

Neritic larval fish assemblages across the Texas shelf in the northwestern Gulf of Mexico following Hurricane Harvey

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Abstract

Fall is an important time of year for fish recruitment in the Gulf of Mexico, with many commercially and recreationally important species spawning during this period. Changes in temperature and salinity regimes through seasonally abnormal freshwater input may change spawning patterns and displace larvae. Such an event occurred off the coast of Galveston Bay, Texas when a freshwater flood plume formed from unprecedented rainfall related to Hurricane Harvey at the end of August 2017. This study investigated the effects of a large-scale flood plume on larval fish assemblages, collected at nearshore and shelf zones one and two months after Hurricane Harvey. Samples from 2017 were compared to historical datasets collected by NOAA Fisheries in September (2000-2004; 2006-2016) and October (2000-2012). Evidence of lowered water temperature and salinity was found in both September and October 2017. Larval community composition changed along cross-shelf gradients and with increasing distance from

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shore. We also found evidence of 2017 assemblages differing from historical data, with the September 2017 assemblage more closely resembling those from October historical samples. Observed differences in 2017 assemblages were most likely explained by an earlier onset in fall sciaenid spawning, suggesting that decreases in water temperature occurring during hurricanes have the potential to alter fish spawning patterns.

Introduction

During their early life stages, fish are highly vulnerable to a variety biological and physical processes (Houde, 1987). Mismatches between the timing of fish spawning and peak zooplankton production can increase the susceptibility of larval fish to starvation and predation mortality, through inadequate nutrition and slower growth rates (Cushing, 1969, Houde, 2008). Environmental parameters, like water temperature and salinity, can influence egg incubation periods (Mihelakakis and Kitajima, 1994, Brown et al., 2011), vertical and horizontal larval distribution (Sanvicente-Añorve et al., 2000, Sloterdijk et al., 2017), larval growth rates (Landaeta et al., 2012, Koenker et al., 2018), and larval swimming performance (Cominassi et al., 2019, Downie et al., 2020). Seasonal changes in water temperature, photoperiod and tidal/lunar cycles can also act as important spawning cues for adult fishes (Miller and Kendall, 2009, Wang et al., 2010), which may contribute towards year-to-year variation in larval assemblage structure (Ramos et al., 2006, Genner et al., 2010). For example, interannual temperature changes can influence the timing of adult spawning migration (Sims et al., 2004), and peak seasonal larval fish abundance (Genner et al., 2010). In addition to adult spawning behavior, predator and prey abundance, water depth, and temperature and salinity gradients (i.e., frontal boundaries) can influence larval growth and survival resulting in a change of assemblage composition and larval distributions (Miller and Kendall, 2009, Hsieh et al., 2016, Axler et al., 2020).

Examining changes in larval fish assemblages driven by fluctuations in biological and environmental variables allow for a better understanding of interannual variations in taxonomic

composition. Extreme environmental events such as hurricanes or coastal flood plumes, can affect these assemblages (Thorrold and McKinnon, 1995, McKinnon et al., 2003, Hsieh et al., 2016), potentially influencing recruitment dynamics. Storms that facilitate strong wind driven currents can increase the dispersal of larval fish (McKinnon et al., 2003), which can allow species to extend their geographic range and supports the mixing of genes (Fuiman and Werner, 2009). However, greater larval dispersal, especially farther from shore, may increase the risk of aberrant drift in which some individuals are lost from a cohort through unfavorable conditions dispersing larvae into regions with insufficient prey or away from suitable juvenile habitat (Hjort 1914). Additionally, hurricanes have been reported to lower sea surface temperature by as much as 10 °C through evaporative cooling, upwelling, and other mechanisms (Vincent et al., 2012), which could potentially cause pronounced changes in larval assemblages, especially during transitional periods between seasons. The number of extreme weather events (i.e., category 3 hurricanes and above) and their associated precipitation levels are predicted to increase over the next century (Bender et al., 2010, Marsooli et al., 2019, Pflieger et al., 2022), so understanding the impact these events have on larval assemblages can provide insight into changes in population for both economic and environmentally important fish species.

In the northern Gulf of Mexico (GOM), larval fish abundance, distribution, and community composition is influenced by seasonality, distance to shore, and physical processes such as water column mixing and freshwater input (Hernandez et al., 2010, Carassou et al., 2012, Meinert et al., 2020). Larval fish assemblages in the northern GOM are typically characterized by high taxonomic richness during the late summer to early fall, with dominant coastal families including Engraulidae, Clupeidae, Sciaenidae, Gobiidae, and Carangidae and oceanic families (past the shelf) including Myctophidae and Gonostomatidae (Ditty et al., 1988, Hernandez et al., 2010). Assemblage composition also changes along cross-shelf gradients, which has been supported by studies in the northern and southern GOM (Espinosa-Fuentes and Flores-Coto, 2004, Carassou et al., 2012), south-western Australia (Muhling et al., 2008), and Taiwan (Hsieh et al., 2016). When cross-shelf currents are weak, seasonal and spatial differences in larval

assemblage composition are likely a result of adult spawning behavior (Muhling et al., 2008, Carassou et al., 2012). River plumes indicated through cross-shelf gradients in temperature and salinity can act as a vector for cross-shelf larval transport (Espinosa-Fuentes and Flores-Coto, 2004, Carassou et al., 2012). Seasonally higher freshwater discharge from the Grijalva-Usumacinta River system creates a freshwater plume in the southern GOM that facilitates an extension of nearshore larval assemblages farther off the shelf (Sanvicente-Añorve et al., 1998, Espinosa-Fuentes and Flores-Coto, 2004). Similarly, for the Mobile River discharge in the northern GOM the resulting freshwater plume has been shown to influence nearshore and shelf larval assemblage structure (Carassou et al., 2012).

