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Abstract
    Serial, cyclonic, mesoscale eddies arise just north of the Charleston Bump, a topographical rise on the continental slope and Blake Plateau, and characterize the U.S. outer shelf and upper slope in the region of the Charleston Gyre. This region was transected during the winters of 2000, 2001, and 2002, and hydrographic data and larval fishes were collected. The hydrodynamics of the cyclonic eddies of the Charleston Gyre shape the distribution of larval fishes by mixing larvae from the outer continental shelf and the Gulf Stream and entraining them into the eddy circulation at the peripheral margins, the wrap-around filaments. Over all years and transects (those that intercepted eddies and those that did not), chlorophyll *a* concentrations, zooplankton displacement volumes, and larval fish concentrations were positively correlated. Chlorophyll *a* concentrations were highest in filaments that wrapped around eddies, and zooplankton displacement volumes were highest in the continental shelf–Gulf Stream–frontal mix. Overall, the concentration of all larval fishes declined from inshore to offshore with highest concentrations occurring over the outer shelf. Collections produced larvae from 91 fish families representing continental shelf and oceanic species. The larvae of shelf-spawned fishes—Atlantic Menhaden *Brevoortia tyrannus*, Round Herring *Etrumeus teres*, Spot *Leiostomus xanthurus*, and Atlantic Croaker *Micropogonias undulatus*—were most concentrated over the outer shelf and in the continental shelf–Gulf Stream–frontal mix. The larvae of ocean-spawned fishes—lanternfishes, bristlemouths, and lightfishes—were more evenly dispersed in low concentrations across the outer shelf and upper slope, the highest typically in the Gulf Stream and Sargasso Sea, except for lightfishes that were highest in the continental shelf–Gulf Stream–frontal mix. Detrended correspondence analysis rendered groups of larval fishes that corresponded with a gradient between the continental shelf and Gulf Stream and Sargasso Sea. Eddies propagate northeastward with a residence time on the outer shelf and upper slope of ∼1 month, the same duration as the larval period of most fishes. The pelagic habitat afforded by eddies and fronts of the Charleston Gyre region can be exploited as nursery areas for feeding and growth of larval fishes within the southeastern Atlantic continental shelf ecosystem of the U.S. Eddies, and the nursery habitat they provide, translocate larvae northeastward.
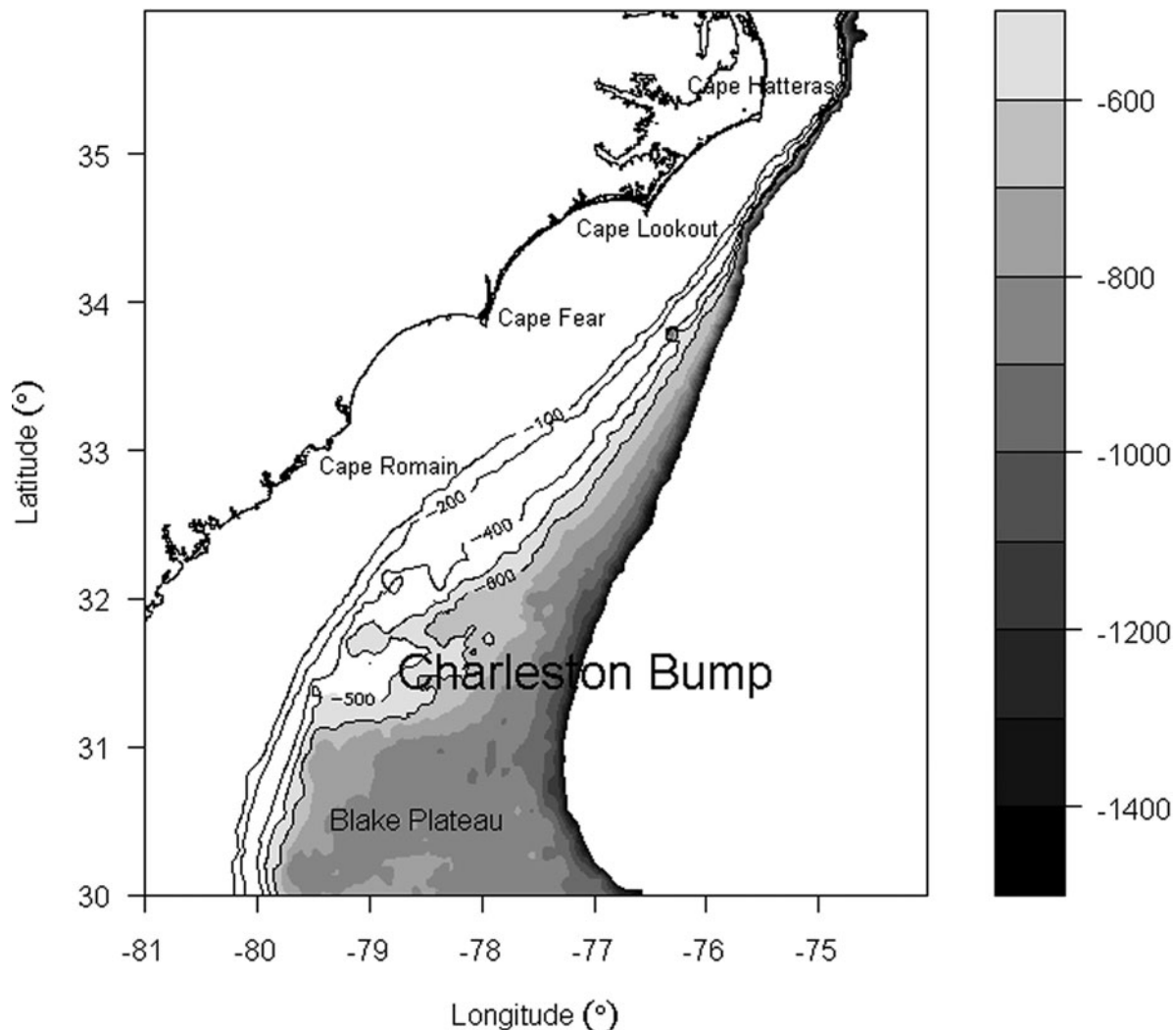
FIGURE 1. The Charleston Gyre region off the southeastern coast of the United States. Gray-scale gradient represents depth >500 m.

A series of recurrent, cyclonic, mesoscale eddies characterize the Charleston Gyre region off the southeastern coast of the United States, and influences the primary, secondary, and fisheries production of the southeastern Atlantic coastal ecosystem (Govoni and Hare 2001). A bathymetric rise on the continental slope above the Blake Plateau, known as the Charleston Bump (Figure 1), forces an eastward deflection of the Gulf Stream, a major western boundary current (Olson 2001) that borders the southeastern U.S. continental shelf to the east. This deflection, a result of the vertical compression and subsequent expansion of the water column as the Gulf Stream overrides the Charleston Bump, gives repetitive rise to a series of meanders. Meander crests pull Gulf Stream water onto the shelf and into the Gulf Stream Front, and also pull shelf water into the Gulf Stream front. Meanders become unstable and break, spinning off cyclonic eddies. Eddies propagate northeastward and decay or coalesce with the Gulf Stream north of Cape Fear, North Carolina. The residence time of eddies within the region ranges from a week to a month if stranded on the shelf (Pietrafesa et al. 1985; Lee et al. 1991; Blanton et al. 2003). The cyclonic circulation of the eddies upwells nutrient-rich water from deep and off the shelf edge to the euphotic zone, which can result in enhanced primary and secondary production (Verity et al. 1993). These eddies develop most frequently and are more pronounced in winter (Mathews and Pashuk 1984, 1986) when the Gulf Stream is in its strongly deflected mode (Lee et al. 1991).

