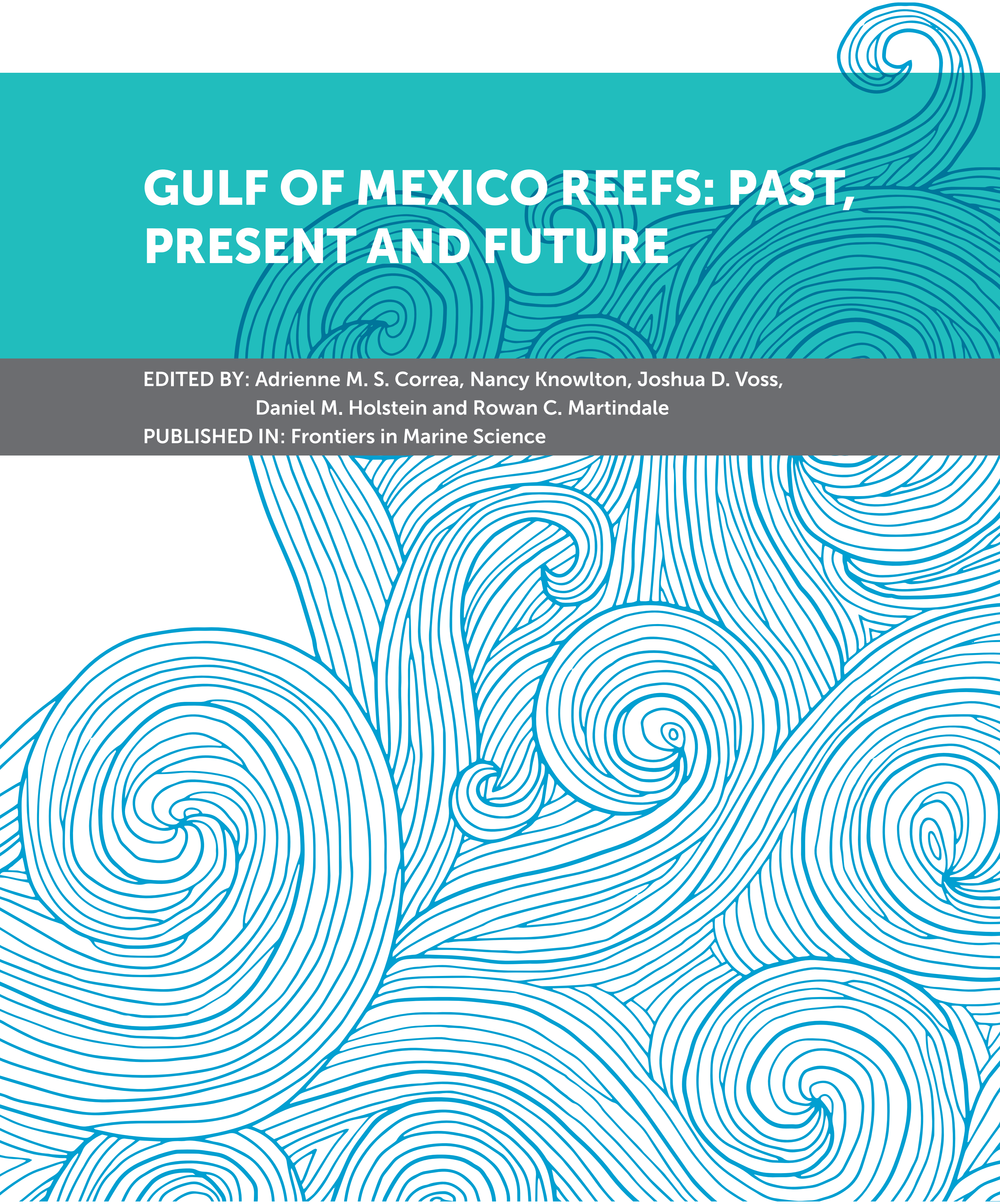

GULF OF MEXICO REEFS: PAST, PRESENT AND FUTURE

EDITED BY: Adrienne M. S. Correa, Nancy Knowlton, Joshua D. Voss,
Daniel M. Holstein and Rowan C. Martindale

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GULF OF MEXICO REEFS: PAST, PRESENT AND FUTURE

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Editorial: Gulf of Mexico Reefs: Past, Present and Future

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Editorial on the Research Topic

Gulf of Mexico Reefs: Past, Present and Future

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1. INTRODUCTION

Bounded by Cuba, Mexico, and the United States, the Gulf of Mexico (GoM) contains vast, relatively understudied modern and geological reefs. GoM reef environments are extremely valuable (Natural Resources Defense Council, 2010) but experience a range of disturbance regimes (Gil-Agudelo et al.; Cummings et al., 2018). Nevertheless, some offshore reefs remain remarkably healthy (e.g., Johnston et al., 2016). The prospects for new discoveries through the study of reefs in the GoM are extensive. To foster interdisciplinary discussions and new collaborations, the "Gulf of Mexico Reefs: Past, Present and Future Symposium" was held at Rice University in Houston (TX, USA) in 2018. This symposium brought together forty scientists (**Figure 1D**) from various institutions, and resulted in several (new) multi-institutional collaborations (**Figures 1A,B**) as well as this Special Topic, which summarizes the state-of-the-field for GoM reef systems (**Figure 1C**) from a transdisciplinary perspective. Below, we highlight findings from 12 contributions (11 Research Articles and 1 Opinion).

2. BIODIVERSITY AND ECOLOGY

Many ecosystems in the GoM lack basic ecological or genomic characterization; several articles herein address this issue. Limer et al. utilized larval transport models to investigate mechanisms enhancing coral larval retention at the Flower Garden Banks on the Texas-Louisiana shelf. These reefs are thought to be relatively isolated from anthropogenic influence (but see Wright et al.; Shore et al.), as well as from larval exchange with Western Atlantic reefs. Limer et al. shows that Loop Current eddies are crucial for coral larval retention, transport between adjacent banks, and redelivery of larvae after initial advection away from natal reefs; the paper also highlights the potential for these reefs as refugia. Wetmore et al. found that fish and coral diversity in the northwestern GoM are strongly linked, with the highest fish diversity at shelf-edge locations.

The GoM also contains mesophotic beds of rhodoliths (free-living spheroids of encrusting organisms). Krayesky-Self et al. cultured *Rhodosorus marinus* collected from such beds in the northern GoM, and discovered endolithic unicellular red algae within biogenic rhodoliths. Their

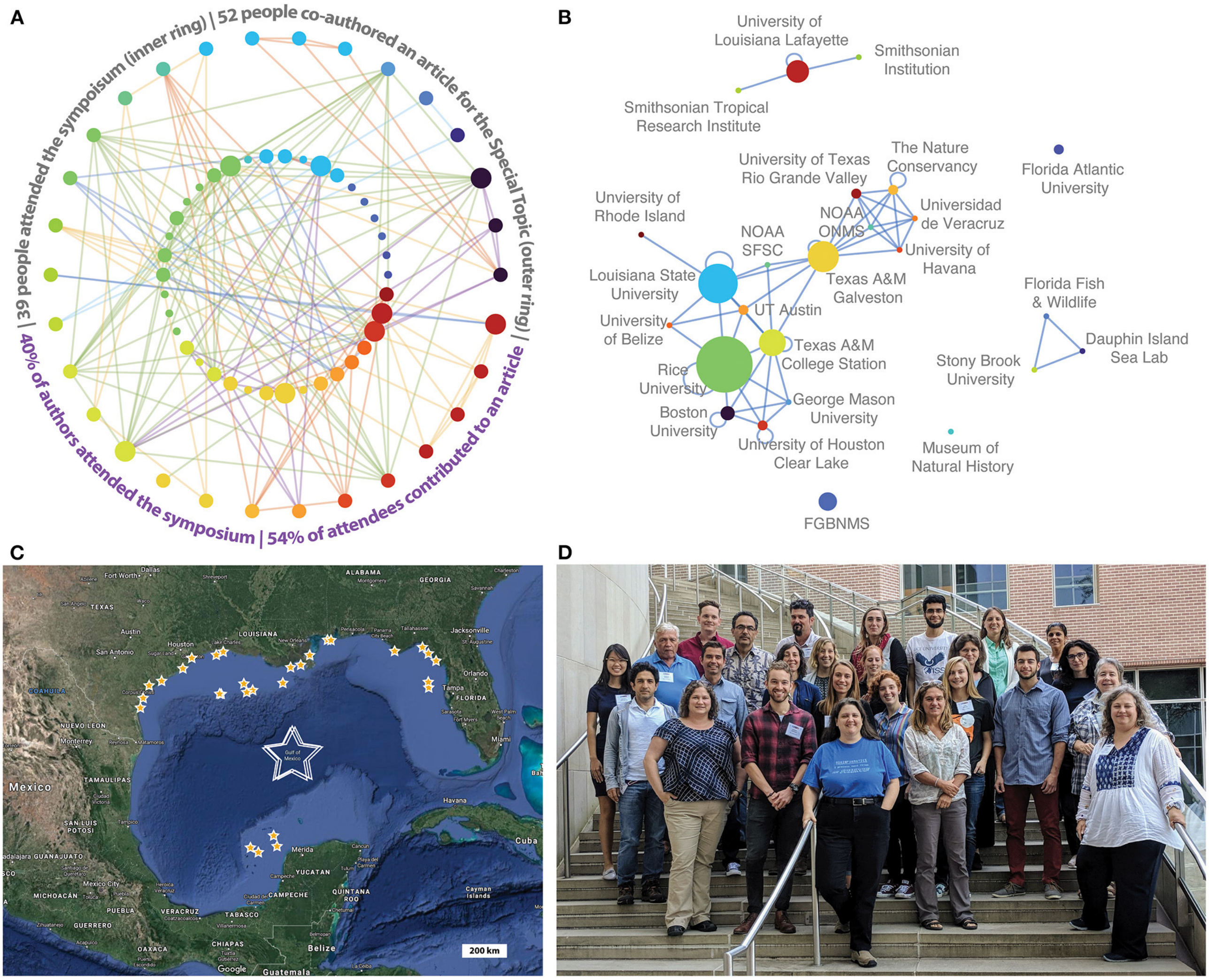

FIGURE 1 | Summary of individual and institutional collaborations in the "Gulf of Mexico (GoM) Reefs: Past, Present and Future" Special Topic. **(A)** Collaboration network in which nodes are individuals shaded by institutional affiliation (key in **B**). Node size scales with the number of papers authored in the Special Topic. Connecting lines depict paper collaborations in the Special Topic, and are shaded by manuscript. The inner circle of nodes are individuals who attended the GoM Reefs Symposium. **(B)** The same network, with collaborations accumulated by institution (same color scheme as **A**). This graph uses a force-directed layout. **(C)** Google Earth map depicting the Gulf of Mexico, indicating the study locations (filled stars) of papers in this Special Topic. The three open stars at the center of the GoM represent papers that span the entire gulf. **(D)** Subset of the participants attending the GoM Reefs Symposium held at Rice University (Houston, TX USA) on October 10-11, 2018.

results suggest rhodoliths are hotspots of biodiversity that potentially act as refugia following periods of environmental stress.

Oyster reefs act as important ecosystem engineers in GoM estuaries; La Peyre et al. summarize oyster-associated fish and decapod diversity and abundance in the northern GoM, with conservation and restoration implications. Schulze et al. discuss the community ecology of organisms that colonize fixed offshore platforms and equipment. These structures function as artificial reefs throughout a significant portion of the GoM but may also facilitate non-native invasions. This article highlights public health concerns and critical knowledge gaps related to the structure and function of these communities.

3. ANTHROPOGENIC DISTURBANCE

GoM reefs have experienced natural disturbances throughout geologic and modern history, with mounting recent anthropogenic pressures. As storm frequency and intensity increases due to climate change (Emanuel, 2017; Fagnant et al., 2020), understanding the associated impact on reef communities is critical. Wright et al. inferred that coastal flooding following 2017's Hurricane Harvey likely caused offshore reef organisms (>100 mi from the Texas coast) to experience sub-lethal physiological stress based on gene expression changes in corals and their symbiotic dinoflagellates. Shore et al. documented that two coastal flooding events impacted these reefs based on shifted sponge microbiota compositions, including detections of fecal coliforms. Together, these papers indicate that offshore ecosystems are not necessarily protected from extreme coastal flooding. The Deepwater Horizon (DWH) oil spill was another major perturbation that recently impacted GoM ecosystems; Venera-Ponton et al. highlight substantial shifts in the genetic populations of a GoM-wide macroalga, *Botryocladia occidentalis*, following the spill. Collectively these three studies highlight the need to establish molecular and/or microbial time series and baselines for what is "typical" in GoM ecosystems. Time series data can also support the characterization and mitigation of disturbance-driven changes to the health and functioning of GoM organisms, populations, communities, and ecosystems.

4. ECOSYSTEM FUTURES

The current status of GoM reefs, their interconnectedness, and conservation priorities are assessed in Gil-Agudelo et al. This article also summarizes the threats reefs experience from bleaching, disease, extreme storms and invasive species. Conservation opportunities such as international sanctuary agreements, funding, and private sector support are highlighted. In a complementary Opinion article, Furman et al. predict that extensive hard bottom habitats in the Big Bend region of Florida may support the development of coral reefs in the near future. Seasonal wind patterns and simulated drifter experiments further suggest this region may be seeded by a supply of diverse coral larvae; the extent to which such larvae are presently being delivered to the Big Bend Area is a critical gap in our understanding of potential range expansion. Therefore, Furman et al. advocate for augmented eastern GoM benthic monitoring programs. Frolova and Miglietta also consider how climate change might impact the distribution of organisms in a warmer GoM. They cultured two species of *Aurelia* jellyfish (one a newly identified species) and found that each is tolerant of different temperature and salinity ranges.

Successful long-term conservation and monitoring strategies require accurate predictions of how environments in the GoM will change and what this means for reefs in 50–100 years. Dee et al. assess the future of GoM reef ecosystems by combining reef occurrence data with climate projections from the RCP8.5 ensemble of the Community Earth System Model v1.2. Their findings highlight the threats of prolonged, elevated temperatures and ocean acidification to GoM reef persistence. Dee et al.'s predictions are contextualized with descriptions of ancient reefs from past analogue hyperthermal climate events. The future projections show that unless long-term conservation strategies are successful and anthropogenic emissions are dramatically reduced, GoM reefs are unlikely to survive the next century of climate change.

5. OPPORTUNITIES FOR FUTURE RESEARCH

This Special Topic brings together disparate fields and we hope it catalyzes future international and cross-disciplinary GoM research. Many GoM reef ecosystems require further characterization and exploration, the crucial foundation for associated conservation and restoration goals. Establishing microbial and molecular time series baseline datasets for key GoM reef-building organisms is critical for recognizing and mitigating natural and anthropogenic disturbance impacts, particularly given novel challenges to Caribbean reefs like stony coral tissue loss disease (e.g., Meiling et al., 2021). The increasing frequency and intensity of disturbances highlight the need for geographically broader and more comprehensive conservation and management strategies for GoM ecosystems. The expansion of the Flower Garden Banks National Marine Sanctuary has partially accomplished this, but without more rigorous study of ecosystem sensitivity and connectivity among the diverse reef and coastal ecosystems of the GoM, ecosystem-based management in the region remains a challenge. Finally, most contributions in this Special Topic focus on the northern Gulf of Mexico (**Figure 1C**), underscoring the need for greater international communication, cooperation, and collaboration among scientists across the GoM.

The 2018 Symposium highlighted the importance of bringing geologists, biologists, conservation experts, and managers together (**Figure 1D**). The meeting catalyzed the completion of projects and fostered new partnerships between researchers in different fields and from different institutions and countries (**Figures 1A,B**); many of these projects and papers would not have been initiated (or completed) without this meeting. We hope that Gulf of Mexico Reef Symposia will continue to be held regularly with broad participation from researchers spanning the gulf. Conferences such as these are particularly valuable networking opportunities for students, other early career scholars, and researchers new to the GoM region.

AUTHOR CONTRIBUTIONS

AC, RM, and DH wrote the manuscript and drafted the figure. All authors made a substantial, direct and intellectual contribution to the work, and have read, edited, and approved it for publication.

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frontiers in Marine Science

ORIGINAL RESEARCH
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Population Structure of the Red Macroalga *Botryocladia occidentalis* (Børgesen) Kylin (Rhodymeniaceae, Rhodymeniales) in the Gulf of Mexico Before the Deepwater Horizon Oil Spill

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Studies on the population structure of common widespread macroalgae in the Gulf of Mexico (GoMx) are scarce, and this knowledge gap limits our understanding on how disturbances affect the genetic diversity of macroalgae in this basin. The latter is due to the lack of a baseline that can be compared with allele frequency surveys conducted after a major disturbance such as the 2010 Deepwater Horizon oil spill (DWH), which leaked 780,000 m^3 of crude oil in the vicinity of highly diverse macroalgal communities. Fortunately, quantitative assessments of the population structure pre-DWH can be accomplished for several macroalgae with dried specimens collected from research cruises conducted before 2010 in the offshore GoMx. Based on three markers (cytochrome c oxidase subunit I, COX II-III intergenic spacer, and the RuBisCO large subunit), this study reconstructed the allele frequencies pre-DWH for a GoMx-widespread macroalga, *Botryocladia occidentalis*, and revealed the existence of distinct populations in each of three distant regions of the GoMx: Florida Middle Grounds (FL), Campeche Banks (CB), and offshore Louisiana (LA). Population structure was assessed with exact tests of population differentiation and Analyses of Molecular Variance. FL harbored the most differentiated and genetically diverse population due to the presence and abundance of unique haplotypes. Interestingly, FL haplotypes were not closely phylogenetically related to each other and included the most divergent lineages of the entire GoMx; this phylogeographic pattern suggests a strong influence of migrants from the Caribbean on the FL population. Additionally, likelihood ratio tests with a small sample collected post-DWH indicated that the LA population underwent strong changes, showing statistically significant differences before (LA) vs. after (L2) the disaster. Whereas the LA population had affinity to CB, L2 showed a FL haplotype

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that, before the disaster, had never been reported in LA or CB. Such changes may not be permanent but rather a temporary response to disturbance; also, they may not necessarily be caused by the spilled oil but by other factors associated with the DWH.

Keywords: Macondo oil spill, genetic diversity, mesophotic, seaweeds, population genetics, molecular ecology, offshore Louisiana

INTRODUCTION

Researching the population structure of marine macroalgae is a challenging endeavor because many species are nearly indistinguishable from each other morphologically and, thus, are virtually impossible to identify *in situ* (e.g., Krayesky et al., 2009; Balata et al., 2011). Since population genetics studies normally require the collection of numerous conspecific individuals for each location of interest (Nei, 1978; Baverstock and Moritz, 1996; Ruzzante, 1998; Excoffier, 2007), population samples of macroalgae are often found to be multispecies mixtures from which multiple individuals must be discarded, reducing sample sizes. This is especially true for highly biodiverse metacommunities like the offshore hard banks of the Gulf of Mexico (GoMx) (Felder and Camp, 2009) which harbor nearly 700 species and over 70 families as recorded in the most recent review of GoMx macroalgae (Fredericq et al., 2009).

Despite this problem, researching the population structure of marine macroalgae is highly valuable due to their economic and ecological importance. For instance, macroalgae provide food and shelter for numerous marine animals, including invertebrates and fishes of economic interest, at different stages of their life (e.g., larvae, juveniles, and adults) (Chemello and Milazzo, 2002; Epifanio et al., 2003; Hasan and Chakrabarti, 2009; Thomsen, 2010; Vergés et al., 2012; Chaves et al., 2013; Milne and Griffiths, 2014; Shaal et al., 2016). Some macroalgae also contribute largely to the building of reef structures that shelter not only a few species but whole ecosystems (Littler and Littler, 1984; Adey, 1998; Hurd et al., 2014). Therefore, changes in the dominant macroalgal populations of marine ecosystems can impact their associated animal communities as well as the human activities (e.g., fishing). Communities largely dominated by marine macroalgae such as the offshore hard banks of the GoMx (e.g., Gavio and Fredericq, 2003, 2005; Gurgel et al., 2004a; Gavio et al., 2005; Mateo-Cid et al., 2013; Arakaki et al., 2014; Fredericq et al., 2014; Richards et al., 2014, 2016; Schmidt et al., 2016, 2017; Leliaert et al., 2016; Camacho et al., 2018; Richards and Fredericq, 2018), may greatly benefit from studies on the population structure of their most common and widespread macroalgal species.

Unfortunately, few studies have been done on the population structure of dominant macroalgae in the GoMx and this knowledge gap limits our understanding of the impacts of human and natural disturbances in this marine basin. For instance, there is no baseline that can be compared with allele frequency surveys performed after a disturbance event. In April 2010, the NW GoMx was affected by the Deepwater Horizon oil spill (DWH) (Felder et al., 2014), regarded as the largest accidental marine oil spill in U.S. territories (Atlas and Hazen, 2011; Liu et al., 2011; Barron, 2012; Paris et al., 2012; Rabalais, 2014; Beyer et al., 2016). This disaster lasted 87 days, during which 780,000 m^3 of crude oil were leaked in the GoMx along with 7,000 m^3 of Corexit oil dispersant (Lehr et al., 2010; OSAT, 2010, 2011; Kujawinski et al., 2011). Since the typical genetic diversity and population structure of the dominant GoMx macroalgae were unknown, evaluating the impact of the DWH disaster on macroalgal populations has been unfeasible. There are a few studies (e.g., Gurgel et al., 2004b; Núñez-Resendiz et al., 2017) examining the phylogeography of particular GoMx species using non-quantitative approaches; one study (Gurgel et al., 2004b) showed the presence of two haplotype lineages characteristic of the eastern and western GoMx. Quantitative assessments of the population structure before the DWH can be accomplished for several macroalgae with specimens from research cruises conducted prior to 2010 in the offshore GoMx. Most of these specimens are deposited in the University of Louisiana at Lafayette Herbarium (LAF).