An extreme weather event occurred along the coast of Texas during the last week of August 2017 (Du and Park, 2019). Unprecedented rainfall from Hurricane Harvey resulted in an estimated 14 billion kL of freshwater being discharged into Galveston Bay, TX, (~3.7 times the Bay's volume) and created a large freshwater plume in the adjacent coastal north-western GOM waters (D'Sa et al., 2018, Du et al., 2020). Following Hurricane Harvey, salinity near the mouth of the Bay was reduced from 30 to 0 and took approximately two months to recover (Du and Park, 2019). During this time, freshwater phytoplankton and zooplankton species replaced estuarine taxa throughout the inner Bay to coastal inlet (Du et al., 2019a, Liu et al., 2019). Outside of the Bay, a reduction in surface temperature, salinity and phytoplankton biomass was observed nearshore (< 50 km from shore) in September and October 2017 (Kurtay et al. 2021). Additionally, nearshore and shelf waters (50-130 km from shore) in September 2017 were characterized by significantly higher abundances of zooplankton as compared to samples collected at the same locations across a six-month period following Hurricane Harvey (Topor et al., 2020). Differences in spatio-temporal patterns of phytoplankton biomass and composition have been linked to storm induced freshwater discharge in the Neuse River Estuary and Pamlico Sound watersheds in North Carolina (Paerl et al., 2006, Paerl et al., 2018) and the Chesapeake Bay watershed in the Mid-Atlantic, USA (Filippino et al., 2017). Increases in copepod egg production and zooplankton abundance associated with storm induced freshwater discharge were

reported near the Great Barrier Reef lagoon, Australia (McKinnon and Thorrold, 1993). Shifts in the distribution of zooplankton biomass in response to increased freshwater inflow (Grant et al., 1977) and wind induced mixing (Roman et al., 2005) after the passage of storms was also found for the Chesapeake Bay watershed.

Given the effect of large-scale storms on phytoplankton and zooplankton communities, which are important prey for larval fishes, changes in temperature and salinity gradients as well as physical mixing are likely to also have a subsequent influence on larval assemblages. Previous studies in Chesapeake Bay reported young of the year *Micropogonias undulatus* abundances as being 30 times higher than the mean abundance for the previous decade following Hurricane Isabel in 2003, which was attributed to increased larval transport into the Bay through strong onshore winds (Houde et al., 2005, Roman et al., 2005, Montane and Austin, 2005). By contrast, a loss of larvae from the Rappahannock and James Rivers in Virginia was reported following Tropical Storm Agnes (1972) due to increased freshwater discharge and river flow (Hoagman and Merriner, 1976). A few other studies, in Australia (Thorrold and McKinnon, 1995, McKinnon et al., 2003) and Taiwan (Hsieh et al., 2016), have investigated the effects of extreme storm events on coastal and marine larval fish assemblages. These studies reported changes in community composition, abundance, and distribution, with the driving mechanisms dependent on the nature of the storm, such as high precipitation or wind intensity (Thorrold and McKinnon, 1995, McKinnon et al., 2003, Hsieh et al., 2016).

The purpose of this study was to assess larval fish community assemblages along a cross-shelf gradient incorporating nearshore and shelf GOM waters adjacent to Galveston Bay, TX following Hurricane Harvey and determine the effects the resulting freshwater plume may have had on larval densities, distribution, and community composition. We hypothesized that i) changes in larval fish assemblages would follow a cross-shelf gradient due to adult spawning patterns of different species, ii) September and October larval fish communities in 2017 would differ significantly from September and October communities of previous years (2000-2016)

with the freshwater plume changing the salinity gradient and allowing nearshore families to extend farther over the shelf.

Methods and Materials

Study Area and Field Sampling

Ichthyoplankton samples were collected at seven stations (S1-S7) along two longitudinally arranged transects outside of Galveston Bay, Texas on board the NOAA Ship Gordon Gunter from September 22-24, 2017 as part of NOAA Fisheries' Southeast Area Monitoring and Assessment Program (SEAMAP) and the RV Point Sur from October 30 to November 3, 2017. Stations, S1-S7, were arranged north-to-south and divided into "nearshore" (16-20 m) and "shelf" (35-72 m) subsets based on distance to shore and bottom depth (Figure 1). Locations for S1-7 are in accordance with the SEAMAP survey grid. Samples on board the Gordon Gunter were collected during 24hr operations, whereas samples on board the RV Point Sur were collected during the day only.

Plankton samples were collected using bongo (61 cm diameter opening, 335 μ m mesh nets) and neuston (1 x 2 m opening, 950 μ m mesh net) gear. Both gear types were deployed over the side according to the standard protocols outlined in the SEAMAP operation manual (GSMFC 2016). Bongos were oblique tows starting at 2 m above the bottom and pulled to the surface with a retrieval rate of 5-10 m/min. at nearshore and 15-20 m/min. at shelf stations. Neustons were towed for 10 minutes along the surface with the frame half submerged. The bottom third of each net was rinsed aboard the ship and the catch was transferred to the ship's wet lab where larval fish were euthanized using hypothermic shock according to the project's Animal Use protocols (TAMUCC AUP 3-16 and TAMUK #2017-11-20-A2). Sampling in Texas state waters was conducted under the Texas Parks and Wildlife Department scientific permit number SPR-0316-065 to S.J. Geist. Plankton samples were preserved on board the ship and larval fish were sorted using mirror-base dissecting microscopes, at Texas A&M University Corpus-Christi. Samples were sorted two times to ensure all larvae were removed. All specimens were identified to family

level following larval identification guides by Richards (2005) and Fahay (2007). Water parameters including temperature (°C), salinity, dissolved oxygen (mg/l), and chlorophyll-a (Chl_a) were collected using a SEABIRD (9plus; SBE 11) CTD instrument suite.