The survival of fish larvae is the principal determinant of population recruitment and an important contributor to fisheries production (Houde 2008). Most marine fishes are pelagic spawners, while their larvae occupy the upper 200 m (Miller and Kendall 2009). While the Charleston Gyre region has the potential to act as spawning and nursery habitat, evidence of the use

TABLE 1. Transects and stations occupied across the outer continental shelf and upper slope in the Charleston Gyre region off the southeastern coast of the United States in the winters of 2000, 2001, and 2002. See Figure 2 for definitions of station abbreviations.

Dates	Number of stations occupied	Transect number	Transect characterization	Stations designations occupied (number)
15 Jan 00	9	1	E deflection	CS (2), CS-GS-FM (5), GS (2)
16–17 Jan 00	10	2	Eddy intersection	CS-GS-FM (3), GS (1), WAF (5), EC (1)
18–19 Jan 00	9	3	NE of eddy	CS-GS-FM (3), GS (6)
24–25 Jan 01	9	4	Eddy intersection	CS-GS-FM (1), GS (2), WAF (4), SS (2)
26 Jan 01	8	5	Eddy intersection	CS (3), CS-GS-FM (1), GS (1), WAF (1), EC (2)
27–28 Jan 01	8	6	Eddy formation	CS (3), CS-GS-FM (1), GS (1), WAF (1), EC (2)
26–27 Jan 02	10	7	Eddy intersection	CS-GS-FM (6), GS (3), WAF (1)
28–29 Jan 02	10	8	Eddy intersection	CS-GS-FM (5), GS (2), WAF (2), EC (1)
29–30 Jan 02	10	9	Between eddies	CS-GS-FM (7), GS (3)
30–39 Jan 02	10	10	Eddy formation	CS-GS-FM (8), GS (2)
31 Jan−1 Feb 02	10	11	E deflection	CS (2), CS-GS-FM (6), GS (2)

of the pelagic habitats afforded by cyclonic eddies in this region is limited. Winter is the spawning season for a suite of fishes, many of which are commercially important (Govoni and Hare 2001; Taylor et al. 2009). High concentrations of larval fishes are evident in the Charleston Gyre region (Fahay 1975; Powles and Stender 1976; Yoder 1983), but there is little indication of high concentrations of fish eggs, aside from those reported for Atlantic Menhaden *Brevoortia tyrannus* (Judy and Lewis 1983). The distribution of larval fishes across the outer shelf and upper slope in association with the passage of the cyclonic eddies is not described, and consequently habitat utilization of these eddies is undetermined.

The objectives of this study were to (1) transect the Charleston Gyre region and intercept eddies that arise there, (2) describe the distribution of chlorophyll *a*, zooplankton, and larval fishes in and around these eddies, and (3) describe the influence of eddies in shaping the distribution of larval fishes.

METHODS

Study area.—The Charleston Gyre region is dynamic across the outer shelf and upper slope, along the shore and in the vertical dimensions, changing with the formation and northeastward propagation of mesoscale cyclonic eddies. In the absence of eddies, a mix of outer continental shelf and Gulf Stream waters separates water over the continental shelf from the Gulf Stream. During formation of an eddy, the mixture of outer shelf and Gulf Stream water is stretched meridionally and zonally to form wrap-around filaments that appear as a lens of water near the surface and extend to ∼25 m depth. Wrap-around filaments close around an eddy with a core.

With its dynamic character, eddies of the Charleston Gyre region can provide favorable pelagic habitat for larval fishes. Localized frontal convergence in the mixed waters of the outer shelf and the Gulf Stream north of the Charleston Gyre region account for elevated concentrations of larval fishes (Govoni

1993; Govoni and Pietrafesa 1994; Govoni and Spach 1999). Within the eddy core, upwelling from below the Gulf Stream is evident (Bane et al. 2001), and this upwelling stimulates primary and secondary production (Verity et al. 1993). This production can provide food for larval fishes (Govoni et al. 2010).

Data collection and processing.—To determine the influence of cyclonic eddies of the Charleston Gyre region on the distribution of larval fishes, ichthyoplankton collections were taken along transects that nominally began on the outer shelf, extended onto the slope, and continued into the Gulf Stream (and on one transect, in 1 year, into the western edge of the Sargasso Sea). Stations along transects were occupied in January of 2000, 2001, and 2002; stations were nominally 16.1 km (10 nautical miles) apart along transects (Table 1; Figure 2). Transects extended zonally across the outer shelf and upper slope and meridionally from the Charleston Bump to Cape Fear (Figure 2). Transects were oblique and not perpendicular to the axis of the physical features of the region. Transect and station locations were modified each year to capture eddy formation and propagation. Some transects intercepted formed eddies, some did not, and some intersected eddy formation.

At each station, casts of conductivity, temperature, and depth (CTD) to a maximum depth of 350 m were taken and surface chlorophyll *a* concentrations were measured. At each station, ichthyoplankton collections were taken with a 60-cm-diameter bongo net fitted with 333-μm-mesh nets fished obliquely from near the bottom on the shelf or from 200 m depth to the surface when they were off the shelf break as described by Powell et al. (2000). Zooplankton displacement volume (including displacement by larval fishes) was measured from ichthyoplankton collections as described by Smith and Richardson (1977). Outer shelf and upper slope sections of temperature were derived from profiles taken from CTD casts.

Larval fishes were sorted from one bongo net and identified to family or order level when specimens could not be

TABLE 2. The nominal characteristics of station designations across the outer continental shelf and upper slope in the Charleston Gyre region off the southeastern coast of the United States in the winters of 2000, 2001, and 2002.

Station designation	Abbreviation	Nominal sea-surface temperature range (°C)	Nominal thermal and halocline characteristics
Continental shelf	CS	11–19[a]	Isothermal and isohaline[a]
Continental sshelf–Gulf Stream–frontal mix	CS-GS-FM	20–24[a]	Variable, begins ∼50–75 m[a,b]
Gulf Stream	GS	24–26[a,b]	Variable, begins ∼50 m[a,b,c]
Wrap-around filament	WAF	20–24[d]	Variable, begins ∼20 m
Eddy core	EC	∼20[d]	Variable, begins ∼30 m[d]
Sargasso Sea	SS	20–23[e]	∼400 m[e]

[a]Xie and Pietrafesa (1995).
[b]Hitchcock et al. (1994).
[c]Schmitz et al. (1993).
[d]Bane et al. (2001).
[e]McGillicuddy et al. (1999).

referred to family because of their condition. Identification followed that described by Richards (2006); classification, some of which were modified owing to recent systematic revisions, generally followed that of Nelson (1994). The larvae of the herrings (Clupeidae)—Atlantic Menhaden and Round Herring *Etrumeus teres*—and the drums (Sciaenidae)—Spot *Leiostomus xanthurus* and Atlantic Croaker *Micropogonias undulatus*—were identified and selected as indicators of fishes spawned on the shelf. Atlantic Menhaden and Spot larvae are among the most abundant species collected on the shelf in winter south of Cape Hatteras (Checkley et al. 1999; Govoni and Spach 1999; Hare and Govoni 2005). Larvae of the bristlemouths (Gonostomatidae), lightfishes (Phosichthyidae), and lanternfishes (Myctophidae) were selected as indicators of fishes spawned off the shelf in the open ocean. The larvae of these fishes are among the most abundant, open-ocean spawned larvae in the western North Atlantic (Evseenko 1982), as well as in western boundary currents (Sassa et al. 2004).

