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PRIMARY RESEARCH PAPER

Abundance and habitat associations of tuna larvae in the surface water of the Gulf of Mexico

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Abstract Summer ichthyoplankton surveys were conducted in the northern Gulf of Mexico from 2007 to 2010 to characterize the distribution and abundance of tuna larvae. Larval assemblages of tunas were comprised of four genera: *Thunnus*, *Auxis*, *Euthynnus,* and *Katsuwonus*. *Thunnus* were the most abundant and four species were detected; *T. atlanticus* [blackfin tuna], *T. obesus* [bigeye tuna], *T. albacares* [yellowfin tuna], and *T. thynnus* [bluefin tuna]. Intra- and inter-annual variability in the distribution and abundance of *Thunnus* species were observed with higher densities in 2008 and 2009, with a decline in abundance observed in 2010. Distribution and abundance of *Thunnus* larvae were influenced by physical and chemical conditions of the water mass, notably sea surface temperature and salinity. Distinct species-specific habitat preferences were observed and the location of mesoscale oceanographic features influenced larval abundance with higher densities of *T. atlanticus, T. obesus,* and *T. albacares* near anticyclonic (warm core) regions and the Loop Current, while *T. thynnus* was observed in higher densities near cyclonic (cold core) regions. This study demonstrates that spatial and temporal variability in the location of mesoscale oceanographic features may be important to partitioning nursery habitat among *Thunnus* species.

Keywords Bluefin · Yellowfin · Bigeye · Blackfin · Eddies · Loop Current

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Introduction

Tunas (family Scombridae) support an important worldwide fishery and represent a highly prized food resource. Overexploitation of tunas has become an important concern over the past few decades as populations of several species have declined below levels required to achieve maximum sustainable yield (ICCAT, 2015, 2016). Declining tuna populations have important economical implications, but also influence the productivity and stability of pelagic ecosystems (Fromentin & Powers, 2005; Baum & Worm, 2009;

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Olson et al., 2010). Similar to other pelagic species, tunas consume large amounts of prey to satisfy their high metabolic rates and, in turn, influence biodiversity, community structure, and trophic relationships in pelagic ecosystems (Stevens et al., 2000; Korsmeyer & Dewar, 2001; Essington et al., 2002). Because of their economical and ecological importance, understanding the factors that affect the distribution and abundance of tunas is critical information and required to protect and manage their populations.

The dynamics of exploited population is greatly impacted by recruitment success (Hsiesh et al., 2006); therefore, it is important to understand the causes of recruitment variability to reduce uncertainty in estimates of spawning biomass and population size. Basic information on the abundance and distribution of tuna larvae can be used to determine the timing and location of spawning (Govoni, 2005; Rooker et al., 2007; Teo et al., 2007; Richardson et al., 2016). Abundance estimates from early life surveys also represent important fishery independent indices that can be used to predict spawning biomass and the recruitment potential of tuna populations (Ingram et al., 2010). As a variety of biological, physical and chemical factors influence growth and survival during early life stages of pelagic fishes, recruitment success may be linked to the oceanographic conditions of the water mass inhabited (Lang et al., 1994; Sponaugle et al., 2005; Wexler et al., 2007; Simms et al., 2010; Rooker et al., 2012). Therefore, density and occurrence data for tunas and other pelagic fish larvae are often combined with environmental data to determine the location of highly suitable habitats or nurseries (Rooker et al., 2013, Kitchens & Rooker, 2014).

The Gulf of Mexico (GoM) is known to support important tuna fisheries and it is recognized as an important spawning and nursery habitat for several pelagic species, including tunas (Lindo-Atichati et al., 2012; Rooker et al., 2012, 2013; Kitchens & Rooker, 2014). Four genera of tunas are observed in this region (*Thunnus*, *Katsuwonus*, *Euthynnus*, and *Auxis*) and "true tunas" in the genus *Thunnus* represent the most valuable tuna stocks and, in turn, are most vulnerable to overfishing (ICCAT, 2015). Although several *Thunnus* species (*T. atlanticus*, Lesson, 1831 [blackfin tuna], *T. obesus*, Lowe, 1839 [bigeye tuna], *T. albacares*, Bonnaterre, 1788 [yellowfin tuna], and *T. thynnus*, Linnaeus, 1758 [bluefin tuna]) are detected in the GoM, investigations of fish-habitat relationships for early life stages of *Thunnus* are incomplete and work to date has centered almost exclusively on one species *T. thynnus* (e.g. Scott et al., 1993; Ingram et al., 2010; Muhling et al., 2010, 2011; Malca et al., 2017). The distribution and abundance of *Thunnus* larvae has been linked to environmental change of their habitat in the GoM (Muhling et al., 2011; Lindo-Atichati et al., 2012; Rooker et al., 2013); however, our understanding of tuna-habitat associations and the importance of the GoM as spawning and nursery habitat for these species warrants further attention.

The importance of mesoscale features in the distribution and abundance of tunas has been demonstrated in the GoM (Lang et al., 1994; Muhling et al., 2010; Rooker et al., 2013). Spatiotemporal environmental changes in tuna habitat were observed due to the presence of the Loop Current (LC) and its associated eddies that create zones of enhanced primary production, creating favorable early life habitat for *Thunnus* species (Richardson et al., 2010; Lindo-Atichati et al., 2012; Muhling et al., 2013; Rooker et al., 2013). Apart from these mesoscale features, the northern GoM is also heavily influenced by freshwater inflow and nutrient loading from the Mississippi River, which also enhances primary and secondary production (Biggs et al., 2008; Dorado et al., 2012). Together, mesoscale oceanographic features and freshwater inflow in the northern GoM likely lead to favorable environmental conditions that improve the growth and survival of *Thunnus* larvae (Lindo-Atichati et al., 2012; Muhling et al., 2013; Rooker et al., 2013). However, influence of mesoscale features on distribution and abundance of tuna in the northern GoM have not yet been adequately determined at the species level. Here, we provide the first detailed assessment of early life habitats of *Thunnus* (*T. atlanticus*, *T. obesus*, *T. albacares*, and *T. thynnus*) and examine the effect of dynamic oceanographic conditions on the distribution and abundance of each species.

Methods

Sample collection

Surveys were conducted over 4 years (2007–2010) in the northern GoM within a sampling corridor that ranged from 26.5 to 29.0°N latitude and 88.0 to 93.0°W longitude (Fig. 1). Sampling was conducted in June

and July to correspond with the spawning period of several tunas in this region (Lang et al., 1994; Teo et al., 2007; Richardson et al., 2010). Paired neuston nets (2-m width × 1-m height frame) equipped with two different mesh sizes (500 and 1,200 μm) were towed through surface waters (<1 m) at approximately 2.5 kt for 10 min. Net tows were conducted during the day (ca. 700–1,900 h) at stations approximately 15-km apart to ensure coverage of a large area encompassing multiple oceanographic features. Overall, 558 stations were sampled with neuston nets over the duration of the study. General Oceanics flowmeters (Model 2030R, Miami, FL) were placed at the opening of each neuston net in order to estimate the volume of water sampled during each tow. This information was then used to calculate the density of tuna larvae collected at each station. Onboard, fish larvae were initially preserved in 70% ethanol, and later transferred to 95% ethanol.