This study reconstructed the allele frequencies before the DWH for a common widespread deepwater red alga in the GoMx, *Botryocladia occidentalis* (Børgesen) Kylin (Gavio and Fredericq, 2003; Fredericq et al., 2009; **Figure 1**), and evaluated its population structure and phylogeography across three distant regions of the GoMx. The main goal of the study was to determine whether the *B. occidentalis* population exposed to the DWH is distinct or belongs to a larger uniform population widespread throughout the GoMx. Additionally, as a secondary analysis, this study evaluated a small sample collected post-DWH for changes in population structure that may be associated with the disaster.

Finally, this study also compared the efficacy of three genetic markers in elucidating the genetic structure of *B. occidentalis*. The value of the mitochondrial cytochrome c oxidase subunit I (*Cox1*) and the COX II-III intergenic spacer region (*Cox2-3*) for evaluating population structure and intraspecific genetic diversity in red macroalgae has been validated in multiple studies (e.g., Zuccarello et al., 1999, 2005, 2006; Yang et al., 2008; Kim et al., 2010, 2012; Hernández-Kantún et al., 2014), whereas the plastid-encoded RuBisCO large subunit (*rbc*L) is generally regarded as a slow-evolving gene with poor resolution at the intra-species level (Yang et al., 2008; Geraldino et al., 2009; Tan et al., 2012). With that said, there are a number of cases in which *Cox2-3* has failed to detect important intraspecific variation detected by other markers (e.g., O'Doherty and Sherwood, 2007), and also, there are specific studies in which *rbc*L has effectively elucidated phylogeographic patterns of Rhodophyta species. One important example for the Western Atlantic and GoMx was studied by Gurgel et al. (2004b) who found 10 haplotypes for *Gracilaria*

FIGURE 1 | Herbarium specimen of *Botryocladia occidentalis* (scale bar: 2 cm) collected in the Florida Middle Grounds (28° 5.20′ N, 83° 46.16′ W) during the research cruise NSFIII (collect date: July 05, 2006) of the University of Louisiana at Lafayette (LAF) Seaweeds Lab. This specimen, referenced NSFIII-7-5-06-8-2 in the LAF Herbarium, is part of the biological material used in this study.

tikvahiae spread in four lineages, including two associated with the Western and Eastern GoMx, respectively. As a final point, *Cox1* has been a reliable marker for red macroalgae (Geraldino et al., 2009; Kim et al., 2010, 2012).

MATERIALS AND METHODS

Study Area

The population structure of *Botryocladia occidentalis* in the GoMx was inferred from DNA samples of 131 individuals collected during multiple research cruises between 2000 and 2008 (**Table 1**). The specimens were collected from offshore banks in three geographically distant regions (Felder and Camp, 2009): (1) offshore Louisiana in the NW Gulf comprising a system of hard banks, including salt domes (Rezak et al., 1985); (2) Florida Middle Grounds in the NE Gulf, a system of vermetid reefs formed by discontinuous limestone outcroppings that extend along the West Florida Shelf and are covered with shells, rocks, and corals (Cheney and Dyer, 1974; Reich et al., 2013); and the Campeche Banks, Mexico, in the SW Gulf, a system of tropical biogenic reefs raised in the Southern GoMx from a submerged limestone plateau (the Yucatan Shelf) with virtually no sedimentation from land runoff (Liddell, 2007; Mateo-Cid et al., 2013; **Figure 2**). These regions are ∼650 km away from each other and include most of the offshore banks and reefs surveyed across the GoMx (Fredericq et al., 2009).

Sample Selection and DNA Extraction

Thirty-eight to fifty-one individuals were sequenced for each region, totaling 131 individuals. Three *B. occidentalis* specimens collected from offshore Louisiana during August 2012 were also available in the University of Louisiana at Lafayette Herbarium (LAF) but they were assigned to a different group (L2) in the population structure analyses since they came from a community exposed to the 2010 DWH (Ewing Bank, see Fredericq et al., 2014; Venera-Pontón et al., 2019) and may not represent the typical population structure of offshore Louisiana. These three individuals were the only *B. occidentalis* specimens collected during seven post-DWH research cruises conducted between 2010 and 2014 (personal observation during field trips by Venera-Pontón et al., 2019)

TABLE 1 | Collection information of *Botryocladia occidentalis* individuals (Inds) used in this study.

Collection date	Region	Location	Coordinates	Depth	Inds
May 2000	LA	Bouma Bank	28° 3.40′ N, 92° 27.35′ W	63.27	17
August 2000	FL	Middle Grounds	28° 12.40′ N, 84° 4.67′ W	43.31	1
June 2001	LA	Ewing Bank	28° 8.06′ N, 90° 54.63′ W	63.03	7
	LA	Bouma Bank	28° 3.40′ N, 92° 27.35′ W	63.27	2
	CA	Cayo Arenas*	22° 11.28′ N, 90° 58.41′ W	48.00	28
June 2005	CA	S.Arenas*	21° 36.46′ N, 91° 1.67′ W	32.56	6
	CA	Pera Bank	20° 40.94′ N, 91° 55.54′ W	26.2	2
	CA	Triangulos Reefs	21° 1.87′ N, 92° 11.86′ W	49.49	5
July 2006	FL	Middle Grounds	28° 12.40′ N, 84° 4.67′ W	43.31	51
August 2008	LA	Bouma Bank	28° 3.40′ N, 92° 27.35′ W	63.27	4
	LA	Parker Bank	27° 57.13′ N, 92° 1.26′ W	63.36	8
August 2012	LA	Ewing Bank	28° 8.06′ N, 90° 54.63′ W	63.03	3

Only the specimens collected before 2010 were used for analyses of population structure. Asterisks indicate that the specimens were not necessarily collected in the named location but in its vicinity. Depths are given in meters.

despite their sampling effort (number of dredges launched) was comparable to other sampling campaigns conducted pre-DWH (see Venera-Pontón et al., 2019). These observations suggest a strong decrease in the *B. occidentalis* abundance offshore Louisiana post-DWH.

DNA samples were extracted from dried specimens of *B. occidentalis* in the University of Louisiana at Lafayette Herbarium (LAF). Specimens were selected with help of collection notes to prevent the DNA sequencing of individuals that were collected together in a same dredge; nevertheless, due to the limited number of specimens, this was not always feasible. DNA extractions followed a modified version of the protocol by Dellaporta et al. (1983). A ∼20 mg sample from each individual was ground to a fine powder with mortar and pestle, and treated with 700 μl of extraction buffer [100 mM Tris (pH 8.0), 50 mM EDTA, 500 mM NaCl, 10 mM 2-Mercaptoethanol], 50 μl of 20% SDS, 10 μl of 0.1 M DTT, and 4 mg of Proteinase K. During this treatment, the samples were incubated overnight at 65°C. To remove polysaccharides, samples were treated with 250 μl of potassium acetate (5 M), incubated on ice during 30 min., and centrifuged at 12,000 g for 30 min. 750 μl of supernatant were then mixed with 750 μl of chloroform and centrifuged at 12,000 g for 15 min, afterward, the supernatant was mixed again with an equal volume of chloroform and centrifuged for 15 min. again. The latter procedure was repeated once more and then, to precipitate the DNA, the supernatant was treated with isopropanol (two-thirds of the supernatant volume), incubated at −20°C overnight, and centrifuged the next day at 12,000 g for 30 min. Afterward, the pellet (which contains the precipitated DNA) was washed twice with 500 μl of 70% ethanol, dried in a Speed-Vac, re-suspended in 50 μl of elution buffer (10 mM Tris-Cl, pH 8.5), and stored at −20°C (Dellaporta et al., 1983).

DNA Sequencing and Data Analyses

Three polymorphic regions were PCR-amplified from each DNA sample using the Mango-*Taq* DNA Polymerase Kit (BioLine, Taunton, MA, United States): the RuBisCO large subunit (*rbc*L, Gurgel et al., 2004a,b; Yang et al., 2008), cytochrome c oxidase subunit I (Cox1, Saunders, 2005; Sherwood et al., 2010), and the COX II-III intergenic spacer region (*Cox2-3*, Zuccarello et al., 1999). *Cox1* and *Cox2-3* are mitochondrial while *rbc*L is a chloroplast gene; all of them, except *Cox2-3*, are protein-coding regions. The primers and PCR conditions associated with each marker are described in **Table 2**. Preliminary analyses of *rbc*L sequences in the first 27 *B. occidentalis* individuals found three polymorphic sites in a region of ∼500 bp between the F57 and R577 primers, whereas no polymorphic sites were found outside this region. Consequently, *rbc*L amplifications of the remaining individuals only included the polymorphic region. PCR products were sequenced using the BigDye Terminator v3.1 Cycle Kit (Thermo Fisher Scientific, Grand Island, NY, United States). DNA sequences were aligned with CLUSTALX2 and used to define haplotypes (alleles) as well as their frequencies.

The best model of sequence evolution based on the Bayesian and Akaike information criteria (Posada and Buckley, 2004) and Maximum Likelihood (ML) phylogeny were inferred for each gene using MrAIC (Nylander, 2004) and MEGA6 (Tamura et al., 2013). Moreover, to determine whether each region represents a different sub-population or is part of a uniform meta-population, the allele frequencies and sequence divergences were compared among regions with exact tests of population differentiation (Raymond and Rousset, 1995) and Analyses of Molecular Variance (AMOVA; Excoffier et al., 1992) using Arlequin 3.5 (Excoffier et al., 2005). The AMOVA considers both the frequency and sequence divergence of alleles (Φst), while the exact test index is solely based on allele frequencies (Fst) (Balding et al., 2007). The latter used a 100,000 steps Markov Chain and 10,000 dememorization steps. The gene diversity (Nei) of each region was measured as the probability of obtaining different haplotypes in two randomly drawn individuals, i.e., heterozygosity (Balding et al., 2007).

The phylogeographic relationships of the alleles were evaluated with haplotype networks using Haplotype Viewer (Center for Integrative Bioinformatics Vienna[1]) which combines

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[1] http://www.cibiv.at/

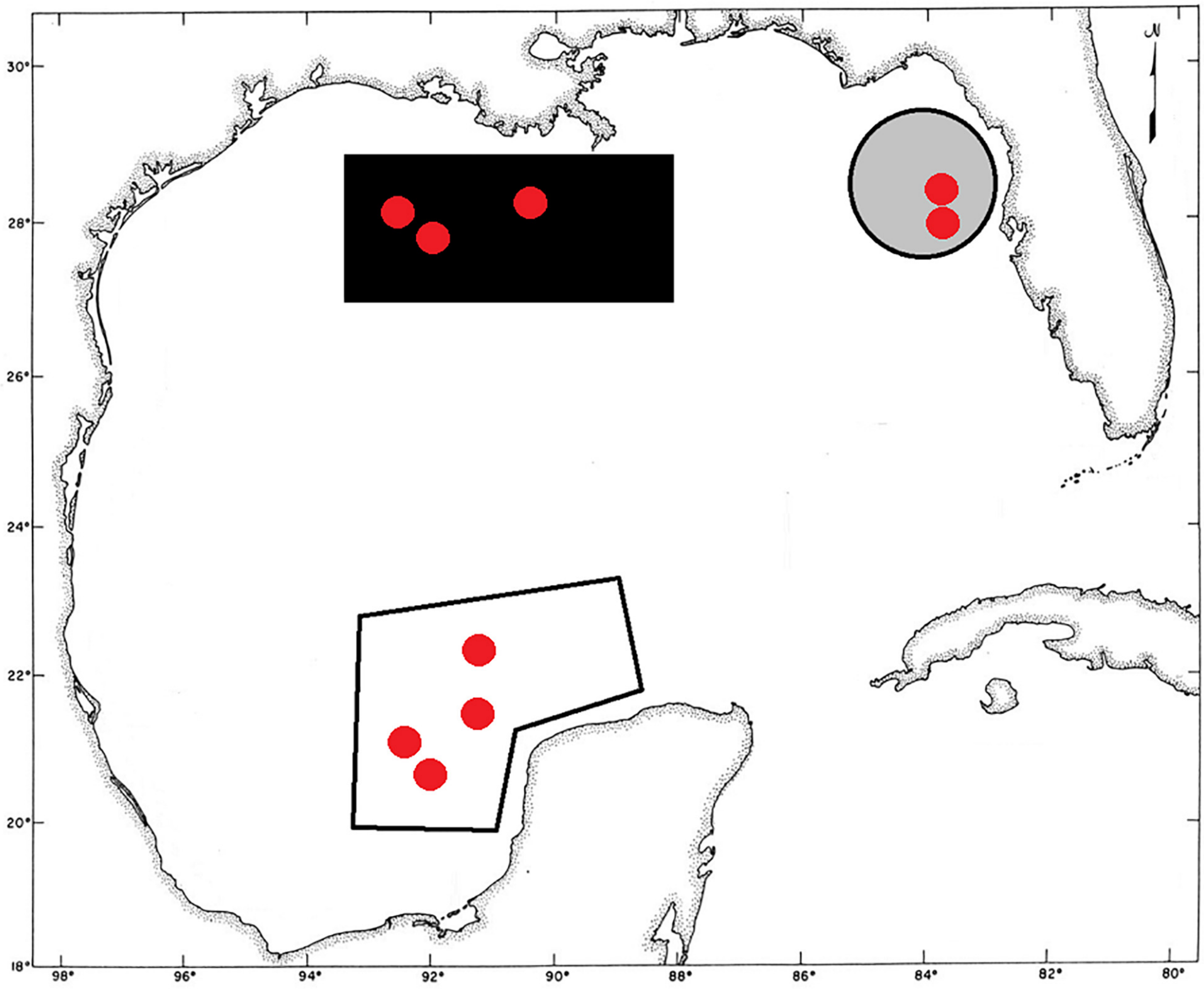

FIGURE 2 | Map of the Gulf of Mexico (GoMx) indicating the three regions evaluated in this study which include most of the offshore banks and reefs surveyed across the basin. The southernmost region (white) corresponds to the Campeche Banks; the easternmost region corresponds to the Florida Middle Grounds (gray); and the NW region (black) corresponds to the offshore banks of Louisiana (black). The collection sites are presented as red points. The coordinate grid shows the position for even degrees of longitude and latitude; two degrees of longitude cover a distance of ~201.5 km at the GoMx latitudes.

their micro-evolutionary history (ML phylogeny) with their regional frequencies. The statistical genetics analyses were separately performed on individual gene sequences as well as on the multigene alleles resulting from concatenating individual genes into single sequences. The distance between multigene haplotypes considered the best model of sequence evolution for each gene as well as the single model that best applied to every region (HKY); both approaches produced the same results and thus only one is presented.

To evaluate potential changes in population structure associated with the 2010 DWH, three individuals collected from Ewing Bank post-DWH were compared with specimens collected pre-DWH in offshore Louisiana using Likelihood Ratio tests (Hernández and Weir, 1989; Weir, 1992a,b) that included the three genes (multi-loci). This test was also applied to evaluate affinities between individuals collected from Louisiana post-DWH (L2) and other GoMx regions.

RESULTS

Among the three genes evaluated, cytochrome c oxidase subunit I (*Cox1*) showed the highest intraspecific variability for *Botryocladia occidentalis* in the GoMx, with eight polymorphic sites and five haplotypes. Conversely, the COX II-III intergenic spacer region (*Cox2-3*) and the RuBisCO large subunit (*rbc*L) each showed three haplotypes based on two polymorphic sites. When individual genes were concatenated into multigene sequences, the number of haplotypes increased to 11, based on a total of 12 polymorphic sites. Details on the gene haplotypes and their geographical distribution in the GoMx regions are provided in **Table 3**.

All the genes supported the existence of two or more *B. occidentalis* populations in the GoMx (**Table 4**). All three genes supported the existence of a unique population in the Florida Middle Grounds (FL) that was greatly differentiated from the rest

TABLE 2 | Conditions and primers of the Polymerase Chain Reactions (PCRs) associated with each gene.

Gene	*Rbc*L	*Cox1*	*Cox2-3*
Forward	5′-GTAATTCCATATGCTAAAATGGG -3′	5′-TCAACAAATCATAAAGATATTGG -3′	5′- GTACCWTCTTTDRGRRKDAAATGTGATGC -3′
Reverse	5′- CCACCTTTTAGACCTTCATATAC -3′	5′- CCACCWGMAGGATCAA -3′	5′- GGATCTACWAGATGRAAWGGATGTC -3′
Cycle types	2	1	2
Denaturation0	95°C, 3 min	94°C, 4 min	94°C, 4 min
Denaturation1	95°C, 1 min	94°C, 1 min	93°C, 1 min
Annealing1	40°C, 1 min	45°C, 1 min	45°C, 1 min
Elongation1	72°C, 2 min	72°C, 1 min	72°C, 1 min
Cycles1	2	40	5
Denaturation2	95°C, 1 min	–	93°C, 30 s
Annealing2	42°C, 1 min	–	55°C, 30 s
Elongation2	72°C, 2 min	–	72°C, 30 s
Cycles2	40	–	30
ElongationF	72°C, 7 min	72°C, 6 min	72°C, 5 min
Hold	4°C	4°C	4°C
References	Hommersand et al., 1994	Saunders, 2005; Sherwood et al., 2010	Zuccarello et al., 1999

RbcL, RuBisCO large subunit; Cox1, cytochrome c oxidase subunit I; Cox2-3, COX II-III intergenic spacer region. Some PCR reactions had two types of cycles with different conditions. The conditions of each cycle type are succeeded with the numbers 1 or 2. Likewise, the conditions of steps performed before the first and last cycle are succeeded with 0 and F, respectively.

of the GoMx (*rbc*L Fst > 0.15; *Cox1* and *Cox2-3* Fst > 0.25). *Cox1* and the multigene haplotypes supported the existence of distinct, highly differentiated populations (Fst > 0.25) in Campeche Banks (CB) and offshore Louisiana (LA) (**Table 4**).

Three individuals collected after the DWH from offshore Louisiana (L2) showed statistically significant differences with individuals collected before the DWH in the same region (LA) (**Table 4**). For every gene, the three L2 individuals shared the same haplotype, which was typically absent in CB and LA but common in FL individuals (**Table 3**). The only exception to this pattern was *rbc*L, whose L2 haplotype was common across all the GoMx and thus did not show differences between L2 and any GoMx region. Nonetheless, *rbc*L showed statistically significant differences between FL and all the groups except L2. The affinity between FL and L2 was further supported by the Likelihood Ratio tests, which showed a *P*-value of 0.1563 for FL vs. L2 and a *P*-value < 0.001 for LA vs. L2.

Amongst all the GoMx regions, FL showed the largest gene diversity, regardless of the gene evaluated (**Table 5**). LA showed the second largest gene diversity with *Cox1* and multigene sequences but presented a single haplotype (gene diversity = 0) with *Cox2-3* and *rbc*L, respectively. Interestingly, CB showed more haplotypes than LA in all the genes but its gene diversity was low due to extreme unevenness in its haplotype frequencies. *Rbc*L and *Cox2-3* showed an equal number of haplotypes in FL and CB whereas *Cox1* and multigene sequences showed more haplotypes in FL, followed by CB; finally, LA showed the lowest number of haplotypes in all the evaluated genes. All the LA haplotypes were present in other GoMx regions whereas some haplotypes from FL and CB were restricted to one region, especially FL before the DWH. Remarkably, none of the six multigene haplotypes of FL were found elsewhere in the GoMx before the DWH (**Table 3** and **Figure 3**).

The haplotype networks of *rbc*L and *Cox2-3* (**Figure 3**) consisted of simple schemes in which rarer haplotypes, restricted to one region (FL and CB, respectively), are connected to each other, phylogenetically, only by their relationship to the dominant haplotype of the entire GoMx. Conversely, the *Cox1* network showed a more complex pattern with two main groups of phylogenetically connected haplotypes: the first group included haplotypes widespread in the entire GoMx and a rare haplotype from CB; the second group included two closely related haplotypes from FL that were relatively genetically divergent from the other group. Finally, the multigene scheme showed that all haplotypes from CB and LA are closely phylogenetically related and appear in the center of the network; the FL haplotypes, on the other hand, came from three separate lineages and include the most divergent alleles of the entire GoMx, which appear in the extremes of the network. Only one FL haplotype was closely related to alleles from LA and CB.

DISCUSSION

Effectiveness of the Genetic Markers

The results of this study further confirm that *Cox1* is an effective marker for evaluating population structure and intraspecific genetic diversity in red macroalgae (see Yang et al., 2008; Kim et al., 2010, 2012). The second most effective marker was *Cox2-3* which did not separate CB and LA into distinct populations but otherwise showed the same results as *Cox1*. On the other hand, *rbc*L only detected the most extreme cases of population differentiation (i.e., FL vs. LA and FL vs. CB). Despite their lower effectiveness, using *Cox2-3* and *rbc*L in the multigene sequences was essential to reveal the divergent origins of FL haplotypes, which was not clearly

TABLE 3 | Haplotypes of *Botryocladia occidentalis* and their regional distribution in the Gulf of Mexico.

