

Habitat characteristics of bluntnose flyingfish *Prognichthys occidentalis* (Actinopterygii, Exocoetidae), across mesoscale features in the Gulf of Mexico

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Abstract The aim of the present study is to investigate the influence of oceanic features on the distribution and abundance of bluntnose flyingfish (*Prognichthys occidentalis*) larvae in the northern Gulf of Mexico (NGoM). Summer ichthyoplankton cruises were conducted from 2009 to 2011 using a neuston net towed through the upper meter of the water column. Interannual variation was detected with densities of bluntnose flyingfish larvae higher in 2009 and 2010 than 2011. Bluntnose flyingfish larvae were present in each month and year sampled, suggesting that this species is a common and important component of the ichthyoplankton assemblage in this region. Generalized additive models were used to evaluate the effect of oceanographic conditions on the abundance

of bluntnose flyingfish, and several environmental variables (sea surface height anomaly, distance to Loop Current, and salinity) were found to be influential in explaining patterns of abundance. Habitat suitability was linked to physicochemical properties of the seawater, and higher larval abundances were found at higher salinities and negative sea surface heights. This study emphasizes the importance of NGoM as a spawning/nursery area of bluntnose flyingfish and suggests that oceanographic conditions play an important role in determining the distribution and abundance of bluntnose flyingfish.

Keywords Flyingfish · Larvae · Gulf of Mexico · HRMA · GAM

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Introduction

Flyingfishes (family Exocoetidae) are epipelagic, subtropical to tropical species found worldwide. Eighty-one species of flyingfish exist throughout the oceans, and many countries in the Caribbean, South East Asia, and the South Pacific rely on these fishes as a source of food and income (Dalzell, 1993; Huang and Ou, 2012). In addition to their economic value, flyingfishes are an essential component of pelagic food webs, serving as both predator and prey. Many pelagic fishes (billfishes, dolphinfishes, and tunas) consume large quantities of flyingfish, and several studies have documented their importance as prey for apex predators residing in coastal and offshore environments (Oxenford and Hunte, 1999; Rudershausen et al., 2010). Seabirds also target flyingfishes and/or their eggs, both being commonly consumed by several groups of tropical seabirds including petrels, frigate birds, and terns (Harrison et al., 1983; Ballance et al., 1997). Apart from their functional role as prey, flyingfishes consume large quantities of zooplankton and ichthyoplankton, with the latter being numerically dominant in the diets of several species (Lewis et al., 1962; Van Noord et al., 2013). In response, predation by the flyingfish assemblage can influence the population dynamics of several marine invertebrates and vertebrates, and therefore play an important functional role in pelagic ecosystems.

Research on the ecology of flyingfishes in the Gulf of Mexico (GoM) is surprisingly limited, particularly studies investigating early life processes (Hunte et al., 1995). Early life studies on marine fishes, such as flyingfishes, provide fundamental information on their life history and population dynamics (Carassou et al., 2012). More specifically, spatial and temporal trends in the distribution and abundance of fish larvae can be used to characterize the timing and location of spawning as well as environmental conditions that favor early life survival (Rooker et al., 2012). An understanding of early life events can also help define processes that affect recruitment and year-class strength (Richardson et al., 2010; Carassou et al., 2012). Because early life survival is tied closely to primary productivity and environmental conditions, changes in larval fish abundance or distribution is useful for understanding the impacts of environmental perturbations, ranging from oil spills (e.g., Deepwater Horizon) to environmental shifts linked to climate

change (Hernandez et al., 2010; Rooker et al., 2013). Therefore, establishing baseline data on the distribution and abundance of flyingfish larvae provides critical information that can be used to better understand population trends of flyingfishes and the pelagic predators that feed on them.

The GoM is an ideal model system for evaluating early life ecology of flyingfishes because increased primary production associated with allochthonous nutrient inputs (i.e., Mississippi River) supports highly productive spawning and nursery areas for several pelagic fishes (Nürnberg et al., 2008; Rooker et al., 2013). In addition, the GoM is characterized by the presence of a dominant mesoscale oceanographic feature (Loop Current), and associated cyclonic and anti-cyclonic eddies (Nürnberg et al., 2008). Cyclonic eddies and areas of frontal convergence associated with the Loop Current represent zones of upwelling (Govoni et al., 2010), causing an increase in both primary and secondary production, and enhancing foraging opportunities for fish larvae (Ross et al., 2010). Previous studies have shown that several taxa of pelagic fishes spawn near convergence zones like fronts and eddies, suggesting that these features may represent important spawning or nursery areas for the larvae (Richardson et al., 2009). This combination of autochthonous and allochthonous drivers of production coupled with the unique oceanographic characteristics of the GoM make it an interesting location for investigating the early life ecology of flyingfish.

The goal of the present study was to characterize the spatial and temporal trends in the distribution and abundance of flyingfish larvae in the outer shelf and slope waters of the northern GoM (NGoM). Additionally, we examined the influence of oceanographic conditions on the distribution and abundance of the most common species, bluntnose flyingfish (*Prognichthys occidentalis*, Parin, 1999), using generalized additive models (GAMs). Our working hypothesis stated that the relative abundance of bluntnose flyingfish larvae will be higher in cyclonic eddies and frontal boundaries because these areas concentrate larvae and are assumed to be areas of increased primary and secondary production. The information gathered from this study will help assess the importance of this region as a spawning/nursery area for bluntnose flyingfish.