Molecular identification

In the laboratory, each neuston net sample was sorted under a Leica MZ stereomicroscope and tuna larvae were isolated and preserved in 70% ethanol. Four genera were visually identified among tuna larvae using pigmentation and morphological characteristics: *Thunnus* spp., *Auxis* spp., *Katsuwonus pelamis*, and *Euthynnus alletteratus* (Richards, 2006). *Thunnus* larvae were identified until the species level; however, small *Thunnus* larvae present very similar pigmentation and morphological characteristics making visual identification to the species level difficult. As an alternative, we used high-resolution melting analysis (HRMA), a highly sensitive and fast genotyping method used previously on fishes (Smith et al., 2010; Fitzcharles, 2012; Randall et al., 2015), for species identification. A non-destructive sodium hydroxide DNA isolation method (Alvarado Bremer et al., 2014) was utilized for DNA isolation on each larva. We used an unlabeled probe HRMA assay developed for GoM tuna species genetic identification by Smith and Alvarado Bremer (unpublished), as follows. The mitochondrial DNA gene NADH dehydrogenase subunit 4 (ND4) was amplified using asymmetric polymerase chain reaction (PCR) in 10 μl reaction volumes containing 10 ng of DNA template, 1× EconoTaqPlus (Lucigen), and 1× LC Green Plus (Biofire Diagnostics, Inc.), and 0.200 μM of the forward primer (5′-AGCAGAAAAGAGCG GAGGAG-3′), 0.028 μM of the diluted reverse primer (5′-ACAGGCTCAATCTGTCTCCCG-3′), and 0.200 μM of an unlabeled phosphorylated probe (5′-GAGGCTTTACGGGGGGCCCTTATCCTT/3Phos/-3′), which is complementary for *T. maccoyii*. Thermal cycling and HRMA were performed on a LightCycler 480 Real-Time PCR system (Roche Applied Science, USA) with an initial denaturation of 10 min at 95°C followed by 35–45 cycles denaturing for 10 s at 95°C, annealing 30 s at 57°C, and extension for 10 s at 72°C. After PCR cycling amplicons were denatured at 95°C

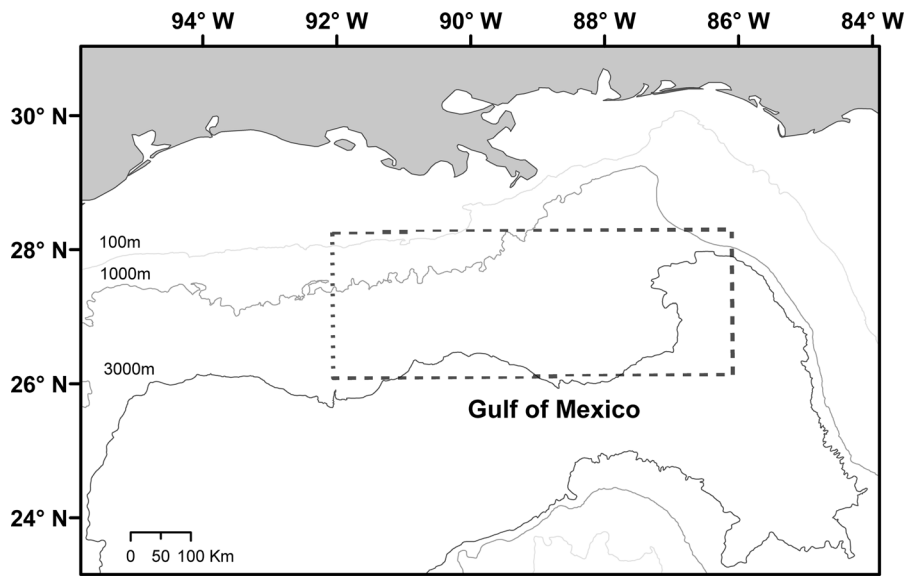


Fig. 1 Map of the ichtyoplankton sampling corridor (*dashed rectangle*) in the northern Gulf of Mexico from 2007 to 2010

for 1 min and then rapidly cooled and incubated at 40°C for 1 min followed by data acquisitions (11/°C) between 48 and 95°C at a melting ramp rate of 0.02°C/s. Species identification was determined by the unlabeled species probe melts that generated species-specific melting curves corresponding to single nucleotide polymorphisms (i.e., point mutations) in the probe-complementary coding sequences (Fig. 2).

Due to the large number of *Thunnus* larvae collected ($n = 16{,}986$), it was not possible to genetically identify to species all larvae collected over the 4-year study. HRMA was performed on larvae from a subset of positive stations (*Thunnus* larvae present, $n = 5{,}744$) from each survey, with molecular identification performed on larvae from 51% of the overall positive stations (range 38–53% from 2007 to 2009, and 100% in 2010). Positive stations used for HRMA were selected randomly among major zones (e.g. 27°N vs 28°N transect) or mesoscale features to provide broad spatial coverage within each sampling corridor. No attempt was made to extrapolate species composition from HRMA-based stations to remaining positive stations, and these stations were excluded from species level descriptions and analyses. If positive stations examined with HRMA contained less than 100 *Thunnus* larvae, each individual was genetically identified to species. If more than 100 *Thunnus* larvae were present, 100 randomly selected larvae were genetically identified and the ratio of species present in this subset was applied to the total number of larvae collected at the station. Before DNA extraction, each larva was measured from the tip of the snout to the tip of the notochord (SL) to the nearest 0.1 mm using the software Image-Pro Plus 7.0.

Environmental data

At each station, sea surface temperature (SST in °C) and salinity (psu) were collected using a Sonde 6920 Environmental Monitoring System (YSI Inc.). Other environmental data were downloaded and extracted from different datasets using the marine ecology toolbox in ArcGIS v.10. Sea surface height anomaly (SSHA in cm) data were generated every 7 days from merged satellite altimetry measurements using Jason-1, ENVISAT/ERS, Geosat Follow-On and Topex/Poseidon interlaced (AVISO, www.aviso.oceanobs.com) and data consisted of averaged time periods with 0.25° resolution. Sea surface chlorophyll *a* concentrations (mg m^{-3}) were downloaded from Moderate

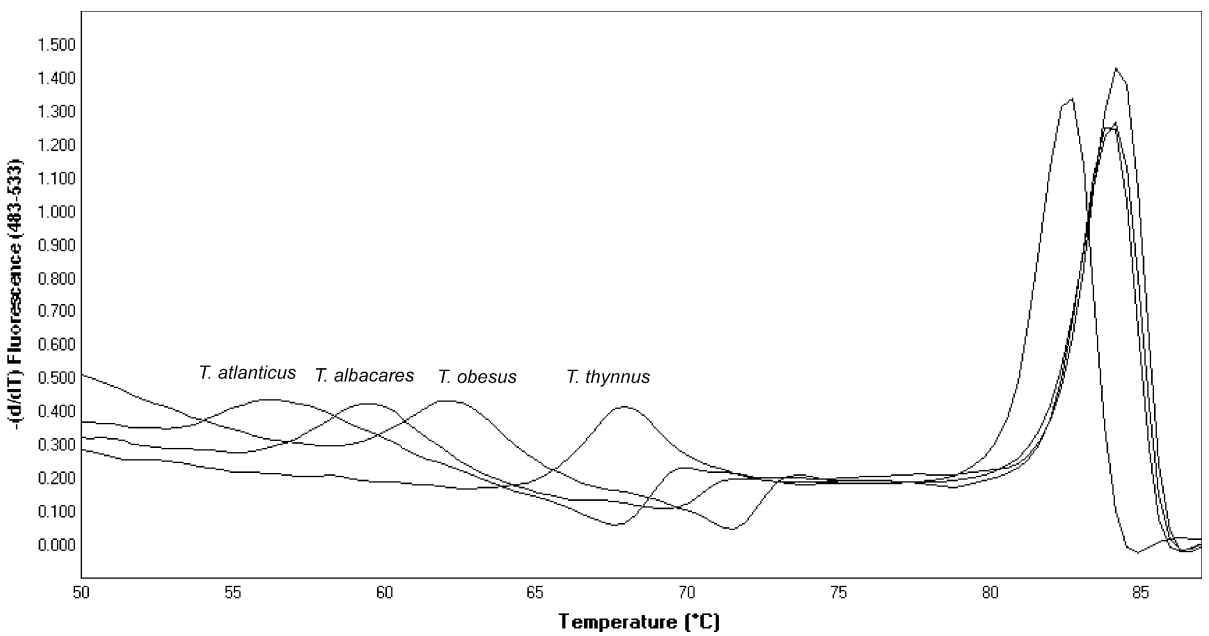


Fig. 2 Species-specific derivative melting curves based on HRMA for *Thunnus atlanticus*, *Thunnus obesus*, *Thunnus albacares*, and *Thunnus thynnus* of a ND4 mtDNA gene segment. Labeled peaks correspond to the maximum rate of melting of the PCR product against a *Thunnus maccoyii* specific probe. The portion of each curve melting >80°C corresponds to the entire amplicon and separates *Thunnus thynnus* from the other three species

Resolution Imaging Spectroradiometer (MODIS Aqua, www.oceancolor.gsfc.nasa.gov). Chlorophyll *a* data consisted of 8-days averaged time periods with 0.04° resolution. Water depth (m) at all sampling stations was extracted from GEODAS U.S. Coastal Relief Model with 3 arc-second grids (www.ngdc.noaa.gov).