Gene	Haplotype	Distribution	GenBank accession #
*Rbc*L	TC	FL	MH521039
	TT	CB, FL, LA, L2	MH521040
	CT	CB	MH521041
Cox2-3	TT	FL, L2	MH537602
	TC	CB, FL, LA	MH537600
	AC	CB	MH537601
Cox1	AGTGAGCT	CB, FL, LA	MH521034
	AGTGAGTT	CB	MH521035
	GGTGAGTT	CB, FL, LA	MH521036
	GACGGATC	FL, L2	MH521037
	GACAGATC	FL	MH521038
Multigene	TC,AGTGAGCT,TT	FL	–
	TT,AGTGAGCT,TC	CB, LA	–
	TT,AGTGAGTT,TC	CB	–
	TT,AGTGAGCT,TT	FL	–
	TT,GGTGAGTT,AC	CB	–
	TC,AGTGAGCT,TC	FL	–
	CT,GGTGAGTT,TC	CB	–
	TT,GGTGAGTT,TC	CB, LA	–
	TC,GGTGAGTT,TC	FL	–
	TT,GACGGATC,TT	FL, L2	–
	TT,GACAGATC,TT	FL	–

Haplotypes are labeled with their sequence of nucleotides at each polymorphic site. CB, Campeche Banks; LA, offshore Louisiana before the Deepwater Horizon Oil Spill (DWH); L2, offshore Louisiana after the DWH; FL, Florida Middle Grounds. GenBank (GB) Accession numbers are provided for the haplotypes of each gene. RbcL, RuBisCO large subunit; Cox1, cytochrome c oxidase subunit I; Cox2-3, the COX II-III intergenic spacer region; multigene, concatenation of the three genes into a single organellar sequence.

TABLE 4 | Population differentiation of *Botryocladia occidentalis* in three distant regions of the Gulf of Mexico and before vs. after the Deepwater Horizon Oil Spill (DWH).

	Rbc*L: Global Fst = 0.22				***Cox1*: Global Fst = 0.48***		
	CB	**LA**	**L2**		**CB**	**LA**	**L2**
CB	0.00			CB	0.00		
LA	0.00	0.00		LA	0.44*	0.00	
L2	−0.20	0.00	0.00	L2	0.95*	0.85*	0.00
FL	0.22*	0.23*	0.02	FL	0.49*	0.39*	0.17
	Cox2-3*: Global Fst = 0.71				**Multigene: Global Fst = 0.49***		
	CB	**LA**	**L2**		**CB**	**LA**	**L2**
CB	0.00			CB	0.00		
LA	0.00	0.00		LA	0.42*	0.00	
L2	0.96*	1.00*	0.00	L2	0.94*	0.87*	0.00
FL	0.70*	0.71*	0.00	FL	0.50*	0.43*	0.14

CB, Campeche Banks; LA, offshore Louisiana before the Deepwater Horizon Oil Spill (DWH); L2, offshore Louisiana after the DWH; FL, Florida Middle Grounds. Each sub-table is based on different genes: the RuBisCO large subunit (rbcL; top-left), cytochrome c oxidase subunit I (Cox1; top-right), the COX II-III intergenic spacer region (Cox2-3; bottom-left) or the three genes concatenated in a single organellar sequence (multigene; bottom-right). The numbers in the sub-tables correspond to the Fixation Indices (Φst) while asterisks indicate that the population differences are statistically significant ($P < 0.05$) in both the Analysis of Molecular Variance and the Exact Test. Fixation indices were interpreted as follows: ≤0: no differences, >0: little differences, >0.05: moderate, >0.15: great, >0.25 very great.

TABLE 5 | Gene diversity (Nei) of *Botryocladia occidentalis* in three distant regions in the Gulf of Mexico, measured as the probability of obtaining different haplotypes in two randomly drawn individuals (heterozygosity).

Gene	CB	LA	L2	FL
*Rbc*L	0.0488 (0.05)	0.0000 (0.00)	0.0000 (0.00)	0.4063 (0.06)
Cox2-3	0.0488 (0.05)	0.0000 (0.00)	0.0000 (0.00)	0.3875 (0.06)
Cox1	0.2244 (0.08)	0.4780 (0.04)	0.0000 (0.00)	0.5388 (0.03)
Multigene	0.2305 (0.09)	0.4780 (0.04)	0.0000 (0.00)	0.6298 (0.05)

The standard deviation is presented within parentheses. CB, Campeche Banks; LA, offshore Louisiana prior to the Deepwater Horizon Oil Spill (DWH); L2, offshore Louisiana after the DWH; FL, Florida Middle Grounds; RbcL, RuBisCO large subunit; Cox1, cytochrome c oxidase subunit I; Cox2-3, the COX II-III intergenic spacer region; multigene, concatenation of the three genes into a single organellar sequence.

evident with *Cox1* alone. The single-gene approaches found 3–5 haplotypes, depending on the marker, whereas the multigene approach found 11, including six FL haplotypes distributed in three separate lineages with the most divergent alleles of the entire GoMx. The latter was not clearly evident with single-gene approaches, highlighting once more the advantages of a multigene approach.

Population Structure of *Botryocladia occidentalis* in the Gulf of Mexico

Both the analyses of molecular variance (AMOVAs) and exact tests of population differentiation supported the existence of distinct populations in each of the regions evaluated. The Florida Middle Ground (FL) harbored the most divergent population of the GoMx which was identified even with the less polymorphic genes (*rbc*L and *Cox2-3*); conversely, individuals from Campeche Banks (CB) and offshore Louisiana (LA) were more closely related and only the most polymorphic gene (*Cox1*) and the multigene haplotypes were able to identify them as separated populations. The affinity between LA and CB was due to the fact that, regardless of the gene, all the LA haplotypes occur in CB too and are closely phylogenetically related to every CB haplotype. The latter is clearly evident in the multigene and *Cox1* networks which shows CB and LA haplotypes closely and continuously connected toward the center of the plot. Conversely, the population differences between LA and CB are likely due to significant disparities in their allele frequencies.

By contrast, the population divergence of FL, from CB and LA, was due to the presence and relatively high frequencies of unique haplotypes in this region. FL haplotypes are not closely phylogenetically related to each other but instead are spread in the three most divergent lineages of the *Cox1* and multigene network. Only one of the FL haplotypes was closely related to LA and CB alleles. This phylogeographic pattern may indicate a strong influence of migrants from outside the GoMx on the FL population. Those migrants would bring haplotypes that considerably diverge from local alleles as well as from each

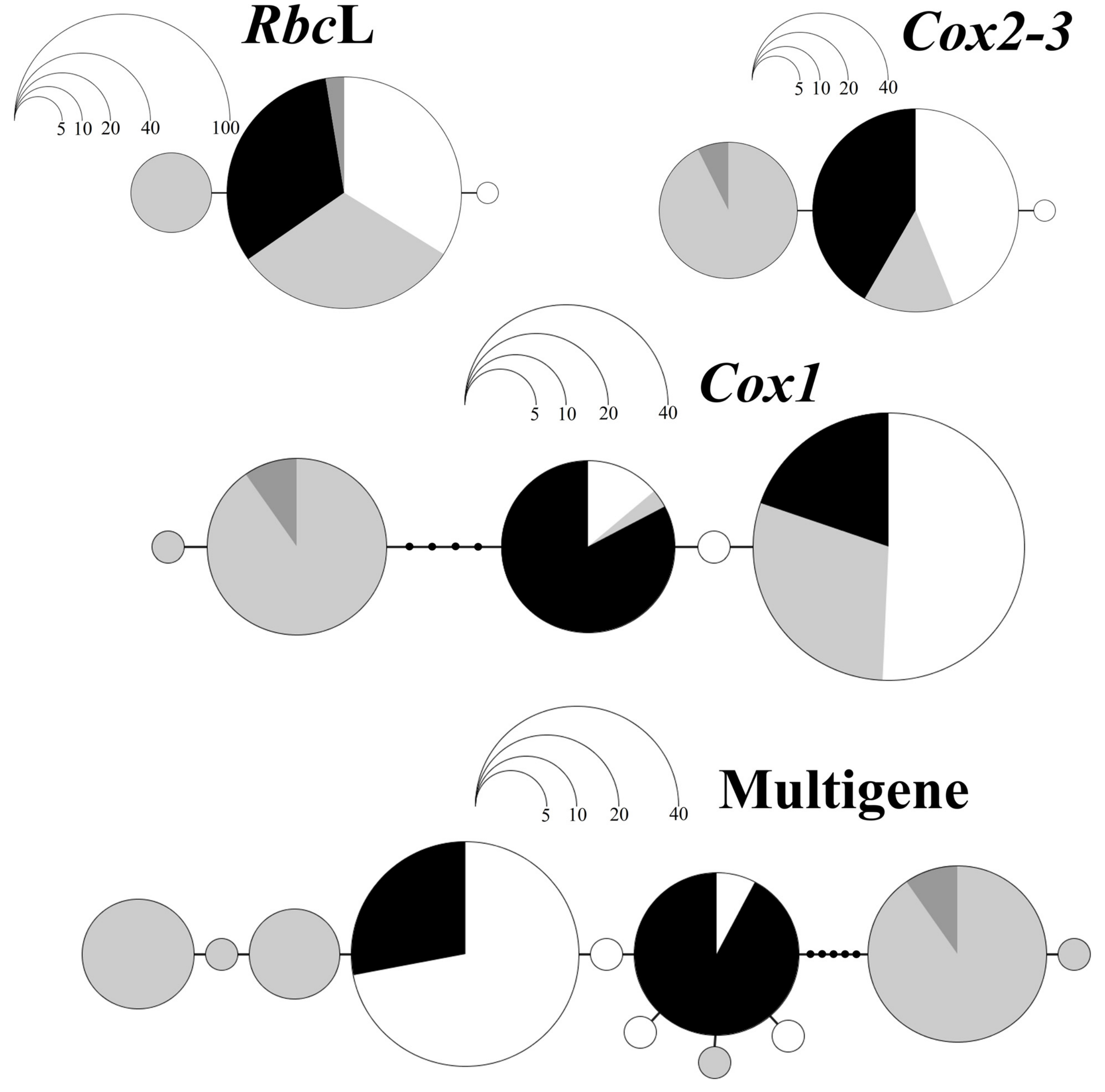

FIGURE 3 | Haplotype Networks of *Botryocladia occidentalis* in three regions of the Gulf of Mexico. CB, Campeche Banks (white); LA, offshore Louisiana before the Deepwater Horizon Oil Spill (DWH; black); L2, offshore Louisiana after the DWH (dark-gray); FL, Florida Middle Grounds (light-gray). The networks are based on different genes: the RuBisCO large subunit (*rbc*L), the COX II-III intergenic spacer region (*Cox2-3*), cytochrome c oxidase subunit I (*Cox1*), or the three genes combined. Each circle represents an allele while their size indicate their abundance in number of individuals. The position of alleles in the diagram reflects their ML phylogeny: closely related alleles are next to each other while more divergent alleles are farther. The genetic divergence was calculated with the T92 model, except in the multigene network, which used the HKY model.

other. Conversely, the populations of CB and LA, represented by local haplotypes, would show the lowest divergence and more phylogenetic relatedness among alleles. Interestingly, the occurrence and relatively high frequencies of unique haplotypes in FL has been also observed in other organisms with planktonic dispersal such as corals (Studivan and Voss, 2018); in their study, one FL population (Pulley Ridge) was identified as a potential sink population with an alternate source population not shared by the other GoMx sites.

It is possible that FL haplotypes occur in other GoMx regions in their early life-stages (e.g., propagules) but are excluded from the substratum by regionally local haplotypes (intraspecific competition) and so their adults would not typically occur in the benthos. This is consistent with previously reported observations at the species level (not haplotypes) by Fredericq et al. (2014, 2019), Sauvage et al. (2016), and Krayesky-Self et al. (2017), who demonstrated the presence of early-life stages (e.g., propagules) inside the interior of rhodoliths of LA for macroalgal species whose adult stages (e.g., sporophytes) had never been reported in the *in situ* benthos. It is possible that under certain environmental conditions, propagules of FL haplotypes can succeed and reach "adulthood" in other GoMx regions.

The above hypothesis does not necessarily assume that CB and LA haplotypes have higher competitive abilities than FL alleles. CB and LA haplotypes may outcompete FL alleles, locally, simply by outnumbering them so that their frequency remains too low to be detected with the relatively small sample sizes of this study; the same may occur in FL if haplotypes from CB and LA are outnumbered by migrant haplotypes. Such pattern of haplotype disparities appears consistent with the activity of three important oceanographic forces: (1) the Louisiana Coastal Current (Wiseman et al., 2004; Jarosz and Murray, 2005), (2) the GoMx Loop (Sturges and Leben, 2000; Oey et al., 2005), and the Westward Yucatan Current (Martínez-López and Parés-Sierra, 1998; Ochoa et al., 2001).

The Louisiana Coastal Current (LCC) flows westwards from the Mississippi mouth toward Texas and Mexico but away from the Florida Continental Shelf (Wiseman et al., 2004; Jarosz and Murray, 2005) and has the potential to reduce the movement of propagules from LA to FL. Moreover, the LCC may be a key step in the flow of propagules (and their haplotypes) from LA toward CA. Conversely, the GoMx Loop flows northwards from the Yucatan Channel, moving most of the inflow from the Caribbean toward the Florida Continental Shelf and then loops east and south to finally leave the GoMx via the Florida straits. The GoMx loop is the strongest surface current of the NE Gulf and has the potential of moving a vast number of migrant propagules (with their haplotypes) from the Caribbean toward FL. Then, a relatively lower inflow of propagules from LA and CB would facilitate the dominance of migrant haplotypes in FL.

The Yucatan current, where the GoMx Loop originates, has a portion that flows westwards toward CB and loops northwards alongside the Mexican and US Gulf coasts. This current has the potential of moving migrant propagules to other regions of the GoMx where, unlike in FL, may be outcompeted by local haplotypes. Eddies originating from the GoMx Loop (Sturges and Leben, 2000; Oey et al., 2005) can also move FL haplotypes westwards. Nevertheless, it is possible that migrant haplotypes increase their abundances temporarily when local haplotypes are affected by disturbances. Importantly, the previous hypotheses on the role of migrant haplotypes should be considered with caution since many of their main assumptions warrant further research; for example, the relative proportion of haplotypes in the early-life stages of *B. occidentalis* has yet to be explored.

Finally, despite the fact that the three populations evaluated occur at different depths (**Table 1**), no correlation appears to occur between the pairwise population differentiations (**Table 3**) and depth differences. For example, the deepest (LA) and shallowest (CB) populations showed the lowest Fst whereas the population with intermediate depth (FL) showed the highest Fsts with LA and CB. Therefore, despite the lack of additional tools or data to further assess this factor, depth does not seem to be a crucial predictor of population structure for *B. occidentalis* in the GoMx.

Changes in Population Structure After the Deepwater Horizon Oil Spill

Three individuals collected from offshore LA after the DWH (L2) showed a haplotype that, before the disaster, had never been reported in LA or CB (**Table 3** and **Figure 3**) but was found in FL. This finding was consistent for all the genes, except *rbc*L, in which the L2 haplotype was common in all the GoMx regions before the DWH. The analyses of molecular variance (AMOVAs), exact tests of population differentiation (Fst > 0.8 and $P < 0.05$), and Likelihood Ratio tests ($P < 0.001$) indicated a significant shift in haplotype frequencies in LA from before and after the DWH. For example, the Likelihood Ratio test indicated that, if L2 and LA are the same population, the probability of obtaining three FL haplotypes in the L2 individuals is nearly zero. Moreover, the LA vs. L2 Fst were supported by statistically significant *P*-values. The affinity between L2 and FL was also confirmed in all the analyses. L2 vs. FL Fsts were close to zero for *rbc*L and *Cox2-3*, and supported by $P < 0.05$. Conversely, *Cox1* and the multigene, showed relatively large Fsts (~0.15) for L2 vs. FL, but their *P*-values were lower than 0.05. The occurrence of FL haplotypes in LA after the DWH is greatly consistent with the hypothesis that early-life stages with FL haplotypes continuously occur in LA and CB but are typically outcompeted or outnumbered by local haplotypes until a disturbance allows for a change in haplotype frequencies.

Additional Considerations and Limitations

Due to the retrospective nature of this study, the research cruise specimen collections were not planned in function of our quantitative assessments of population structure. The pre-DWH specimens were collected during different sampling periods, between 2000 and 2008, at each region (**Table 1**); to group the specimens into three putative regional populations our study assumed that the allele frequencies within each region has been relatively stable between 2000 and 2008. This assumption is not unrealistic in our study area since no major disturbance appears to have impacted the natural dynamics of the GoMx between 2000 and 2008. Therefore, this study is still highly valuable for understanding the population structure of a common widespread GoMx macroalgal species in the context of the DWH. This type of assumption is necessary when the data are not ideal but can produce valuable information under certain considerations.

Likewise, due to the retrospective nature of this study, the use of herbarium specimens was our best possible approach. Such an approach may lead to pseudoreplication and frequency overestimation of haplotypes if fragments of the same specimen are treated as separate individuals; for that reason, we used the collection notes associated to each specimen to decide which individuals would be included in this study.

We avoided specimens collected from the same dredge but, unfortunately, due to the limited number of specimens it was not always feasible. Despite this limitation, individuals sequenced from the same dredge often showed different haplotypes.

Finally, due to the decreased abundance of *Botryocladia occidentalis* offshore Louisiana after the DWH personal observations during field trips by Venera-Pontón et al. (2019), only three individuals were available for the analyses of the post-DWH population (L2) in spite that the sampling effort (number of dredges launched) of the post-DWH research cruises was comparable to the sampling campaigns conducted pre-DWH (see Venera-Pontón et al., 2019). Even with this extremely low sample size, the fact that none of the L2 individuals showed the *Cox1* or *Cox2-3* haplotypes collected offshore Louisiana between 2000 and 2008 (LA) is, by itself, strong evidence of a change in allele frequencies. Undersampling typically favors the exclusion of rare haplotypes (which require larger sampling efforts to be detected) and an overestimation of frequencies in the common haplotypes (which require a smaller effort to be detected); consequently, the fact that a previously undetected haplotype (absent in a sample of 41 individuals) occurred only in the three samples collected post-DWH is solid evidence that its frequency significantly increased. Since such change may be temporary, we encourage new studies to test whether the haplotypes found offshore Louisiana post-DWH are still found in the region or whether the pre-DWH haplotypes regained their frequency in the present Louisiana population. Nevertheless, the population changes occurred after the DWH may not necessarily be a consequence of crude oil contamination but could be caused by other DWH factors such as the release of Corexit oil dispersant (OSAT, 2010; Kujawinski et al., 2011) or the closure of fisheries for a prolonged period, temporarily increasing the abundance of fishes that graze on macroalgae. Likewise, it is a possibility too that these population changes were driven by factors unrelated to the DWH. Unfortunately, further assumptions or conclusions on the L2 population are very problematic due to the small sample size.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in GenBank, MH521039, MH521040, and MH521041 (*rbcL*); MH537602, MH537600, and MH537601 (*Cox2-3*); MH521034, MH521035, MH521036, MH521037, and MH521038 (*Cox1*).

AUTHOR CONTRIBUTIONS

DV-P conceived the study, conducted the laboratory work, and performed the data analyses. DV-P wrote the manuscript with contributions from SF and WS. All authors edited the manuscript before submission.

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Oyster Reefs in Northern Gulf of Mexico Estuaries Harbor Diverse Fish and Decapod Crustacean Assemblages: A Meta-Synthesis

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Oyster reefs provide habitat for numerous fish and decapod crustacean species that mediate ecosystem functioning and support vibrant fisheries. Recent focus on the restoration of eastern oyster (*Crassostrea virginica)* reefs stems from this role as a critical ecosystem engineer. Within the shallow estuaries of the northern Gulf of Mexico (nGoM), the eastern oyster is the dominant reef building organism. This study synthesizes data on fish and decapod crustacean occupancy of oyster reefs across nGoM with the goal of providing management and restoration benchmarks, something that is currently lacking for the region. Relevant data from 23 studies were identified, representing data from all five U.S. nGoM states over the last 28 years. Cumulatively, these studies documented over 120,000 individuals from 115 fish and 41 decapod crustacean species. Densities as high as 2,800 ind m^{-2} were reported, with individual reef assemblages composed of as many as 52 species. Small, cryptic organisms that occupy interstitial spaces within the reefs, and sampled using trays, were found at an average density of 647 and 20 ind m^{-2} for decapod crustaceans and fishes, respectively. Both groups of organisms were comprised, on average, of 8 species. Larger-bodied fishes captured adjacent to the reef using gill nets were found at an average density of 6 ind m^{-2}, which came from 23 species. Decapod crustaceans sampled with gill nets had a much lower average density, <1 ind m^{-2}, and only contained 2 species. On average, seines captured the greatest number of fish species ($n = 33$), which were made up of both facultative residents and transients. These data provide general gear-specific benchmarks, based on values currently found in the region, to assist managers in assessing nekton occupancy of oyster reefs, and assessing trends or changes in status of oyster reef associated nekton support. More explicit reef descriptions (e.g., rugosity, height, area, adjacent habitat) would allow for more precise benchmarks as these factors are important in determining nekton assemblages, and sampling efficiency.

Keywords: essential fish habitat, estuary, fisheries, restoration, *Crassostrea virginica*

INTRODUCTION

Understanding the impacts of habitat change on natural resources remains a key component for informing restoration and management policy (Barbier et al., 2011; Bennett et al., 2015). Fisheries policy in particular, through the 1996 amendment to the U.S. Magnuson-Stevens Act (passed 1976), introduced a mandate on defining and protecting Essential Fish Habitat, which include "all waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity" (Magnuson Stevens Fishery Management Conservation Act, 1996, 16 U.S.C. section 1801–1804). This placed high importance on species-habitat associations (Magnuson Stevens Fishery Management Conservation Act, 1996: 50 CFR, sections 600.805–930). Since then, data on habitat-specific fisheries and associated species have been used to justify, inform, and guide policy and management activities (Rondinini and Chiozza, 2010; Vasconcelos et al., 2015; NRC, 2017). Thus, documenting species richness and assemblages within a habitat type is a first crucial step to defining habitat support and ensuring collection of proper baseline data. These baseline data can be used to support modeling, evaluate restoration outcomes (Dufrêne and Legendre, 1997; NRC, 2017), and, as highlighted recently, to evaluate resource injury (i.e., under the U.S. Oil Pollution Act, 1990[1], section 1006I(1) for coastal resources).