Stations were classified as location-based designations (Table 2) and were not linked to water mass, because water masses are often separated vertically in the region; collections were neither depth nor water-mass discrete. Bongo-net casts obliquely integrated larval fishes within the water column from 200 m to the surface, or from near the bottom to the surface in depths shallower than 200 m. Consequently, larval fishes could be collected vertically from different water masses within retrograde frontal zones or from within eddies of the Charleston Gyre region. Whereas the lack of vertical separation of larval fish collections could result in the combination of larval fishes from different water masses, the spatial scale of stations along transects and location-based station designations ameliorated the effects of the lack of discrete water-mass sampling.

Examination of advanced very high resolution radiometer (AVHRR) images (Figure 2) of sea-surface temperature (SST), temperature (T) and salinity (S) profiles for each station (Figure 3), and sections of T over the outer shelf and upper slope (Figure 4) were used to classify collections along transects. Stations were designated as CS, CS-GS-FM, GS, WAF, EC, and

SS (see Table 2 for definitions). Stations WAF and EC were not evident on transects that did not intercept an eddy. Station designations were closely concordant with the surface expression of frontal zones along outer shelf transects north of Cape Fear (Govoni et al. 2010). These location-based designations were consonant with the methods employed for ordination of the larval fish assemblage north of the Charleston Gyre region (Quattrini et al. 2005).

Data analyses.—For analysis, parametric statistics were preferred, but nonparametric methods were used when variances within groups were not homogenous (Zar 1999). Overall concentrations of chlorophyll *a*, zooplankton displacement volumes, and concentrations of all larval fishes were tested for association with Kendall's correlations. For comparisons, ANOVA was preferred, but Kruskall–Wallis (K-W) nonparametric ANOVA was used when the variances of concentrations were not homogenous (Levene's tests). Multiple comparison tests identified differences among station designations.

Detrended correspondence analysis (DCA) provided ordination (Ter Braak and Prentice 1988; Legendre and Legendre 1998) of station designations and of families and indicator taxa of larval fishes. The DCA minimizes edge effects that can interfere with the interpretation of the ordination by simple correspondence analysis. Concentrations of families and indicator taxa from all station designations were normalized by using percentage composition. Scores from the first and second axes, identified by eigenvalues, were plotted for station designations and concentrations of families and indicator taxa. The proximity families, indicator taxa, and station designation on axis plots indicated the coherence of taxa groups with station designations.

RESULTS

Hydrography

Cyclonic eddies were intercepted and traversed in each year with other transects to the south or north of eddies (Table 1). Overall, most collections were taken in the CS-GS-FM ($n = 51$), followed by the GS ($n = 28$), WAF ($n = 14$), CS ($n = 7$), EC
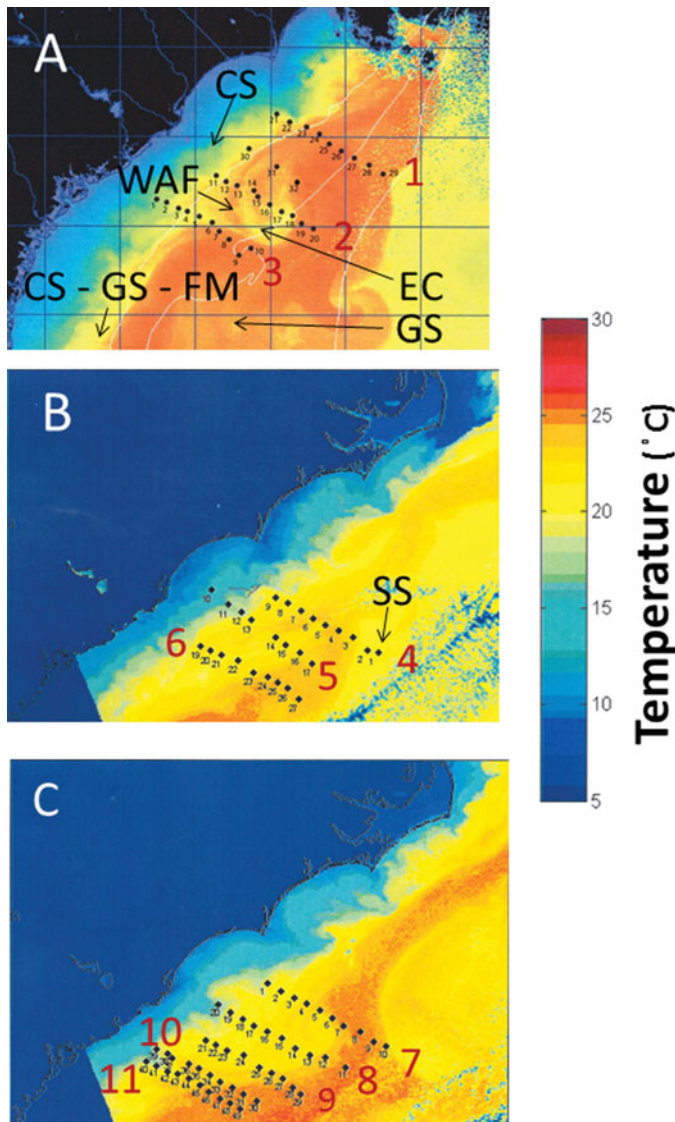
FIGURE 2.   Stations (dots), transects (red numerals), and station designations (black letters) occupied in the Charleston Gyre region off the southeastern United States, superimposed on representative advanced very high resolution images of sea-surface temperatures: (**A**) 16 January 2000; (**B**) 10 January 2001; (**C**) 09 January 2002. CS: continental shelf; CS-GS-FM: continental shelf–Gulf Stream–frontal mix; GS: Gulf Stream; WAF: wrap-around filament; EC: eddy core; SS: Sargasso Sea. Stations occupancy and images are not temporally synoptic; color on images is relative, not absolute, with the temperature scale.

($n = 4$), and SS ($n = 2$). With the exception of CS stations, where the water column was vertically isothermal, the water column was stratified, and the thermocline and halocline occurred at varying depths (Figures 3, 4).