Methods

Sampling design

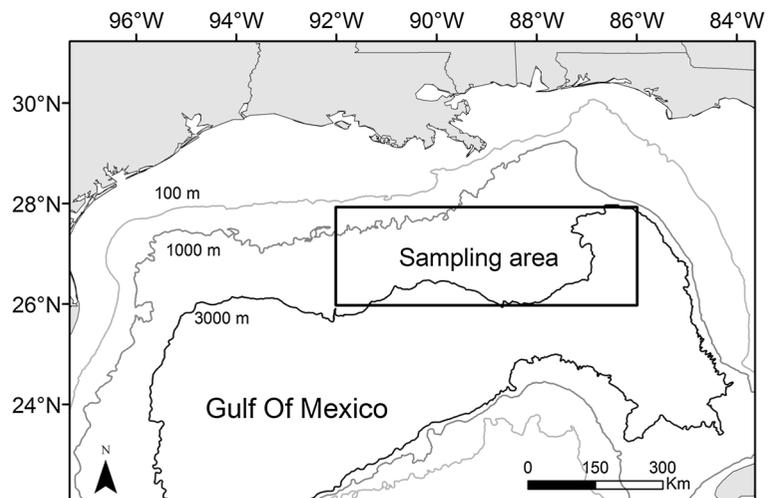
Six ichthyoplankton surveys were conducted in the outer shelf and slope waters of the NGoM during June and July from 2009 to 2011. The sampling region encompassed the area 26–28°N latitude and 86–93°W longitude (Fig. 1). Flyingfish larvae were collected with paired 2 m by 1 m neuston nets with different mesh sizes, 500 and 1200 μm , during 2009 and 2010. In 2011, the sampling design was modified and only a single 1200 μm mesh neuston net was used to collect the larvae. Nets were towed through the upper meter of the water column for 10 min at a speed of approximately 2.5 knots. Approximately 48 stations, spaced 8 nautical miles apart, were sampled during each survey allowing for a variety of oceanographic features to be sampled. A General Oceanics flowmeter (Model 2030R, Miami, FL) was placed in the center of each neuston net to record the total surface area filtered during each tow. The total number of bluntnose flyingfish from both the 500 and 1200 μm nets was pooled and then divided by the combined surface area towed of both nets to determine abundance (density, larvae $1,000\text{ m}^{-2}$) of bluntnose flyingfish at each station sampled. Percent occurrence of bluntnose flyingfish was determined based on the number of stations where flyingfish were present divided by the total number of stations sampled during the survey. Geographic information system (GIS) was then used

to visually display the abundance of bluntnose flyingfish (larvae $1,000\text{ m}^{-2}$) across the sampling area.

All ichthyoplankton and associated zooplankton collected were stored onboard in 70% ethanol, and then transferred to 100% ethanol after 48 h. *Sargassum* biomass collected in the neuston nets at each station was also recorded. In the laboratory, all flyingfish larvae were sorted from other taxa and enumerated using a Leica MZ stereomicroscope and placed into individual vials with 70% ethanol before identified to species.

Due to similarity in larval characteristic, a genetic protocol using high-resolution melting analysis (HRMA), as outlined in Smith et al. (2010), was used to identify a subset of flyingfish ($n = 390$) to species level before visually identifying the remaining larvae. DNA of larvae was isolated with a sodium hydroxide DNA isolation method (Alvarado Bremer et al., 2014). The protocol was slightly modified with flyingfish larvae transferred to 600 μl microfuge tubes containing 200 μl of 70% ethanol and vortexed vigorously for 50 s. A 1 μl aliquot was used as DNA template for HRMA. The 16S-RNA gene was targeted for an asymmetric unlabeled probe high-resolution melting analysis (UP-HRMA) using the forward primer 16S-Exo-INT-F2 (5'-ATCTCCCCGTGCAGAAGCGG-3'), a diluted 1:10 reverse primer 16S-Exo-INT-R2 (5'-CGTGGTCGCC CCAACCGAAG-3'), and the unlabeled probe 16S-Exo-UPHRM-1R (5'-TAGGGCGATGTCCAATTGG CTTAGTTCCT/3Phos/-3'). The UP-HRMA amplifications were performed in 10 μl reactions on the

Fig. 1 Ichthyoplankton sampling area (rectangle) in the outer shelf and slope waters of the northern Gulf of Mexico conducted during June and July of 2009–2011



LightCycler 480 (Roche Diagnostics) containing 0.5 μ l of LCGreen[®] Plus (BiofireTechnologies), 5.0 μ l of EconotaqPlus (Lucigen), 0.5 μ l of each primer, 0.5 μ l of unlabeled probe, 2 μ l of ddH₂O, and 1 μ l of DNA template. Samples were denatured, annealed, and extended for 38 cycles at 94°C for 10 s, 52°C for 30 s, and 72°C for 10 s, respectively, followed by 26 stepdown cycles where the annealing temperature was lowered to 44°C. High-resolution melting profiles of the unlabeled probes produced species-specific melting curves, which were compared to reference samples of known adult flyingfish collected in the GoM (Fig. 2). Flyingfish larvae identified to the species level genetically with HRMA were then used in conjunction with larval descriptions provided by Fahay (1983) and Richards (2006) to visually identify bluntnose flyingfish larvae in our samples. The efficacy of the visual identification was then evaluated using the above UP-

HRMA genetic identification on a random subsample of the visually identified bluntnose flyingfish larvae ($n = 161$).

At each station, temperature (°C), salinity (psu), and dissolved oxygen (mg/l) were measured using a Sonde 6920 Environmental Monitoring System (YSI Inc.). Other environmental parameters at each station were determined using remotely sensed data accessed through the marine geospatial ecology toolbox (version 0.8a44) in ArcGIS (version 10.0). Sea surface height anomaly (SSHA, cm) data were calculated weekly at a resolution of 1/3° using merged satellite altimetry measurements from Topex/Poseidon, Jason-1 and 2, Geosat Follow-On, ERS-1 and 2, and EnviSat (AVISO, <http://www.aviso.oceanobs.com/duacs/>). Distance to the Loop Current was estimated by measuring the linear distance from the edge of the feature, based on the 20 cm SSHA contour, to each