Reefs built by the eastern oyster, *Crassostrea virginica,* have been recognized as Essential Fish Habitat (Coen and Grizzle, 2007). Historically valued for their economic impact as a direct food commodity, oysters also create reefs, providing valuable three-dimensional habitat within coastal environments. In recent decades, significant efforts to conserve, and restore oyster reefs have been justified based on the valuable ecosystem services they provide, including water quality improvements, shoreline protection, and habitat creation for commercially and recreationally important fisheries (Coen and Grizzle, 2007; Grabowski et al., 2012). Importantly, for fisheries and restoration policy, oyster reefs are recognized as key biogenic habitat for a diverse assemblage of fishes and decapod crustaceans (e.g., Mobius, 1877; Frey, 1946; Wells, 1961; Coen et al., 1999; Coen and Grizzle, 2007, 2016). The reported functional decline in oyster reefs (Beck et al., 2011; Zu Ermgassen et al., 2012) is likely to have broad consequences for habitat provision, and thus biodiversity and fisheries production (Peterson et al., 2003; Humphries and La Peyre, 2015; Zu Ermgassen et al., 2015), but a lack of established benchmarks hinders our ability to assess impacts.

Recent guidelines for monitoring oyster reefs suggest setting explicit goals for assessing habitat support (Baggett et al., 2015; NRC, 2017). Goals for restoration projects may focus simply on provision of habitat (i.e., La Peyre et al., 2014a; Baggett et al., 2015), or, they may be expanded to include local enhancement of ecosystem services (i.e., Coen and Luckenbach, 2000). Central to either of these goals, however, is an understanding of what the nekton assemblages look like on the desired habitat in terms of expected assemblages, abundance, and biomass of species. As such, many oyster reef restoration planning documents call for the use of project-specific reference sites (Coen et al., 2004; SER Society for Ecological Restoration, 2004; Baggett et al., 2015; NRC, 2017); however, such sites are often not available, or monitoring efforts fail to collect these data. An alternative is to establish desirable conditions, or benchmarks to measure changes in resource status (Ehrenfeld, 2000; Kentula, 2000).

Benchmarks provide a tool to assess the status of natural, managed, or restored ecosystems (Angermeier and Karr, 1994; McClanahan et al., 2019). Ideally, benchmarks are set using baseline data derived from natural or pristine systems, which are defined by functional and evolutionary limits of the ecosystem (Pickett et al., 1992). For many resources and regions, effects of altered landscapes (e.g., river management, climate change), and a lack of historical data confound efforts to set benchmarks representing pristine conditions (Toledo et al., 2011). Lacking these historical data, useful benchmarks can still be established for current ecosystem status against which future assessments of natural resource condition or management effects can be measured. Across the northern Gulf of Mexico (nGoM), significant coastal restoration, river management, and climate change impacts have affected local hydrology, water quality, and landscape configurations (Pendleton et al., 2010; Montagna et al., 2011). These changes alter oyster population dynamics and reef characteristics which ultimately impacts the oyster reef's provision of ecosystem services, including nekton habitat. Benchmarks representing reef-resident and transient assemblages based on the current range or means of values from recent assessments would provide useful tools to assess changes in status of natural reefs, as well as managed and restored reefs.

The nGoM supports extensive natural oyster reefs (Kilgen and Dugas, 1989), and recently has experienced significant restoration activities related to oyster reefs, with a goal of providing fisheries habitat (La Peyre et al., 2014a). Reports from the Atlantic coast of the United States document occupancy of eastern oyster reefs by 50 to over 300 species, with the wide range of reported species depending on whether the surveys include fish, decapod crustaceans, molluscs or other organisms, such as protozoans, sponges and flatworms (e.g., Frey, 1946; Wells, 1961; Coen and Grizzle, 2007). Similar data do not exist for the nGoM, despite the exceptional fisheries support and habitat characteristics of the region. For example, the nGoM is characterized by a microtidal regime (<0.5 m) where water level changes are driven mostly by winds, precipitation, and runoff (Kim and Park, 2012). As such, depth and exposure of Gulf coast oyster reefs can vary and be difficult to predict (Kilgen and Dugas, 1989). Importantly, water depth and substrate or reef exposure influence reef formation, which impacts oyster population dynamics (Ridge et al., 2015). Oysters in the nGoM have higher growth rates and reduced mortality rates compared to other regions, despite experiencing lower salinity, and higher temperatures than other regions (Lowe et al., 2017). These differences in reef formation, water quality, and growth characteristics likely influence the associated nekton communities, suggesting a need for region specific benchmarks.

This study aims to quantify fish and decapod crustacean assemblages associated with nGoM oyster reefs. The goal is to

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[1] Oil Pollution Act of 1990 (OPA) (101 H.R.1465, P.L. 101–380).

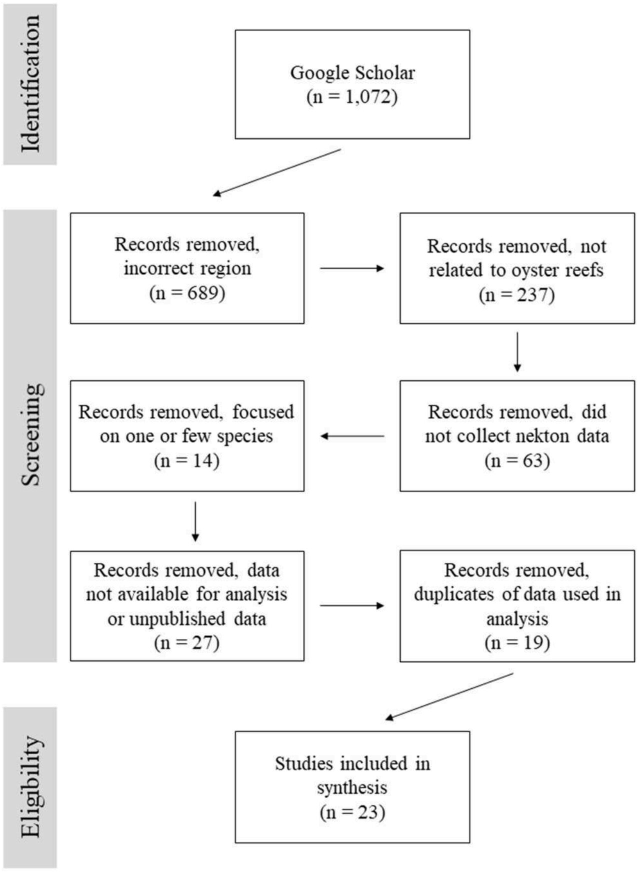

FIGURE 1 | Flow diagram for records search documenting number of records identified and screened for inclusion in this data review.

provide benchmarks using available data collected on nekton occupancy across a broad spectrum of oyster reefs. These benchmarks will be useful as a guideline to assess policy and restoration outcomes in the nGoM, as well as inform future injury assessments (Geist and Hawkins, 2016). These needs have been identified in previous studies and planning documents and represent a critical information gap for assessing restoration and policy goals (Baggett et al., 2015; Coen and Humphries, 2017; NRC, 2017).

METHODS

Peer Reviewed Study Selection

A literature search for fish and decapod crustacean sampling on oyster reefs across the nGoM was conducted by searching Google Scholar using the following search terms: “oyster reef” AND (Texas OR Louisiana OR Mississippi OR Alabama OR Florida) AND (macrofauna OR nekton), for all papers dated through April 2019. Only peer-reviewed, regional nGoM shallow water (<3 m) studies that provided oyster reef location, sample size, sample methods (i.e., gear), species identities, and density information were included in the final database. Also, only studies targeting oyster reef fish and/or decapod crustacean communities (and not individual species focused studies) were included for the targeted evaluation of community composition, and not specific species.

Nekton Variables

Nekton variables were collected by gear type, and standardized across studies. To address the issue of unequal sampling effort, all nekton density data were standardized to individuals m^{-2} for all gear types, except gill net, which was standardized to individuals hr^{-1} of net soak time. Sampling effort was calculated by multiplying the number of samples taken by either the total area sampled, or total hours fished.

Reef and Water Quality Characteristics

Variables describing reef characteristics and water quality, where available, were added to the database. Data availability was examined for tidal height, reef elevation, exposure, and water quality for selected study reefs and locations. Water quality data for salinity, temperature (°C), and dissolved oxygen (mg L^{-1}) were the only three variables consistently available. We recorded reef type (natural vs. constructed) as there were few data sets for natural reefs, and using data from only natural reefs resulted in a very limited database. For the purposes of this study, we define natural reefs as reefs that had not, to the best of our knowledge, been anthropogenically enhanced, restored, or created in any way. We define “constructed” reefs as those that were anthropogenically enhanced, restored, or created using shell or other materials such as rock or cement with the goal of reef restoration and not oyster production for human consumption. Reefs were classified as intertidal or subtidal based on information from the original studies. Any reef not explicitly identified as intertidal was classified as subtidal, although we acknowledge that some subtidal reefs in this region are occasionally exposed from weather events (i.e., La Peyre et al., 2017).

Final Database

The final database included density or catch per unit effort (CPUE) of fish and decapod crustaceans, number of fish and decapod crustacean species, list of species collected, sample size, sampling gear, reef type (natural, constructed), tidal status (intertidal vs. subtidal), and a few discrete environmental parameters (water temperature, salinity, dissolved oxygen).

Data are presented and discussed using statistical means and distributions by gear type. We use the means for fish and decapod crustacean density and species number separately, by dominant gear type quantifying “on-reef” and “near reef” values to suggest potential benchmarks based on the range and means of values currently found across the nGoM (R 3.5.1; R Core Team, 2018).

RESULTS

From a total of 1,072 search results, 23 articles were selected for this analysis based on their overall goals and data availability (**Figure 1**; **Table 1**). The majority of studies were excluded

TABLE 1 | List of studies identified as sampling for nekton assemblages on oyster reefs within estuaries across the northern Gulf of Mexico.

Code	Reference	Location	Reef type	Exposure	Salinity	Temperature (°C)	Dissolved oxygen (mg L^{-1})
A	Zimmerman et al., 1989	Galveston Bay, TX	Natural	Intertidal	n/a	n/a	n/a
B	Glancy et al., 2003	Citrus County, FL	Natural	Subtidal	12.0–25.0	16.5–32.4	3.0–9.6
C	Plunket and La Peyre, 2005	Barataria Bay, LA	Natural	Subtidal	4.3–22.1	13.7–28.8	3.3–10.2
D	Tolley and Volety, 2005	Tarpon Bay, FL	Natural	Intertidal	28.2–36.8*	26.0–28.3*	n/a
E	Tolley et al., 2006	Estero Bay, FL	Natural	Intertidal	9.3–26.4*	28.1–29.0*	5.1–5.9*
F	Shervette and Gelwick, 2008	Grand Bay, MS	Natural	Intertidal	3.0–22.8	25.1–33.1	4.7–7.0
G	Simonsen, 2008; Simonsen and Cowan, 2013	Barataria Bay, LA	Natural	Subtidal	8.1–32.7	11.8–32.1	2.1–9.8
H	Gregalis et al., 2009	Mobile Bay, AL	Constructed, 2004	Subtidal	5.0–23.0	9.6–32.8	3.5–15.7
I	Gain, 2009; Gain et al., 2017	Corpus Christi Bay, TX	Natural	Intertidal	31.0–36.1	20.3–28.1	5.8–6.1
J	Stunz et al., 2010	Galveston Bay, TX	Constructed, 2003	Subtidal	20.1–37.4*	16.9–31.2*	5.8–8.8 *
K	Robillard et al., 2010	Lavaca Bay, TX	Natural	Subtidal	8.6–21.7	13.6–27.4	6.1–9.8
L	Humphries et al., 2011a	Sister Lake, LA	Constructed, 2009	Subtidal	0–23.0	2.0–34.0	4.0–11.0
M	Scyphers et al., 2011	Mobile Bay, AL	Constructed, 2007	Subtidal	8.7–31.8#	11.3–31.5#	n/a
N	La Peyre et al., 2013	Breton Sound, LA	Constructed, 2009	Subtidal	8.3–20.5	12.9–34.7	0.4–8.8
O	Brown et al., 2013	Gulf-wide	Constructed, 1990-2010	Subtidal	0.2–31.7	28.5–30.7*	4.5–9.5
P	Nevins et al., 2014	Sabine Lake, TX, LA	Natural	Subtidal	4.2–27.5	13.3–31.9	4.3–9.7
Q	La Peyre et al., 2014b	Sister Lake, LA	Constructed, 2010	Subtidal	0.3–29.8	2.2–34.4	0.4–17.3
R	Beck and La Peyre, 2015	Louisiana	Natural	Subtidal	12.0–20.0	24.9–31.1	4.4–6.9
S	George et al., 2015	St. Charles Bay, TX	Natural[1]	Subtidal	22.0–25.0	25.0–28.0	7.0–7.1
T	Graham et al., 2017	Aransas Bay, TX	Constructed, 2013	Subtidal	16.3–34.0	6.8–29.7	5.2–10.8
U	Rezek et al., 2017	Aransas Bay, TX	Natural & Constructed, 2012	Subtidal	30.6–39.5*#	10.9–30.4*#	n/a
V	Aguilar, 2017; Aguilar Marshall et al., 2019	Matagorda Bay, TX	Constructed, 2013-2014	Subtidal	8.2–31.2	8.7–40.6	4.7–10.6
W	Blomberg et al., 2018b	Copano Bay, TX	Natural & Constructed, 2011	Subtidal	26.6–38.8	13.8–30.1	4.6–8.7

Reef type (natural vs. constructed), and exposure (intertidal vs. subtidal) are listed. Environmental conditions for water quality parameters are reported as a range as most studies report only discrete sample data.

[1] *Study compares trays of constructed material adjacent to natural reef.*

[2] *Reef construction years vary, some unknown.*

**Range of means reported from discrete sampling.*

\#*Range was downloaded from data recorders for the study sites.*

because they focused on a region other than the Gulf of Mexico, the study was not related to oyster reefs, or data were not reported for all species. Within the Gulf of Mexico, there were many studies examining various aspects of fisheries, nekton production, and trophic changes on oyster reefs, but they failed to meet our criteria for inclusion in the final dataset. A number of studies focused exclusively on indicator species, economically important species, a subset of the reef community, or failed to report all catch data. While valuable, such studies were not included.

The studies selected for analyses covered all five Gulf Coast states and used multiple gear types. Texas had the most data (9 studies), followed by Louisiana (6 studies), Florida (3 studies), Alabama (2 studies), and Mississippi (1 study), and 2 studies covered multiple states (**Figure 2**). Across the 23 studies, seven different gear types were used with most studies using more than one gear type on a single oyster reef. Trays (TR) were the most frequently used gear type ($n = 12$). Gill nets (GN) were the next most used gear type ($n = 8$), although the lengths, mesh sizes and soak times varied. Drop-samplers (DS), throw traps (TT), and lift nets (LN) were grouped in one category (DS/TT/LN; $n = 8$). Seines (SN; $n = 4$) and epibenthic sleds (ES; $n = 3$) represented the remainder of sampling gear included in these analyses. We classified TR, DS/TT/LN and ES as sampling "on-reef," and GN and SN as sampling "near-reef" assemblages.

Reefs sampled across the selected studies included a mix of reef types, tidal status, and location. Studies sampled either natural reefs ($n = 12$) or constructed reefs ($n = 9$), with two studies comparing natural and constructed. Constructed reef habitats ($n = 9$) were built at different times (1990–2014) using different base materials that included shell, limestone, and concrete base materials. There was a mix of intertidal and subtidal reefs (intertidal = 5; subtidal = 18). Due to lack of site-specific water level data, we were unable to determine exposure levels of reefs or exposure time. Intertidal reefs were all located nearshore (identified as < 25 m from shore), along with a few of the subtidal reefs ($n = 3$); the remainder of reefs were located offshore (>25 m from shore).

Water quality parameters commonly reported included salinity, temperature, and dissolved oxygen. Oyster reefs were

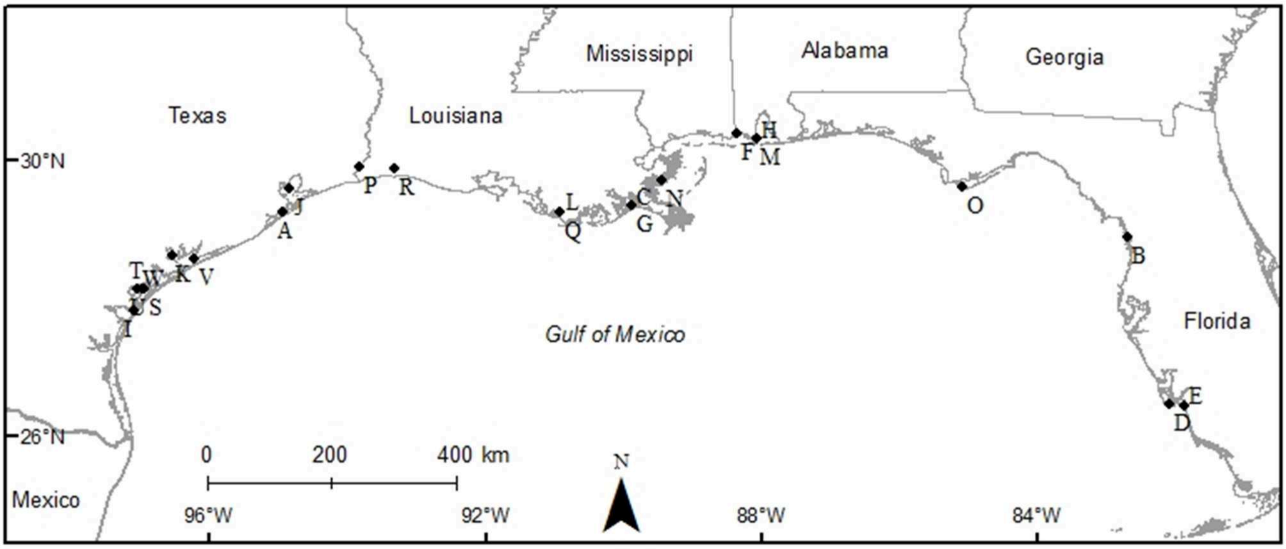

FIGURE 2 | Map of study sites used to examine the diversity and abundance of fish and decapod crustacean communities on oyster reefs across the northern coast of the Gulf of Mexico (Texas, Louisiana, Mississippi, Alabama, and Florida Gulf coast). See **Table 1** for explanation of study codes.

sampled through a broad range of salinities (0–39.5) from Florida to Texas with most studies reporting ranges of salinities >20, reflecting the highly variable nature of the estuarine environments where many oysters are found in the nGoM (**Table 1**). Temperature reflected the annual range in the region, from 2.0° to 40.6°C, encompassing winter and summer samples, while dissolved oxygen conditions ranged from 0.4 to 17.3 mg L^{-1}. No other environmental parameters were reported consistently across studies.

A total of 115 fish species, based on over 32,000 individual fish, were reported on or near oyster reefs (**Table 2**, **Supplementary Table 1**). Of the 115 reported fish species, 22 species (∼19%) were collected in eight or more of the studies (**Table 3**), and 40 species were only reported in one study (**Supplementary Table 1**). The number of fish species collected ranged from 4 to 46 per study (**Table 2**; **Figure 3**; **Supplementary Table 1**). Species assemblages varied among gear types with TR and DS/TT/LN capturing more known reef residents, such as gobies and blennies, which included 15 species found only in these gear types. Gill nets captured larger and more mobile transient fish species, such as sheepshead (*Archosargus probatocephalus*) and red drum (*Sciaenops ocellatus*), while seines captured a mix of both the transient fish species and some of the smaller more ubiquitous resident species (**Table 3**; **Supplementary Table 1**). Seine and gill net data included 51 fish species not captured with any of the other methods. Of these, 23 species were captured exclusively by gill net, including many of the shark species, and 15 species were captured exclusively by seine. Combined, the SN and GN gear types uniquely captured 44% of the fish species (**Supplementary Table 1**). Densities reported were gear-dependent, with TR and TT/DS/LN having mean densities of 20.2 ± 4.3 ind m^{-2} (mean ± SE) and 15.6 ± 2.8 ind m^{-2}, respectively (**Figure 4**). GN, capturing larger bodied fish, reported mean densities of 6.7 ± 8.4 ind m^{-2}. SN and ES reported low densities (< 1 ind m^{-2}).

A total of 56 decapod crustacean species, based on over 90,000 individuals were identified (**Table 2**, **Supplementary Table 2**). The number of decapod crustacean species ranged up to 26 per study. Of the 56 reported crustacean species, 11 species (snapping shrimp, blue crabs, depressed mud crabs, brown shrimp, white shrimp, Gulf stone crabs, *Palaemonetes pugio* and *P. vulgaris* grass shrimp, Panopeid mud crabs, green porcelain crabs, Harris mud crabs) were listed in eight or more of the studies (**Table 4**) while 27 species were only listed in one study (**Supplementary Table 2**). Species composition differed between gear types, with TR, TT/DS/LN, and ES capturing the most species. TR consistently captured highest densities (mean ± SE: 647.9 ± 245.9; **Figure 4**), while GN and SN captured few decapod crustaceans (**Figure 4**, **Supplementary Table 2**).

DISCUSSION

Modern day natural and constructed reefs across the nGoM support diverse and dense assemblages of fishes and decapod crustaceans. Nekton density was as high as 2,800 ind m^{-2} and some reefs had >50 species of fish and decapod crustaceans. Using the available published data, gear-dependent means for density and species richness of dominant "on-reef" sampling (tray) and "near reef" sampling (gill net) serve as useful benchmarks. These benchmarks provide quantitative measures that can be used to assess changes in the status of existing and constructed oyster reefs. Management of coastal habitat and fisheries requires data on species-habitat associations to delineate Essential Fish Habitat, better implement restoration, perform injury assessments, and set policy goals. These suggested benchmarks, based on current reef status, may be used to assess

TABLE 2 | Synthesis of sampling effort and catch for studies for the northern Gulf of Mexico.