In addition to environmental data (SST, chlorophyll *a*, and depth) stations were classified based on salinity and SSHA. Over the four sampling years, salinity varied from 20.5 to 39.3 psu and a natural break in salinity data was observed at 35 psu. This break was used to define two different regions depending on salinity: lower salinity regions (≤35 psu) and higher salinity regions (>35 psu). To characterize mesoscale features (Loop Current and eddies) associated with each station, SSHA values < -5 and >10 cm were defined here as cyclonic and anticyclonic regions, respectively (Leben et al., 2002). Intermediate SSHA values (-5 cm $<$ SSHA $<$ 10 cm) were defined as open water regions.

Data analysis

Densities at each station were expressed as larvae 1,000 m^{-3} and based on pooled catches between the 500 and 1,200 µm mesh neuston nets. Moreover, it has been observed that the difference in vertical distribution among tuna genera might influence the catch rate of the *Thunnus* spp., *Auxis* spp., *Euthynnus alletteratus*, and *Katsuwonus pelamis* larvae (Habtes et al., 2014). To determine the influence of the sampling gear in the present study, we compared larval fish collected with both oblique bongo tows to 100 m (frame 61 cm, 333 and 500 µm mesh size) and neuston net collections in the upper 1 m of the water column (1,200 µm mesh size) in our sampling corridor from 2011 to 2013 and 2015. Significant differences in density were observed for *E. alletteratus* and *Auxis* spp. larvae between bongo nets (8.10 and 2.62 larvae 1,000 m^{-3}) and neuston nets (0.92 and 0.26 larvae 1,000 m^{-3}) (Welch test $P < 0.01$), while *K. pelamis* larvae were rare in our samples. Except for *T. albacares*, no significant difference in density was observed between neuston and oblique bongo tows (Welch test; $P > 0.05$), suggesting that both sampling gears efficiently sampled *Thunnus* larvae (Fig. S1). This result is consistent with previous study that indicated no significant difference in density between neuston net and bongo net for *T. thynnus* and other *Thunnus* (Habtes et al., 2014). While we acknowledge that the surface sampling gear used for this study may not be suitable characterizing the entire assemblage of tuna larvae, it does provide representative estimates of density for the primary genera (*Thunnus*) under investigation here.

Temporal and spatial variability in densities of *Thunnus* larvae were investigated using PRIMER V6.1.15 (Clarke & Gorley, 2006) and permutational multivariate analysis of variance PERMANOVA V1.0.5 (Anderson et al., 2008). PERMANOVA analyses were used because they can handle non-normally distributed data and unbalanced designs (unequal number of stations collected and larvae analyzed per surveys). Statistical significance was calculated by permutations (9,999) (Anderson, 2001). Prior to the analysis, untransformed densities were used to calculate a Bray–Curtis similarity resemblance matrix for each species and a Euclidean distances matrix was calculated with normalized environmental variables. Densities of each species over the sampling period were compared using PERMANOVA (type-III) performed in a two-way crossed design, with year (4 levels: 2007, 2008, 2009 and 2010) and month (2 levels: June and July) as fixed factors. The relative importance of environmental parameters on the density of each *Thunnus* species was determined using univariate PERMANOVAs (type-I) with environmental data as covariates (SST, salinity, SSHA, chlorophyll *a*, and depth).

The influence of the environmental variables on each species was also investigated using principal coordinate analysis (PCoA). This approach explores the similarities in oceanographic regions and in densities of each species among stations in relation to environmental conditions (Van Oostende et al., 2012). Vector overlays (Pearson correlation) were superimposed onto PCoA plots to show which environmental variables were influencing densities, with the length and the direction of each vector providing information on the degree of correlation and the relationship between the environmental variables and the ordination axes. All statistical analyses were performed with alpha set at 0.05.

Results

A total of 18,251 tuna larvae was collected in the GoM including *Thunnus* spp. (93%), *Auxis* spp. (5%), *E. alletteratus* (<2%), and *K. pelamis* (<1%). Variations in occurrence and densities were observed among genera over the four sampling years (Table 1). *Thunnus* spp. were the most common and abundant tuna larvae with percent frequency of occurrence ranging from 63 to 88% and density ranging from 21.3 larvae 1,000 m^{-3} (2009) to 8.5 larvae 1,000 m^{-3} (2010). *Auxis* spp. and *E. alletteratus* larvae were moderately abundant with percent frequency of occurrence ranging from 3 to 23% and 2 to 14%, respectively. Maximum density of *Auxis* spp. was observed in 2009 (0.7 larvae 1,000 m^{-3}), while *E. alletteratus* maximum densities were recorded in 2008–2009 (1.1 larvae 1,000 m^{-3}). For both *Auxis* spp. and *E. alletteratus*, lowest densities were recorded in 2007 (0.2 and 0.01 larvae 1,000 m^{-3}). *Katsuwonus* was the least common tuna genera observed in our samples and was absent in 2007. Highest percent frequency of occurrence and density of *K. pelamis* were recorded in 2010 (8% and 0.2 larvae 1,000 m^{-3}).

Four species of *Thunnus* larvae were identified in our samples from the GoM with HRMA: *T. atlanticus*, *T. albacares*, *T. obesus*, and *T. thynnus*. The most abundant was *T. atlanticus*, accounting for 81% of the *Thunnus* larvae; *T. albacares* and *T. obesus* comprised 9 and 8% of the *Thunnus* larvae, while *T. thynnus* represented the smallest portion of *Thunnus* at 2% (Fig. 3). The size frequency distributions of *Thunnus* larvae ranged from 2 to 11 mm standard length (SL) (Fig. 4). Spawning period of *Thunnus* was estimated using the length-frequency distribution and growth curves previously established in the GoM. Because no age–length relationships *T. obesus* and *T. atlanticus* larval growth existed in this region, growth curve of *T. albacares* were used to estimate the spawning period of *T. atlanticus*, *T. obesus*, and *T. albacares* (Lang et al., 1994). The result indicated that a large number of *T. atlanticus*, *T. obesus,* and *T. albacares* larvae hatched 10 days before collection (<6 mm SL), while *T. thynnus* larvae hatched more than 10 days before collection (>6 mm SL) (Malca et al., 2017).

Temporal variation in density and percent frequency of occurrence of *Thunnus* larvae was also detected, with both inter- and intra-annual effects observed (Table 2; Fig. 5). *T. atlanticus* larvae were present at frequency greater than 50% of the stations sampled in each survey except in July 2008 (Table 2). Mean density of *T. atlanticus* larvae across all surveys was 9.7 larvae 1,000 m^{-3} and a significant effect of month ($P(\text{perm}) < 0.05$), year ($P(\text{perm}) < 0.01$), and interaction between month and year ($P(\text{perm}) < 0.05$) was detected (Table 3). Minimum and maximum densities of *T. atlanticus* larvae from surveys were observed in June 2010 (3.3 larvae 1,000 m^{-3}) and July 2009 (33.4 larvae 1,000 m^{-3}). Maximum density of *T. atlanticus* at a single station was recorded in July 2009 with 402.4 larvae 1,000 m^{-3}. *T. obesus* and *T. albacares* larvae were also regularly collected and percent frequency of occurrence ranged from 22 to

Table 1 Catch data of tuna larvae in the northern Gulf of Mexico from 2007 to 2010 using neuston nets

Year	Month	# Stations	*Thunnus* spp.		*Euthynnus alletteratus*		*Auxis* spp.		*Katsuwonus pelamis*	
			n	Frequency (%)	*n*	Frequency (%)	*n*	Frequency (%)	*n*	Frequency (%)
2007	June	59	1,381	81	1	2	28	7	0	0
	July	55	3,509	95	1	2	0	0	0	0
2008	June	72	1,343	74	2	3	6	8	2	1
	July	83	1,151	63	51	8	296	12	4	5
2009	June	92	1,242	82	0	0	3	3	0	0
	July	101	6,452	88	238	29	370	43	7	2
2010	June	48	749	44	31	10	170	13	49	10
	July	48	1,159	81	0	0	3	4	3	6
Total		558	16,986		324		876		65	