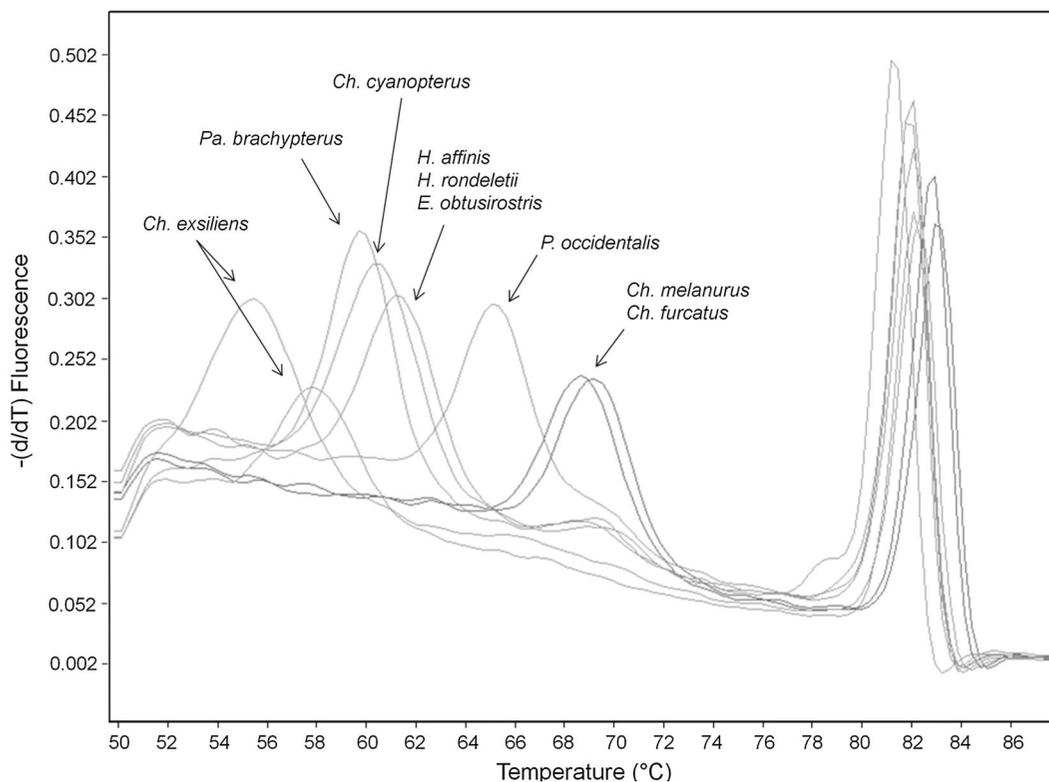


Fig. 2 Species-specific derivative melting profiles targeting the 16S-RNA region for flyingfish larvae based on UP-HRMA (unlabeled probe high-resolution melting analysis) as a function of fluorescence over temperature (°C). Melting profiles for the nine species of flyingfish are presented: *Cheilopogon exsiliens* (bandwing flyingfish), *Parexocoetus brachypterus* (sailfin

flyingfish), *Ch. cyanopterus* (marginated flyingfish), *Hirundichthys affinis* (fourwing flyingfish), *H. rondeletii* (blackwing flyingfish), *Exocoetus obtusirostris* (oceanic two-winged flyingfish), *P. occidentalis* (bluntnose flyingfish), *Ch. furcatus* (spotfin flyingfish), and *Ch. melanurus* (Atlantic flyingfish)

sampling station using the Spatial Analyst toolbox in ArcGIS. Sea surface chlorophyll concentration (mg m^{-3}) was obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) sensor onboard the Aqua satellite over an 8-day period at 4 km spatial resolution (Aqua, <http://oceancolor.gsfc.nasa.gov>). Water depth information for the GoM was accessed from NOAA National Geophysical Data Center using the GEODAS US Coastal Relief Model Grid with a grid cell size of 6 (http://www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html). To visually show the impact of certain variables on bluntnose flyingfish abundance, Ocean Data View (Schlitzer, 2013) was used to create density plots using the variables of temperature, salinity, SSHA, and distance to Loop Current (DisLC) as the independent variables and bluntnose flyingfish density across all 3 years as the response variable. These variables were selected because they were shown to be influential on bluntnose flyingfish abundance.

Statistical analysis

Abundance of larval bluntnose flyingfish at each station was estimated using larvae collected in both nets during each cruise, except in 2011 when only a 1200 μm mesh neuston net was used. Variation in mean density of larval bluntnose flyingfish for each cruise was analyzed using a full factorial two-way analysis of variance (ANOVA) with month and year as the main factors. Post hoc differences among means of the main effects were examined using a Tukey's Honestly Significant Difference test (Tukey HSD). Additionally, a non-parametric test, Kruskal–Wallis, was used when data violated assumptions of normality or homogeneity of variance. Because the Kruskal–Wallis test produced the same results as the ANOVA, and parametric tests are more robust and have greater power than non-parametric tests (Sheskin, 2004), only the ANOVA results are reported. All statistical analysis were run with SPSS Statistical software (version 16.0.1) with $\alpha = 0.05$.

The influence of biotic and abiotic environmental variables on bluntnose flyingfish abundance was analyzed using generalized additive models (GAMs) in R (version 3.0.0). GAMs, a non-parametric extension of the generalized linear models, allow for non-linear relationships between the response variable and many explanatory variables by fitting smoothing functions to

the explanatory variables (Zuur et al., 2009). This is an improvement over the generalized linear model because rarely does species abundance data and environmental data follow a linear trend (Maggini et al., 2006). For modeling purposes, density estimates were rounded to the nearest non-negative integer. The explanatory variables used in the GAM were month, year, sea surface temperature, SSHA, distance to Loop Current, chlorophyll-*a* concentration, salinity, depth, and *Sargassum* weight. The general GAM model for the negative binomial distribution follows the equation:

$$E[y] = g^{-1} \left(\beta_0 + \sum_k S_k(x_k) \right),$$

where $E[y]$ represents the predicted values for the response variable (density), g represents the link function, β_0 denotes the intercept, k represents the number of explanatory variables used in the model, and S_k is the smoothing function of each explanatory variable, x_k . Models were fit with cubic regression splines within the *mgcv* library using R 3.0 software (The R Foundation for Statistical Computing, 2010). Cubic splines were limited to three degrees of freedom (df) to avoid creating unrealistic models (over fitting) with less predictive powers (Sandman et al., 2008). GAMs with lower and higher levels of smoothing complexity (df = 2 and df = 4) were also examined, but the smoothing value (df = 3) was deemed more appropriate based on the total number of variables and model complexity (Guisan et al., 2002; Sandman et al., 2008). The best model was chosen based on minimizing the Akaike Information Criterion (AIC), which measures both model complexity and goodness of fit (Burnham & Anderson, 2004).