Study	Reef Type	Gear type	No. samples	No. fish collected	No. crustaceans collected	Effort (m^{-2} or hrs)	Mean fish density (ind m^{-2} OR ind hr^{-1})	Mean crustacean density (ind m^{-2} OR ind hr^{-1})	No. fish species	No. crustacean species
Plunket and La Peyre, 2005	N	TR	22	226	1,560	6.7 m^2	33.2 (4.5)	168.4 (16.1)	8	5
Gregalis et al., 2009	C	TR	576	4,985	13,970	115.2 m^2	41.5 (5.6)	116.4 (15.9)	9	8
Brown et al., 2013	C	TR	80	201	15,004	7.2 m^2	2.4 (4.3)	188.5 (33.8)	5	12
La Peyre et al., 2014b	C	TR	60	784	302	19.8 m^2	38.9 (16.6)	18.2 (14.2)	7	8
Beck and La Peyre, 2015	N	TR	58	1,273	5,360	12.8 m^2	56.2 (5.5)	223.7 (12.6)	10	10
George et al., 2015	N	TR	50	–	–	37.5 m^2	19.6 (–)	414.5 (–)	13	9
Graham et al., 2017	C	TR	72	–	–	10.8 m^2	20.7 (–)	1031.9 (–)	8	10
Rezek et al., 2017	N	TR	15	56	3,142	2.025 m^2	27.7 (–)	1551.5 (–)	5	3
Rezek et al., 2017	C	TR	15	24	5,758	2.025 m^2	11.9 (–)	2843.6 (–)	7	7
Aguilar, 2017; Aguilar Marshall et al., 2019	C	TR	72	–	–	20.16 m^2	19.5 (–)	393.4 (–)	4	13
Blomberg et al., 2018b	N	TR	36	217	5,769	15.84 m^2	13.95 (–)	371.6 (–)	15	10
Blomberg et al., 2018b	C	TR	36	285	7,046	15.84 m^2	18.35 (–)	453.86 (–)	13	9
Plunket and La Peyre, 2005	N	GN	18	234	0	32 h	6.4 (1.9)	0.0	16	0
Simonsen, 2008; Simonsen and Cowan, 2013	N	GN	28	2,156	66	28 h	68 (13.2)	< 1.0	25	2
Gregalis et al., 2009	C	GN	288	–	0	1,152 h	8.4 (5.3)	0.0	40	0
Robillard et al., 2010	N	GN	16	470	2	40 h	11.8 (–)	< 0.1 (–)	18	2
Scyphers et al., 2011	C	GN	–	4,647	0	1,258 h	3.87 (–)	0.0	46	0
La Peyre et al., 2013	C	GN	18	36	4	18 h	2.0 (0.6)	0.2 (0.1)	9	1
Brown et al., 2013	C	GN	104	217	2	104 h	1.3 (0.3)	< 0.5	22	2
La Peyre et al., 2014b	C	GN	60	845	87	120 h	7.0 (0.8)	0.7 (0.2)	23	3
Zimmerman et al., 1989	N	DS	16	791	2,937	41.6 m^2	4.3 (1.0)–34.0 (16.9)	36.4 (4.3)–104.8 (18.8)	15	11
Shervette and Gelwick, 2008	N	DS	24	345	1,122	28.1 m^2	12.3 (–)	39.9 (–)	26	16
Stunz et al., 2010	C	DS	40	609	2,491	104 m^2	17.2 (1.9)	62.3 (9.9)	26	26
Humphries et al., 2011a	C	DS	40	244	324	40 m^2	6.9 (1.5)	9.1 (1.9)	16	6
Simonsen, 2008; Simonsen and Cowan, 2013	N	SN	28	1,993	2	560 m^2	0.7 (0.39)	< 0.1	34	2
Scyphers et al., 2011	C	SN	–	3,385	776	55,440 m^2	0.5 (–)	0.23 (–)	42	7
La Peyre et al., 2013	C	SN	36	836	141	2,160 m^2	0.8 (0.3)	0.1 (0.04)	14	4
La Peyre et al., 2014b	C	SN	117	4,839	1,883	14,625 m^2	0.3 (0.09)	0.1 (0.04)	44	7
Robillard et al., 2010	N	ES	16	433	635	1,600 m^2	0.3 (–)	0.4 (–)	16	11
Nevins et al., 2014	N	ES	48	1,001	1,411	3,744 m^2	0.15 (0.10)	0.14 (0.03)	14	10
Aguilar, 2017; Aguilar Marshall et al., 2019	C	ES	40	–	–	5,760 m^2	0.11 (–)	3.42 (–)	10	21
Tolley and Volety, 2005	N	LN	30	300	1,920	30 m^2	10 (–)	64 (–)	16	10
Tolley et al., 2006	N	LN	90	299	5,187	45 m^2	6.6 (–)	115.3 (–)	12	11
Glancy et al., 2003	N	TT	76	n/a	11,543	76 m^2	n/a	155.4 (–)	n/a	15
Gain, 2009; Gain et al., 2017	N	TT	27	~600	~2,300	27 m^2	25.1 (2.1)	157.1 (30.2)	28	15

*Natural, Reef type is either N; or C, Constructed. TR, Gear type includes tray; GN, gill net; DS, drop sampler; SN, seine; ES, epibenthic sled; LN, lift net; TT, throw trap. Details on exact gear dimension are available within the sources. All gear types are standardized; effort is calculated as the number of samples * area sampled (or hours fished), and reported in m^{-2} (or h^{-1}) for comparison. Standard error for mean density, when available, is reported in parentheses.*

TABLE 3 | List of fish species reported in 8 studies or more, with sampling gear, location, and source.

Fish species	Common name	Sampling gear	Location	Source
Anchoa mitchilli	Bay anchovy	DS, ES, SN, TR	LA, MS, TX	A, F, G, J, K, N, P, Q, S, V
Ariopsis felis	Hardhead catfish	GN, SN	AL, LA, TX	C, G, H, K, M, N, O, Q
Archosargus probatocephalus	Sheepshead	DS, GN, LN, SN, TR	AL, FL, LA, TX	A, C, D, E, H, J, L, M, Q, S
Bagre marinus	Gaftopsail catfish	GN, SN, TR	AL, LA, TX	C, G, H, K, M, N, O, Q, S
Bairdiella chrysoura	Silver perch	DS, ES, GN, LN, SN, TR, TT	AL, FL, LA, TX	C, D, G, H, I, J, K, L, M, N, Q, S, V
Brevoortia patronus	Gulf menhaden	DS, ES, GN, SN	AL, LA, TX	A, C, G, H, J, K, M, N, O, Q
Chaetodipterus faber	Atlantic spadefish	DS, GN, SN, TR	AL, LA	C, G, H, L, M, O, Q, R
Chasmodes bosquianus	Striped blenny	DS, ES, TR, TT	LA, MS, TX	A, C, F, I, J, K, O, Q, R, S
Ctenogobius boleosoma	Darter goby	DS, ES, SN, TR, TT	AL, LA, MS, TX	C, F, G, H, I, J, K, L, P, Q, R, W
Cynoscion arenarius	Sand seatrout	GN, SN	AL, LA, TX	C, G, H, K, M, N, O, Q
Cynoscion nebulosus	Spotted seatrout	DS, ES, GN, SN, TT	AL, LA, TX	C, G, H, I, J, K, M, N, O, P, Q
Gobiesox strumosus	Skilletfish	DS, ES, LN, SN, TR	AL, FL, LA, MS, TX	A, C, E, F, H, J, L, N, O, P, Q, R, S, T, U, V, W
Gobiosoma bosc	Naked goby	DS, ES, LN, SN, TR, TT	AL, FL, LA, MS, TX	A, C, E, F, H, I, J, K, L, N, P, Q, R, S, T, U, W
Hypsoblennius hentz	Feather blenny	DS, ES, LN, TR	AL, FL, LA, MS, TX	C, D, E, F, H, P, S, V, W
Lagodon rhomboides	Pinfish	DS, ES, LN, GN, SN, TR, TT	AL, FL, LA, MS, TX	A, C, D, E, F, G, H, I, J, K, M, N, Q, S
Leiostomus xanthurus	Spot	DS, GN, SN, TR	AL, LA, MS, TX	C, F, G, H, J, K, M, Q, W
Lutjanus griseus	Mangrove/gray snapper	DS, GN, LN, SN, TR, TT	AL, FL, LA, TX	D, E, G, I, J, L, M, Q, R, W
Micropogonias undulatus	Atlantic croaker	DS, ES, GN, SN, TR	AL, LA, TX	C, G, H, J, K, M, O, P, Q, V
Myrophis punctatus	Speckled worm eel	DS, TR	AL, LA, MS, TX	A, F, H, J, L, M, Q, R, W
Opsanus beta	Gulf toadfish	DS, LN, SN, TR, TT	AL, FL, LA, TX	A, C, D, E, H, I, J, L, M, O, Q, R, S, T, U, V, W
Pogonias cromis	Black drum	ES, GN, SN	AL, LA, TX	C, G, H, K, M, N, O, P, Q
Symphurus plagiusa	Blackcheek tonguefish	DS, ES, LN, GN, SN	AL, FL, LA, MS, TX	D, F, G, J, K, L, M, P

TR, Gear type includes tray; GN, gill net; DS, drop sampler; SN, seine; ES, epibenthic sled; LN, lift net; TT, throw trap. Source is indicated in ***Table 1*** *by letter.*

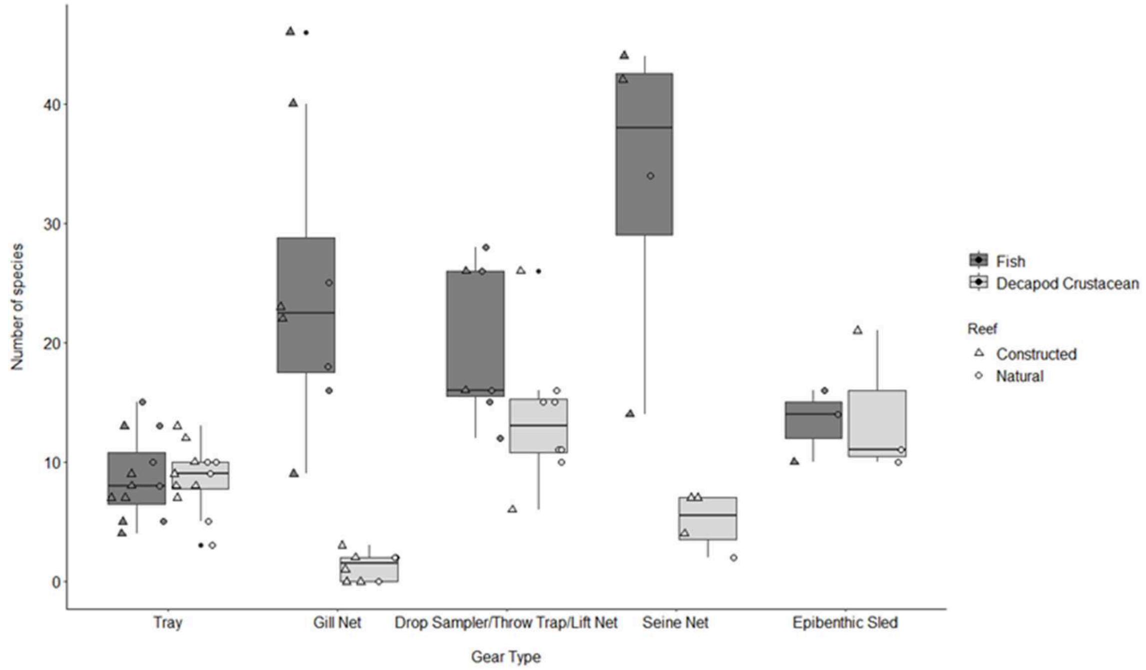

FIGURE 3 | Boxplot of number of fish and decapod crustacean species presented by gear type TR, tray; GN, gill net; DS, drop sampler; LN, lift net; TT, throw trap; SN, seine; ES, epibenthic sled. Box represents 25, 50, and 75% quantilets, with whiskers at ±1.5*IQR.

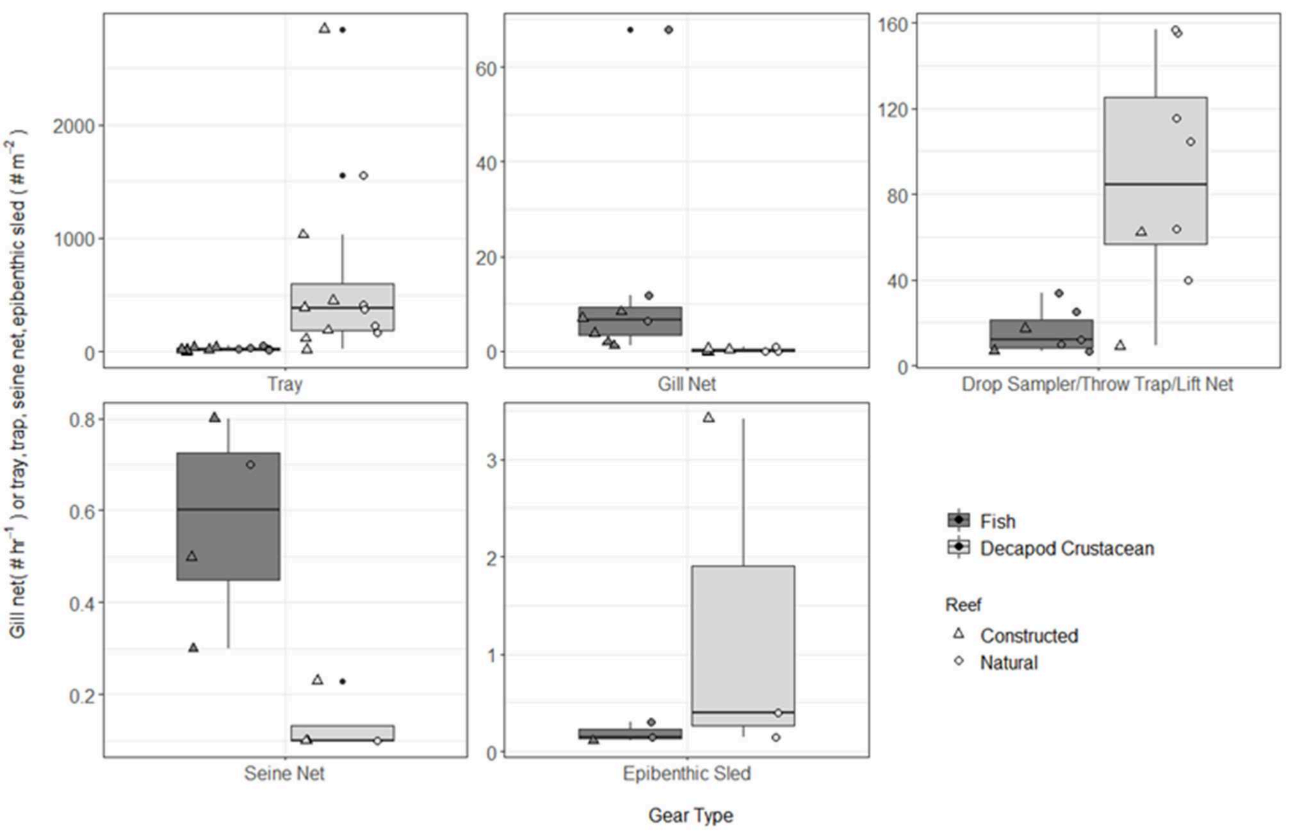

FIGURE 4 | Boxplot of fish and decapod crustacean density presented by gear type TR, tray; GN, gill net; DS, drop sampler; LN, lift net; TT, throw trap; SN, seine; ES, epibenthic sled. Note different y-axes for each gear type. Box represents 25, 50, and 75% quantilets, with whiskers at ±1.5*IQR.

trends in oyster reef habitat support of fisheries and ecosystem functioning for this region.

Relating specific assemblages or densities to reef characteristics or across locations was problematic due to a lack of gear standardization, established gear conversion factors for oyster reefs, and reef habitat metrics. For example, some studies only used gill nets and seines to sample whereas others used drop samplers; given differences in catch efficiencies based on species' identity and size, and variable efficiency of different gear types across reefs, results from different gear types are not directly comparable (Zimmerman et al., 1984). As more data are collected, methodologies are standardized, or conversion factors developed, these fish and decapod crustacean benchmarks will become more targeted to specific locations, reef complexity or reef type.

Reef Characteristics and Complexity

Reef characteristics, such as adjacent habitats, connectivity, habitat redundancy, and water quality all affect fish and decapod crustacean assemblages, and are thus vital metrics for interpreting benchmark data. In general, data synthesized for this study lacked consistent reporting of reef location, in terms of adjacent habitats, connectivity or habitat redundancy, or complexity even though these factors influence nekton assemblages. For example, in Texas, Nevins et al. (2014) hypothesized that low faunal densities observed on natural oyster reefs may be a result of adjacent habitats, as well as difficulties sampling the complex habitat. Tolley et al. (2006) highlighted the impacts of salinity and freshwater flow on reef assemblages identifying flow rates and salinity as key location characteristics influencing reef communities. For constructed reefs, Gregalis et al. (2009) demonstrated that reef height affected fish abundance, while resident species abundance and transient fish assemblages varied by reef location. In some cases, reefs have been proposed as potentially redundant habitat due to their location adjacent to or near other high-quality habitat (i.e., Geraldi et al., 2009; La Peyre et al., 2014a; Heck et al., 2017). Reporting distance to adjacent habitats, reef exposure, and water quality/level at sampling would be useful for studies to better understand drivers of fish and decapod crustacean occupancy of oyster reefs.

Habitat complexity may also affect nekton assemblages through direct and indirect effects on trophic cascades, predation and habitat availability (e.g., Grabowski et al., 2008; Humphries et al., 2011a). Quantifying complexity, particularly across various constructed reef materials remains challenging. In particular, while habitat complexity may be important, some studies have suggested a potential complexity threshold due to failure of finding increasing nekton numbers with increased complexity (e.g., Humphries et al., 2011b; George et al., 2015). For example,

TABLE 4 | List of decapod crustacean species reported in 8 studies or more, with sampling gear, location, and source.

Decapod crustacean species	Common name	Sampling gear	Location	Source
Alpheus heterochaelis	Snapping shrimp	DS, ES, LN, TR, TT	AL, FL, LA, TX	A, B, D, E, H, I, J, K, L, O, P, Q, R, S, T, U, V, W
Callinectes sapidus	Blue crab	DS, ES, GN, LN, SN, TR, TT	AL, FL, LA, MS, TX	A, B, C, D, E, F, H, I, J, K, L, M, N, O, Q, R, S, T, W
Eurypanopeus depressus	Depressed/flatback mud crab	DS, LN SN, TR, TT	AL, FL, LA, MS, TX	A, B, D, E, F, H, I, J, O, Q, R,U
Farfantepenaeus aztecus	Brown shrimp	DS, ES, GN, SN, TR	LA, MS, TX	F, G, I, J, K, L, N, O, P, Q, R, U, W
Litopenaeus setiferus	White shrimp	DS, ES, GN, SN, TR, TT	LA, MS, TX	F, G, I, J, K, L, N, O, P, Q, W
Menippe adina	Gulf stone crab	DS, ES, TR, TT	LA, MS, TX	F, I, K, O, R, S, T, U, V, W
Palaemonetes pugio	Grass shrimp	DS, SN, TR, TT	FL, LA, MS, TX	A, B, F, I, J, L, N, O, Q, T, W
Palaemonetes vulgaris	Marsh grass shrimp	DS, LN, TR	FL, MS, TX	A, D, E, F, J, T, U, W
Panopeidae/Xanthidae	Mud crab sp.	DS, ES, LN, SN, TR, TT	AL, FL, LA, MS, TX	A, B, C, D, E, F, H, I, J, K, L, M, O, P, Q, R, S, U, V, W
Petrolisthes armatus	Green porcelain crab	DS, LN, TR, TT	FL, LA, TX	A, B, D, E, I, J, O, R
Rhithropanopeus harrisii	Harris mud crab	DS, LN, SN, TR, TT	FL, LA, MS, TX	B, E, F, I, J, O, Q, R

TR, Gear type includes tray; GN, gill net; DS, drop sampler; SN, seine; ES, epibenthic sled; LN, lift net; TT, throw trap. Source is indicated in ***Table 1*** *by letter.*

George et al. (2015) found no difference in nekton assemblages or prey mortality in experimental studies comparing five possible substrate materials. Similar densities of resident nekton despite increasing oyster density led the authors of one study to hypothesize that there might be a low threshold for habitat complexity (Beck and La Peyre, 2015). These studies highlight the difficulty of relating nekton density and assemblage composition to habitat complexity; some of the differences, however, might also relate to faulty comparisons across studies as a result of sampling gear issues.

Impact of Sampling Gear

Sampling gear are selective for specific size ranges or species, and are not equally effective across, or within, complex habitats (Rozas and Minello, 1997). For oyster reefs in particular, the natural and constructed reefs include a wide range of reef complexity, heterogeneity, reef sizes, reef history, and reef locations. All of these factors influence the assemblages found on or around oyster reefs (Grabowski et al., 2005; Luckenbach et al., 2005; Geraldi et al., 2009; Nevins et al., 2014; Beck and La Peyre, 2015), as well as the effectiveness of gear types. While gear-dependent benchmarks for fish and decapod crustacean density and species number provide general region-wide values, the effects of the interaction of gear type with reef complexity, type, and location remain unknown.