Historical Data

To investigate potential changes in ichthyoplankton community assemblage following Hurricane Harvey, samples collected during the September and October-November 2017 cruises were compared to historical data from the annual Fall SEAMAP ichthyoplankton surveys. Additional historical ichthyoplankton data was used for comparison from collections made on SEAMAP Fall groundfish trawl surveys for years which also included ichthyoplankton sampling. Data from the ichthyoplankton surveys, hereinafter referred to as “historical September” cruises, was available for the years 2000-2004 and 2006-2016 (Supplemental Table 1), with sampling dates ranging from August 27 to September 22. By contrast, groundfish survey data, hereinafter referred to as “historical October” cruises, was available for 2000-2012 (Supplemental Table 1), with sampling dates ranging from October 14 to November 5. In 2005, Hurricane Katrina prevented September sampling. In 2008, Hurricanes Gustav and Ike shortened sampling time, with S1, S3, and S5 being excluded as a result, and shifted sampling for S2, S4, and S6 to mid-September. The same procedures and gear were used in the fall SEAMAP surveys to collect larval fish and water parameter data as described above. Larval fish were sorted and identified to the lowest possible level (typically family) at the Sea Fisheries Institute, Plankton Sorting and Identification Center, Gdynia and Szczecin, Poland.

Data Analysis

To assess potential changes in temperature and salinity, surface and bottom temperatures (°C) as well as surface and midwater column salinities within September and October were compared between all available years at S1-5, which were the stations primarily affected by the Hurricane Harvey flood plume (Figure 2; Kurtay et al., 2021). One-way ANOVAs followed by Tukey post-hoc comparisons were used to analyze September surface, October surface, and

October bottom temperatures. Kruskal-Wallis tests followed by Dunn's post-hoc comparisons were used to analyze September bottom temperature as well as September and October surface and midwater column salinities, as the residuals from these datasets did not meet the ANOVA test assumptions.

Differences in larval assemblages between the categories "zone" (nearshore and shelf), "cruise" (historical September, September 2017, historical October, and October 2017), and their interaction were investigated separately for bongo and neuston nets through non-metric multidimensional scaling analysis (NMDS) and permutational multivariate analysis of variance (PERMANOVA) using Primer 7. Family level density (bongo = Ind./100 m³; neuston = Ind. per 10 mins.) data was log (X+1) transformed, to down-weight the contribution of the dominant families, with NMDS and PERMANOVA performed on Bray-Curtis dissimilarity matrices using the recommended Primer 7 settings (Anderson et al., 2008). A PERMDISP was performed using the "centroid" and "permutation" setting in Primer 7 to test for homogeneity of multivariate dispersion among categories with both zone (df1 = 1, df2 = 208, $f = 1.998e-7$, $p = 1$) and cruise (df1 = 3, df2 = 206, $f = 0.0856$, $p = 0.991$) meeting this assumption. Pairwise post-hoc comparisons were run for significant main effects and interaction differences between respective categories indicated by the PERMANOVA. For post-hoc comparisons of cruise (main effect) and the interaction of zone and cruise, p -values were Bonferroni adjusted to correct for family-wise error (Armstrong, 2014). The similarity percentage test (SIMPER) was used to identify taxa driving dissimilarities between significantly different zones or cruises based on the pairwise post-hoc comparisons.

The BIOENV analyses (Clarke and Ainsworth, 1993) were used to evaluate potential environmental drivers for the bongo and neuston assemblages. Assemblage dissimilarity matrices followed the same procedure described above. Environmental data was "normalized" by subtracting the mean and dividing by the standard deviation for each variable across all years (2000-2017). The environmental matrix was calculated between samples (each station per year)

using Euclidean distance. Prior to creating the environmental matrix, water parameters were checked for collinearity. Surface and bottom temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/l), mid-water column salinity, and Chl_a max were included in the bongo net analysis. For the neuston net analysis, surface temperature, dissolved oxygen, salinity and Chl_a were included. Midwater column salinity was chosen for the bongo net analysis as high collinearity among surface, mid-water, and bottom salinity measurements was indicated through a draftsman's plot and corresponding correlation coefficients. For the BIOENV, only stations with both assemblage and CTD data were included in the analysis. In addition to stations or years not sampled (Supplemental Table 1), data not included in the analysis from historical September cruises were stations S1-7 from 2007 as well as S7 from 2008, due to the CTD winch malfunctioning. Similarly, S5 from both 2002 and 2008 for historical October cruises were also left out for this reason.

Results

Larval Fish Densities and Environmental Parameters

The dataset is based on 3,202 larval fishes collected in September 2017; 2,356 larvae collected in October 2017; 85,888 collected throughout historical September (2000-2004; 2006-2016); and 47,134 collected throughout the historical October (2000-2012) cruises that were identified to family level. Comparing the larval fish densities (bongo = Ind./100 m^3 ; neuston = Ind. per 10 mins.) during the 2017 cruises with respective September and October historical cruises, median densities collected with the bongo were lower in September 2017 and higher in October 2017 but still fell within the range of all historical cruises (Table 1). For the neuston data, median densities fell within the range of all historical cruises (Table 1). However, densities were higher in September 2017 and lower in October 2017 compared to the respective historical medians. Larval fishes representing 38 families were identified between the two 2017 cruises and 96 families across all historical cruises (Supplemental Table 2). In 2017, Sciaenidae was the dominant family in terms of abundance, composing 30.3% of the total larval density collected with the bongo in September and 50.3% in October. By contrast, Sciaenidae (10.4%) had the

fifth highest density across the September historical cruises, following Gobiidae (17.6%), Carangidae (15.4%), Engraulidae (15.3%), and Clupeidae (15.2%). Across the October historical cruises, Sciaenidae (20.7%) had the second highest density following Gobiidae (39.9%).