Prior to running GAMs, multi-collinearity among explanatory variables was examined using the Spearman's rank correlation coefficient (Spearman's ρ) to remove highly correlated variables. If two variables had a Spearman's ρ greater than 0.5, the variables were analyzed in separate models to determine the relative influence of each predictor. The predictor with the lower AIC remained in the initial model prior to the backwards stepwise selection process. After checking for multi-collinearity using the Spearman's ρ method, all remaining variables were further examined with the variance inflation factor (VIF) to check for multi-collinearity among the variables. A VIF over the threshold value (VIF > 5) indicates that variables

are correlated and should be removed (O'Brien, 2007). Once multi-collinearity was checked, a manual backwards stepwise selection process was used to remove the non-significant explanatory variables that influenced larval abundance. Backwards stepwise selection ended when all remaining variables were significant ($P < 0.05$) or the AIC value started to increase when non-significant variables were removed, unless the increase was less than 1%. Percent deviance explained (DE) was calculated for each model to examine the overall fit:

$$DE = ([\text{null deviance} - \text{residual deviance}] / \text{null deviance}) \times 100.$$

Once the final model was selected, each variable was individually removed to examine the change in AIC and DE to assess the relative importance of each predictor variable to the response variable.

Prior to GAM development, initial Spearman's ρ analysis indicated a significant correlation between two variables: salinity and chl-*a* concentration. The full model was run separately with salinity and chl-*a* concentration removed to determine which variable had a greater impact on the initial model. Because both variables are common oceanographic measurements and the VIF was less than five, salinity and chl-*a* concentration were kept in the initial model. The subsequent addition of other variables such as distance to nearest eddy, distance to nearest temperature front, current velocity, latitude, longitude, and hours after sunrise resulted in an increase in the AIC value, which were collinear with at least one of the initial parameters so these variables were kept out of the initial model.

Results

Over the 3 years sampled, a total of 12,390 flyingfish larvae were collected from 385 stations in the NGoM. Bluntnose flyingfish (*P. occidentalis*) was the most common species, accounting for 76.9% ($n = 9,533$) of all flyingfish larvae collected (Table 1). The other species collected, *Cheilopogon cyanopterus* (marginated flyingfish), *Ch. exsiliens* (bandwing flyingfish), *Ch. furcatus* (spotfin flyingfish), *Ch. melanurus* (Atlantic flyingfish), *Hirundichthys affinis* (fourwing

flyingfish), *H. rondeletii* (blackwing flyingfish), *Exocoetus obtusirostris* (oceanic two-wing flyingfish), and *Parexocoetus brachypterus* (sailfin flyingfish), accounted for 19.1% ($n = 2,370$) of the total catch. The remaining 4% ($n = 487$) could not be visually identified because of damage. Mean density of bluntnose flyingfish ranged from 0.62 to 16.39 larvae $1,000 \text{ m}^{-2}$, with an average of 7.05 larvae $1,000 \text{ m}^{-2}$ (Table 1). The highest abundance for bluntnose flyingfish at a single station occurred in June 2009 with a density of 198.02 larvae $1,000 \text{ m}^{-2}$. Frequency of

occurrence was high for bluntnose flyingfish, with larvae collected in every month and year sampled. Percent frequency of occurrence for bluntnose flyingfish ranged from 39.6% in July 2011 to 100% in June and July 2010. In all years surveyed, except 2010, percent frequency of occurrence was higher in June than July.

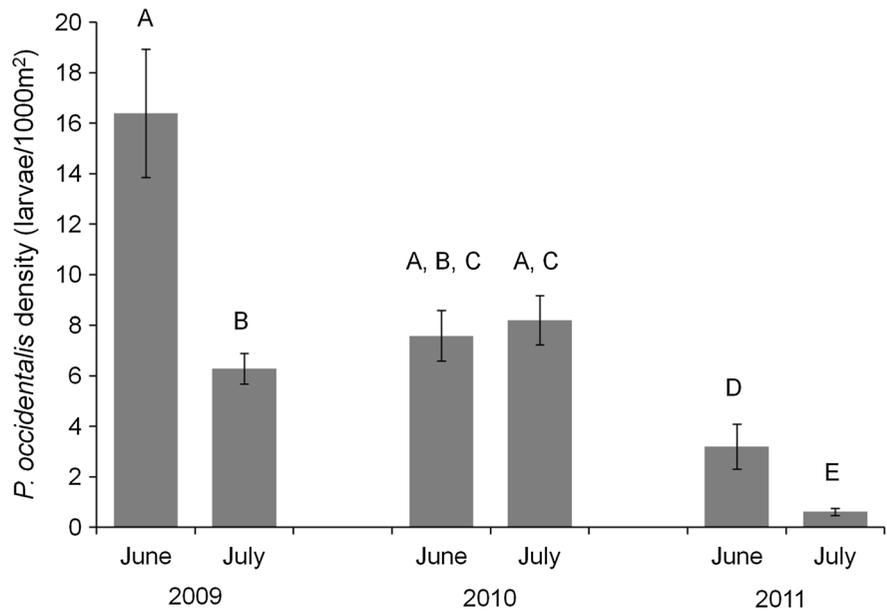
Abundance of bluntnose flyingfish varied significantly among the 3 years surveyed (ANOVA, $F_{(2,384)} = 16.966$, $P < 0.001$). Mean density of bluntnose flyingfish for years 2009 and 2010 (11.35 and 7.89 larvae $1,000 \text{ m}^{-2}$, respectively) was significantly higher than the mean density for 2011 (1.91 larvae $1,000 \text{ m}^{-2}$). Mean density also varied significantly between the months sampled (ANOVA, $F_{(1,384)} = 8.298$, $P < 0.004$), with densities in June (9.06 larvae

Table 1 Catch statistics for bluntnose flyingfish collected during 2009–2011 in the northern Gulf of Mexico

Survey	<i>n</i>	Count	Density (SD)	% Freq.
3–9 June, 2009	92	4,572	16.39 (24.33)	98.91
22–29 July, 2009	101	1,693	6.30 (6.09)	95.05
15–18 June, 2010	48	1,454	7.59 (6.94)	100.00
27–30 July, 2010	48	1,533	8.20 (6.72)	100.00
14–18 June, 2011	48	229	3.20 (6.21)	77.08
17–20 July, 2011	48	52	0.62 (1.02)	39.58
	385	9,533	7.05	85.10

Number of stations sampled during each cruise (*n*), total number of larvae collected (count), mean density (larvae $1,000 \text{ m}^{-2}$), standard deviation (SD), and percent frequency of occurrence (% Freq) are given for bluntnose flyingfish (*P. occidentalis*)

Fig. 3 Mean density of bluntnose flyingfish (*P. occidentalis*) collected in June and July for each sampling year 2009–2011. Bars with different letters denote significant differences among months based on Tukey HSD post hoc groupings ($P < 0.05$). Error bars represent one standard error of the mean



1,000 m⁻²) greater than July (5.04 larvae 1,000 m⁻²). A significant interaction was observed between month and year (ANOVA, $F_{(2,384)} = 6.282$, $P < 0.002$). In all years except 2010, abundance of bluntnose flyingfish larvae was higher in June (Fig. 3). Of all the surveys, June 2009 had the highest mean density (16.39 larvae 1,000 m⁻²) and July 2011 had the lowest mean density (0.62 larvae 1,000 m⁻²). Bluntnose flyingfish larvae were widespread and detected along much of the area sampled, but spatial differences in the distribution and abundance were detected among the six surveys (Fig. 4). In 2009 and 2010, bluntnose flyingfish were present at nearly all stations surveyed (97 and 100% occurrence, respectively), but in 2011 the presence of bluntnose flyingfish decreased with larvae absent from more stations than the previous 2 years (58% occurrence).