Total number of stations sampled, number of larvae caught, and percent of frequency are presented

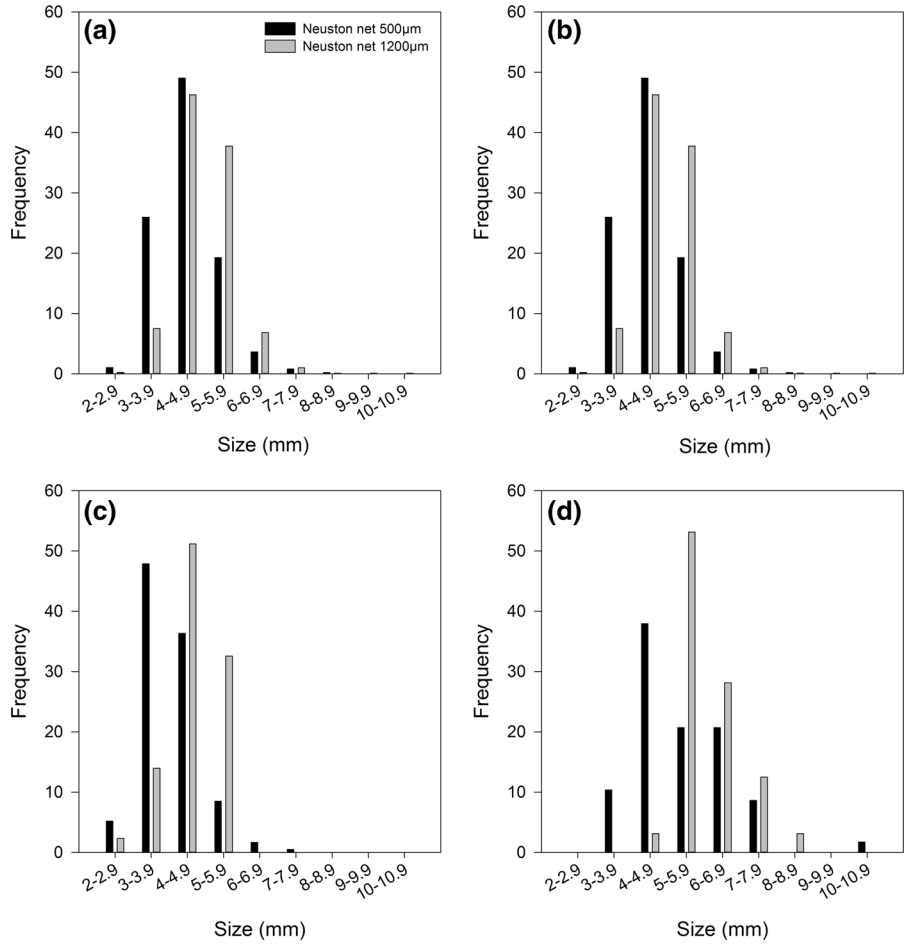


Fig. 3 Length-frequency of *Thunnus* larvae from 2007 to 2010; **a** *Thunnus atlanticus*, **b** *Thunnus obesus*, **c** *Thunnus albacares*, **d** *Thunnus thynnus*

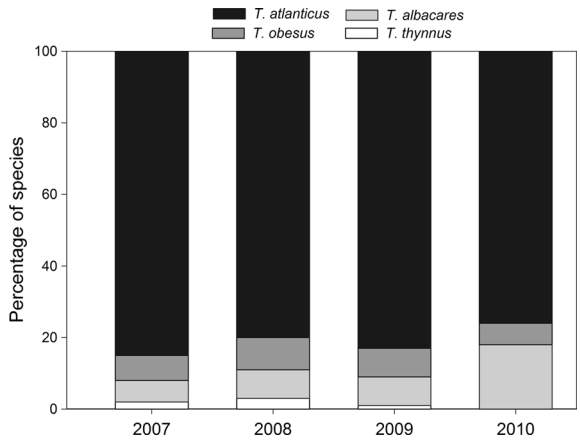


Fig. 4 Species composition of *Thunnus* larvae in the northern Gulf of Mexico from 2007 to 2010

79% and 13 to 57% among surveys, respectively (Table 2). *T. obesus* densities varied significantly between months and among years (P(perm) < 0.01), while *T. albacares* densities varied significantly only among years (P(perm) < 0.01) (Table 3). Peak of densities of *T. obesus* (2.7 larvae 1,000 m^{-3}) and *T. albacares* (3.5 larvae 1,000 m^{-3}) were both observed in July 2009, while the lowest densities were observed in July 2010 for *T. obesus* (0.2 larvae 1,000 m^{-3}) and July 2008 for *T. albacares* (0.1 larvae 1,000 m^{-3}) (Fig. 5). For the two aforementioned species, a significant interaction between month and year (P(perm) < 0.05) on density was observed (Table 3). *T. thynnus* larvae were absent from all July surveys and percent frequency of occurrence in June surveys ranged from 4 to 25% (Table 2). Mean density of *T. thynnus* larvae in all June surveys was (0.2 larvae 1,000 m^{-3}), with the highest density recorded in June 2007 (0.5 larvae 1,000 m^{-3}). Similar to the other species, *T. thynnus* densities varied significantly among years (P(perm) $= 0.03$; Table 3), and the lowest recorded density was observed in 2010 with

Table 2 Catch data of *Thunnus* larvae in the northern Gulf of Mexico from 2007 to 2010 using neuston nets

Year	Month	# Stations	*T. atlanticus*		*T. obesus*		*T. albacares*		*T. thynnus*	
			n	Frequency (%)	*n*	Frequency (%)	*n*	Frequency (%)	*n*	Frequency (%)
2007	June	22	420	79	32	50	54	39	25	25
	July	22	659	92	63	79	16	42	0	0
2008	June	25	472	52	48	40	82	21	42	19
	July	24	531	43	62	23	11	13	0	0
2009	June	32	623	76	71	48	16	19	31	19
	July	34	1,193	81	102	55	162	57	0	0
2010	June	28	316	62	24	22	157	31	2	4
	July	33	464	75	37	25	29	25	0	0
Total		220	4,678		440		527		100	

Total number of stations genetically identified, number of larvae identified, and percent of frequency are presented

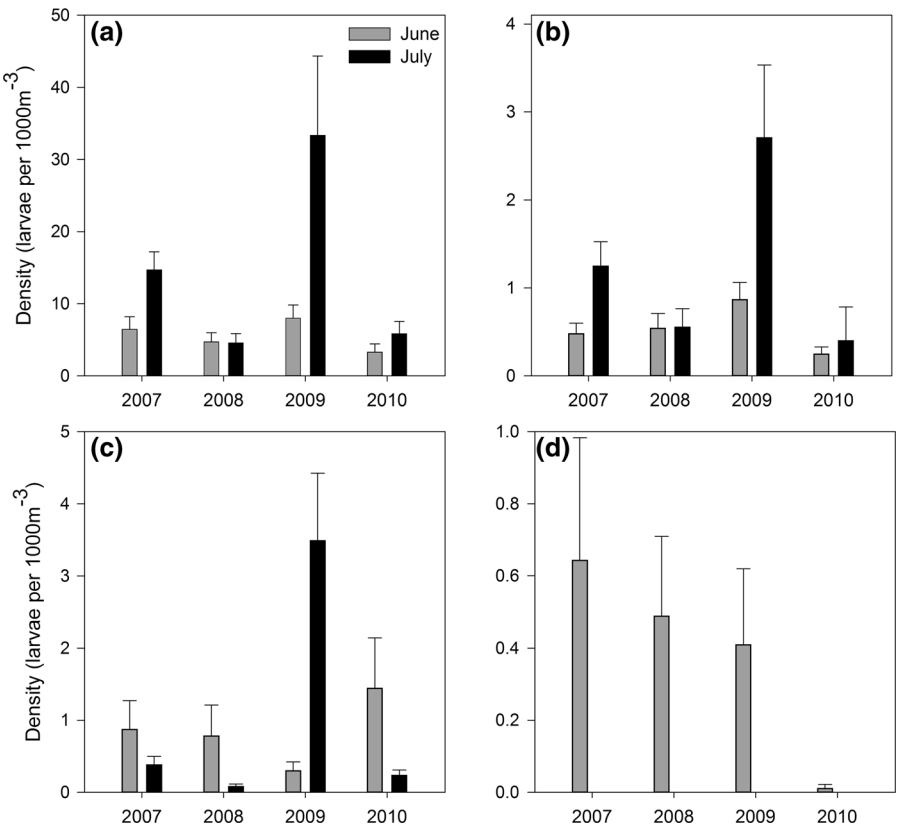


Fig. 5 *Thunnus* larvae densities (larvae 1,000 m^{-3}) in the northern Gulf of Mexico between 2007 and 2010; **a** *Thunnus atlanticus*, **b** *Thunnus obesus*, **c** *Thunnus albacares*, **d** *Thunnus thynnus. Error bars* represent standard error of the mean

only two larvae caught during this survey (<0.01 larvae 1,000 m^{-3}).