Environmental variables measured from CTD casts from the September and October 2017 surveys fell within recorded values from the historical surveys (2000 – 2016) during the same respective months (Table 1). However, surface temperature and midwater column salinity at the five stations nearest to shore (S1-5) were near the lower end of the range. Further analysis of S1-5 suggested a significant difference in surface temperatures across years within September (ANOVA, $df = 14, f = 17.1, p < 0.0001$) and October (ANOVA, $df = 10, f = 7.6, p < 0.0001$; Supplemental Figure 1). During September surface temperature was significantly lower in 2017 (Tukey post-hoc, $p < 0.02$) compared to all years except 2001. During October surface temperature was significantly lower in 2017 (Tukey post-hoc, $p < 0.02$) compared to all years except 2000 and 2001. No difference in bottom temperature across years was found for September (KW, $p > 0.05$). However, a significant difference was found for October (ANOVA, $df = 10, f = 5.9, p < 0.0001$; Supplemental Figure 1), with bottom temperatures in 2017 being lower than all years except 2000, 2001, and 2003 (Tukey post-hoc, $p < 0.03$).

Evidence of freshwater input in 2017 was supported by S1-5 having the lowest median surface salinities in September (29.3) and second lowest in October (32.8), following 2005 (31.8). A significant difference in surface (KW, $df = 14, X^2 = 55.3, p < 0.0001$) and midwater column (KW, $df = 14, X^2 = 45.9, p < 0.0001$; Supplemental Figure 2) salinity was found across years in September. However, several years showed high interstation variation which led to surface and midwater column salinities in 2017 only being lower than 2000 and 2011 (Dunn's post-hoc, $p < 0.01$), where all stations had fully marine salinities (> 36.0). No difference in surface or midwater column salinity was found across years for October (KW, $p > 0.05$; Supplemental Figure 2).

Larval Fish Community Composition

Larval community assemblage was significantly different between (i) zone, (ii) cruise, and (iii) their interaction based on the PERMANOVA (Table 2) for samples collected with both gear types, bongo and neuston. Assemblages collected with the bongo showed more structure than those collected with the neuston, indicated by higher pseudo- f values (Table 2). For the bongo, zone (pseudo- f = 29.24) showed the strongest separation in larval assemblage structure followed by cruise (pseudo- f = 11.58) whereas for the neuston, zone (pseudo- f = 4.26) and cruise (pseudo- f = 4.49) had a similar effect. The interaction of zone with cruise had the weakest effect for both gear types, indicated by low pseudo- f values (Table 2).

For larvae collected throughout the water column (bongo net), there was a clear separation in assemblage structure between nearshore and shelf zones based on pairwise post-hoc comparisons and NMDS analysis (Table 3 and Figure 3). Abundant families in nearshore samples included Clupeidae, Engraulidae, Carangidae, Sciaenidae, and Gobiidae (Figure 4). By contrast, shelf samples were characterized by Gobiidae, Bregmacerotidae, Synodontidae, Lutjanidae, and the three Pleuronectiformes families all having higher densities than nearshore. The three families driving dissimilarities between nearshore and shelf zones were Sciaenidae, Clupeidae, and Gobiidae (Table 4). Analysis of cruise suggested differences between historical September and historical October assemblages and that the September 2017 larval assemblage was different from past years and more closely resembled historical October assemblage (Table 3 and Figure 3). Comparison of the two historical cruise months showed that September was characterized by high Clupeidae, Engraulidae, and Carangidae densities and October by high Gobiidae, Sciaenidae, and Bregmacerotidae densities (Table 5 and Figure 5). The same five important nearshore families primarily explained dissimilarity between historical September larval assemblage compared to September 2017 and historical October assemblages (Table 5). Of those five families, Clupeidae, Engraulidae, and Carangidae densities were notably lower in September 2017 as compared to historical September densities (Figure 5). Densities of several families were similar between September 2017 and historical October cruises, including Engraulidae, Synodontidae, Ophidiidae, Carangidae, Sciaenidae, and Paralichthidae (Figure 5).

Sciaenidae, Gobiidae, Bregmacerotidae, and Engraulidae were the top families explaining differences between October 2017 and historical October assemblages (Table 5), with Sciaenidae densities being higher and Engraulidae entirely absent from the October 2017 assemblage (Figure 5). The interaction between zone and cruise confirmed differences in larval assemblages between historical September and October cruises for all zones (Supplemental Table 3). Additionally, October 2017 assemblages were different from historical September cruises for nearshore and shelf zones (Supplemental Table 3).

For larvae collected at the water surface (neuston net), there was evidence of the same cross-shelf assemblage gradient as found for the depth integrated samples (Table 3). However, separation between the nearshore and shelf zones was comparatively weaker than the bongo, as indicated by a low pseudo- f value (Table 3), and a 2D NMDS ordination showed a high level of stress (0.23; Supplemental Figure 3). Nearshore, the same families as in the bongo catches dominated in terms of density except for Gobiidae (Figure 6). Different from the bongo, Sciaenidae dominated larval shelf densities for neuston samples. Larval assemblages were different between the two historical cruise months and the two historical cruise months were also both different from October 2017 (Table 3). Comparison of the two historical cruise months showed that September neuston catches were characterized by high Clupeidae, Engraulidae, and Carangidae densities and October by high Sciaenidae density (Figure 7). The family Sciaenidae dominated larval densities in September 2017, with mean densities being 5 times higher than historic September cruises and were the dominant family for historical October and October 2017 cruises (Figure 7). Similar to the bongo, the family Engraulidae was almost entirely absent from neuston assemblages during October 2017. The interaction between zone and cruise confirmed differences in larval assemblages between historical September and October cruises for nearshore and shelf zones and a marginal difference between October 2017 and historic September cruises for the shelf (Supplemental Table 3).