Chlorophyll *a* Concentrations, Zooplankton Displacement Volumes, and Larval Fish Correlations

Chlorophyll *a* concentrations were weakly, but positively, correlated with zooplankton displacement volumes and larval fish concentrations (Table 3). Zooplankton displacement
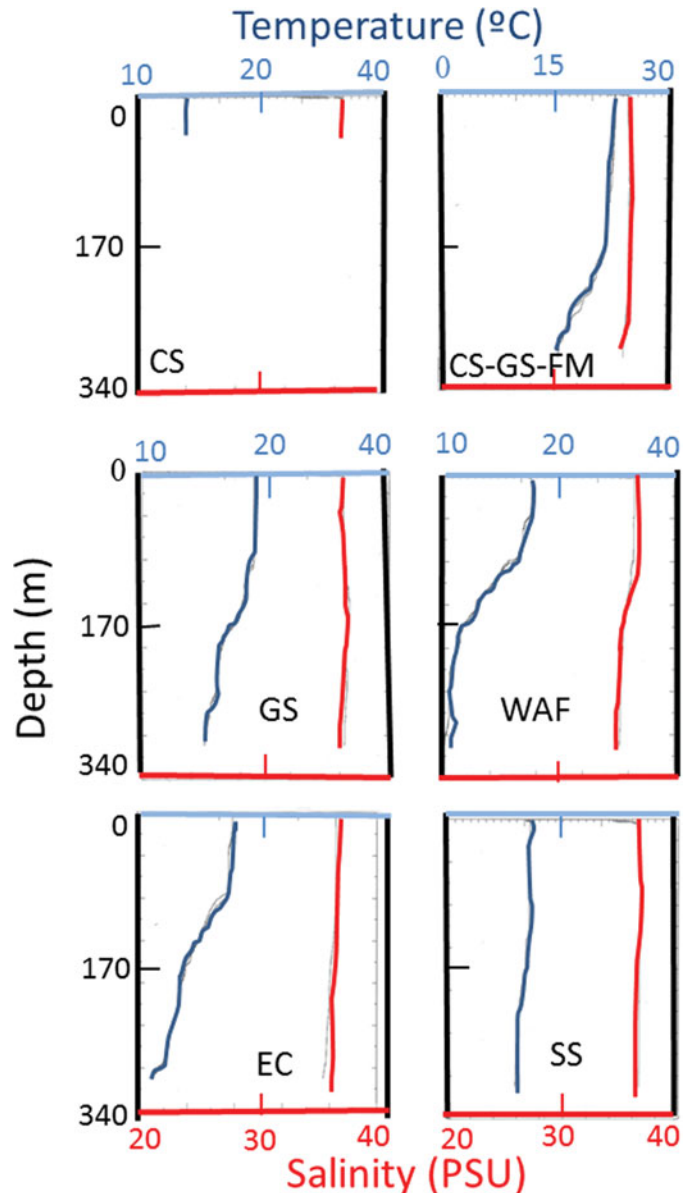
FIGURE 3.   Representative temperature (blue) and salinity (red) profiles (downcast and upcast smoothed) for stations designations. See Figure 2 for definitions of station abbreviations.

volumes had a stronger, positive correlation with larval fish concentrations than did chlorophyll *a* concentrations, though zooplankton displacement volume included, volumetrically, larval fishes and therefore was not completely independent of larval fish concentration. Larval fish concentrations had a stronger positive correlation with zooplankton displacement volumes than with chlorophyll *a* concentration.

Chlorophyll *a* Concentration, Zooplankton Displacement Volume, and Concentration of Larval Fishes

Over all years and transects (those that intersected the eddies and those that did not), mean chlorophyll *a* concentrations,

TABLE 3. Kendall's rank correlations (τ) and test statistics (S) of chlorophyll *a* concentrations, zooplankton displacement volumes, and concentrations of larval fishes in the winters of 2000, 2001, and 2002 in the Charleston Gyre region off the southeastern coast of the United States (an asterisk [*] denotes significant difference at $P < 0.05$).

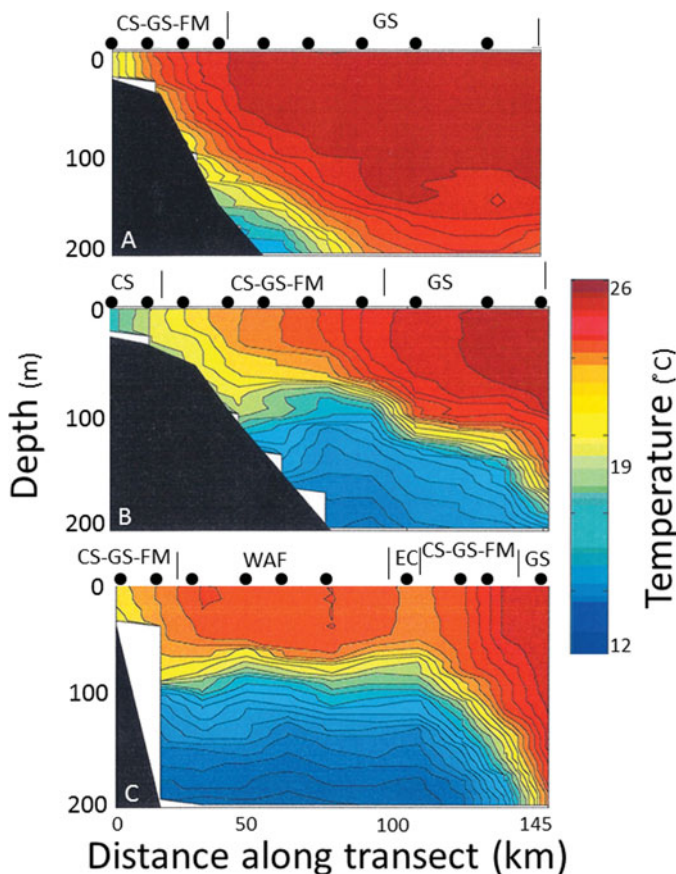| Correlation	τ	Test statistic (S)	P
Larval fish concentration versus zooplankton displacement volume	0.54	7.34	<0.001*
Larval fish concentration versus chlorophyll *a* concentration	0.15	2.23	0.02*
Zooplankton displacement volume versus chlorophyll *a* concentration	0.13	1.78	0.08

FIGURE 4. Representative sections of the outer continental shelf and upper slope of the Charleston Gyre region in 2000: (**A**) no eddy present; (**B**) eastward deflection of the Gulf Stream at the Charleston Bump; and (**C**) eddy present. See Figure 2 for definitions of station abbreviations.

zooplankton displacement volumes, and concentrations of all larval fishes differed among years and station designations with no significant interaction between years and station designations (Table 4). Multiple comparison tests indicated significantly higher concentrations of chlorophyll *a* in WAF than in the GS; concentrations in the CS-GS-FM were significantly higher than in the GS (Figure 5A). Zooplankton displacement volumes were significantly higher in the CS-GS-FM than in the GS (Figure 5B). Concentrations of all larval fishes were significantly higher on the CS than in the GS and EC; concentrations in the CS-GS-FM were significantly higher than in the GS (Figure 5C).

Taxa of Larval Fishes

Collections produced 91 families of larval fishes representing the larvae of coastal ground, reef, and pelagic fishes and oceanic, meso- and benthopelagic, and benthic fishes (Table 5). Of the indicators of shelf-spawned fishes, Atlantic Menhaden and Round Herring, comprised almost all of the clupeids and were consistently present in high concentrations. Spot and Atlantic Croaker comprised almost all of the sciaenids. Of the indicators of ocean-spawned fishes, most of the bristlemouths were *Cyclothone* spp., but *Diplophos taenia*, *Bonapartia pedaliota*, and *Gonostoma* spp., were included. Most of the lightfishes were *Vinciquerria* spp. Lanternfishes included *Electrona risso*, *Gonichthys cocco*, *Hygophum* spp., *Myctophum* spp., *Ceratoscopelus* spp., *Diaphus* spp., and *Lepidophanes* spp. Lanternfishes and bristlemouths were consistently present.