Spatial variability in larval densities was observed during the 4-year survey in the GoM, with conspicuous species-specific patterns observed for some taxa (Figs. 6, 7). *T. atlanticus* and *T. obesus* larvae were widely distributed on the continental shelf and the continental slope. *T. albacares* distributions were narrower with peak densities of larvae on the continental slope and in zones impacted by the Mississippi

Table 3 PERMANOVA results showing the temporal difference in densities from *Thunnus* larvae from 2007 to 2010 in the northern Gulf of Mexico using neuston nets

Source of variation	df	*T. atlanticus*			*T. obesus*		
		MS	Pseudo-F	*P*	MS	Pseudo-F	*P*
Year	3	12,516	7.4349	**0.0001**	4,964.7	9.5989	**0.001**
Month	1	9,823.7	5.8357	**0.0054**	2,931.6	5.668	**0.0104**
Year*Month	3	4,080.9	2.4242	**0.0311**	1,711.6	3.3093	**0.0109**
Residuals	332	1,683.4			517.22		
		T. albacares			*T. thynnus*		
Year	3	2,717	5.1571	**0.0006**	346.21	2.5186	**0.0396**
Month	1	1,424.2	2.7033	0.0797	2,573.4	18.72	**0.0001**
Year*Month	3	5,797.9	11.005	**0.0001**	326.8	2.3773	0.0525
Residuals	332	526.84			137.46		

Bold values represent significant differences

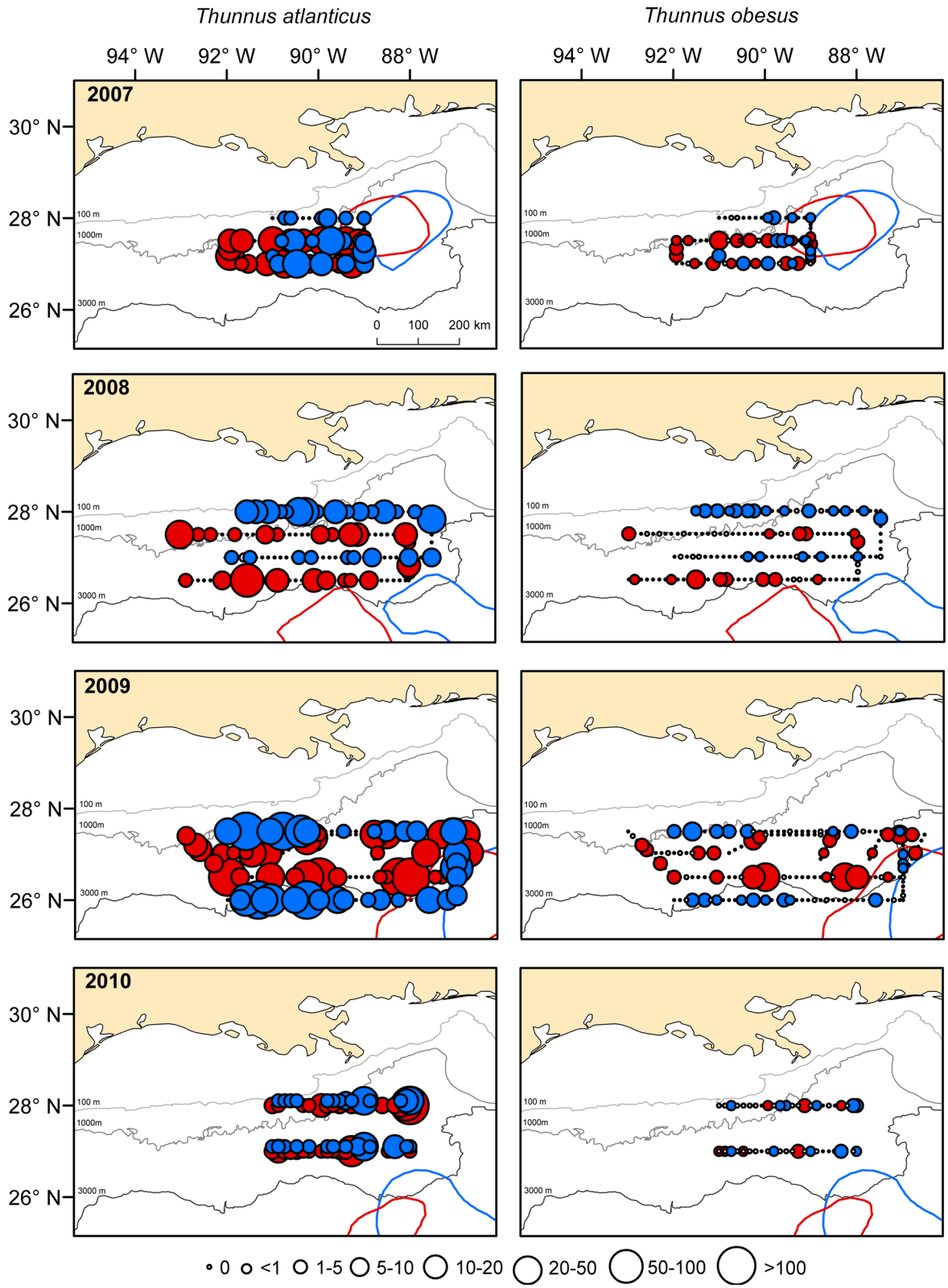
River plume (28°N and 88–89°W). In contrast, the distribution of *T. thynnus* was more limited with highest densities observed on the continental slope. In certain years, the presence of anticyclonic eddies and the Loop Current (LC) seemed to influence the distribution and abundance of all four *Thunnus* species. Years with the highest northward extension of the LC and associated anticyclonic eddies (2007 and 2009) coincided with peaks in the density of *Thunnus* larvae. Mean densities for *T. atlanticus*, *T. obesus*, and *T. albacares* were greatest in July 2009 during the maximum northward penetration of the LC, with peak densities observed at stations in close proximity to the northern margin of the LC or its associated eddies (Figs. 6, 7).

PCoA was conducted on all stations sampled to observe the influence of oceanographic conditions on the density of *Thunnus* larvae, with the contribution of environmental variables shown with directional vectors (Fig. 8). PCoA axis 1 explained 35.6% of the total variation among stations and was highly correlated to salinity ($|r| = 0.87$), chlorophyll *a* concentration ($|r| = 0.80$), and SST ($|r| = 0.59$), while PCoA axis 2 explained 22.3% of total variation among stations and was highly correlated to SSHA ($|r| = 0.89$). Environmental conditions and oceanographic features varied across our sampling corridor, and distinct physical and chemical characteristics were observed in cyclonic, anticyclonic, and open water regions (Fig. 8). Cyclonic regions characterized by lower salinity (mean 35.8 psu), lower SST (mean 28.5°C), and higher chlorophyll *a* concentration (mean 0.23 mg m^{-3}), while anticyclonic regions were characterized by higher salinity (mean 36.3 psu), higher SST (mean 29.6°C) and lower chlorophyll *a* concentration (mean 0.11 mg m^{-3}). In addition, open water regions were distinctly different from cyclonic and anticyclonic regions, and characterized by lower salinity (mean 35.2 psu), intermediate SST (mean 29.4°C), and higher chlorophyll *a* concentration (mean 0.27 mg m^{-3}).

