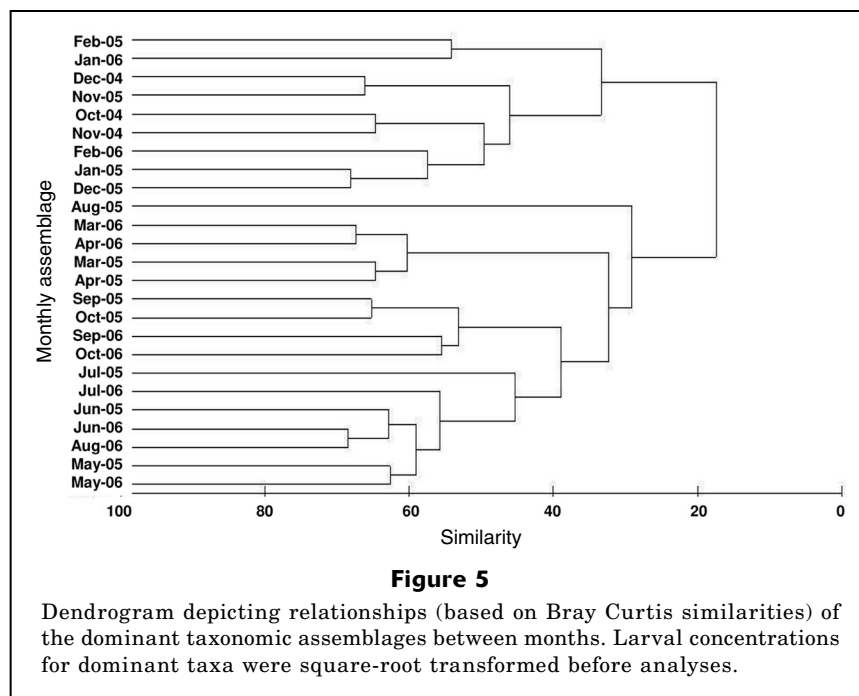
Fifty-eight different families of fishes were collected in our ichthyoplankton collections, the adult forms of which represent diverse zoogeographic regions and ecological niches. As expected, larvae of nearshore and inner shelf species were the most dominant, such as coastal pelagic (e.g., engraulids, carangids, clupeids, stromateids, gerreids) and coastal demersal (e.g., sciaenids, paralichthyids, gobiids, cynoglossids, synodontids) species. Unidentified engraulids were the most abundant larval fish group in our survey (ap-