The final GAM based on the abundance of bluntnose flyingfish included five oceanographic and temporal variables: month, year, SSHA, distance to Loop Current, and salinity. The final model had an AIC of 2108 and percent DE was 42.9% (Fig. 5). Associated Δ AIC and Δ DE from the final model were used to further evaluate the relative influence of each parameter in explaining natural variation in the abundance of bluntnose flyingfish. The most influential parameter in the final model, based on Δ AIC, was SSHA (37), followed by year (20), distance to Loop Current (14), and salinity (13). Similarly, Δ DE was highest for SSHA (7.2%), followed by year (4.0%), and distance

to Loop Current (2.9%), and salinity (2.7%) (Table 2). Removal of the remaining variable, month, from the final model resulted in changes in Δ AIC of less than 2 and Δ DE of less than 0.8%. Variables not retained in the final model were chl-*a* concentration, depth, sea surface temperature, and *Sargassum* biomass.

Response plots from the final GAM showed a negative relationship with SSHA and abundance of bluntnose flyingfish larvae with the highest abundances found in waters with a negative sea surface height, correlating with cold-core eddies (Figs. 5, 6). Overall, densities were greater in areas with negative sea surface height anomalies (12.5 larvae 1,000 m⁻²) compared to areas with positive anomalies (6.2 larvae 1,000 m⁻²). Density of bluntnose flyingfish larvae was greater (18.4 larvae 1,000 m⁻²) in waters of higher salinities (>35 psu) than in lower salinity waters (8.1 larvae 1,000 m⁻²) regardless of sea surface temperatures (Fig. 5). These higher salinity waters are typically associated with oceanic water masses over the continental shelf and slope. Although sea surface temperature was not a significant variable in the final GAM, the stations with the highest catches of flyingfish occurred in waters with lower temperature (Fig. 6). Additionally, bluntnose flyingfish abundance and distance to Loop Current were positively related (Figs. 5, 6), and densities were higher at sites greater than 200 km from the Loop Current (12.3 larvae 1,000 m⁻²) relative to sites 0–200 km from this feature (5.7 larvae 1,000 m⁻²).

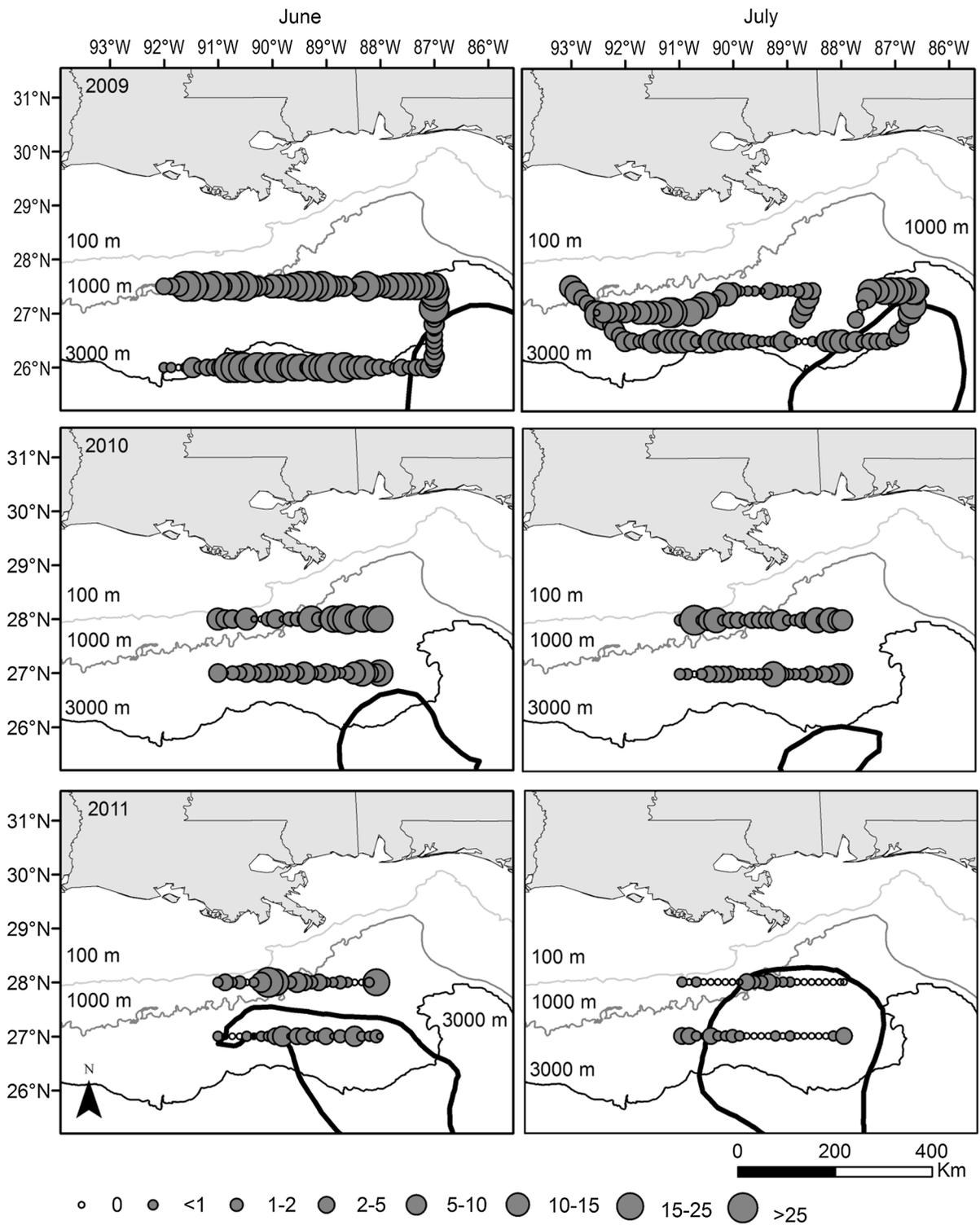


Fig. 4 Spatial and temporal variability in the distributions of bluntnose flyingfish during summer ichthyoplankton cruises from 2009 (*top*), 2010 (*middle*), and 2011 (*bottom*) and June (*left column*) and July (*right column*). The location of the Loop Current during the sampling period is outlined in *thick black*. Density (larvae/1,000 m²) at each sampling station is denoted by *circle size*