The PCoA plots indicated that larval densities of all four *Thunnus* species were influenced by oceanographic conditions (Fig. 8). *T. atlanticus* and *T. obesus* were positively associated with SST, SSHA, and chlorophyll *a* concentration (Fig. 8). Also, the highest densities of *T. atlanticus* and *T. obesus* were recorded in regions with relatively high salinity (>36 psu), which are typically found in anticyclonic water masses. *T. albacares* were highly correlated with SST and chlorophyll *a* concentration, with the highest densities recorded in open water and lower salinity regions of our survey area (Fig. 8). In contrast to other *Thunnus* larvae, *T. thynnus* densities were negatively associated with SSHA, SST, and chlorophyll *a* concentrations and the highest densities were correlated with stations in cyclonic and open waters regions (Fig. 8).

Discussion

Larval assemblages of tunas during the course of the study in the northern GoM were dominated by *Thunnus* spp., followed by *Auxis* spp., *Euthynnus alletteratus*, and *Katsuwonus pelamis*. This finding is

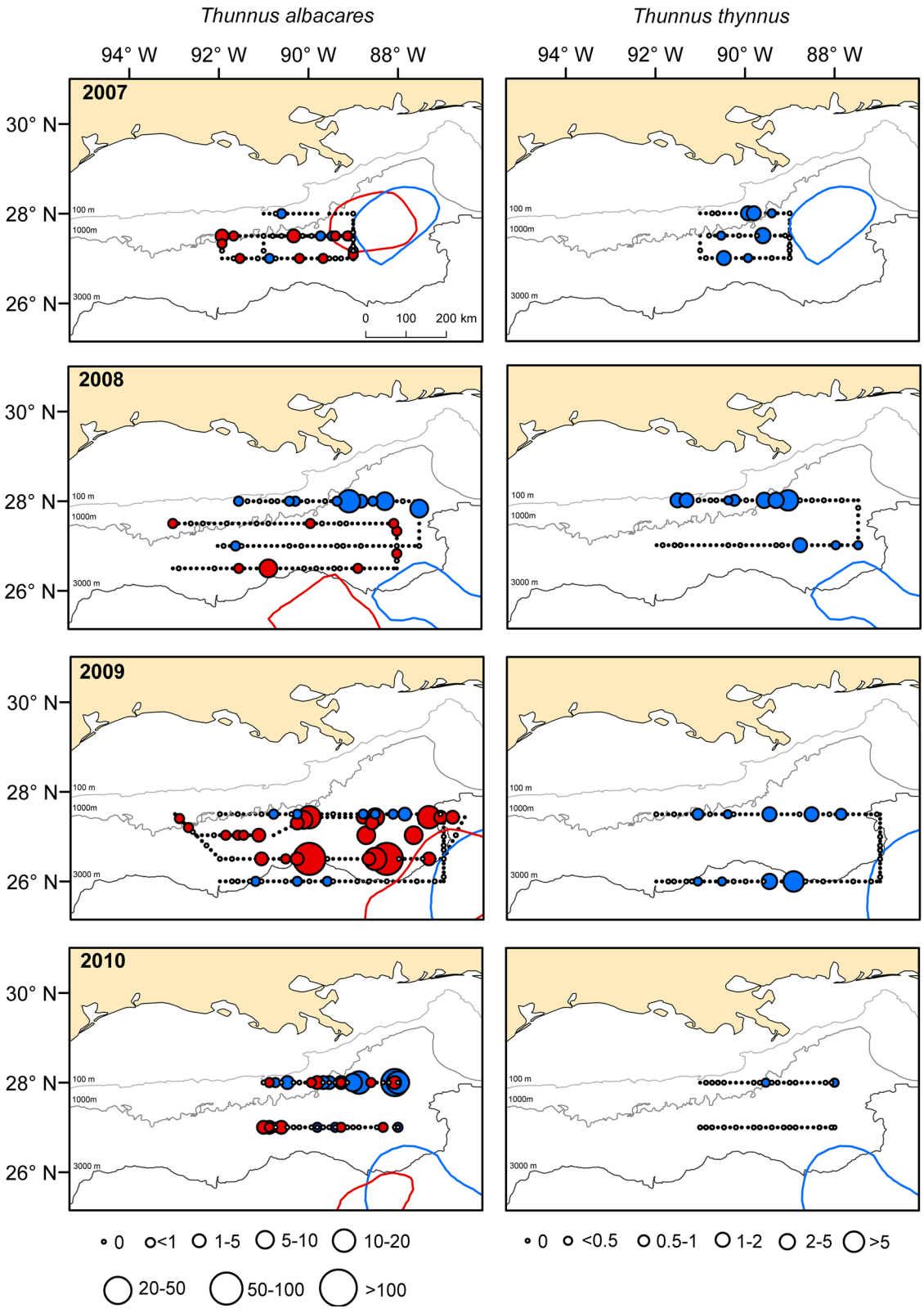

Thunnus atlanticus
Thunnus obesus
94° W
92° W
90° W
88° W
30° N
28° N
26° N
2007
2008
2009
2010
100 m
1000m
3000 m
0 100 200 km
0 <1 1-5 5-10 10-20 20-50 50-100 >100

◀**Fig. 6** Distribution and abundance of *Thunnus atlanticus* and *Thunnus obesus* larvae in June (*blue*) and July (*red*) from 2007 to 2010 in the northern Gulf of Mexico. *Circles* symbolize densities, scale of *T. atlanticus* and *T. obesus* is from 0 to >100 larvae 1,000 m^{-3}. *Black dots* represented the stations sampled but not genetically analyzed. Location of the LC is represented in June (*blue line*) and July (*red line*)

in accord with previous studies in the GoM (Richardson et al., 2010; Habtes et al., 2014); however, the density of *Thunnus* spp. larvae were higher than previously reported, while *Auxis* spp., *E. alletteratus* and *K. pelamis* densities were lower (Habtes et al., 2014). Although variation in densities was observed among previous studies, *Thunnus* was consistently reported as the dominant tuna taxa in this area (Richards et al., 1993; Rooker et al., 2007; Richardson et al., 2010; Lindo-Atichati et al., 2012; Epinosa-Fuentes et al., 2013). In the present study, *Thunnus* larvae were commonly collected over the 4-years sampling with mean densities of four species (9.6, 0.9, 0.8, and 0.2 larvae 1,000 m^{-3} for *T. atlanticus*, *T. albacares, T. obesus, T. thynnus*) often comparable or higher than reported values for other putative spawning areas, suggesting that the northern GoM may be a valuable spawning and nursery area. We found that *T. atlanticus* larvae were most abundant followed by *T. albacares* and *T. obesus*, while *T. thynnus* were present in limited numbers in our summer surveys. Richards et al. (1990) and Richardson et al. (2010) reported the composition of *Thunnus* larvae from ichthyoplankton surveys in the GoM and observed similar species structure with *T. atlanticus* accounting for 73–95%, *T. albacares* representing 5%, and *T. thynnus* larvae only 1%. Similar to the present study, Richards et al. (1990) detected *T. obesus,* and this species accounted for 4.9% of their *Thunnus* larvae. More recent work by Richardson et al. (2010) did not detect *T. obesus* larvae in their samples, but this may be due the difference in geographic location (Straits of Florida); nevertheless, the general make up of *Thunnus* larvae was similar to the present study with higher occurrence of other *Thunnus* species than *T. thynnus* (Richardson et al., 2010; Habtes et al., 2014).