Figure 4 (continued)
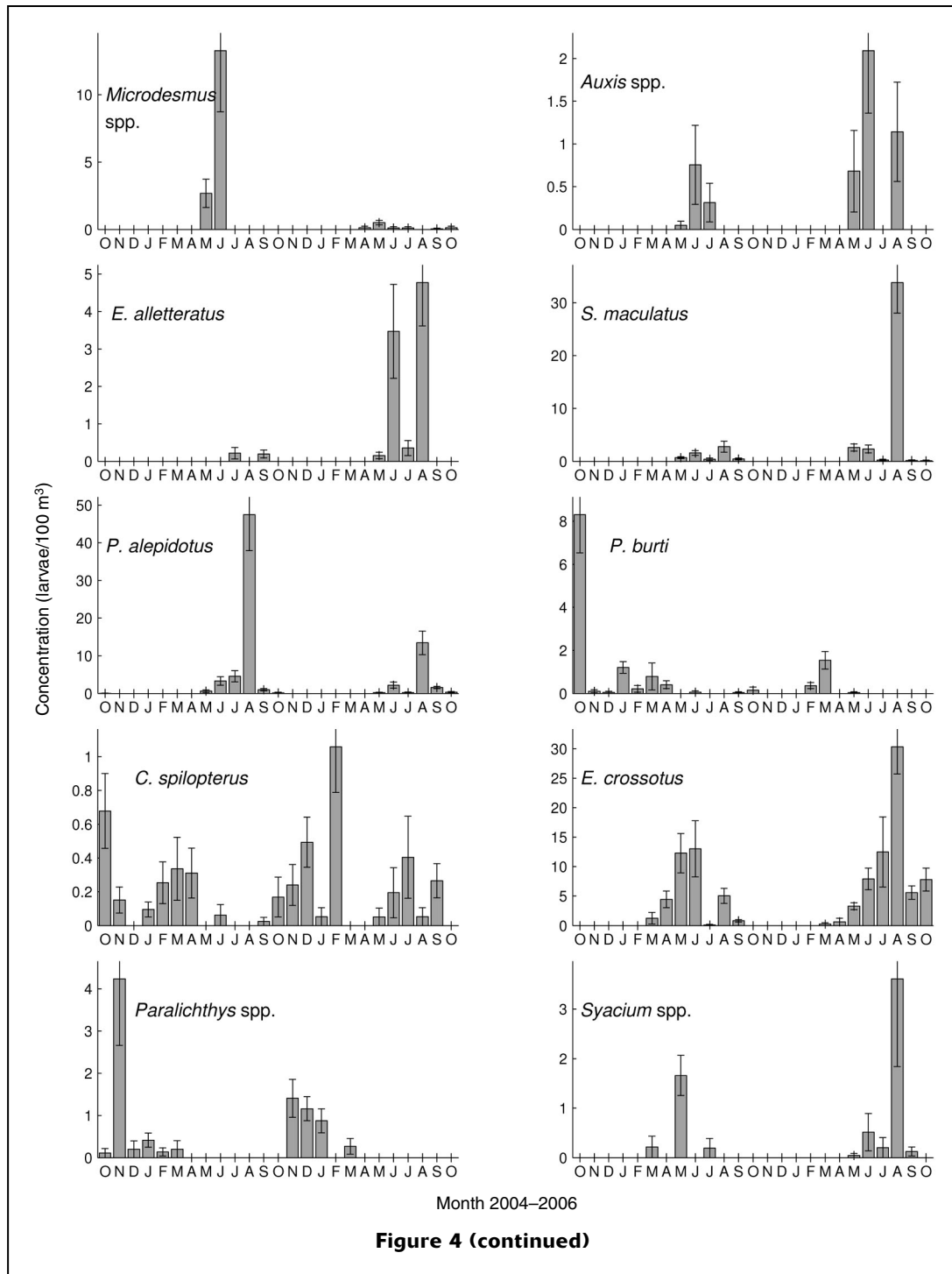
proximately 50%) and in the aforementioned regional surveys (Table 3). Engraulid larvae appear to be more abundant in protected coastal waters, as indicated by their higher dominance in the surveys of Mobile Bay (82%) and Mississippi Sound (69%), both of which are shallow estuarine regions. On the basis of identification of larger specimens, most of the engraulids collected in Mobile Bay and Mississippi Sound were *Anchoa mitchilli* and *A. hepsetus* (Williams, 1983; Rakocinski et al., 1996), whereas our collections contained these species as well as the coastal species *A. nasuta* and *Engraulis eurystole*. The inner shelf taxa *Brevoortia patronus, Cynoscion arenarius, Micropogonias undulatus, Chloroscombrus chrysurus,* and unidentified gobies were among the most dominant ichthyoplankton in all surveys, including ours. As adults, these fishes are ex-

Figure 5

Dendrogram depicting relationships (based on Bray Curtis similarities) of the dominant taxonomic assemblages between months. Larval concentrations for dominant taxa were square-root transformed before analyses.

tremely abundant in estuarine and inner shelf waters and serve important ecological roles as forage fishes (e.g., *B. patronus*, *C. chrysurus*) and as predators linking primary consumers to higher trophic levels (e.g., *M. undulatus*, *C. arenarius*) (Naughton and Saloman, 1981; Overstreet and Heard, 1982; Sheridan et al., 1984; Franks et al., 2003). The larvae of these relatively few taxa often comprise the majority of ichthyoplankton in surveys throughout the northern Gulf of Mexico (Ditty, 1986; Cowan and Shaw, 1988; Tolan et al., 1997).

Flatfish larvae (e.g., paralichthyids and cynoglossids) represented another dominant coastal group. Cynoglossids (*Symphurus* spp.) were common year-round in our study, which indicates that our collections contained multiple species. These fishes are commonly reported in ichthyoplankton surveys throughout the Gulf of Mexico, but identification of larvae (and adults) is problematic owing to high species richness and overlapping meristics (Farooqi et al., 2006b). Similarly, *Citharichthys* spp. were abundant year-round, as were *C. spilopterus.* Again, identification down to species is problematic because five species (*C. arctifrons*, *C. cornotus*, *C. gymnorhinus*, *C. macrops,* and *C. spilopterus*) are found in the study region (Lyczkowski-Shultz and Bond, 2006). Although efforts were made to identify larvae conservatively, some of our *C. spilopterus* may have included congeners. This issue of questionable identification appears less likely for the *Etropus* species complex, which was also abundant, primarily *E. crossotus* and *E. microstomus.*