The three environmental parameters that best explained larval fish community structure captured in the bongo were surface water temperature, bottom water temperature, and mid-water column salinity (BIOENV correlation 0.529; Table 6). Only one parameter, surface water temperature, best explained community structure for larvae captured in the neuston (BIOENV correlation 0.183; Table 6).

Discussion

Following Hurricane Harvey, sea surface temperatures (SST) across Galveston Bay dropped by 5 °C (Huang et al., 2021) and a reduction in mean SST from > 30 °C to 28.5 °C, was reported across a broad region of the Gulf of Mexico (GOM) in September (Trenberth et al., 2018). Cooler water temperature in the GOM was primarily attributed to evaporative cooling, which leaves behind a “cold wake” following the passage of a hurricane (Trenberth et al., 2018). Meanwhile, lowered water temperatures within the Bay were most likely a result of both evaporative cooling and cool freshwater from the riverine tributaries being mixed into the Bay (Huang et al., 2021). A reduction in SST from pre- to post-storm was evident across the stations used in this study, with temperatures lowering from 29.7-30.8 °C in July to 28.2-28.9 °C in September (Kurtay et al., 2021). This study presents evidence that SST in late September and late October 2017 at stations \leq 88 km from shore were lower compared to most years since 2000 based on NOAA SEAMAP data.

In addition to lower water temperatures, a dramatic decrease in salinity within Galveston Bay and the adjacent coastal waters was observed by many studies following Hurricane Harvey (Du et al., 2019a, Yan et al., 2020, Kurtay et al., 2021). The SEAMAP historical data showed high variation in salinity at our nearshore and two inner shelf stations (S1-5) with lower salinities caused by freshwater discharge from Galveston Bay and the Mississippi-Atchafalaya River system, as the prevailing longshore transport during the fall can carry freshwater discharge along the Texas coast (Zavala-Hidalgo et al., 2003, Du et al., 2019b). This resulted in late September

2017 salinities only to be different from 2000 and 2011, which were extreme drought years (Nielsen-Gammon, 2012).

The effect of distance from shore on the composition of larval assemblages has been well documented before for the GOM (Sanvicente-Añorve et al., 1998, Espinosa-Fuentes and Flores-Coto, 2004, Carassou et al., 2012) and other areas of the world (Muhling et al., 2008, Hsieh et al., 2016). Analysis of larval assemblages in our dataset confirmed that both distance to shore and seasonality were important factors influencing community structure in all years studied, including 2017. The predominant nearshore families reported in this study were consistent with the findings of other larval assemblage studies in the northern GOM (Hernandez et al., 2010, Meinert et al., 2020), with nearshore families including Clupeidae, Engraulidae, Carangidae, and Sciaenidae. The primary difference in catches from the two nets occurred at the shelf with Gobiidae dominating the bongo and Sciaenidae dominating the neuston, which may indicate differences in vertical structuring of larval assemblages at these stations. There was also a seasonal effect on the cross-shelf pattern of larval assemblages, with historical September and October assemblages being different from one another. The monthly difference is likely explained by larvae from abundant species with spawning periods that extend into the late summer, such as *Chloroscombrus chrysurus* (Carangidae), *Harengula jaguana* (Clupeidae), and *Anchoa mitchilli* (Engraulidae; Ditty, 1986, Hernandez et al., 2010, Carassou et al., 2012), being present at higher densities in September compared to October. For example, the mean density for *C. chrysurus* larvae during September compared to October was four times higher in the nearshore waters of Dauphin Island, Alabama (Hernandez et al., 2010) and nearly six times higher in the nearshore waters adjacent to Caminada Pass, Louisiana (Ditty, 1986).

Community composition of larval assemblages collected one and two months following Hurricane Harvey were different from historical cruises in the respective month, with sciaenids dominating larval assemblages. The limited studies on coastal and shelf larval assemblage composition following a large-scale storm also reported significant changes in community

structure (Thorrold and McKinnon, 1995, McKinnon et al., 2003, Hsieh et al., 2016), however each reported different driving mechanisms. High rainfall from Cyclone Joy (1991) created a freshwater plume off the coast of the Great Barrier Reef lagoon, Australia, which led to family specific changes in abundance and translocation of coastal larval fish communities farther offshore (Thorrold and McKinnon, 1995). Notable changes in larval community composition and increased diversity along the northwestern shelf of Australia was facilitated by strong winds from Cyclone Tiffany (1998), which increased vertical water column mixing and southward along-shore transport of planktonic communities (McKinnon et al., 2003). Increased abundance of larval fishes, but decreased taxonomic diversity, and changes in dominant species in southwestern Taiwan after Typhoon Tembin (2012) were thought to be related to increased nutrients and zooplankton availability in coastal waters (Hsieh et al., 2016).