Our study highlighted that different gear types capture different assemblages and numbers of nekton. The highest densities of fish and decapod crustaceans were consistently quantified using methods sampling "on-reef" despite reporting the lowest sampling effort. Specifically, trays, and/or enclosure samplers (lift nets, throw traps, drop-samplers), report sampling "on-reef," where they capture species generally occupying interstitial spaces within the reef structure. Some variance between these gear types likely reflects differences in location as they cannot be used across all reef types (i.e., throw traps and drop-samplers require water depth < 1.5 m), or require small patches of reefs where the sampler can fully enclose the reef (i.e., Stunz et al., 2010; Humphries et al., 2011a). Substrate trays sampled similar resident faunal assemblages as other "on-reef" gear, but can be used at greater depths and on larger reef patches. Trays are often criticized for allowing organisms to escape during retrieval in deeper waters, although modifications including nets that can be drawn closed have been suggested (Beck and La Peyre, 2015). Overall, resident decapod crustaceans (e.g., panopeid crabs) and resident fishes (e.g., gobies, blennies) were ubiquitous on the nGoM oyster reefs. In coral reef systems, these cryptobenthic fauna have been shown to provide as much as 70% of the energy consumed in the ecosystem (Brandl et al., 2019). However, many of these species were captured only with tray sampling, suggesting that without these sampling approaches, an important part of the oyster reef community would not be captured.

In contrast, lower numbers were generally captured using gear sampling adjacent to the reef; specifically, by seines and gill nets. Due to the nature of the reef, these techniques limit sampling to near the reef. These approaches however captured the larger commercially and recreationally important fish species of interest, such as red drum (*Sciaenops ocellatus*), and Spanish mackerel (*Scomberomorus maculatus*). For both gill net and seine sampling, variation in mesh size, time of day, water flow, and distance covered all influence catch rates (e.g., Vandergroot et al., 2011; Hubert et al., 2012). While techniques exist for standardizing data for some of these differences (i.e., mesh size; Shoup and Ryswky, 2016), other details may be more difficult to reconcile (i.e., interaction with hydrology, reef characteristics), and are often not fully reported.

Gear conversion factors have been developed for comparing different sampling gear, using a variety of statistical techniques (i.e., Pelletier, 1998; Gibson-Reinemer et al., 2016). This might be a useful technique to standardize reported densities and species' numbers for oyster reefs, if effects of habitat location and complexity can be reconciled. For example, even when similar gears can be used, their catch efficiencies and deployment techniques can vary dramatically across conditions. Drop samplers were found to have over 90% catch efficiency at small Texas oyster reefs (Zimmerman et al., 1984; Stunz et al., 2010), but this rate is highly correlated to water clarity and wave action (Rozas and Minello, 1997), two variables that are not frequently reported. Improved reporting of full environmental conditions, standardization of gear type for specific habitats, and, as data permit, exploring possible gear conversion factors could help in developing more targeted reef benchmarks than what we present here.

Reef Restoration, Monitoring, and Benchmarks

If we consider the current state of oyster reefs to be the desired reference condition for assessing changes in status and setting goals and policy for restoration (Coen and Luckenbach, 2000; NRC, 2017), this synthesis provides a set of benchmarks based on means and ranges of current values found across the region. These benchmarks help provide an abundance, density and composition of fish and decapod crustaceans expected to occupy a reef. We suggest these benchmarks as gear-dependent goals, using trays and gill nets, the two most versatile gear types used to sample "on-reefs" (tray), and "near-reefs" (gill nets). To effectively develop and use this approach, habitat characteristics that may be driving the differences between reef assemblages, densities, and species richness need to be better documented. Specifically, habitat characteristics, including reef location, complexity, water quality, and reef exposure critically influence occupancy of reefs by nekton, and benchmarks should be developed to reflect these variations. These same habitat characteristics, along with sampling conditions (i.e., winds, currents, waves, tidal conditions) may also impact sampling gear efficiency. Suggested benchmarks should be treated as a general guide for this region, with adjustments made based on knowledge of local reef habitat characteristics and conditions during sampling. Ideally, future data collection will provide for more targeted benchmarks for this region.

Over the last decade, the oyster reef restoration community has developed and increasingly follows detailed guidance for selection of restoration sites (Coen et al., 2004, and further discussed in Coen and Humphries, 2017) and monitoring reef restoration (i.e., Baggett et al., 2015). However, the difference between these original criteria for guiding site selection, and assessing occupancy by fish and decapod crustaceans, is that the characteristics of the species assemblage using a reef may be dependent on variables that do not necessarily limit oyster reef development (e.g., structural complexity). As a result, better quantification of occupancy of oyster reefs by fish and decapod crustaceans would significantly help in predicting effects of reef complexity, or location (Gilby et al., 2018).

With enormous investments targeted for habitat restoration in the nGoM, and continued emphasis on habitat-species linkages through Essential Fish Habitat policy, quantitative and standardized baseline data to establish benchmarks are increasingly important for managers and policy-makers (Baggett et al., 2015; NRC, 2017; Blomberg et al., 2018a). In the nGoM, over 6 billion USD has been designated for restoration of ecosystems (Environmental Law Institute, 2016) as a result of injury settlements. To ensure effective use of these funds, and to support existing policies related to fisheries and habitat management, generation of standardized monitoring metrics and clear benchmarks to help assess restoration and policy outcomes remains critical.

DATA AVAILABILITY STATEMENT

Datasets were taken from the published literature identified in **Table 1**.

AUTHOR CONTRIBUTIONS

ML, DA, and LM reviewed the literature, analyzed and graphed the data. ML and AH conceived the idea, and led the writing. DA and LM contributed to writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00666/full#supplementary-material

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Gene Expression of Endangered Coral (*Orbicella* spp.) in Flower Garden Banks National Marine Sanctuary After Hurricane Harvey

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About 190 km south of the Texas–Louisiana border, the East and West Flower Garden Banks (FGB) have maintained > 50% coral cover with infrequent and minor incidents of disease or bleaching since monitoring began in the 1970s. However, a mortality event, affecting 5.6 ha (2.6% of the area) of the East FGB, occurred in late July 2016 and coincided with storm-generated freshwater runoff extending offshore and over the reef system. To capture the immediate effects of storm-driven freshwater runoff on coral and symbiont physiology, we leveraged the heavy rainfall associated with Hurricane Harvey in late August 2017 by sampling FGB corals at two time points: September 2017, when surface water salinity was reduced (∼34 ppt); and 1 month later when salinity had returned to typical levels (∼36 ppt in October 2017). Tissue samples (N = 47) collected midday were immediately preserved for gene expression profiling from two congeneric coral species (*Orbicella faveolata* and *Orbicella franksi*) from the East and West FGB to determine the physiological consequences of storm-derived runoff. In the coral, differences between host species and sampling time points accounted for the majority of differentially expressed genes. Gene ontology enrichment for genes differentially expressed immediately after Hurricane Harvey indicated increases in cellular oxidative stress responses. Although tissue loss was not observed on FGB reefs following Hurricane Harvey, our results suggest that poor water quality following this storm caused FGB corals to experience sub-lethal stress. We also found dramatic expression differences across sampling time points in the coral's algal symbiont, *Breviolum minutum*. Some of these differentially expressed genes may be involved in the symbionts' response to changing environments, including a group of differentially expressed post-transcriptional RNA modification genes. In this study, we cannot disentangle the effects of reduced salinity from the collection time point, so these expression patterns could also be related to seasonality. These findings highlight the urgent need for continued monitoring of these reef systems to establish a baseline for gene expression of healthy corals in the FGB system across seasons, as well as the need for integrated solutions to manage stormwater runoff in the Gulf of Mexico.

Keywords: coral reef, Flower Garden Banks (FGB) National Marine Sanctuary, *Orbicella faveolata*, *Orbicella franksi*, gene expression, Hurricane Harvey

INTRODUCTION

Reef-building corals are among the tropical marine species most vulnerable to the effects of hurricanes (Woodley et al., 1981; Gardner et al., 2005). Coral colonies can be impacted by hurricanes via physical damage from waves, smothering by sediments (Highsmith et al., 1980; Bries et al., 2004), and reductions in water quality (e.g., Manzello et al., 2013; Edmunds, 2019; Nelson and Altieri, 2019). Low salinity caused by heavy rainfall associated with extreme storms can trigger mass loss of the algal endosymbionts of corals (Family Symbiodiniaceae, Goreau, 1964; Bries et al., 2004; LaJeunesse et al., 2018; Pengsakun et al., 2019). Increased turbidity due to terrestrial runoff during storms can significantly reduce light penetration over reefs, which diminishes the algal symbionts' photosynthetic efficiencies. For example, Hurricanes Irma and Maria caused temporary periods of complete daytime darkness at a depth of 19 m on a reef off St. John in the US Virgin Islands in 2017 (Edmunds, 2019). As a result, these storms caused a 20% reduction in daily integrated underwater photosynthetic photon flux density over a period of 69 days. Coral calcification can be directly impacted by reduced water quality following hurricanes. For example, Tropical Storm Isaac in 2012 caused a week-long reduction in aragonite saturation state along the Florida Keys reef tract, which could potentially cause a decrease in coral calcification (Manzello et al., 2013). Terrestrial runoff following extreme storms can increase nutrient levels in these normally oligotrophic reef-associated waters, causing bacterial blooms that can ultimately trigger oxygen drawdown and suffocation of reef organisms (e.g., Kealoha, 2019; Nelson and Altieri, 2019). An overview of the diverse mechanisms by which shifts in water quality can trigger low dissolved oxygen conditions is provided in Nelson and Altieri (2019).

Flower Garden Banks (FGB) National Marine Sanctuary, in the northwest Gulf of Mexico, which harbors one of the few remaining reef systems in the wider Caribbean with > 50% coral cover (Gardner et al., 2003; Johnston et al., 2016), sits southeast of Galveston Bay and thus is at risk of exposure to terrestrial freshwater runoff generated by hurricanes. Hurricane Harvey, the focal storm of this study, intensified to a Category 4 storm over the Gulf of Mexico on 24 August 2017 and made landfall on the Texas coast shortly after. The storm stalled over land for several days, resulting in an estimated 33 trillion gallons of rainfall and more than 100,000 damaged homes in Texas and Louisiana (Shultz and Galea, 2017; van Oldenborgh et al., 2017). In the weeks following the storm's retreat, Galveston Bay experienced heavy freshwater outflow, that elevated sea levels for more than four days and reduced salinity to nearly zero at multiple monitoring stations in the bay (Du et al., 2019). Besides being hyposaline, this storm-derived runoff contained high nutrients levels and other compounds of terrigenous origin, that had the potential to shift pelagic bacterial and zooplankton communities and their associated processes (Lefebure et al., 2013; Jonsson et al., 2017), and to impact the health of organisms that came in contact with the runoff (Liñán-Cabello et al., 2016).

While Hurricane Harvey did not cause direct physical damage to FGB coral reefs, impacts from the storm runoff were of particular concern given that approximately 1 year earlier (July 2016) benthic invertebrates in a 5.6 ha area (2.6% of the site) of the East FGB experienced a highly localized mortality event that was associated with freshwater runoff. The 2016 mortality event caused partial or full mortality of an estimated 82% of monitored coral colonies, as well as many other benthic invertebrates, within the affected area (Johnston et al., 2019). While no water quality data were collected near the coral cap at the mortality site during the 2016 die-off, surface and deep (200 m) salinity, temperature, and carbonate chemistry measurements collected from the area soon after the event suggest low dissolved oxygen played a critical role (Kealoha, 2019). Heavy rainfall along the coast immediately before the 2016 mortality event resulted in unusually high levels of freshwater runoff. This runoff extended offshore to the FGB but was restricted to a thin surface layer that did not directly interact with the reefs, however, it likely contributed to an increase in net respiration on the reef, water stratification, and reduced gas exchange at the affected site (Kealoha, 2019). Given the FGB's recent history of coral mortality following high levels of freshwater runoff, the aim of this study was to identify the immediate physiological impacts of a major storm (Hurricane Harvey in 2017) in the same reef system: the East and West FGB. Two congeneric coral species (*Orbicella faveolata* and *Orbicella franksi*) were sampled at two time points: immediately after Hurricane Harvey in September 2017 and 1 month later. Global gene expression profiling of these corals and their photosynthetic algal symbionts (*Breviolum minutum*) was conducted to determine the physiological consequences of runoff generated by an extreme storm on dominant reef-building coral species in the FGB.

MATERIALS AND METHODS

Pelagic Water Properties After Hurricane Harvey

Water properties, including salinity (ppt) and temperature (°C), were measured by the Texas Automated Buoy System

(TABS) Real Time Ocean Observations, Buoy V (27° 53.7960′N, 93° 35.8380′W; sensor depth 2m), before, during, and after coral sampling. Buoy V is approximately 3km from the EFGB and 25km from the WFGB. Data were downloaded from the archives: http://tabs.gerg.tamu.edu/tglo/tabsqueryform.php?buoy=V. Unfortunately, water property data at TABS Buoy V do not exist for much of August 2017, including when Hurricane Harvey formed over the Gulf of Mexico (approximately 25 August 2017). Surface salinity and temperature were reduced in the days prior to the September coral collection (red lines in **Figure 1**), presumably due to anomalous freshwater runoff effects from the storm. Surface salinity returned to normal levels by the second collection time point (October 2017; **Figure 1** top right dashed line). Henceforth, we refer to the first sampling time point (September 2017) as "sub-lethal stress" and the second sampling time point (October 2017) as "recovery" to describe the hypothesized effects of the storm on the coral and its algal symbiont at those times.

Coral Collections

Tissue fragments were collected from individually tagged *O. faveolata* and *O. franksi* coral colonies in FGB (northwest Gulf of Mexico) during periods of "sub-lethal stress" (on 16 September 2017, EFGB only) and "recovery" (October 21–24, 2017, East and West Banks, **Supplementary Table 1**). In total, 23 samples of *O. faveolata* and 24 samples of *O. franksi* were collected over the two sampling periods (**Table 1**).

The depths of sampled colonies ranged from 19.2 to 24.1 m. Details on the locations and depths of samples collected for each coral species are provided in **Supplementary Table 1**. Samples were collected from the tops of colonies using a hammer and a species-specific chisel and were immediately placed in pre-labeled upside-down 15 mL falcon tubes containing 200 proof molecular grade EtOH free of air bubbles.

Gene Expression Library Preparation

RNA was isolated from 47 coral tissue samples using the RNAqueous-Micro Total RNA Isolation Kit (Invitrogen). Coral fragments (∼1 cm^2 tissue) were fully submerged in tubes containing 150 μL of lysis buffer and glass beads (Sigma, 150–212 μm). Samples were placed in a bead blaster at 5 m/s for 1 min and then centrifuged at a speed of 16.5 × g for 1 min. The supernatant was transferred to a new tube and centrifuged again at 16.5 × g for 2 min, and then transferred to a final tube. RNA was eluted, washed, and DNased using 10 × DNase I. First-strand synthesis, cDNA amplification, barcoding, and pooling were performed according to an established protocol (Meyer et al., 2011; Dixon et al., 2015). We used a polyT primer to enrich for polyadenylated mRNA during first-strand synthesis. A total of 47 gene expression libraries were prepared in-house following the Tag-Seq protocol mentioned above (Meyer et al., 2011), with 20 from September 2017 and 27 from October 2017. Libraries were sequenced on the HiSeq 2500 (Illumina) at Tufts University Core Facility (Boston, MA). Sequenced reads have been uploaded to the National Center for Biotechnology Information Short Read Archive under accession number PRJNA552981.

Gene Expression Analysis

Adapter sequences were trimmed and low quality reads (minimum quality score = 20; minimum percent bases above

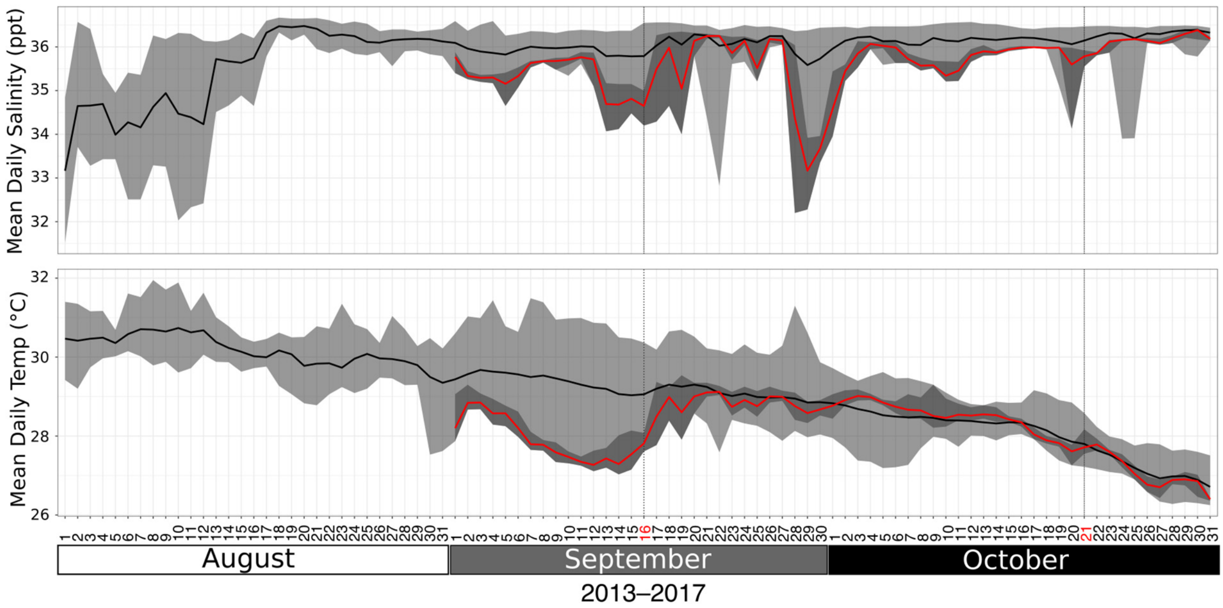

FIGURE 1 | Salinity (ppt, **top**) and temperature (°C, **bottom**) at buoy V near the coral sampling sites at the East and West Flower Garden Banks for the weeks surrounding the time of sampling. Black lines represent daily means from 2013–2017. Light gray ribbons encompass minimum and maximum values from 2013–2017. Red lines and dark gray ribbons encompass daily means and ranges, respectively, throughout September 2017 and October 2017. Dates in red (16 September and 21 October, vertical dashed lines) highlight the sampling days in 2017.

TABLE 1 | Overview by species, location, and time of the 47 coral colonies sampled from the East and West Banks of Flower Garden Banks National Marine Sanctuary (northwest Gulf of Mexico) in this study.

	East FGB	West FGB	Total
Orbicella faveolata			
September 2017	10	0	10
October 2017	6	7	13
Total	16	7	23
Orbicella franksi			
September 2017	10	0	10
October 2017	6	8	14
Total	16	8	24

minimum quality score = 90%) were filtered using FASTX tools (Hannon, 2010). Reads were mapped to a composite coral host and algal symbiont transcriptome, which included concatenated sequences from the coral, *O. faveolata* (Pinzon et al., 2015), and its algal symbiont, *B. minutum* (Parkinson et al., 2016), using Bowtie 2 (Langmead and Salzberg, 2012). Given that only *B. minutum* and its haplotypes have been reported from *O. faveolata* and *O. franksi* in the FGB to date (Santos and LaJeunesse, 2006; Green et al., 2014), this species was the only algal reference transcriptome used. Statistical analyses were conducted in R version 3.4.0 (R Core Team, 2017). Isogroups (henceforth called "genes") with a base mean < 3 across all samples were removed from the analysis. Expression sample outliers were detected using *arrayQualityMetrics* (Kauffmann et al., 2009). Differentially expressed genes (DEGs) were identified using *DESeq2* (Love et al., 2014). Wald tests were performed to calculate contrasts between sampling time points, host species, and collection location (i.e., EFGB or WFGB). Additionally, we performed Wald tests on the subset of samples from only the second collection to further investigate site effects. Log-fold change (LFC) values for sampling time point are expressed relative to the October collection (e.g., negative LFC indicates upregulation in September relative to October or, equivalently, downregulation in October relative to September). False-discovery rate (FDR) *p*-values were adjusted using the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995). Permutational analysis of variance testing on Manhattan dissimilarity matrices was performed using *vegan* (Dixon, 2003) to assess overall transcriptomic differences across samples. Gene expression heat maps were generated using *pheatmaps* (Kolde, 2012) and gene ontology enrichment was performed based on signed adjusted *p*-values using *GO-MWU* (Wright et al., 2015).