Discussion

Flyingfish larvae were commonly collected in our ichthyoplankton surveys and observed densities were relatively high, suggesting that this group represents an important component of the larval fish assemblage in the NGoM. Although nine flyingfish species were collected in the survey area, bluntnose flyingfish dominated the overall catch, representing 77% of the total flyingfish collected. Abundances of bluntnose flyingfish larvae were generally higher when compared to other larval pelagic fishes collected within the survey area (Rooker et al., 2012, 2013). Average densities of larval blue marlin (0.19 larvae 1,000 m⁻³), sailfish (0.55 larvae 1,000 m⁻³), and dolphinfish (0.72 larvae 1,000 m⁻³), in 2009 and 2010

were much lower than densities of bluntnose flyingfish (7.70 larvae 1,000 m⁻³) during the same 2 years, whereas densities of blackfin tuna (11.89 larvae 1,000 m⁻³) were higher than bluntnose flyingfish (Rooker et al., 2013). Comparable assessments of flyingfish abundances in the GoM and other regions are rare; nevertheless, a study by Hunte et al. (1995) within the eastern Caribbean examined abundance of larval flyingfishes and found a relative density of bluntnose flyingfish at 0.04 larvae 1,000 m⁻², which is markedly lower than mean densities observed in our study (7.05 larvae 1,000 m⁻²).

Over the 3-year sampling period, 85% of the neuston net tows captured bluntnose flyingfish, suggesting that the NGoM may represent an important spawning and nursery area for this species. Conversely, previous research in the Caribbean Sea during April and May showed that the tropical two-winged flyingfish (*Exocoetus volitans*) and sailfin flyingfish (*P. brachypterus*) dominated the flyingfish assemblage (Hunte et al., 1995). Regional differences in the flyingfish assemblage between the Caribbean Sea and the NGoM were expected. In addition to geographic differences in species ranges, variation may also be

Fig. 5 Response plots for oceanographic variable on the density of bluntnose flyingfish (*P. occidentalis*) from final generalized additive model (GAM). Plots include distance to Loop Current (km), sea surface height anomaly (SSHA, cm), and salinity (psu). *Solid lines* represent smoothed values and the *shaded area* represents 95% confidence intervals. *Dashed line* displayed at $y = 0$ on each response plot

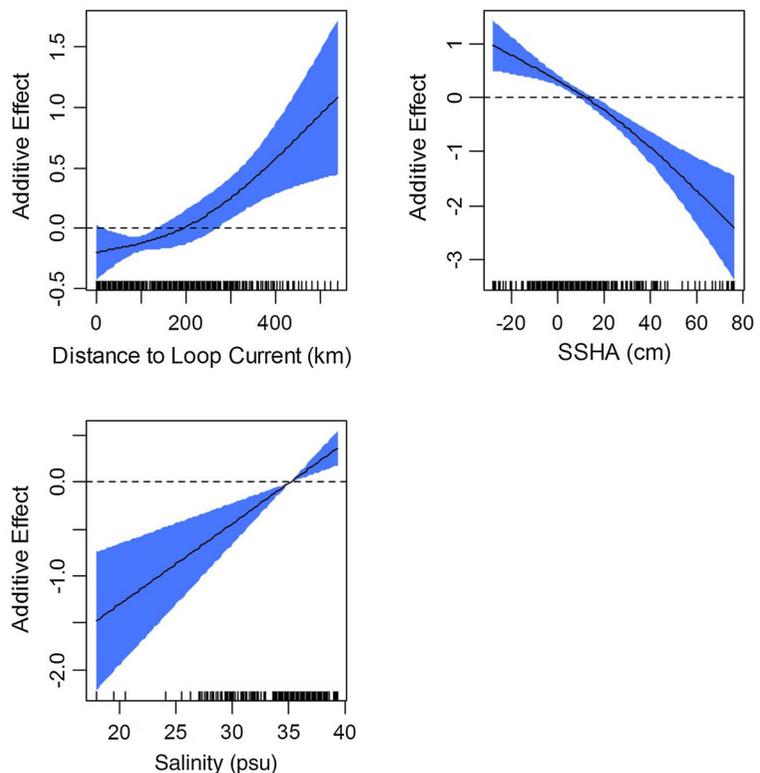


Table 2 Environmental and temporal variables in the final bluntnose flyingfish (*P. occidentalis*) GAM with the relative influence of each final variable indicated by Δ AIC (Akaike's Information Criterion) and Δ DE (deviance explained)

Bluntnose flyingfish GAM Variables	AIC = 2,108.074 Δ AIC	DE = 42.9% Δ DE
Month	2.101	0.8
Year	20.018	4.0
DisLC	14.019	2.9
SSHA	36.580	7.2
Salinity	12.586	2.7