Equally notable in our survey was the absence (or rarity) of larvae from taxa that are common in our sampling region as adults. For example, serranine (seabasses) serranid larvae were collected, but epi-

nepheline (grouper) larvae were not. Similarly absent (or rare) were larvae from other recreational and commercially important species such *Coryphaena hippurus* (Coryphaenidae), *Rachycentron canadum* (Rachycentridae), *Balistes capriscus* (Balistidae), *Lobotes surinamensis* (Lobotidae), *Chaetodipterus faber* (Ephippidae), and *Mugil cephalus* (Mugilidae), all of which spawn in coastal or offshore waters of Alabama. The fact that we did not collect some of these taxa is not surprising (e.g., *B. capriscus*, *M. cephalus*) because they are more commonly collected in the neuston (which we did not sample). The absence of grouper larvae is perplexing, even though the rarity of epinepheline larvae has been documented in the northern Gulf of Mexico. For example, only 37 grouper larvae were collected in gulfwide SEAMAP ichthyoplankton surveys between 1982 and 1999 (>7000 samples) (Lyczkowski-Shultz et al.[1]). Most of the grouper larvae were collected at offshore SEAMAP sampling stations, which indicates that their occurrence in nearshore environments may be rare. It is possible that the limited spatial extent of our survey (i.e., a single station) may have influenced our estimates of larval fish concentrations and variability, because coastal marine processes that influence larval fish dynamics are often site-specific (e.g., local wind regimes, tidal flows, river discharge), but the overall seasonal supply of larvae available at our sampling station is likely representative of the ichthyofauna from a larger northcentral Gulf of Mexico region between the 87°W and 89°W longitude (Boschung, 1992).

The main objective of this study was to describe taxon-specific seasonality for larval fishes collected in the survey region. For several reasons, we limited our seasonal analyses to water temperature, as opposed to

a suite of environmental parameters. First, temperature has long been proposed as an important factor in the initiation of spawning for marine fishes (Orton, 1920), and numerous field and laboratory (primarily aquaculture-related) studies have provided support for temperature as a primary influence (Arnold et al., 2002; Sheaves, 2006). Second, water temperature varies predictably at seasonal scales (e.g., months), as opposed to other factors that vary at shorter time scales. Our salinity data (Fig. 3), for example, showed no seasonal trends and were not correlated with egg or larval fish concentrations. The monthly mean salinity values calculated during each cruise likely reflect short-term variability related to tidal flow, riverine outflow, local wind conditions, and related factors that affect salinity at our sampling station. In addition, salinity, although an important factor for many estuarine-spawning species, is generally considered less important than temperature to the timing of marine fish spawning (Bye, 1984; Sheaves, 2006).

Defining seasonality in terms of water temperature also provides a framework for monitoring fisheries dynamics with respect to anticipated rises in sea temperature due to global climate change. Our monthly observed depth-integrated temperatures were relatively consistent with those for the previous ten-year average for the region, although winter (December–January) and late summer (August–October) values were generally higher (Fig. 2). Fodrie et al. (2009) noted a significant increase in sea surface temperature near the mouth of Mobile Bay over a 20-year period (1987–2007). The authors also noted a concurrent increase in the number and occurrence of juvenile subtropical and tropical fishes collected in seagrass meadows along the northern Gulf of Mexico. For example, in 2006–2007 surveys, juveniles of tropical species such as *Chaetodon ocellatus* (Chaetodontidae), *Fistularia tabacaria* (Fistulariidae), *Ocyurus chrysurus* (Lutjanidae), *Thalassoma bifasciatum* (Labridae), *Sparisoma viride* (Scaridae), and unidentified acanthurids were collected in coastal habitats where they were not collected during previous surveys (1971–79) (Livingston, 1985). Notably, in our ichthyoplankton survey larvae from all of these families, except Chaetodontidae, were collected but regrettably, comparable ichthyoplankton data from the 1970s were not available and our identifications were made only to the family level.

Conclusions

Increases in regional water temperatures may have significant impacts on the reproductive success of marine fishes and the subsequent survival of early life stages, including early gonad maturation and spawning in adults, altered larval transport pathways, extended pelagic larval durations, changes in larval assemblage structure, and mismatched timing of larval fish occurrence with food resources and physiological optima, among other effects (Sheaves, 2006; O'Conner et al.,

2007; Genner et al., 2009). Establishment of long-term baseline surveys provides a means of monitoring larval fish assemblages and the factors that influence larval fish dynamics in order to provide early indicators of ecosystem changes due to environmental perturbations. The ichthyoplankton survey efforts described here for the October 2004–October 2005 period have since continued and expanded to include near monthly (depth-discrete) ichthyoplankton sampling at five stations along a cross-shelf transect from inside Mobile Bay extending offshore to a station approximately 54 km south of Dauphin Island. The expanded survey program (Fisheries Oceanography of Coastal Alabama, or FOCAL) will allow us to estimate and monitor the variability in ichthyoplankton seasonality, abundance, assemblage structure, and vertical distribution over multiple temporal and spatial scales.

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