Overall, concentrations of the indicators of shelf-spawned fishes differed and were highest in the CS or CS-GS-FM (Figure 6), and some significant differences were apparent among station designations (Table 6). Multiple comparison tests indicated that concentrations of Atlantic Menhaden were not significantly different among station designations (Figure 6A). Concentrations of Round Herring larvae were significantly higher in the CS-GS-FM than in the GS and WAF (Figure 6B). Concentrations of Spot larvae were significantly higher in the CS than in CS-GS-FM and WAF (Figure 6C). Concentrations of Atlantic Croaker were not significantly different among station designations. No larvae of shelf-spawned fishes were collected in the SS.

Concentrations of the larvae of ocean-spawned target fishes were low and static across the outer shelf and upper slope (Figure 7), and some significant differences occurred among station designations (Table 6). Concentrations of lanternfishes were significantly higher in the GS than in the CS, CS-GS-FM, and WAF (Figure 7A). Concentrations of lightfishes and bristlemouths did not differ significantly among station designations (Figure 7B, C). No lightfishes were collected in the CS.

Hydrodynamics and the Distribution of Larval Fishes

The hydrodynamics of the eddies of the Charleston Gyre region shape the outer shelf and upper slope distribution of

TABLE 4. Two-way ANOVA of mean chlorophyll *a* concentrations, zooplankton displacement volumes, and concentrations of larval fishes among years and station designation in the winters of 2000, 2001, and 2002 in the Charleston Gyre region off the southeastern coast of the United States.

Parameter	Groups compared	df	Sum of squares	Mean square	*F*-value	Pr($>F$)
Chlorophyll *a*	Year	2	1.66	0.83	1.79	0.17
	Station Designation	5	6.34	1.27	2.73	0.02
	Year × Station Designation	8	4.15	0.52	1.12	0.36
Zooplankton displacement volume	Year	2	0.36	0.18	4.95	0.01
	Station Designation	5	0.78	0.16	4.35	0.00
	Year × Station Designation	8	0.16	0.02	0.54	0.82
Larval fish concentration	Year	2	14.88	7.44	3.00	0.06
	Station Designation	5	42.36	8.47	3.41	0.01
	Year × Station Designation	8	12.43	1.55	0.63	0.75

larval fishes by mixing larval fishes from the CS and the GS into the CS-GS-FM and entraining them into the eddy circulation at the peripheral margins of filaments, the WAF (Figures 2, 4). In eddy formation, the Gulf Stream veers toward the east at the Charleston Bump, the CS-GS-FM and WAF stretches, toward the south, then the east (Figures 2A, 4B), then north as the filament closes (Figure 4C). Larvae, which were in high concentrations on the CS and in CS-GS-FM (Figure 6), were entrained into eddy circulation, the WAF. The overall decrease in concentrations of the larvae of shelf-spawned fishes across eddies and in the WAF and ED (Figure 6), and the more even distribution of the larvae of ocean-spawned fishes (Figure 7), indicated mixing across eddies by the circulation of the eddies and by eddy diffusion.

Ordination of larval Fishes

The assemblage of families and indicator taxa of larval fishes grouped along two axes (Table 7). Overlap in taxa groupings within station designations is indicated by overlapping polygons that encompass station designations (Figure 8). A gradient was evident principally along axis 2. The herrings (Clupeidae) that comprise Atlantic Menhaden and Round Herring, and were the most abundant family, were consistently grouped toward the lower end of axis 2, while the Sciaenidae that comprise Spot and Atlantic Croaker grouped toward the upper end of axis 2 (Figure 8). Spot and Atlantic Croaker typically occupy more inshore habitats, most frequently the station designation CS, whereas Atlantic Menhaden and Round Herring occupy more offshore habitats, the CS-SG-FM. The lanternfishes and bristlemouths grouped toward the far right of axis 1. The CS-GS-FM, EC, and WAF overlap between them and are closer to, or over, the origin, indicating that these stations contained some of the indicator taxa. The EC was more similar to the GS than the CS. Overall, the taxa grouped by the DCA conform with the station classification, which supports the validity of station classification.

DISCUSSION

The action of the eddies of the Charleston Gyre region is to mix larval fishes from the outer continental shelf (CS) and Gulf Stream (GS) into the CS-GS-FM and entrain the CS-GS-FM into the water that wraps around the eddy core (WAF). Fronts and eddies of the Charleston Gyre region are areas of elevated abundance of larval fishes. In this region the abundance of larval fishes were greatest on the outer shelf, CS, and CS-GS-FM, and thirdly in the WAF, because the Gulf Stream and continental shelf waters contribute larvae that are concentrated and mixed within this frontal mix. Eddy diffusion (Blanton 1971; Lillibridge et al. 1990; Churchill et al. 1993) affects this mixing, as is evident in frontal zones to the north of the Charleston Gyre region (Govoni 1993; Govoni and Spach 1999).

The dynamics of eddies of the Charleston Gyre region shape the distribution of chlorophyll *a*, zooplankton, and larval fishes by concentrating these attributes in and about eddies in ways similar to those of other mesoscale cyclonic eddies elsewhere in the world's oceans. Entrainment of larval fishes and zooplankton into fronts associated with eddies is evident elsewhere, particularly along western boundary currents (Nakata et al. 2000; Everett et al. 2011; Mullaney 2011). In eddies along the western front of the Kuroshio Current extension, Eulerian and Langrangian observations indicated increased chlorophyll *a* concentrations stimulated by upwelling of nutrients within the eddy core, followed by a decline in chlorophyll *a* as eddies mature with a concomitant increase in the concentration of copepod nauplii and small copepods (Kimura et al. 1997; Okazaki et al. 2002). Chlorophyll *a* concentrations, zooplankton abundance, and larval fish concentrations were positively correlated within mesoscale cyclonic eddies of the Loop Current, the progenitor of the Florida Current and the Gulf Stream, in the northern Gulf of Mexico (Biggs and Ressler 2001). Mesoscale eddies formed in the wake of oceanic islands also result in elevated chlorophyll *a* concentrations (Onitsuka et al. 2009), and positive correlations were evident among chlorophyll *a* concentrations,
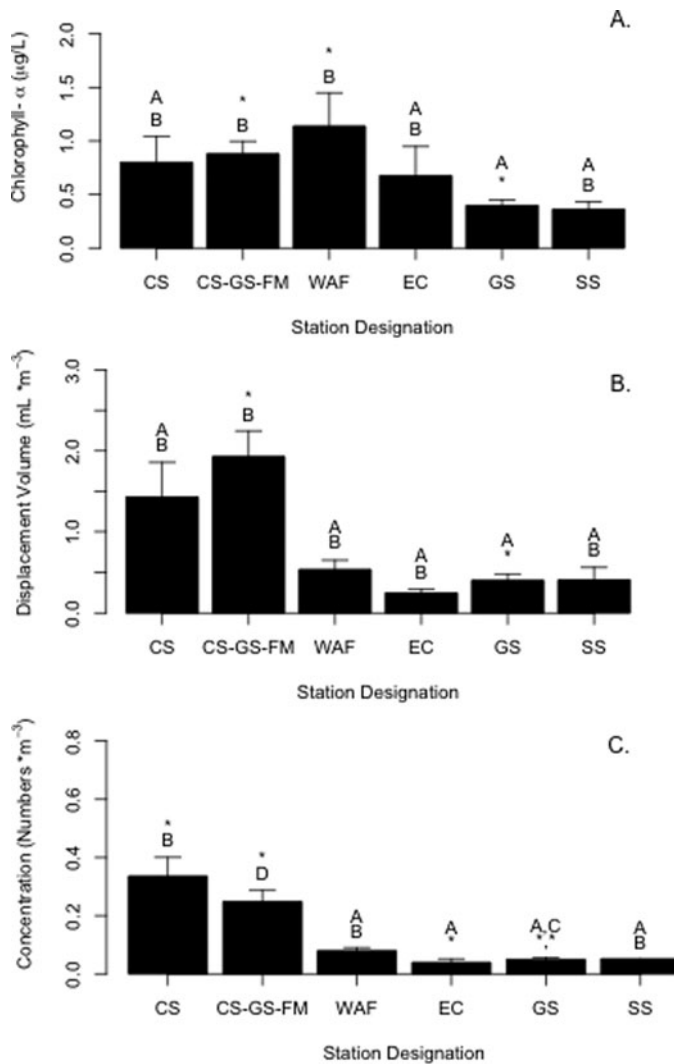
FIGURE 5. Comparison of means grouped by station designation for (**A**) chlorophyll *a* concentrations, (**B**) zooplankton displacement volumes, and (**C**) larval fish concentrations. See Figure 2 for definitions of station abbreviations. Error bar represents 1 SE of the mean; letters above bar plots indicate the results of multiple comparison tests; the asterisk (*) above the letters "B" or "D" denote significant differences in comparison with the * below the letter "A" or "C" ($P < 0.05$); the letter "A" above the letter "B" denotes no significant difference.