RESULTS

Gene Expression Associated With Coral Host, Sampling Time Point, and Collection Site

An average of 1.85×10^6 host reads per sample and 0.2×10^6 symbiont reads per sample remained after quality filtering and mapping to the *O. faveolata* and *B. minutum* transcriptomes. Both coral host species were mapped to the *O. faveolata* transcriptome, but we observed no significant difference in mapping efficiency between *O. faveolata* (50.7 ± 7.9%) and *O. franksi* (47.0 ± 10.3%, analysis of variance [ANOVA] $p = 0.179$, $F = 1.9$). In the coral host, differences between *Orbicella* species (analysis of variance using a distance matrix [ADONIS] $p = 0.008$, $F = 2.3$) and sampling time points (ADONIS $p = 0.026$, $F = 2.0$) explain the majority of the observed differences in gene expression profiles (**Figure 2A**). There was no significant variance in host gene expression associated with sampling locations

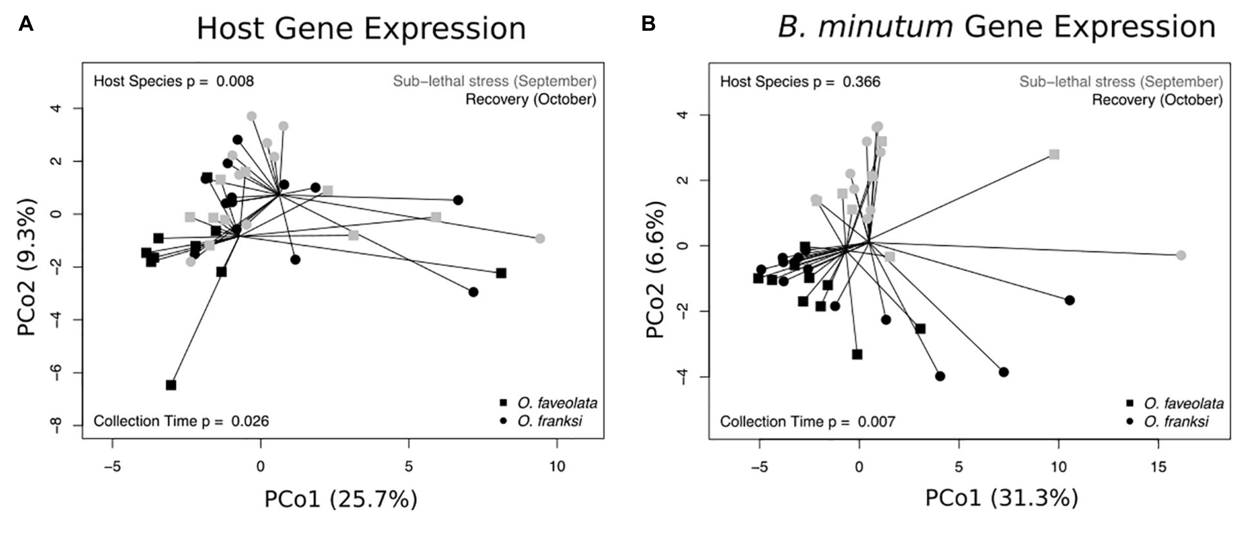

FIGURE 2 | Principal coordinates analysis for coral host **(A)** and *B. minutum* **(B)** gene expression profiles. Each point is a sample and points closer together exhibit more similar expression profiles. Spider lines connect samples originating from the same coral species (*Orbicella faveolata* or *Orbicella franksi*), as indicated. Colors indicate whether the sample was collected during the sub-lethal stress (September, gray) or recovery (October, black) period. *P*-values were generated by permutational multivariate analysis of variance using distance matrices.

(ADONIS $p = 0.063$, $F = 0.037$). *B. minutum* expression profiles were impacted by sampling time point (ADONIS $p = 0.007$, $F = 3.1$), but not host species (ADONIS $p = 0.366$, $F = 0.99$) or sampling location (ADONIS $p = 0.125$, $F = 1.4$) (**Figure 2B**).

We used an adjusted p-value threshold of 0.05 calculated by the Wald test to identify significantly differentially expressed genes (DEGs) in the coral host (**Figure 3A**) and algal symbiont, *B. minutum* (**Figure 3B**). In the coral host, we identified 769 (3.9% of transcriptome) and 265 (1.3% of transcriptome) DEGs when comparing between species (*O. faveolata* vs. *O. franksi*) and time (September sub-lethal stress vs. October recovery), respectively. Fifteen genes were significantly differentially expressed between the EFGB and WFGB sampling locations in the coral host (0.08% of transcriptome). In *B. minutum*, we identified 1,471 (4.6% of transcriptome) and 21 (0.07% of transcriptome) DEGs when comparing between time (September sub-lethal stress vs. October recovery) and sampling location (EFGB vs. WFGB), respectively. We found only two DEGs when comparing *B. minutum* expression between the two coral host species (<0.01% of transcriptome).

When we performed differential expression analysis to model differences by coral species and site on a subset of the data (second time point only; first time point excluded because data for WFGB were not available), we still found little differential expression between site. Only one gene was differentially expressed across coral hosts between EFGB and WFGB, and 13 DEGs were identified between algal symbionts from different banks.

Gene Ontology Enrichment

In the coral host, gene ontology (GO) categories enriched during the sub-lethal low salinity stress event (September 2017) included antioxidant activity (Mann–Whitney U [MWU] $p = 0.013$), cell redox homeostasis (MWU $p = 0.039$), and mitochondrial membrane parts (MWU $p = 4.04e{-7}$) (**Supplementary Table 2**). When normal salinity levels had returned, during the "recovery" time point, many categories related to growth and cellular propagation were enriched within up-regulated genes, such as cell division (MWU $p = 0.003$) and organelle fission (MWU $p = 0.003$). No GO terms were significantly enriched when comparing genes differentially expressed by either host species or sampling location.

The annotated coral host genes differentially regulated across the sub-lethal stress and recovery periods are shown in **Figure 4**. Relative to the recovery period, corals under sub-lethal low salinity stress up-regulated small cysteine rich protein 4 (LFC = −3.48, FDR = 4.2e–8) and down-regulated protein WNT-5 (LFC = 1.76, FDR = 0.006).

In the algal symbiont, *B. minutum,* enriched GO categories under sub-lethal low salinity stress conditions (September 2017) included oxidoreductase activity ($p = 0.03$) and transmembrane transport ($p = 2.76e{-5}$) (**Supplementary Table 3**). When average salinity levels had returned in October 2017 (i.e., during "recovery"), many GO categories related to DNA replication and RNA splicing were enriched with up-regulated genes (**Supplementary Table 3**). RNA splicing was also enriched in algal symbionts hosted by *O. faveolata* relative to algal symbionts hosted by *O. franksi* (**Supplementary Table 3**).

In *B. minutum*, the majority of significant DEGs were upregulated during the recovery period (October 2017) or, equivalently, downregulated during the sub-lethal salinity stress event in September 2017 (**Figure 5**). These genes include an RNA helicase (LFC = 2.0, FDR = 4.85e–5) and a nonsense-mediated mRNA decay protein (LFC = 1.5, FDR = 1.80e–5).

DISCUSSION

Transcriptomic Effects of Freshwater From Hurricane Harvey on Coral Holobionts

The objective of this study was to use global gene expression profiling to determine the effects of a low salinity event associated with freshwater from Hurricane Harvey on two species of coral hosts and their algal symbionts in the FGB (northwest Gulf of Mexico). Based on differences in pelagic water parameter data and coral holobiont gene expression differences between the two sampled time periods, we interpret that FGB coral and their symbionts were exhibiting early signs of stress as a result

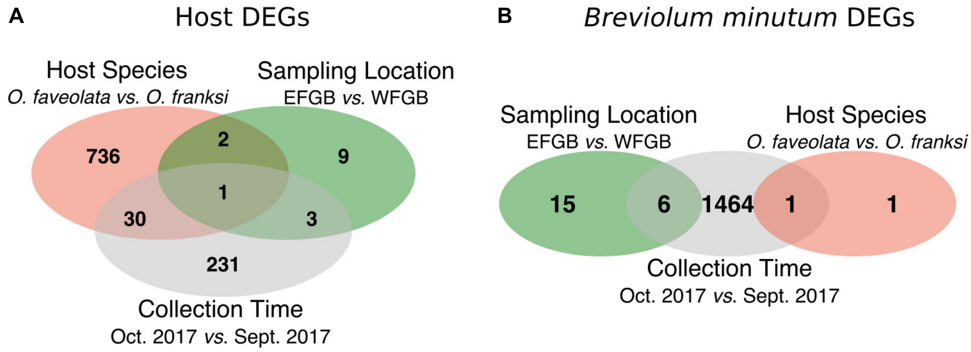

FIGURE 3 | Venn-diagrams specifying the number of unique and shared differentially expressed genes (adjusted p-value < 0.05) by *Orbicella* host species, sampling location, and collection time point (September sub-lethal stress and October recovery) in the coral hosts **(A)** and *Breviolum minutum* **(B)**.

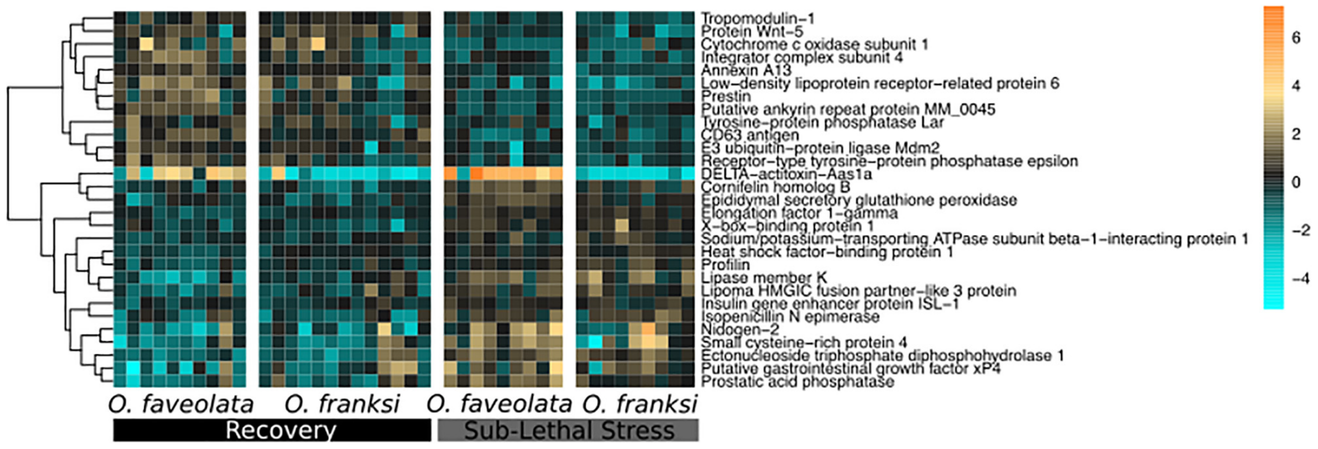

FIGURE 4 | *Orbicella* spp. host gene expression differences across collection time points: sub-lethal stress vs. recovery (September 2017 vs. October 2017, FDR < 0.01). Rows are genes and columns are samples. The color scale indicates log2-fold change relative to the mean expression of each gene across all samples. Genes are hierarchically clustered based on Pearson's correlations of expression across samples. Coral species are indicated below each column. Rectangles below coral species labels indicate the collection time point (black = October 2017 recovery; gray = September 2017 sub-lethal stress).

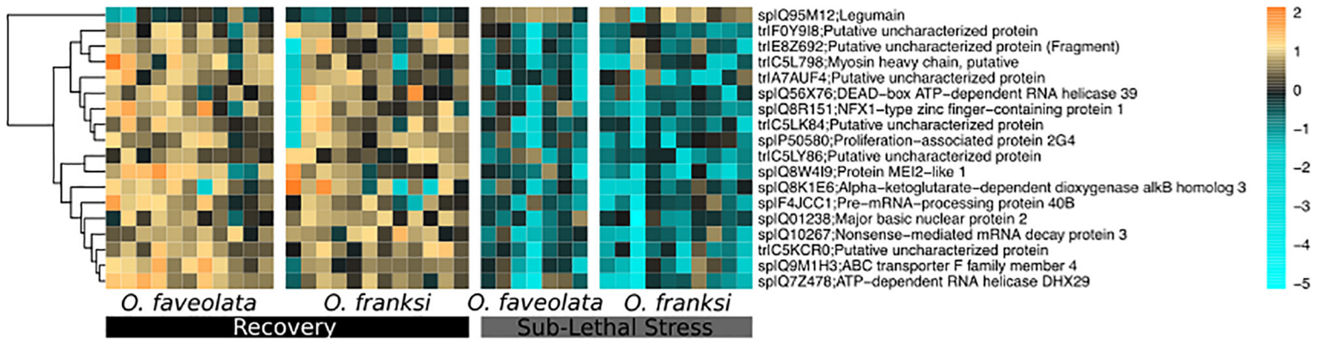

FIGURE 5 | *Breviolum minutum* gene expression differences across sampling time: sub-lethal stress vs. recovery (September 2017 vs. October 2017, FDR < 0.0001). Rows are genes and columns are samples. The color scale indicates log2-fold change relative to the mean expression of each gene across all samples. Genes are hierarchically clustered based on Pearson's correlations of expression across samples. Coral species are indicated below each column. Rectangles below coral species labels indicate the collection time point (black = October 2017 recovery; gray = September 2017 sub-lethal stress.

of freshwater runoff in September 2017, but that the influence of this freshwater influx was alleviated (i.e., recovered) by late October 2017. Conditions at the time of collection did not allow a complete sampling scheme that included individuals from each at both time points. We accounted for differences in expression by site by including sampling location as a covariate in the statistical model. Additionally, we ran differential expression analysis on a subset of the data that included both species from the East and West FGB. In either instance, we observed fewer than 30 genes differentially expressed across sites from either the coral host or algal symbiont compared with hundreds of DEGs by coral species or collection time point, suggesting that sampling location had a minimal effect on holobiont expression.

The TABS buoy that provided salinity data used in this analysis measured salinity near the surface and thus may not represent salinity experienced at depth (19–24 m for corals observed in this study). The analysis for contributing causes of coral mortality from the 2016 mortality event also rely on observations of reduced surface salinity (minimum 23 ppt; Johnston et al., 2019). While we cannot confirm saline conditions experienced by the corals at depth during the 2016 mortality event or after Hurricane Harvey in 2017, this study adds to mounting evidence that hyposaline surface conditions contribute to stress in benthic organisms.

Oxidative Stress in the Coral Host

Corals are osmoconformers: when exposed to hyposaline conditions, water flows into their cells, thereby reducing internal cellular osmotic pressure (Titlyanov et al., 2000). The amount of damage cells sustain under reduced salinity depends on the extent of this osmotic pressure reduction and the length of time that cells are exposed to the stress (Berkelmans et al., 2012). *Stylophora pistillata* fragments exposed to five salinity concentrations ranging from 20–32 ppt showed increasingly severe cellular pathologies, including cell swelling and symbiont expulsion, with decreasing salinity (Downs et al., 2009). Within the coral cell, osmotic changes disrupt electron transport at mitochondrial membranes and increase reactive oxygen species produced by mitochondria. Consequently, robust mitochondrial antioxidant function is thought to be a major determinant of cellular management of osmotic stress (Pastor et al., 2009).

In both coral host species, GO categories were enriched with genes involved in antioxidant activity and mitochondrial structural components, suggesting the presence of oxidative damage that may compromise mitochondrial function (**Supplementary Table 2**). A recent experimental study in *Acropora millepora*, a reef-building coral in the Great Barrier Reef, also found a strong antioxidant response to reduced salinity (Aguilar et al., 2019), suggesting that this response mechanism is conserved across coral genera. The upregulation of antioxidant-encoding genes has been described in corals exposed to a variety of biotic and abiotic threats, including increased temperature (Barshis et al., 2013; Dixon et al., 2015), acidification (Davies et al., 2016; Lopes et al., 2018), and disease (Wright et al., 2015, 2017; Daniels et al., 2015).

Given the diversity of stressors that trigger redox responses in corals, sub-lethal oxidative damage resulting from one stressor may contribute to coral declines when multiple threats occur simultaneously or successively (Adjeroud et al., 2009; Carilli et al., 2009). This study adds to the large body of evidence that genetic markers for antioxidant capability may be useful reef management tools to monitor coral health in the face of multiple climate change-related stressors (Jin et al., 2016).

Expression Responses in *B. minutum*

At the FGB, both *Orbicella* species investigated here have been found to exclusively host *B. minutum* (Santos and LaJeunesse, 2006; Green et al., 2014), although subtle haplotype differences within *B. minutum* have been detected between these two host species as well as between the East and West FGB (Green et al., 2014). When comparing gene expression of the algal symbiont, we found only one *B. minutum* gene uniquely differentially expressed between coral hosts and 15 *B. minutum* DEGs between sampling locations (**Figures 3B**, **5**). In *B. minutum*, collection time point had the strongest association with the observed variance in gene expression (**Figure 2B**).

This gene expression response is in contrast to previous studies investigating the effects of multiple stressors on algal symbiont gene expression, which generally detect a paucity of expression changes and these changes are muted relative to their coral hosts (Leggat et al., 2011; Barshis et al., 2014; Davies et al., 2018, but see Baumgarten et al., 2013). One potential explanation is that we sampled before host buffering or acclimatization mechanisms diminished the symbiont response (e.g., Takahashi et al., 2013; Maboloc et al., 2015). Furthermore, our findings may be influenced by additive or interactive effects between post-storm water quality metrics and seasonal fluctuations (Brown et al., 1999), which have not been explicitly characterized in Symbiodiniaceae *in hospite* to our knowledge.

A major category of genes differentially expressed in *B. minutum* across time points is associated with RNA-modification (**Supplementary Table 3**; **Figure 5**). These candidates include a gene encoding a nonsense-mediated RNA decay protein (LFC = 1.5, FDR = 1.8e–5; **Figure 5**) and a gene encoding Regulator of Nonsense Transcripts 1 homolog (sp| Q9HEH1, LFC = 1.7, FDR = 0.03), which were both downregulated in September 2017 during the storm-induced low salinity period. In plants and mammals, nonsense-mediated decay (NMD) is inhibited during stress to allow proper activation of stress response functions. For example, inhibition of NMD under hypoxia augments the cellular stress response in mammalian cells (Gardner, 2008) and inhibition of NMD in plant cells under pathogen attack stimulates plant defenses (reviewed in Shaul, 2015). In our study, the downregulation of NMD-related genes may indicate symbiont stress sustained as a result of hyposalinity. Furthermore, a gene encoding Regulator of Nonsense Transcripts 1 homolog was also found to be differentially expressed in another coral symbiont, *Durusdinium* (formerly *Symbiodinium*) *trenchii*, within a juvenile *Acropora tenuis* host under benign conditions (Yuyama et al., 2018), suggesting that the gene product may play a role in normal interactions between the coral host and algal symbiont.

While these gene expression differences may be responses to the sub-lethal low salinity stress event associated with Hurricane Harvey experienced in September 2017, we also cannot disentangle responses to this event from seasonal changes occurring between the sampling time points, which would include lower light levels associated with slightly shorter and cooler days on average (**Figure 1**). Based on previous experimental studies conducted in other systems, the salinities observed at FGB in September 2017 may not have been low enough to trigger a response in the symbiont. Experimental exposures to low salinity (15–33.5 ppt) in *S. pistillata* caused symbiont loss coincident with reductions in photosynthetic efficiency (Kerswell and Jones, 2003). However, in that experiment, salinities above 29 ppt failed to elicit an algal response. In another experiment, Symbiodiniaceae hosted by juvenile *Tridacna gigas* (giant clam) exhibited cell swelling, degradation, and pigment reductions at 18 ppt for 14 days, but algal cells within the clams were able to acclimatize to reduced salinity at 25 ppt (Maboloc et al., 2015). Thus, tank-based salinity stress experiments on *Orbicella* spp. holobionts from FGB can further confirm (or undermine) the conclusion that reduced salinity caused the gene expression changes we observed in *B. minutum* in the September 2017 samples. Regardless, our results inform our broader understanding of when and to what extent algal symbionts respond to changing environments and hosts.

Transcriptomic Differences Between *Orbicella* Species

In the animal host, differences between congeneric coral species explained the most variation in expression (**Figures 2**, **3A**). Coral transcripts from both species represented in this study were mapped to the *O. faveolata* transcriptome and both species had similar mapping efficiencies to this reference. Previously classified as sister species within the genus *Montastraea*, *Orbicella faveolata,* and *O. franksi* are largely sympatric (Weil and Knowlton, 1994) and have many shared physical attributes that make them difficult to distinguish morphologically, though genetic variant analysis can resolve each species (Manzello et al., 2018). Differential gene expression between the two species that occurs independently of the effects of Hurricane Harvey are not the focus of this study, but do deserve consideration. The sequence datasets generated here can contribute to further research into species-specific coral expression, which, to our knowledge, has not been directly compared in these species. The top DEG between the two coral species shares substantial homology with an anemone (*Anthopleura asiatica*) toxin: DELTA-actitoxin-Aas1a (Kohno et al., 2009). This transcript, which was much more highly expressed in *O. faveolata* (LFC = 7.44, FDR = 3.98e−22), may indicate species-specific toxins that have yet to be characterized in these corals. We did not find any enriched GO categories between these coral species.

In *B. minutum*, coral host species had almost no effect on gene expression (**Figures 2**, **3B**). The one transcript that was differentially regulated between the two host species (LFC = 2.18, FDR = 1.03e−6) was unannotated in the transcriptome but shares sequence homology with an S-antigen protein (identity = 40.9%, *E*-value = 7.9e−68). Characterization of this protein is largely limited to variants associated with immune reactions in humans (e.g., Nussenblatt et al., 1982). Given the importance of host immune activation during the establishment and maintenance of symbiosis in corals (Mansfield et al., 2019) and the fact that these species have been found to host subtly different symbiont populations (Green et al., 2014), this differentially regulated transcript with antigenic potential deserves further investigation for its potential role in host–symbiont recognition.

Implications for Impacts of Future Storms on Reefs

The water surge that completely reduced salinity within Galveston Bay during Hurricane Harvey (Du et al., 2019) did not reduce salinity beyond levels observed in the past 5 years at FGB (**Figure 1**), probably because the water mass did not pass directly over the reef itself. Fortunately, the coral holobionts observed in this study were not exposed to extreme hyposalinity and the salinity reduction that did occur was quickly alleviated. Sustained reductions in salinity can result in mass coral mortality. In 1963, Hurricane Flora reduced coral reef salinity on several reefs in Eastern Jamaica to 3 ppt days after the storm and the region remained below 30 ppt for more than 5 weeks (Goreau, 1964). As a result, multiple genera of corals in the region experienced substantial coral bleaching, though many colonies recovered fully within a few months. In 1987, heavy rains in Kaneohe Bay, Hawaii substantially reduced salinity and caused mass coral mortality (Jokiel et al., 1993). Some species of corals (e.g., *Porites compressa*) in Kaneohe Bay recovered well, and comparisons to past mortality events support the ability of entire reefs to recover within 5–10 years if other stressors, such as pollution, are minimized. Coral reefs today suffer increasingly frequent stress events (Hughes et al., 2018). A recent study shows that hurricanes in the Gulf of Mexico are expected to increase in frequency and intensity, leading to increased flooding and runoff from coastal regions (Marsooli et al., 2019). Our findings indicate that floodwaters following storms can trigger sub-lethal stress in corals, even when salinities remain fairly high; these impacts should be monitored and considered when assessing the cumulative threats to reef health.