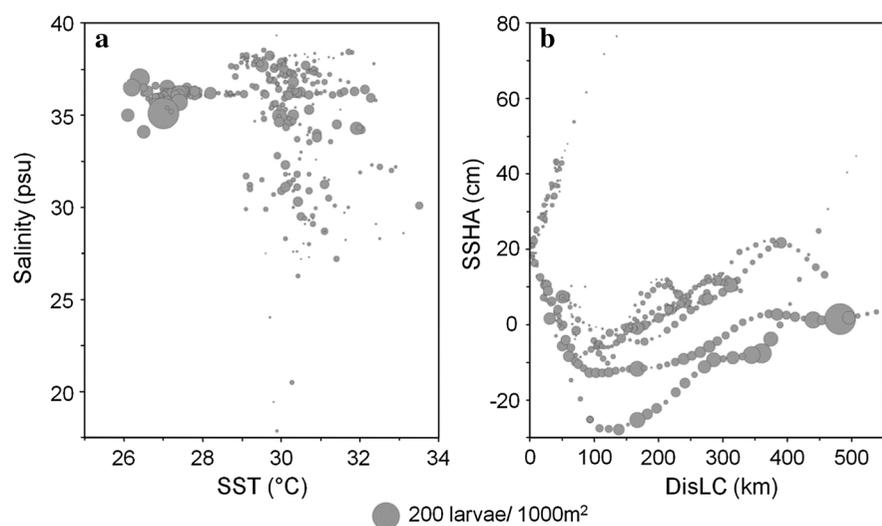
DisLC Distance to the Loop Current; *SSHA* sea surface height anomaly

due in part to other spatial (e.g., shelf position) and temporal (e.g., sampling months) factors. In particular, both the timing of peak spawning and the location where adults spawn are species specific (Lewallen et al., 2011). Some species spawn in coastal waters (e.g., *P. brachypterus*), while others spawn in oceanic waters (e.g., *E. volitans*), which are heavily impacted by currents and upwelling and will influence the distribution and availability of larvae (Hunte et al., 1995; Stevens et al., 2003). Moreover, some species spawn on substrate (*H. affinis*), and therefore the availability of larvae from such species will be determined by the presence of flotsam and benthic substrate (Hunte et al., 1995).

High fluctuation in abundance is common for pelagic fishes within the GoM because larval survival is tightly coupled with oceanographic conditions and

food availability (Cury & Roy, 1989; Fiksen et al., 2007). In our study, significant seasonal (monthly) differences occurred during the sampling period with abundances in June higher than July (exception 2010), indicating spawning times of bluntnose flyingfish in the NGoM correspond to spawning times of other flyingfishes in the eastern Caribbean Sea (Hunte et al., 1995) and western Atlantic Ocean (Casazza et al., 2005). Although no spawning data on adult bluntnose flyingfish are available, results from this study suggest that in the NGoM this species spawns during the summer over a large region of the continental shelf and slope. The increase in larval abundance during the early sampling period (June) could be a result of greater food availability earlier in the summer. In the sampling corridor, primary productivity is impacted by both coastal (Mississippi River) and oceanic (upwelling) nutrient sources (Dorado et al., 2012). The continental shelf in the GoM receives considerable nutrient inputs from the Mississippi River that promotes primary productivity; therefore, changes in river discharge could impact food availability to fish larvae (Lehrter et al., 2009). During the 3 years sampled, freshwater inflow from the Mississippi River and Atchafalaya River to the NGoM was higher in June (35,633 m³/s) than July (22,600 m³/s) (Aulench et al., 2007), thus causing an influx of nutrients into the NGoM earlier in the summer, increasing primary and secondary productivity within the region (Biggs, 1992; Davis et al., 2002; Ross et al., 2010). Also within the NGoM, June typically has a higher abundance of phytoplankton biomass than July

Fig. 6 **a** Density (larvae/1,000 m²) of bluntnose flyingfish at each station ($n = 385$) plotted against salinity (psu) and sea surface temperature (SST, °C) from all 3 years combined. **b** Density (larvae/1,000 m²) of bluntnose flyingfish at each station ($n = 385$) plotted against sea surface height anomaly (SSHA, cm) and distance to the Loop Current (DisLC, km) from all 3 years combined



(Fennel et al., 2011), further suggesting that food availability is greater in June. Furthermore, *Trichodesmium*, an oceanic cyanobacterium, is an important primary producer and plays a critical role in fixing nitrogen that can then be incorporated into coastal and pelagic food web and increase secondary production in the NGoM (Dorado et al., 2012). Within the study region, *Trichodesmium* abundance was shown to be higher in June than July (Dorado et al., 2012), and therefore it appears that bluntnose flyingfish may match spawning times to peaks in phytoplankton abundance.

Interannual variability across the 3 years sampled was pronounced, with densities in 2011 markedly lower than the two previous years sampled. Temporal changes in abundance are common and have been linked to a variety of factors, including shifts in the spawning locations of adults, egg production and quality, or variability in early life survival, all of which are influenced by oceanographic conditions (Wright and Trippel, 2009; Rooker et al., 2012). Yearly differences in the abundance of larvae could be attributed to shifts in oceanographic features or conditions, particularly the location of the Loop Current, which is known to affect the distribution and abundance of pelagic larvae in the NGoM (Lamkin, 1997; Rooker et al., 2013). In 2011, the Loop Current penetrated farther north than the previous 2 years (Fig. 4), potentially creating unfavorable spawning habitat for bluntnose flyingfish because of the warm, nutrient depleted waters associated with the Loop Current (Biggs, 1992). The oligotrophic waters of the Loop Current are associated with lower primary and secondary production compared to areas of cyclonic circulation, possibly reducing foraging opportunities for larval flyingfish (Wormuth et al., 2000). In addition to the location of the Loop Current, the Mississippi River plume can also impact the distribution and abundance of fish larvae within the NGoM. The summer of 2011 was a major flooding event for the Mississippi River (Bianchi et al., 2013), and the NGoM saw a greater influx of freshwater to the region. This increase in freshwater to the sampling area would cause salinities to decrease and possibly reduce suitable habitat for bluntnose flyingfish larvae because bluntnose flyingfish occupy a more oceanic habitat. Additionally, the decline in 2011 could also be attributed to anthropogenic factors such as the 2010 Deepwater Horizon oil spill. This event released

4.4×10^6 barrels of oil (Crone & Tolstoy, 2010), and had the potential to impact both early life survival and the distribution of the spawning stock biomass of pelagic fishes in the NGoM (Rooker et al., 2013). Given their epipelagic nature and close association with surface waters it is possible that flyingfish were affected by the Deepwater Horizon oil spill, and observed declines in 2011 may be due in part to the effect of oil and dispersants on larvae mortality and development. However, more information on movement patterns of adults and spatiotemporal variability in spawning and early life survival is needed to fully evaluate the impact of this event on the early life ecology of bluntnose flyingfish.