This study adds to the understanding of biological responses to changes in abiotic parameters following a large-scale storm with extreme levels of rainfall. Water temperature and salinity best explained structuring within larval communities, which is consistent with the findings of other larval assemblage studies (Espinosa-Fuentes and Flores-Coto, 2004, Carassou et al., 2012, Sloterdijk et al., 2017). For example, in the northern GOM larval *C. chrysurus* and *Sciaenops ocellatus* (Sciaenidae) were predominately collected in water temperatures greater than 26 °C (Hernandez et al., 2010). It was hypothesized that changes in salinity gradients from the freshwater plume would allow for nearshore families to extend farther over the shelf, which is supported by studies in the southern GOM (Sanvicente-Añorve et al., 1998, Espinosa-Fuentes and Flores-Coto, 2004) and Australia (Thorrold and McKinnon, 1995). Within the first month following Hurricane Harvey, parallel studies found downstream displacement of freshwater and oligohaline fish species in Galveston Bay (Oakley and Guillen, 2019), and observed freshwater phytoplankton and zooplankton species near the Bay's inlet (Du et al., 2019a, Liu et al., 2019). It is possible that families or species within nearshore assemblages also extended their distribution farther over the shelf within the first few weeks (less than one month) following Hurricane

Harvey. However, strong evidence of nearshore families extending their distribution farther over the shelf or being displaced was not present in our datasets.

Here we propose that changes in water temperature associated with evaporative cooling and cool freshwater from the riverine tributaries, led to an earlier onset of fall spawning resulting in an extended peak spawning window, which caused the observed shift in larval community composition following Hurricane Harvey. While changes in salinity can shift the spawning locations of fishes (Miller and Kendall, 2009), temperature is a well-known spawning trigger (Khan and Thomas, 1996, Sims et al., 2004, Hall et al., 2019). In south-west England, *Platichthys flesus* spawning migration was shown to occur 1-2 months earlier during winters up to 2 °C cooler (Sims et al., 2004) and changes in the timing of peak spring and summer abundances of larval fishes were correlated with interannual temperature variability (Genner et al., 2010). Members of the family Sciaenidae are highly abundant within fall larval assemblages in the northern GOM, with peak abundance of species such as *Cynoscion nothus*, *Larimus fasciatus*, *Micropogonias undulatus*, and *S. ocellatus* occurring between September to October (Ditty et al., 1988, Hernandez et al., 2010). Temperature is a known spawning cue for both *M. undulatus* and *S. ocellatus* with spawning migrations in the northern GOM coinciding with drops in water temperature during the fall (Khan and Thomas, 1996, Hall et al., 2019), with cold fronts usually starting to roll in near mid-September in Texas. This may explain why sciaenid densities are usually higher in October compared to September based on historic NOAA SEAMAP data.

The September 2017 larval fish assemblages, which were characterized by high abundance of Sciaenidae and low abundance of Clupeidae, Engraulidae, and Carangidae larvae, closely resembled the historical October assemblages. Temperature and photoperiod are generally understood as the main cue for spawning periodicity for most marine fish species (Miller and Kendall, 2009). The low abundances of larvae from taxa of the three families mentioned above during September 2017 may be related to an earlier than usual cooling of water temperatures as an effect of Hurricane Harvey. Abundant species from these families such as *C.*

chrysurus, *H. jaguana*, and *A. mitchilli*, typically spawn during the late summer when water temperatures are still warm (Ditty, 1986, Hernandez et al., 2010, Carassou et al., 2012). In addition, Synodontidae, another dominant family within summer northern GOM larval assemblages (Hernandez et al., 2010, Carassou et al., 2012), had similar densities in September 2017 to historical October cruises, which were both lower than historical September cruises. By contrast, a possible explanation for elevated larval sciaenid densities observed during September 2017 is a several weeks earlier than usual start of spawning, probably triggered by cooler than normal water temperatures following Hurricane Harvey. Our observation therefore fits into the larger pattern of extended spawning periods described for many sciaenid species in the northern GOM, which were attributed to ongoing climate change (Hernandez et al., 2010). In addition, Ophidiidae had similar densities in September 2017 to historical October cruises, which were both higher than historical September cruises. Members from this family typically show peak spawning and larval abundance in the northern GOM during the fall (Retzer, 1991, Hernandez et al., 2010, Carassou et al., 2012).

An alternative explanation for elevated sciaenid densities during September 2017 is higher larval survivorship, which may have been supported through high zooplankton densities (Topor et al., 2020) during this same month. Another factor contributing to the observed differences may be related to the historical dataset used in this study, which is based on a long-term monitoring program with fixed station grids from dedicated NOAA SEAMAP plankton surveys in early September and opportunistic plankton sampling during groundfish surveys in October. Challenges with weather and instrument failure can lead to shortcomings in the form of incomplete station sampling (unbalanced sampling design) and shifts in the timing of cruises, which need to be considered when interpreting the data. The delay of September sampling by two weeks in 2017 caused by the closure of the Gulf waters after Hurricane Harvey may have contributed to some of the observed differences in larval assemblage composition as that time of year marks the change from summer to fall spawning species (Ditty et al., 1988, Hernandez et al., 2010). The cool water temperatures together with the two week delay of sampling for the

September cruise in 2017 may have contributed to the observed low Clupeidae, Engraulidae, and Carangidae densities, which include abundant species that spawn near the end of summer (Ditty, 1986, Hernandez et al., 2010, Carassou et al., 2012).