zooplankton displacement volumes, and larval fish concentrations. Zooplankton displacement volumes were highest in the eddy core, while concentrations of larval fishes were highest in the periphery of an oceanic, mesoscale, cyclonic eddy formed adjacent to the Hawaiian Islands (Lobel and Robinson 1986). Lagrangian model simulations that conform with empirical observations indicate that invertebrate and vertebrate larvae can aggregate in high-concentration packets randomly distributed along SST fronts associated with filaments that spin off the California Current, an eastern boundary current (Harrison et al.

2013). Lagrangian observations in and about an eddy of the Charleston Gyre region indicated that initially high concentrations of chlorophyll *a* decreased, while copepod nauplii and small copepodites and some other planktonic invertebrates important in the diets of larval fishes increased as eddies propagated northeastward (Govoni et al. 2010). In the eddies examined, and with the classification of stations used here, chlorophyll *a* concentrations were highest in the WAF, while zooplankton displacement volumes were highest in the CG-GS-FM; the concentration of all larval fishes was second highest in the CG-GS-FM and third highest in WAF.

The high taxa richness of larval fishes registered in collections from the Charleston Gyre region with 91 families was higher than in cross-shelf collections that penetrated the Gulf Stream to the north and to the south off the southeastern United States. Year-round between Cape Canaveral, Florida, and Cape Fear, Fahay (1975) recognized 51 families and Powles and Stender (1976) recognized 48. North of the Charleston Gyre region, Powell and Robbins (1994), Powell et al. (2000), and Quattrini et al. (2005) recognized 85 families from April through December, and Govoni and Spach (1999) recognized 75 families in the coalesced outer shelf and Gulf Stream fronts in similar areas in winter. Marancik et al. (2005) recognized 34 families along a cross-shelf transect south of the Charleston Gyre region, from near shore to the Gulf Stream in spring and winter. To the south, over the Florida Keys and proximal Gulf Stream, Limouzy-Paris et al. (1994) recognized 91 families in May and June, and Sponaugle et al. (2005) recognized 66 families year-round. Farther south in the Florida Straits and along transects across the Florida current (the progenitor of the Gulf Steam), Richards et al. (1993) recognized 52 families. While advances in larval fish taxonomy and changes in systematic classification through time influence the number of families recognized, mixing of Gulf Stream water and shelf water in the outer shelf front can explain much of the high taxa richness of larval fishes in the Charleston Gyre region.

The distribution of taxa and of taxa groups within eddies and associated fronts of the Charleston Gyre region indicates mixing of shelf and oceanic water. This observation is consonant with observations in and about anticyclonic, mesoscale eddies in the Gulf of Alaska, wherein ordination of taxa of larval fishes resulted in grouping by location inside and outside of eddies and associated frontal zones (Atwood et al. 2010). Elsewhere, Lobel and Robinson (1988) found the larvae of pelagic and mesopelagic fishes and coastal and shore fishes in an eddy off the Hawaiian Islands, and Sabatés and Olivar (1996) found the larvae of coastal and mesopelagic fishes displaced by the position of the shelf-slope front in the Mediterranean Sea. The dynamics that drive elevated concentrations of larval fishes are evident also in the Mediterranean Sea (Sabatés 1990; Sabatés and Masó 1990; Sabatés and Olivar 1996; Olivar et al. 2010), eddies along the margins of western boundary currents (Okazaki et al. 2002; Sponaugle et al. 2005), and eddies juxtaposed to

TABLE 5. Abundance of the families of larval fishes collected in the Charleston Gyre region off the southeastern United States in the winters of 2000, 2001, and 2002.

Family	Mean concentration (number/m^3)	Number of occurrences (n)	SE	Percent of total composition (%)	Rank total composition
Anguillidae	0.0042	1		0.05	1
Moringuidae	0.0032	3	0.0003	0.16	18
Ophichthidae	0.0367	54	0.0150	2.97	79
Congridae	0.0062	26	0.0019	1.43	67
Clupeidae	0.6560	75	0.1408	4.12	88
Engraulidae	0.0108	6	0.0045	0.33	34
Argentinidae	0.0045	17	0.0005	0.93	58
Microstomatidae	0.0071	3	0.0020	0.16	18
Gonostomatidae	0.0725	82	0.0064	4.50	89
Chauliodontidae	0.0066	11	0.0027	0.60	50
Sternoptychidae	0.0114	50	0.0015	2.75	77
Phosichthyidae	0.0056	19	0.0009	1.04	60
Stomiidae	0.0044	3	0.0012	0.16	18
Astronesthidae	0.0040	1		0.05	1
Melanostomiidae	0.0035	6	0.0004	0.33	34
Malacosteidae	0.0033	2	0.0001	0.11	12
Aulopidae	0.0045	4	0.0012	0.22	29
Synodontidae	0.0230	57	0.0038	3.13	82
Scopelarchidae	0.0059	27	0.0007	1.48	68
Notosudidae	0.0061	19	0.0007	1.04	60
Paralepididae	0.0170	43	0.0032	2.36	76
Evermannellidae	0.0044	7	0.0007	0.38	39
Myctophidae	0.0778	91	0.0070	5.00	91
Moridae	0.0053	2	0.0017	0.11	12
Bregmacerotidae	0.0230	68	0.0049	3.73	85
Phycidae	0.0839	59	0.0233	3.24	83
Merlucciidae	0.0052	3	0.0010	0.16	18
Macrouridae	0.0031	4	0.0002	0.22	29
Ophidiidae	0.0319	56	0.0060	3.08	81
Carapidae	0.0059	9	0.0019	0.49	46
Antennariidae	0.0022	1		0.05	1
Ceratiidae	0.0034	10	0.0002	0.55	48
Holocentridae	0.0027	1		0.05	1
Melamphaeidae	0.0073	27	0.0018	1.48	68
Trachichthyidae	0.0036	1		0.05	1
Diretmidae	0.0033	3	0.0005	0.16	18
Caproidae	0.0038	3	0.0003	0.16	18
Fistulariidae	0.0037	2	0.0001	0.11	12
Macrorhamphosidae	0.0040	6	0.0007	0.33	34
Scorpaenidae	0.0252	53	0.0036	2.91	78
Triglidae	0.0629	55	0.0171	3.02	80
Acropomatidae	0.0045	11	0.0005	0.60	50
Howellidae	0.0105	1		0.05	1
Serranidae	0.0213	69	0.0023	3.79	86
Opistognathidae	0.0041	1		0.05	1