High occurrence of larvae across our sampling corridor suggests that bluntnose flyingfish occupy a wide range of habitat types and oceanographic conditions, and therefore appears less sensitive to changes in oceanographic conditions than other pelagic fishes (i.e., billfishes) (Rooker et al., 2012). The capability of bluntnose flyingfish to reproduce and hatch in a wide range of oceanographic conditions could be a result of their life history strategy. The short life span of adults (maximum 2 years) and heavy predation by pelagic predators (Oxenford et al., 1994) could limit the time available for adults to seek ideal spawning habitat. Therefore, spawning may occur across multiple oceanographic features, implying that bluntnose flyingfish are adapted to a wider range of ecological conditions than other pelagic species (i.e., dolphinfishes and billfishes). Additionally, when compared to adult billfishes and tunas that travel long distances to spawn (Teo et al., 2007), adult flyingfish are more limited in their movement patterns (Oxenford, 1994), and this reduced mobility of adult flyingfish could limit their ability to seek out favorable habitat for the larvae. The widespread distribution of bluntnose flyingfish and reduced sensitivity to environmental parameters likely explain the lower overall fit of the final GAM and reduced DE when compared to the predictive capability of models using species that are less abundant and have more restricted distributions (Planque et al., 2007; Rooker et al., 2012).

Physicochemical processes of a nursery like salinity have been shown to influence the distribution of larval fishes, and the interaction between a larva and its environment determines survival and ultimately recruitment success (Fogarty et al., 1991; Bruce et al., 2001). Temperature and salinity are known to impact

larval distribution (Hernandez et al., 2010), and other studies on pelagic larvae (billfishes, tunas, and dolphinfishes) have shown that salinity and temperature are important factors in determining quality of early life habitat (Rooker et al., 2012, 2013; Kitchens and Rooker, 2014). Within this study, the abundance of bluntnose flyingfish larvae increased at higher salinities; however, no temperature effect was observed. Near-shore waters in the NGoM are impacted by freshwater input from the Mississippi River plume which can extend more than 100 km offshore (Govoni et al., 1989) bringing lower salinity waters to the northern region of the sampling corridor. The abundance of bluntnose flyingfish larvae decreased in areas of low salinity, suggesting that waters near the Mississippi River plume provide unfavorable habitat for flyingfish larvae as the waters near the plume tend to have sharp changes in physicochemical properties (Govoni & Grimes, 1992). In the NGoM, areas with higher salinities (>35 psu) are typically found near the outer margin of continental shelf and beyond (i.e., slope waters), implying that bluntnose flyingfish larvae are associated with oceanic waters far removed from coastal processes such as freshwater inflow from the Mississippi River (Carassou et al., 2012).

Fish larvae spawned on the outer shelf and slope waters of the NGoM are heavily influenced by the Loop Current and associated eddies that impact the physical and chemical environments occupied by larvae (Lindo-Atichati et al., 2012). The final GAM indicated an increase in bluntnose flyingfish abundance in areas of negative sea surface height or areas associated with cyclonic features (i.e., cold-core eddies). Cyclonic circulation is typically associated with areas of upwelling which brings up cold, nutrient-rich waters from the depths to the surface (Ross et al., 2010). These areas of upwelling often enhance biological productivity (Bakun, 2006; Govoni et al., 2010) and in turn increase foraging opportunities (Wormuth et al., 2000; Bakun, 2006). As a result, these areas may represent favorable environments for pelagic fishes during early life (Rooker et al., 2012). Although areas with negative sea surface height appear to represent suitable early life habitat for bluntnose flyingfish because of a potential increase in primary productivity, chl-*a* concentration (primary productivity) was not retained as a variable in the final GAM model. Grazing by zooplankton (secondary

productivity) often leads to mismatches between chl-*a* and zooplankton biomass (Govoni et al., 2010), possibly explaining why chl-*a* concentration was not a significant factor in our final GAM for bluntnose flyingfish. Alternatively, densities of bluntnose flyingfish larvae may simply appear to be lower in anti-cyclonic and frontal regions because predation-induced mortality is higher in these features, where predators (i.e., juvenile tunas and dolphinfishes) are present in higher densities than cyclonic features (Lindo-Atichati et al., 2012).

Our final model indicated that the abundance of bluntnose flyingfish larvae was greater in waters near or within cold-core eddies but lower in areas of convergence typically associated with high larval catches such as the western margin of the Loop Current. This finding differs from previous research on other larvae that have emphasized the importance of temperature fronts and convergent zones as critical early life habitat of pelagic fishes (Lamkin, 1997; Richardson et al., 2009; Simms et al., 2010; Lindo-Atichati et al., 2012; Rooker et al., 2012). Previous work on other taxa of pelagic fishes (billfishes, dolphinfishes, tunas) have shown that abundances of larvae increase with proximity to the Loop Current (Rooker et al., 2012, 2013), signifying that the location of the Loop Current will influence their spatial distribution in the NGoM. Areas of convergence or fronts are typically characterized by sharp gradients in salinity, turbidity, and primary productivity (Lamkin, 1997), which can accumulate both fish larvae and their prey (Govoni et al., 1989; Lamkin, 1997). Here we observed the opposite for bluntnose flyingfish with an increase in abundance of bluntnose flyingfish as distance to the edge of the Loop Current increased. This indicates that larval bluntnose flyingfish may preferentially spawn offshore in the more stable, nutrient-rich waters of cyclonic eddies that shed off the Loop Current rather than the mixed waters of the Loop Current edge.

This study represents the first attempt to characterize the distribution and abundance of larval bluntnose flyingfish, and identify critical spawning and nursery areas for this species within the NGoM. Previous studies on the early life ecology of flyingfishes have focused on populations in the Caribbean Sea, but comparable studies do not exist for species inhabiting other regions of the western Atlantic Ocean. The high abundance and broad distribution of this species highlights the importance of the NGoM as early life habitat, and suggests that flyingfish are an integral

component of the pelagic ecosystem in this region. Given the growing interest in ecosystem-based management (EBM) of marine fisheries, there is a great need to better understand the population dynamics of ecologically important forage fishes at lower trophic levels in the pelagic ecosystem, such as flyingfishes. Understanding factors that influence the distribution, abundance, and population dynamics of lower trophic species such as bluntnose flyingfish is an important step in improving the knowledge base for EBM of pelagic ecosystems and may provide insight into the spatial distribution of other pelagic fishes that are both ecologically and economically important.

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