The presence of tuna larvae can be used to determine the timing and location of tuna spawning in the GoM (Reglero et al., 2014; Richardson et al., 2016), but information on spawning events of each *Thunnus* species in the northern GoM is limited. The presence of young *Thunnus* larvae in our sampling corridor indicated that *Thunnus* spawning events occur in the northern GoM. Moderate to high frequency of occurrence of young larvae (<10 days) observed in our June and July surveys for *T. atlanticus, T. obesus*, and *T. albacares* suggests that each species spawns in the northern GoM in late spring or early summer, and possibly for more protracted periods which could not be determined given the limited temporal extent of our sampling. Spawning period of *T. albacares* has been defined from May to August in the GoM (Arocha et al., 2001; Richardson et al., 2010), which support our findings and indicate a seasonal periodicity of spawning for *T. albacares* in the northern GoM. In comparison, it has been reported that *T. atlanticus* has a prolonged spawning period from April to November with a peak in June and July (Richardson et al., 2010; Mathieu et al., 2013). Our study was restricted to summer months but indicates similar results with abundant densities of *T. atlanticus* larvae observed in summer. Basic information on the distribution and abundance of both early life stages and adult *T. obesus* in the GoM is lacking, limiting our ability to compare our findings on the spawning in this region. Previously *T. obesus* larvae were reported in the GoM (Richards et al., 1990); however, no spawning events were identified. Over 4-years sampling, we frequently collected *T. obesus* larvae in both June and July and this species accounted for 5–10% of *Thunnus* assemblage, suggesting for the first time the importance of the GoM as spawning habitat. In contrast to the other three species, *T. thynnus* larvae were only encountered in June surveys. This result is in accord with previous studies which indicated that the spawning period of *T. thynnus* is limited from April to June in the GoM (Rooker et al., 2007; Muhling et al., 2010, 2011; Knapp et al., 2014). Thus, lower overall mean densities observed here for *T. thynnus* is likely due in part to our July surveys being conducted at times outside the spawning period of this species.

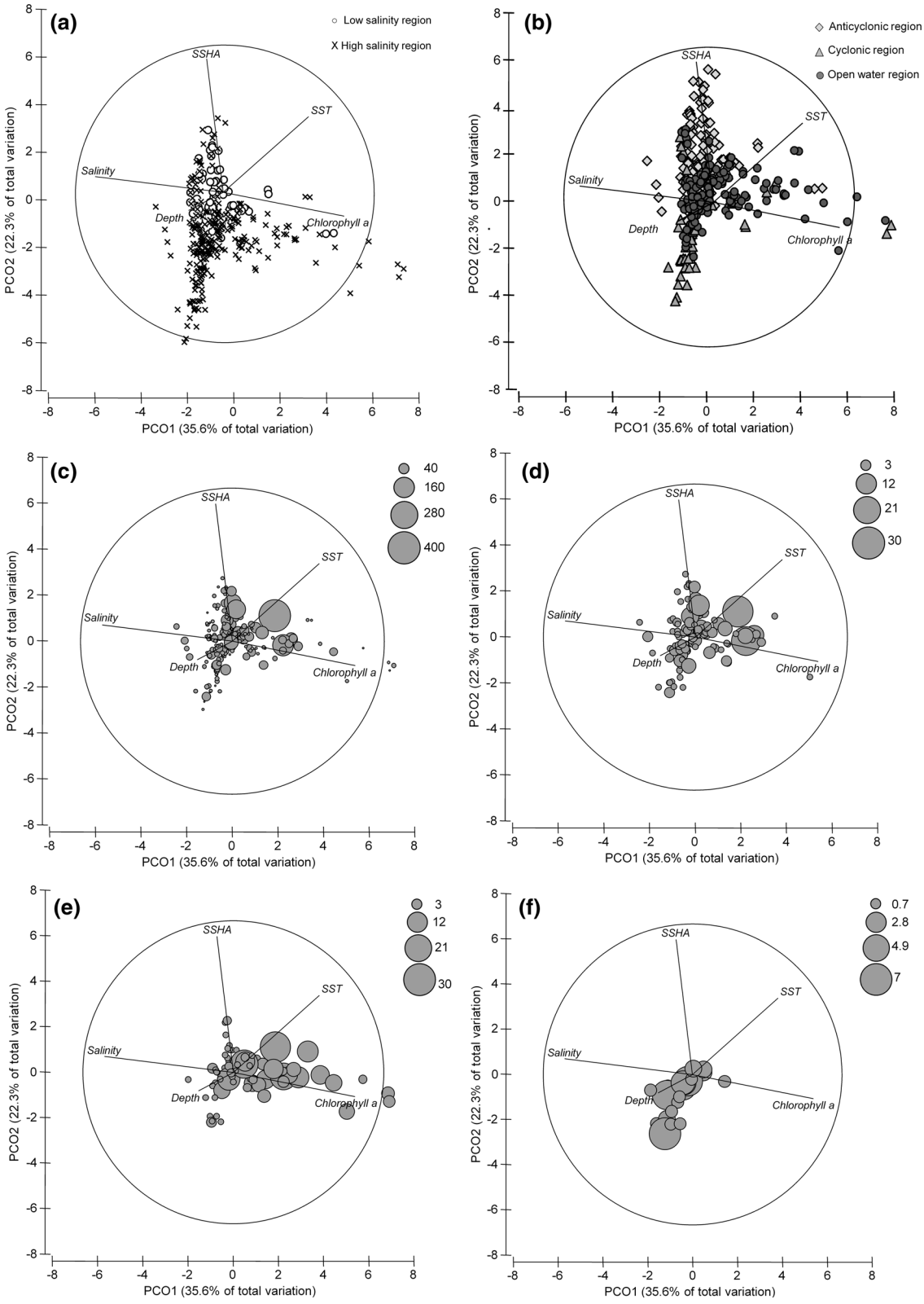
Significant interannual variation in the abundance of *Thunnus* larvae was detected with years of high abundances (2007–2009) and years of low abundances (2010) in the GoM, which may be a consequence of habitat changes or/and degradation. For instance, with the exception of *T. albacares*, densities of *Thunnus* larvae and other tuna genera were lowest in 2010, which is the period directly following the Deepwater Horizon (DWH) oil spill that discharged


Thunnus albacares
Thunnus thynnus
94° W
92° W
90° W
88° W
30° N
28° N
26° N
2007
2008
2009
2010
100 m
1000m
3000 m
0 100 200 km
0 <1 1-5 5-10 10-20
20-50 50-100 >100
0 <0.5 0.5-1 1-2 2-5 >5

◀**Fig. 7** Distribution and abundance of *Thunnus albacares* and *Thunnus thynnus* in June (*blue*) and July (*red*) from 2007 to 2010 in the northern Gulf of Mexico. *Circles* symbolize densities, scale of *T. albacares* is from 0 to >100 larvae 1,000 m^{-3} and scale of *T. thynnus* from 0 to >5 larvae 1,000 m^{-3}. *Black dots* represented the stations sampled but not genetically analyzed. Location of the LC is represented in June (*blue line*) and July (*red line*)

approximately 4.9 million barrels of oil into the northern GoM (Camilli et al., 2010; Crone & Tolstoy, 2010). Therefore, it is possible that the DWH oil spill impacted the spawning activities of adults and/or the survival of *Thunnus* larvae in the summer of 2010 (Rooker et al., 2013). Shifts in spawning location due to habitat loss or degradation have been observed in other pelagic fishes (Rooker et al., 2013), and it is possible that adult tunas moved away from areas impacted by the DWH oil spill and spawned in different areas. Alternatively, oil near the surface may have impacted survival of tuna larvae as experimental studies have demonstrated that oil causes abnormal cardiac functions in *Thunnus* larvae (Brette et al., 2014; Incardona et al., 2014). Therefore, the presence of oil in our sampling corridor could have led to increased mortality and explained the decrease in larval densities of tunas observed during the present study. Still, temporal changes in environmental conditions due to the presence of Mississippi River plume and the northern penetration of the Loop Current (LC) are also known to affect *Thunnus* spawning habitat and the spatiotemporal distribution of adults (Teo et al., 2007) and larvae (Lindo-Atichati et al., 2012; Rooker et al., 2013; Domingues et al., 2016), which may have contributed to the observed variations in the density of *Thunnus* larvae.