TABLE 5. Continued.

| Family	Mean concentration (number/m^3)	Number of occurrences (n)	SE	Percent of total composition (%)	Rank total composition
Priacanthidae	0.0044	3	0.0012	0.16	18
Apogonidae	0.0045	15	0.0005	0.82	56
Epigonidae	0.0093	7	0.0028	0.38	39
Malacanthidae	0.0060	13	0.0010	0.71	53
Haemulidae	0.0081	8	0.0014	0.44	44
Sparidae	0.1652	41	0.0474	2.25	74
Sciaenidae	0.1346	67	0.0332	3.68	84
Gerreidae	0.0815	2	0.0568	0.11	12
Mullidae	0.0104	17	0.0029	0.93	58
Chaetodontidae	0.0073	7	0.0018	0.38	39
Pomacanthidae	0.0048	2	0.0013	0.11	12
Carangidae	0.0084	24	0.0014	1.32	64
Rachycentridae	0.0051	6	0.0019	0.33	34
Coryphaenidae	0.0028	1		0.05	1
Bramidae	0.0047	8	0.0007	0.44	44
Lutjanidae	0.0234	7	0.0129	0.38	39
Mugilidae	0.0077	14	0.0020	0.77	54
Pomacentridae	0.0034	7	0.0004	0.38	39
Labridae	0.0082	38	0.0010	2.09	72
Scaridae	0.0081	42	0.0011	2.31	75
Chiasmodontidae	0.0038	4	0.0001	0.22	29
Labrisomidae	0.0089	5	0.0025	0.27	33
Uranoscopidae	0.0061	14	0.0012	0.77	54
Percophidae	0.0071	4	0.0029	0.22	29
Chaenopsidae	0.0153	1		0.05	1
Blenniidae	0.0102	3	0.0028	0.16	18
Callionymidae	0.0100	34	0.0047	1.87	71
Gobiidae	0.0236	73	0.0033	4.01	87
Luvaridae	0.0076	3	0.0039	0.16	18
Acanthuridae	0.0036	12	0.0003	0.66	52
Sphyraenidae	0.0031	2	0.0001	0.11	12
Gempylidae	0.0061	21	0.0015	1.15	63
Trichiuridae	0.0063	6	0.0018	0.33	34
Scombridae	0.0262	25	0.0063	1.37	66
Nomeidae	0.0150	24	0.0038	1.32	64
Ariommatidae	0.0124	27	0.0024	1.48	68
Tetragonuridae	0.0041	1		0.05	1
Stromateidae	0.0058	10	0.0011	0.55	48
Bothidae	0.0451	82	0.0050	4.50	89
Scophthalmidae	0.0034	3	0.0001	0.16	18
Paralichthiidae	0.0240	39	0.0042	2.14	73
Cynoglossidae	0.0086	15	0.0018	0.82	56
Soleidae	0.0034	3	0.0000	0.16	18
Monacanthidae	0.0053	9	0.0006	0.49	46
Tetraodontidae	0.0059	19	0.0012	1.04	60
Molidae	0.0070	1		0.05	1
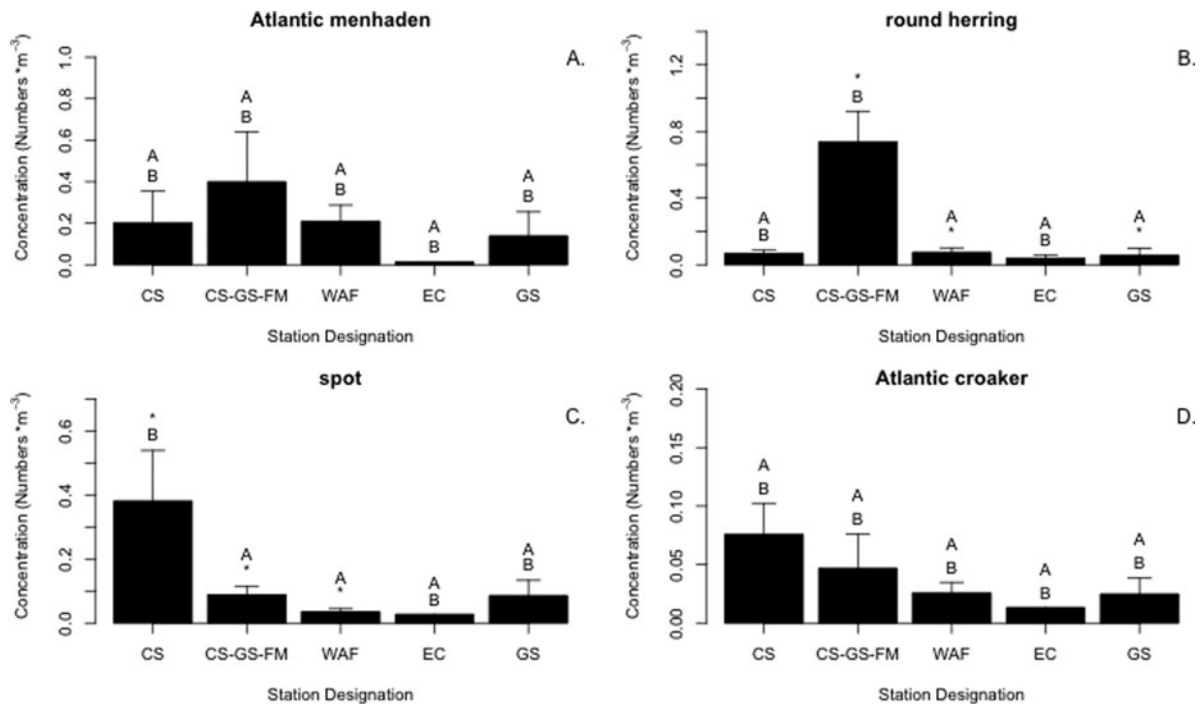
FIGURE 6. Comparison of means grouped by station designation for indicator taxa of the larvae of shelf-spawned fishes in the Charleston Gyre region off the southeastern coast of the United States. See Figure 2 for definitions of station abbreviations. Error bar represents 1 SE of the mean: letters above bar plots indicate the results of multiple comparison tests; the asterisk (*) above the letter "B" denotes significant differences in comparison with the * below letter "A" ($P < 0.05$); the letter "A" above the letter "B" denotes no significant difference.

deepwater currents (Brandt 1983; Lobel and Robinson 1986, 1988; Smith et al. 1999).