With future climate change predicting more frequent large-scale storms with high levels of rainfall (Bender et al., 2010, Marsooli et al., 2019, Reed et al., 2022), post-storm conditions that support increased larval survivorship and recruitment success must outweigh potential risks such as aberrant drift, mismatches between larval recruitment and suitable prey, or predation. The observed difference in larval assemblage composition after Hurricane Harvey in September compared to the composition in most of the previous 20 years, together with its marked similarity to typical larval assemblages for October led to our hypothesis that the most prominent effect structuring the neritic larval assemblage following Hurricane Harvey was an earlier shift from summer to fall spawning taxa, whose main spawning cue is usually temperature. Cool water temperature following Hurricane Harvey likely initiated earlier sciaenid spawning migrations. Water temperature also directly influences the growth rate of larval fish (Miller and Kendall, 2009), with cooler than normal water temperature during September and October 2017 possibly lowering larval growth rates. While high zooplankton densities can lower starvation risk, slower growth can lead to longer stage duration and increased predation risk among larvae (Houde, 1987). Future study investigating coupled differences in post-storm environmental conditions and zooplankton densities is needed to understand how large-scale storms influence larval fish survivorship and recruitment success.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contribution

SM collected samples during the September 2017 cruise and led the lab processing of samples including identification, data analyses, and manuscript preparation. JT assisted with data analyses, results interpretation, and editing of the manuscript. GZ provided and processed the historical data sets and provided comments for the manuscript. SG conceptualized the study supported by NSF#1760674, collected samples during the October 2017 cruise, provided training on methods and analyses, and prepared the manuscript together with SM. All authors read and approved the final document.

Data Availability Statement

The datasets generated for this study are available on request to the corresponding author.

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Table 1. Summary of the total number of bongo and neuston (bongo/neuston) nets and number of larval fish collected, larval densities (bongo = Ind./100m³; neuston = Ind. per 10 mins.), and environmental parameters later used in the BIOENV analysis recorded during historical (2000-2004, 2006-2016; Hist. Sept.), post-Hurricane Harvey September (Sept.) 2017, historical October (2000-2012; Hist. Oct.), and October (Oct.) 2017 cruises. Shown are median, maximum, and minimum larval densities. Environmental variables include surface and bottom temperature (°C); dissolved oxygen (mg/L); mid-water column salinity; surface and maximum chlorophyll a (Chl_a).

	Hist. Sept.	Sept. 2017	Hist. Oct.	Oct. 2017
Total bongo/neuston nets	125/121	7/6	71/73	7/7
Median Density	571.7/8.5	344.6/17.0	257.3/11.6	331.5/2.2
Max Density	4298.6/226.1	518.6/55.2	3075.6/242.1	444.9/36.7
Min Density	25.3/0.1	21.2/0.1	6.3/0.3	52.3/0.2
Surface Temperature	26.6-31.6	28.2-28.9	23.2-28.5	22.9-26.4
Bottom Temperature	12.7-31.2	20.0-28.3	18.0-28.3	22.9-26.3
Surface Salinity	20.9-36.8	22.0-36.2	24.9-36.6	30.5-36.2
Midwater Salinity	22.2-36.8	25.0-36.4	27.1-36.6	30.6-36.2
Surface Dissolved Oxygen	3.3-9.3	6.3-6.9	4.6-7.2	4.4-5.0
Bottom Dissolved Oxygen	0.9-6.9	3.2-6.1	3.6-6.7	3.4-4.6
Surface Chl_a	0.1-37.0	0.2-2.5	<0.1-9.4	0.3-1.2
Chl_a Maximum	<0.1-37.0	0.8-2.5	<0.1-14.9	0.6-2.1

Table 2. Two-way PERMANOVA results comparing community family assemblage structure between zones, cruise, and their interaction for larval fish captured in bongo and neuston nets. Zones include nearshore and shelf. Cruise includes historical September (2000-2004, 2006-2016), September 2017, historical October (2000-2012), and October 2017 cruises. Shown are degrees of freedom (df), sums of squares (SS), mean sums of squares (MS), pseudo-*f*, and *p*-value (*p*) at $\alpha = 0.05$.

Source	df	SS	MS	pseudo-<i>f</i>	<i>p</i>
Bongo					
Cruise	3	39554	13185	11.58	0.001
Zone	1	33289	33289	29.24	0.001
Cruise*Zone	3	9850.7	3283.6	2.88	0.001
Residuals	202	2.3e5	1138.6		
Total	209	3.87e5			
Neuston					
Cruise	3	40951	13650	4.49	0.001
Zone	1	12941	12941	4.26	0.001
Cruise*Zone	3	15552	5184	1.71	0.002
Residuals	199	6.0431e5	3036.7		
Total	206	7.142e5			

Table 3. Pairwise post-hoc comparisons of community family assemblage structure for the main effects zone and cruise from the PERMANOVA analyses for bongo and neuston nets. Zones include nearshore (near.) and shelf. Cruise includes historical September (2000-2004, 2006-2016; Hist. Sept.), September (Sept.) 2017, historical October (2000-2012; Hist. Oct.), and October (Oct.) 2017 cruises. *P*-values (*p*) for year-cruise comparisons were Bonferroni adjusted at $\alpha = 0.0083$.

Distance	<u>Bongo</u>		<u>Neuston</u>	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Near.-Shelf.	5.41	0.001*	2.06	0.001*
Cruise	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Hist. Sept.- Hist. Oct.	5.03	0.001*	3.11	0.001*
Hist. Sept.- Sept. 2017	2.15	0.001*	1.28	0.07
Hist. Sept.- Oct. 2017	3.32	0.001*	1.78	0.002*
Hist. Oct.- Sept. 2017	0.74	0.883	1.09	0.247
Hist. Oct.- Oct. 2017	1.85	0.003*	1.62	0.002*
Sept. 2017- Oct. 2017	1.43	0.060	0.94	0.527

Table 4. Similarity percentage (SIMPER) post-hoc analysis of larval fish family densities (Ind./100m³) captured in the bongo net between nearshore (near.) and shelf zones. Densities are log (x + 1) transformed. Shown are mean dissimilarity (Avg. Diss), standard deviation (SD), and percent contributions (% Cont.). Dashes (-) indicate taxa which were not included in the 70% cumulative percent contribution (Cum. Cont.) cut-off. Taxa order follows Richards (2005).