The Mississippi River plume is responsible for seasonal freshwater inputs that modify salinity and productivity in the northern GoM (Dagg & Breed, 2003) and has been described as a major factor influencing the survival and growth of *Thunnus* larvae (Lang et al., 1994). Along the salinity gradient created by freshwater discharges, a change in biological activity is observed as nutrient-rich riverine waters sustain high primary and secondary production. Regions of confluence between riverine and oceanic waters aggregate fish larvae and nutrients through physical processes and these regions have been described as favorable habitat for fish larvae as food opportunities increase, which in turn supports larval growth, survival, and recruitment (Grimes & Finucane, 1991). Chlorophyll *a* concentration can be used as a proxy to determine the increase of biological productivity due to riverine plume penetration (Walker & Rabalais, 2006). In the present study, high chlorophyll *a* concentrations were observed at stations along the northern extent of our sampling corridor (28°N) and most likely corresponded to regions where oceanic waters were impacted by the Mississippi River plume. During our 4-year survey, the Mississippi River discharges were temporally and spatially variable ranging from 395,800 $ft^3\ s^{-1}$ (June 2007) to 899.800 $ft^3\ s^{-1}$ (June 2009) (U.S. Geological Surveys, 2016, Fig. S2), and changes in the riverine inputs appeared correlated with shifts in the density of *Thunnus* larvae. Increased densities of *T. atlanticus*, *T. obesus*, and *T. albacares* in year (2009) with above average chlorophyll *a* concentrations (3.17 mg m^{-3}) and lower salinities (27 psu), potentially indicate that physical and chemical conditions associated with the Mississippi River discharges may be favorable to these species. In particular, *T. albacares* larvae were frequently more abundant in lower salinity (2.66 larvae 1,000 m^{-3}) than in high salinity (0.43 larvae 1,000 m^{-3}) regions of the northern GoM. Lang et al. (1994) reported that the physical and chemical conditions associated with freshwater inputs from the Mississippi River positively impacted the growth of *T. albacares* and therefore may enhance early life survival of this species. From 2007 to 2010, *T. atlanticus* and *T. obesus* were detected in a wide range of salinity (28.3–38.6 psu) and chlorophyll *a* concentration (0.02–3.8 mg m^{-3}). The broad salinity tolerance of *T. atlanticus* and *T. obesus* seemed to allow them to take advantage of the highly productive waters associated with the intrusion of the Mississippi River plume in the northern GoM. However, high densities of *T. atlanticus* and *T. obesus* were also recorded at stations with high salinity (>36 psu) and lower chlorophyll *a* concentration (0.18 mg m^{-3}), suggesting that the environmental conditions observed in oceanic waters are also favorable to these species. The presence of *T. atlanticus* and *T. obesus* in different water masses indicates that these species were broadly distributed in the northern GoM. *T. thynnus* was the only species absent or in lower abundance close to the areas impacted by the Mississippi River plume or in lower salinity regions. Generally *T. thynnus* larvae


(a)
Low salinity region
X High salinity region
(b)
Anticyclonic region
Cyclonic region
Open water region
(c)
40
160
280
400
(d)
3
12
21
30
(e)
3
12
21
30
(f)
0.7
2.8
4.9
7
SSHA
SST
Salinity
Depth
Chlorophyll a
PCO1 (35.6% of total variation)
PCO2 (22.3% of total variation)

◀**Fig. 8** PCO plots of environmental data representing the different regions crossed from 2007 to 2010 in the northern Gulf of Mexico; **a** salinity regions, **b** oceanographic regions. *Bubble plots* represent the density of each *Thunnus* species (larvae 1,000 m^{-3}) depending on the sampling location with, **c** *Thunnus atlanticus*, **d** *Thunnus obesus*, **e** *Thunnus albacares*, **f** *Thunnus thynnus*. The *circle* presents the vector overlay (Pearson correlation) illustrating the contribution of the respective environmental variables to the PCO axes. SST represents sea surface temperature and SSHA sea surface height anomaly

were observed in regions with high salinities (>36 psu), deep waters (>1,000 m), and intermediate chlorophyll *a* concentration (0.15 mg m^{-3}), indicating that larvae of this species are generally distributed in areas off the continental shelf. Similar larval distributions have been previously reported for *T. thynnus* in the Mediterranean Sea and the GoM (Alemany et al., 2010; Muhling et al., 2013), supporting the assertion that sudden changes in water mass conditions due to Mississippi River discharges (e.g. lower salinity, turbidity) may negatively impact *T. thynnus* larvae. Consequently, riverine discharges potentially create favorable conditions for certain species (*T. albacares, T. atlanticus*, *T. obesus*) and unfavorable conditions for other species (*T. thynnus*), with habitat quality also being influenced by the presence and location of other mesoscale oceanographic features in the northern GoM, namely the LC and associated features.

Seasonal penetration of the LC and mesoscale eddies are highly variable from year-to-year and are known to influence the spatial distribution of *Thunnus* larvae in the northern GoM (Lindo-Atichati et al., 2012; Rooker et al., 2013). The maximum northward penetration of the LC and associated features during our study was observed in 2007 and 2009 (28°N), which also corresponded to the highest densities of *T. atlanticus*, *T. obesus*, and *T. albacares*. In contrast, the lowest mean densities of several species (*T. atlanticus*, *T. obesus*, and *T. thynnus*) were recorded in 2010 when the northern extent of the LC (26°N) did not reach our study area. The presence of the LC and anticyclonic (warm core) eddies influences the SST in this region by creating areas of higher temperature (>29°C). Temperature has been described as an important factor for hatching and larval development of *T. albacares, T. obesus*, and *T. atlanticus*, and the optimal temperature range is 28–29°C (Wexler et al., 2011; Reglero et al., 2014). Thus, the increase in larval density of these species in the LC and anticyclonic regions (SST > 29°C) suggest that these regions offer a favorable environmental conditions to maximize larval growth and survival. Moreover, peaks in density were typically observed at frontal zones, areas of confluence between two eddies, and anticyclonic regions (SSHA > −5 cm). Because physical processes at the edge of these mesoscale features accumulate both fish larvae and their prey, larvae are often entrained in productive waters where their chance of encountering prey is higher. Thus frontal zones at the margin of the LC and mesoscales eddies likely enhance foraging opportunities and provide high quality habitat for tuna larvae (Grimes & Kingsford, 1996; Lamkin, 1997; Bakun, 2006; Rooker et al., 2012). In contrast, *T. thynnus* densities were negatively correlated with the years of high northward penetration of the LC, and *T. thynnus* larvae were usually observed in areas of negative or intermediate SSHA corresponding to cyclonic regions (cold core). The affinity of *T. thynnus* larvae to cyclonic regions may be driven by temperature as SST observed in cyclonic regions match their preferred thermal range (22–28°C) in the GoM (Muhling et al., 2010; Reglero et al., 2014). Moreover, cyclonic regions are also associated with upwelling of nutrients and enhanced primary productivity, which can lead to increase condition or growth of fish larvae (Bakun, 2006). Given that all areas outside cyclonic regions in our surveys were generally above 28°C, cyclonic regions may provide both favorable thermal conditions and prey resources for *T. thynnus*. Our results are in agreement with previous studies that showed the importance of physical and chemical boundaries or fronts associated with mesoscale oceanographic features (cyclonic and anticyclonic) in the distribution of *Thunnus* larvae in the GoM (Lindo-Atichati et al., 2012; Muhling et al., 2013) and the Mediterranean Sea (Alemany et al., 2010).

The diverse group of congeners from the genus *Thunnus* (*T. atlanticus, T. obesus, T. albacares*, and *T. thynnus*) make up the larval assemblage present in the northern GoM, indicating that this region may represent valuable spawning and/or nursery habitat for *Thunnus* as well as other tuna genera (*Auxis*, *Euthynnus, Katsuwonus*). Our study demonstrates that the distribution and abundance of *Thunnus* larvae were influenced by biological, physical, and chemical characteristics of the northern GoM, and distinct species-

specific habitat preferences observed may reduce resource overlap (i.e., habitat partitioning) among the four congeners examined. This study indicates that the abundance of *Thunnus* larvae was influenced by the presence of mesoscale features and oceanic conditions which underscores the necessity to integrate these data into abundance indices for each *Thunnus* species. Because fisheries-independent indices are used in stock assessment models, a habitat-adjusted index of abundance for each *Thunnus* species will lead to more accurate estimates of population parameters (i.e., spawning stock size/biomass) to evaluate population dynamics and ensure the long-term suitability of *Thunnus* stocks in the GoM.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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