Upwelling and eddy diffusion within eddies and fronts of western boundary currents (Olson 2001) can provide enhanced primary and secondary productivity, as well as favorable habitat for feeding and consequent growth of larval fishes (Bakun 2006; Richardson et al. 2009). For larval fishes, enhanced feeding could shorten larval duration, lower cumulative mortality, and increase population recruitment (Houde 2008). The enhanced

trophic environments in and about the mesoscale cyclonic eddies of the Charleston Gyre region as they propagate northeastward (Govoni et al. 2010) indicate the potential importance of these pelagic habitats to the growth, survival, and subsequent population recruitment of larval fishes (Munk et al. 2003; Godø et al. 2012). The residence time on the outer shelf and upper slope is ~1 month, the same duration as the larval period of most fishes. These eddies also translocate larvae to the east and north.

TABLE 6. Results of one-way ANOVAs of the mean concentrations of the larvae of indicator taxa among station designations and Kruskal–Wallis tests of the ranks of the median concentrations among station designations.

Taxon	df	Sum of squares	Mean square	F-value	χ^2	P-value
		One-way ANOVA				
Bristlemouths	5	3.3×10^{-2}	6.6×10^{-3}	2.1		7.4×10^{-2}
Lightfishes	4	6.2×10^{-5}	1.6×10^{-5}	1.1		3.8×10^{-1}
Atlantic Menhaden	4	5.3×10^{-1}	1.3×10^{-1}	1.1×10^{-1}		9.8×10^{-1}
Round Herring	4	7.5	1.9	2.6		4.2×10^{-2}
Atlantic Croaker	4	9.9×10^{-3}	2.5×10^{-3}	2.2×10^{-1}		9.3×10^{-1}
		Kruskal–Wallis tests				
Lanternfishes	5				3.69×10	6.15×10^{-7}
Spot	4				1.06×10	3.15×10^{-2}

TABLE 7. Detrended correspondence analysis (DCA) (axes and eigenvalues) of families of larval fishes collected in the Charleston Gyre region off the southeastern United States in the winters of 2000, 2001, and 2002.

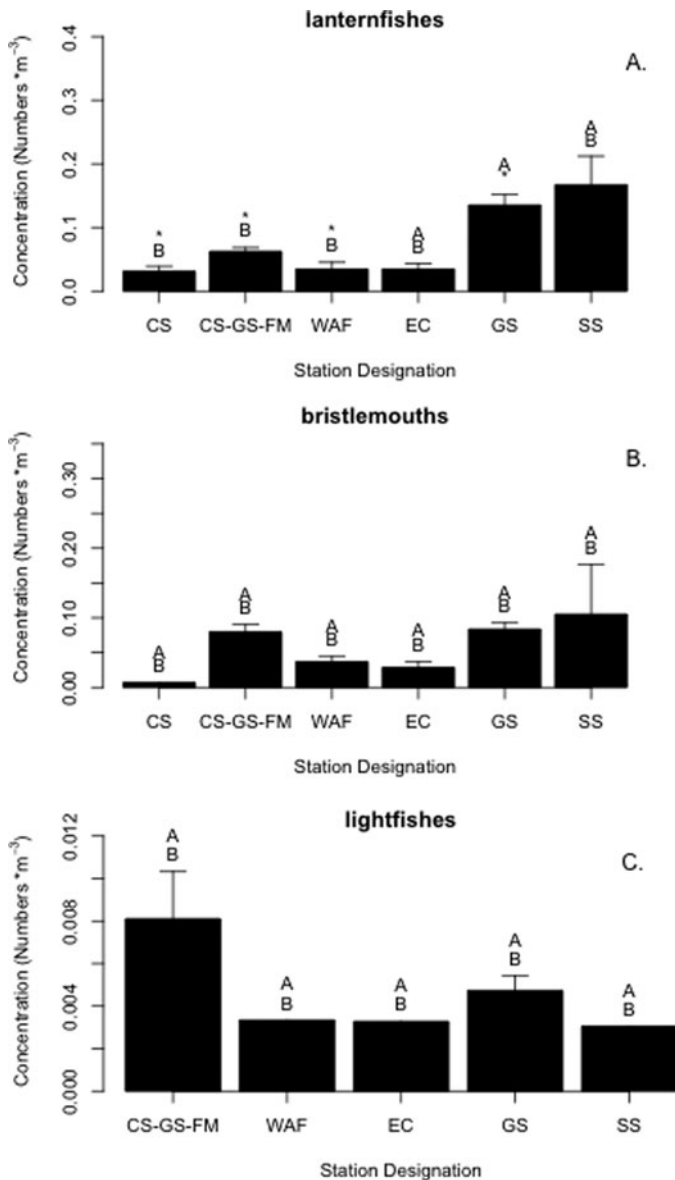| DCA1	DCA2	DCA3	DCA4
0.4824	0.3204	0.2451	0.0685

FIGURE 7. Comparison of means grouped by station designation for indicator taxa of the larvae of ocean-spawned fishes in the Charleston Gyre region off the southeastern coast of the United States. See Figure 2 for definitions of station abbreviations. Error bar represents 1 SE of the mean: letters above bar plots indicate the results of multiple comparison tests; the asterisk (*) above letter "B" denotes significant differences in comparison with the * below the letter "A" ($P < 0.05$); the letter "A" above the letter "B" denotes no significant difference.
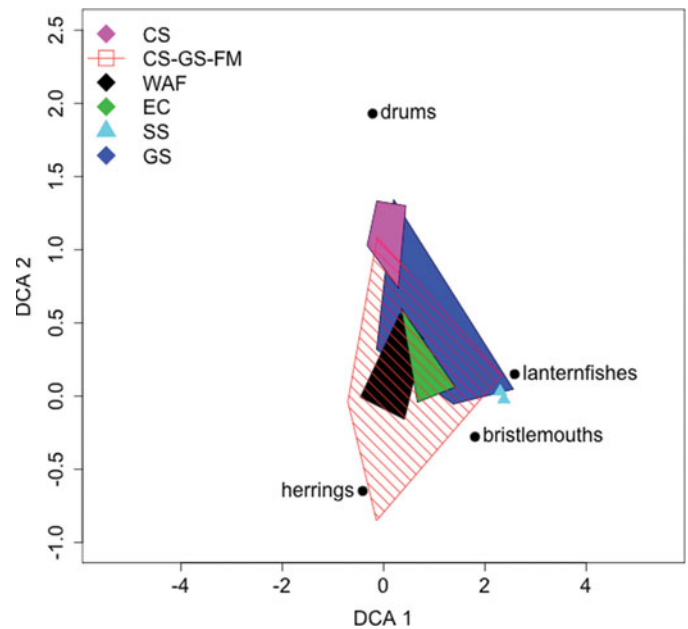

FIGURE 8. Detrended correspondence analysis (axes and eigenvalues) of families of larval fishes collected in the Charleston Gyre region off the southeastern United States in the winters of 2000, 2001, and 2002. Polygons encompass groupings and symbols denote groupings of station designations; see Figure 2 for definitions of station abbreviations.

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