Family	Near. vs Shelf		
	Avg. Diss.	SD	% Cont.
Clupeidae	5.34	1.51	7.79
Engraulidae	3.93	1.38	5.73
Synodontidae	3.18	1.20	4.63
Bregmacerotidae	4.41	1.57	6.44
Ophidiidae	2.75	1.27	4.01
Carangidae	4.30	1.48	6.28
Lutjanidae	2.12	1.10	3.09
Sciaenidae	5.87	1.54	8.57
Gobiidae	5.05	1.44	7.38
Scombridae	2.71	1.25	3.95
Paralichthyidae	3.54	1.46	5.17
Bothidae	2.29	1.26	3.34
Cynoglossidae	2.84	1.38	4.14
Cum. Cont.			70.52

Table 5. Similarity percentage (SIMPER) post-hoc analysis of larval fish family densities (Ind./100m³) captured in the bongo net between historical September (2000-2004, 2006-2016; Hist. Sept.), September (Sept.) 2017, historical October (2000-2012; Hist. Oct.), and October (Oct.) 2017 cruises. Only significantly different comparisons supported by pairwise post-hoc tests from the PERMANOVA are shown. Densities are log (x + 1) transformed. Shown are mean dissimilarity (Avg. Diss), standard deviation (SD), and percent contributions (% Cont.). Dashes (-) indicate taxa which were not included in the 70% cumulative percent contribution (Cum. Cont.) cut-off. Taxa order follows Richards (2005).

Family	Hist. Sept. vs Hist. Oct.			Hist. Sept. vs Sept. 2017			Hist. Sept. vs Oct. 2017			Hist. Oct. vs Oct. 2017		
	Avg. Diss.	SD	% Cont.	Avg. Diss.	SD	% Cont.	Avg. Diss.	SD	% Cont.	Avg. Diss.	SD	% Cont.
Ophichthidae	-	-	-	1.95	1.23	3.13	-	-	-	-	-	-
Clupeidae	3.86	0.98	6.31	4.06	0.96	6.53	4.52	1.14	6.52	3.50	0.89	5.63
Engraulidae	3.68	1.29	6.01	3.84	1.21	6.17	5.97	1.53	8.61	4.14	1.12	6.66
Synodontidae	2.57	1.09	4.20	2.74	1.04	4.40	2.85	1.04	4.11	2.52	1.17	4.06
Myctophidae	1.82	0.87	2.97	-	-	-	-	-	-	-	-	-
Bregmacerotidae	3.36	1.28	5.49	3.04	1.18	4.89	3.01	1.18	4.34	4.31	1.36	6.94
Ophidiidae	2.88	1.31	4.71	2.79	1.27	4.49	2.63	1.37	3.79	3.19	1.26	5.14
Carangidae	4.09	1.17	6.69	4.35	1.06	6.99	5.59	1.39	8.05	2.10	1.12	3.38
Lutjanidae	1.94	1.08	3.16	2.08	1.04	3.34	2.32	1.05	3.35	-	-	-
Sciaenidae	4.32	1.26	7.06	4.93	1.12	7.92	5.93	1.27	8.55	6.19	1.08	9.97
Opistognathidae	-	-	-	-	-	-	2.00	0.96	2.88	2.15	0.94	3.46
Gobiidae	3.85	1.21	6.28	4.13	1.24	6.64	4.99	1.35	-	5.60	1.36	9.02
Microdesmidae	-	-	-	1.57	0.93	2.52	-	-	-	-	-	-

Scombridae	3.29	1.60	5.38	3.61	1.50	5.80	4.25	1.85	6.12	-	-	-
Stromateidae	-	-	-	-	-	-	-	-	-	2.21	1.23	3.55
Paralichthyidae	2.93	1.27	4.78	3.14	1.28	5.05	3.38	1.51	4.87	3.29	1.54	5.29
Bothidae	1.94	1.15	3.17	-	-	-	-	-	-	2.30	1.26	3.70
Cynoglossidae	2.54	1.30	4.15	2.63	1.29	4.22	3.07	1.42	4.42	3.10	1.32	4.99
Cum. Cont.			70.37			72.11			72.80			71.80

Table 6. Results from BIOENV analyses for larval assemblages collected during all September and October cruises (2000-2017) using bongo and neuston nets. Bongo model included surface (Surf.) and bottom (Bot) temperature (Temp.) and dissolved oxygen (DO), midwater column salinity (Mid. Sal.), and chlorophyll-a maximum (Chl_a Max). Neuston model included Surf. Temp., Sal., DO, and Chl_a. Bold Spearman's correlations (Corr.) denote the best combination of environmental parameters. N = number of variables in model.

<u>Variables</u>	<u>N</u>	<u>Corr.</u>
<u>Bongo</u>		
Mid. Sal	1	0.394
Bot. Temp., Mid. Sal.	2	0.466
Surf. Temp., Bot. Temp., Mid. Sal.	3	0.529
Chl _a Max, Surf. Temp., Bot. Temp., Mid. Sal.	4	0.518
Chl _a Max, Surf. Temp., Bot. Temp., Mid. Sal., Bot. DO	5	0.474
Chl _a Max, Surf. Temp., Bot. Temp., Mid. Sal., Surf. DO, Bot. DO	6	0.440
<u>Neuston</u>		
Surf. Temp.	1	0.183
Surf. Chl _a , Surf. Temp.	2	0.168
Surf. Temp., Surf. Sal., Surf. DO	3	0.158
Surf. Chl _a , Surf. Temp., Surf. Sal., Surf. DO	4	0.151