CONCLUSION

Though the observed corals survived the effects of Hurricane Harvey in the summer of 2017, storm-driven flooding from the Tax Day Flood in Houston, TX, United States on this reef the previous summer caused a highly localized die-off event of corals and other marine invertebrates (Johnston et al., 2019; Kealoha, 2019). These events emphasize the urgency to closely monitor the health of coral reefs subjected to multiple anthropogenic threats of increasing severity. Experimental evidence demonstrates that osmotic challenges more extreme than those observed in the FGB following Harvey can cause coral mortality and compromise photosynthetic function of their algal symbionts (Kerswell and Jones, 2003; Downs et al., 2009). However, our genome-wide gene expression analysis of two coral species and their associated symbionts in the FGB following Hurricane Harvey suggests that these endangered animals suffered sub-lethal stress, specifically related to redox state and mitochondrial function, which may compromise their ability to withstand subsequent stress (Adjeroud et al., 2009). Although these corals were able to recover following Harvey, they are likely to experience storm runoff associated stress in the future as tropical storms increase in frequency and intensity. Monitoring coral health in the Gulf of Mexico is especially urgent considering the massive ongoing coral declines throughout the Caribbean (Rippe et al., 2019). Healthy coral colonies at the FGB sustain the local ecosystem and produce larvae that disperse throughout the Caribbean (Davies et al., 2017), which may help restore those devastated reefs. Establishing baseline physiological measurements, including global gene expression, for this important group of corals can help managers disentangle normal seasonal fluctuations from sub-lethal stress events that may contribute to future mortality events.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the National Center for Biotechnology Information Short Read Archive under accession number PRJNA552981.

AUTHOR CONTRIBUTIONS

RW analyzed gene expression and wrote the manuscript. SD designed the experiment and contributed to the manuscript. AC contributed to the experimental design, collected the samples, and contributed to the manuscript. LQ prepared the gene expression libraries and contributed to the manuscript. LS-V and KS assisted in sample collection and contributed to the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00672/full#supplementary-material

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The Future of Reef Ecosystems in the Gulf of Mexico: Insights From Coupled Climate Model Simulations and Ancient Hot-House Reefs

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Shallow water coral reefs and deep sea coral communities are sensitive to current and future environmental stresses, such as changes in sea surface temperatures (SST), salinity, carbonate chemistry, and acidity. Over the last half-century, some reef communities have been disappearing at an alarming pace. This study focuses on the Gulf of Mexico, where the majority of shallow coral reefs are reported to be in poor or fair condition. We analyze the RCP8.5 ensemble of the Community Earth System Model v1.2 to identify monthly-to-decadal trends in Gulf of Mexico SST. Secondly, we examine projected changes in ocean pH, carbonate saturation state, and salinity in the same coupled model simulations. We find that the joint impacts of predicted higher temperatures and changes in ocean acidification will severely degrade Gulf of Mexico reef systems by the end of the twenty-first century. SSTs are likely to warm by 2.5–3°C; while corals do show signs of an ability to adapt toward higher temperatures, current coral species and reef systems are likely to suffer major bleaching events in coming years. We contextualize future changes with ancient reefs from paleoclimate analogs, periods of Earth's past that were also exceptionally warm, specifically rapid "hyperthermal" events. Ancient analog events are often associated with extinctions, reef collapse, and significant ecological changes, yet reef communities managed to survive these events on evolutionary timescales. Finally, we review research which discusses the adaptive potential of the Gulf of Mexico's coral reefs, meccas of biodiversity and oceanic health. We assert that the only guaranteed solution for long-term conservation and recovery is substantial, rapid reduction of anthropogenic greenhouse gas emissions.

Keywords: climate change, coral reefs, coral bleaching, hot-house paleoclimates, adaptation, ocean acidification

1. INTRODUCTION

Coral Reefs constitute some of the most biodiverse ecosystems in Earth's oceans. They are critical to the socioeconomic health of 500 million people globally, providing billions of dollars in tourism and food sources for island and coastal communities (Frieler et al., 2013). Coral reefs support 25% of all of Earth's marine species during various stages of their life cycle (NOAA Ocean Service Education, 2017) and throughout geological time reefs have produced high diversity in Earth's oceans (Kiessling et al., 2010). Anthropogenic climate change is threatening reefs globally via multiple stressors including higher water temperatures, changes in water acidity, and fluctuating salinity. Today, there are no coral reefs left on the planet in pristine condition (Jackson et al., 2001; Hughes et al., 2003). Long-term surface temperature observations show a rate of global warming of 0.13°C per decade since 1979 (Trenberth et al., 2007), with an increase to 0.27°C per decade measured from 1985 to 2009 (Chollett et al., 2012).

Anthropogenic climate change affects coral biology via multiple compounding pathways (Rodolfo-Metalpa et al., 2011; Prada et al., 2017); multiple pressures (e.g., warming and acidification) combine to be significantly more damaging than either stressor alone. The majority of shallow-water, reef building corals are a holobiont consisting of an animal host (the coral) and zooxanthellae (photosynthetic endosymbiotic dinoflagellates of the family Symbiodiniaceae; LaJeunesse et al., 2018); this holobiont produces a skeleton made of calcium carbonate (aragonite). Scleractinian corals (or stony corals) are stenohaline and typically prefer a narrow range of water temperatures and carbonate saturation states. While they do have the ability to modify the saturation state ($\Omega_{aragonite}$) of the fluid from which they calcify their skeleton (e.g., Cohen and Holcomb, 2009; Ries et al., 2010; Anthony et al., 2011; Comeau et al., 2017a,b), changes in seawater pH and seawater carbonate chemistry can significantly reduce coral biomineralization, diversity, recruitment, and abundance (Fabricius et al., 2011). During times of extreme stress, in particular elevated sea surface temperatures (SST) or acidification, coral will expel their zooxanthellae, resulting in coral bleaching (Anthony et al., 2008; Baird et al., 2009; Frieler et al., 2013); in some cases on a global, sustained scale (Eakin et al., 2019; Skirving et al., 2019).

While much attention has been cast toward the sharp decline of coral reef systems in the Australia's Great Barrier Reef and across the tropical Pacific since the early 1980s (Frieler et al., 2013), considerably less work has been devoted to examining climate projections focused on corals and reef organisms from the Gulf of Mexico (GoM hereafter). The GoM is home to many coral reefs growing along coastal Texas, Louisiana, Florida, and Mexico in the upper ∼1,500 m, and houses a wide array of deep sea coral species (as well as other reef builders, such as sponges) found along the continental shelf and slope (**Figure 1**, **Figures S1, S2**). Most of these reefs are within managed areas including Dry Tortugas National Park and Veracruzano Coral Reef System National Park, Flower Garden Banks and Florida Keys National Marine Sanctuaries, and Florida State Park John Pennekamp. Other coral reefs include Campeche Bank, Tuxpan, Tuxtlas, Yucatan Shelf, Florida Middle Grounds, and Pulley Ridge, the deepest stony coral reef in the US (Waddell and Clarke, 2008; Wilkinson and Souter, 2008; Ortiz-Lozano et al., 2013).

GoM reef systems are subject to myriad anthropogenic stressors including rising SSTs, over-fishing, bleaching, chemical pollution and increasing terrestrial runoff, coral mining, and unrestricted tourism (Jordán-Dahlgren and Rodríguez-Martínez, 2003), as well as disease and sedimentation (Tunnell et al., 2007; Carricart-Ganivet et al., 2011; Horta-Puga et al., 2015). The once structurally complex coral reefs in the GoM and Caribbean have declined since the 1970s, and very few reefs still exhibit a mean live coral coverage >10% (Waddell and Clarke, 2008; Wilkinson and Souter, 2008). The majority of GoM coral reefs are reported to be in poor or fair condition with the exception of Flower Garden Banks (a protected National Marine Sanctuary) in the northern Gulf and Dry Tortugas National Park in the westernmost Florida Keys (Waddell and Clarke, 2008; Wilkinson and Souter, 2008; Johnston et al., 2017). The largest changes, documented since the 1970s, indicate that the most prevalent branching corals, the Acroporid corals, have experienced population declines >90% (Acropora Biological Review Team, 2005). Two of these corals, *Acropora palmata* and *Acropora cervicornis*, are listed as threatened species under the Endangered Species Act of 2006 (Hogarth, 2006). In 2010, the National Marine Fisheries Service found significant evidence to list 82 coral species as threatened species, including eight Caribbean species (NOAA, 2010).

At present, there is strong evidence that GoM reefs have experienced thermal stress since 1878 (Kuffner et al., 2015) with recent bleaching events in 2016/2017 (Johnston et al., 2019a). *In situ* SST records show a 0.8°C increase over the last century in the Florida Keys, where corals have declined especially in the later part of the twentieth century. Observed rates of SST warming are spatially and temporally variable throughout the Gulf, but the highest warming rates tend to occur in summer months (June, July, and August); most recently, the highest heating rates have been observed in the central GoM in the Loop Current region (Chollett et al., 2012; del Monte-Luna et al., 2015; Allard et al., 2016). Multiple studies suggest higher probabilities of coral bleaching in mid-latitude reefs (15–20° of latitude) despite similar levels of thermal stress compared to equatorial reefs (Sully et al., 2019). Coral accretion rates must keep up with the current rate of sea level rise for these ecosystems to survive (Toth et al., 2015); today, sea level rise threatens Florida Keys reefs and other GoM reefs, which cannot keep pace (Shinn, 1976).

Many of the climatic changes affecting the future of coral reefs have been examined in climate model projections. Given a business as usual (RCP8.5) greenhouse gas forcing scenario, simulations from the Climate Model Inter-Comparison Project (CMIP5) indicate that by 2090–2100, temperatures will increase, pH will decrease, oxygen content in the oceans will drop, and there will be a decrease in primary productivity (Bopp et al., 2013; Freeman, 2015). Tropical oceans are warming the fastest of any region globally in most of the CMIP5 projections, but with lower acidification rates. GoM SSTs are projected to rise by 0.37°C per decade. This substantial rise in SST would severely stress GoM coral reefs. Indeed, research shows that Gulf corals are stressed when SSTs approach 31°C; today, summertime temperatures frequently reach 30°C in the Florida Keys and Veracruz. These simulations suggest that more than 50% of coral reefs globally will undergo frequent and severe thermal stress by the year 2080 (Donner et al., 2005).

For this special issue on GoM coral reef systems, we zero in on climate change in the GoM and future threats to the region's reef ecosystems. Recent catastrophic environmental events, such as hurricanes Harvey and Irma (Hickerson et al., 2008; Viehman, 2017), have cast justified attention to GoM

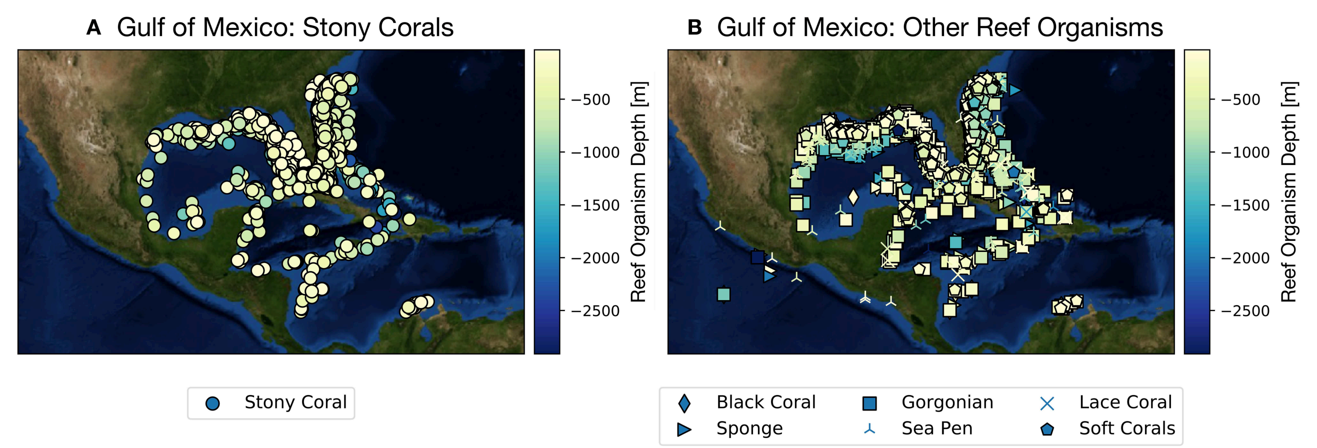

FIGURE 1 | Gulf of Mexico shallow and deep sea coral and sponge sites as reported in the deep sea coral database (NOAA, **Figures S1, S2**). Color scale along y-axis indicates depth of reef organism and symbols denote organism type (e.g., scleractinian coral vs. sponge). **(A)** Scleractinian corals (stony corals), **(B)** all other species reef locations. See also **Figures S1, S2**. From https://deepseacoraldata.noaa.gov/website/AGSViewers/DeepSeaCorals/mapSites.htm.

climate and ocean dynamics, including the well-being of Gulf species and ecosystems (Zavala-Hidalgo et al., 2014). This motivates careful examination of future climate predictions of all relevant variables to accurately capture spatial heterogeneity in reef response. In this work, we address the question: *what changes in climate and ocean chemistry will influence the corals and reef systems in the Gulf of Mexico?* We hypothesize that new model simulations confirm that the GoM will warm and acidify such that substantial coral bleaching will occur. A general circulation model (GCM) with a fully coupled ocean model is employed to test for changes in multiple environmental stressors that impact coral reefs in the GoM through 2100. The individual impacts of changes in temperature, salinity, and ocean acidification are partitioned to drive a more targeted reef impact mitigation plan. We contextualize future impacts to GoM reefs through the lens of geological time, exploring how present-day corals' predecessor species were able to adapt to analogous climate change events in the past. Finally, we discuss the future of GoM reefs in the Anthropocene, and provide a preview of the threats these ecosystems will soon face in this particular region.

2. METHODS

2.1. GCM Simulations

To build a Gulf of Mexico-centric forecast of the various conditions that interfere with coral reef health over the next several decades, we evaluated simulations from the Community Earth System Model version 1.2 (CESM) (Kay et al., 2015). CESM is a state-of-the-art, Intergovernmental Panel on Climate Change (IPCC)-class general circulation model (GCM) developed at the National Center for Atmospheric Research. We compared two periods from a high-CO_2 forcing IPCC representative concentration pathway (RCP) scenario (RCP8.5, which corresponds to 8.5 W/m^2 of radiative imbalance due to anthropogenic greenhouse gas emissions). RCP8.5 assumes a "business as usual" radiative forcing consistent with minimal mitigation; we chose to employ this high-forcing model ensemble in light of the fact that emissions trends over the past few decades track slightly above RCP8.5 (Peters et al., 2012). CESM 1.2 simulations include a large ensemble (n = 33) of simulations spanning the period 2006–2100, from which we extracted four decades (2006–2026 and 2080–2100) for a modern vs. future comparison. From the early twenty-first century control period and the high-CO_2 RCP8.5 scenario, the model ensemble mean was computed for the following variables: SST, salinity (SALT), alkalinity (ALK), dissolved inorganic carbon (DIC), and pH for the upper-most ocean layer of POP2, the ocean model component of CESM. We additionally analyzed the RCP4.5 medium ensemble of CESM1.2 to contextualize the changes in RCP8.5 with those likely under a lower emissions scenario. Note that all of the scripts used in the extraction and analysis of climate model output are documented in section S2, and provided directly in the **Supplementary Material**.

While the CESM model keeps track of the saturation state of seawater with respect to the carbonate minerals calcite and aragonite, these values are not directly included as part of the standard model output. Thus, we recomputed saturation states (Ω) using the MATLAB implementation of the CO2SYS software (https://www.nodc.noaa.gov/ocads/oceans/CO2SYS/co2rprt.html) (Lewis and Wallace, 1998). The CESM model outputs of Alkalinity, DIC, salinity, water depth (pressure), and temperature were used alongside assumptions of phosphate and silicate concentrations of 0 μM, and the dissociation constants of carbonic acid, bicarbonate, and sulfuric acid from Mehrbach et al. (1973); Dickson and Riley (1979); Dickson and Millero (1987), and Dickson (1990). This "offline" approach to evaluating carbonate mineral saturation states also allows us to apportion the predicted changes between each of the input variables by sequentially holding each variable constant at its 2006–2026 mean values and allowing the remaining variables to change.

To evaluate the accuracy of the model predictions for the modern period, the model output was compared to field data from multiple sites within the GoM. The field data were all taken from the Global Ocean Data Analysis Project Version 2 (GLODAPv2) and include sites off of the coasts of Texas, Louisiana, and Florida that range in depth from the surface to 500 m water depth. Using the same CO2SYS approach, the field measurements of alkalinity, DIC, salinity, and temperature were used to calculate $\Omega_{aragonite}$.

2.2. Defining Coral Reef Stress Factors

Based on CESM's available output history files, we define the following stressors on GoM reefs, and examine changes in these stressors from 2006–2026 to 2080–2100. It should be noted that many of these factors are synergistic (e.g., Rodolfo-Metalpa et al., 2011; Prada et al., 2017).

- Degree Heating Months (DHM), a standard predictor for coral bleaching (Gleeson and Strong, 1995; Liu et al., 2003). DHM = 1 refers to heating in excess of or equal to 1°C above the long-term monthly climatology of the warmest month in a given region (Sully et al., 2019). DHM gives a measure of thermal stress applied to corals, which leads to bleaching. DHM is easier to compute given that coupled GCMs usually archived at monthly time steps; however, degree heating weeks (DHW) is considered the more accurate predictor of bleaching (Liu et al., 2003; Kayanne, 2017; Sully et al., 2019).
- SST Variance: Sully et al. (2019) show in a global survey of coral bleaching from 1998 to 2017 that higher SST variance zones over reefs are less susceptible to bleaching.
- Mean annual SST: an upper temperature limit for coral bleaching in the Pacific has been reported as 28.1°C, but more recent work shows an increasing bleaching threshold of 28.7°C (Sully et al., 2019). In the GoM, reported bleaching thresholds are higher, approaching 30–31°C. Wilkinson and Souter (2008) found corals bleached in the Caribbean when SST reached 31°C and were sustained; Florida Keys and Flower Garden Banks reefs bleach when SST reached 30–31°C (Johnston et al., 2019b) or 29.5°C if temperatures were sustained for 50 days (Johnston et al., 2019a). We consider mean annual SSTs approaching 30°C as high risk for coral bleaching in the GoM.
- Salinity: in laboratory experiments, some species of *Acropora* corals are sensitive to low salinity values, exhibiting threshold behavior below ∼22 g/kg (Berkelmans et al., 2012).
- Carbonate Chemistry: The saturation state of seawater with respect to aragonite ($\Omega_{aragonite}$) is an important control on coral growth as modern scleratinian (stony) corals biomineralize an aragonite skeleton. The saturation state of seawater is also a factor in coral growth and reef stabilization. The modern distribution of coral reefs is largely limited to regions of the ocean where $\Omega_{aragonite}$ exceeds 3 (modern distribution threshold; Kleypas et al., 1999; Fine and Tchernov, 2007; Hoegh-Guldberg et al., 2007; Guinotte and Fabry, 2008) and experimental studies suggest that the calcification rate of corals drops to zero when $\Omega_{aragonite}$ reaches 2 (experimental calcification threshold; Langdon et al., 2000; Albright et al., 2008). Nevertheless, there are some examples of corals and low diversity reefs growing in more acidified waters in both natural systems (Fabricius et al., 2011; Shamberger et al., 2014) and in controlled experiments (Cohen and Holcomb, 2009; Ries et al., 2010; Anthony et al., 2011). Finally, $\Omega_{aragonite} = 1$ is a strong thermodynamic limit as, below this value, it is more likely for aragonite to dissolve in seawater than to precipitate.

3. THE FUTURE OF GULF OF MEXICO REEFS IN 21ST CENTURY PROJECTIONS

3.1. SST Changes

Corals demonstrate species-specific variable responses to increasing surface ocean temperatures (Sully et al., 2019) as well as changing carbonate chemistry (Bahr et al., 2018); this response can also vary regionally and within micro-climates. In the GoM, the CESM RCP8.5 ensemble mean SSTs rise to 28.5°C in the northernmost sector of the Gulf, and 29–30°C in the central and southeastern regions (**Figure 2**) for the end of the twenty-first century. There is some indication that global mean thermal bleaching thresholds may be shifting toward warmer temperatures as global SSTs rise (Sully et al., 2019). Nevertheless, the projected annual mean warming for the GoM exceeds the most recent thermal threshold estimates of 30°C (Johnston et al., 2019b) in several locations in the southern and central GoM, especially in the Caribbean.

The difference in 2080–2100 and 2006–2026 average SST is given in **Figure 3**. In most areas of the Gulf of Mexico, temperatures rise by ∼3°C; in the central GoM and the Caribbean, the SST changes are closer to ∼2.2–2.7°C. At 100 m depth, ocean temperatures increase more modestly by 1–1.5°C (**Figure S3**). The corals lining the Texas, Louisiana, and Florida coastlines are likely to experience the greatest temperature stress in the coming decades. Previous analyses of coupled climate model simulations (CMIP3) indicate that SST increases of just 1–1.5°C relative to the pre-industrial era places most reefs at a high risk for long-term degradation; an increase of 2°C will increase the risk of degradation or bleaching to 100% (Frieler et al., 2013). In all zones of the GoM, the change in surface ocean temperatures exceeds 2°C. Thus, the RCP8.5 changes in SST suggest wide-spread bleaching is likely by 2100 if a more aggressive mitigation strategy is not adopted in the coming decades.

To explore the potential influence of increased climate mitigation, we performed the same analysis of SST changes in the CESM RCP4.5 medium ensemble, corresponding to a lower greenhouse gas emissions scenario (**Figure S4**). GoM temperatures rise more modestly by 2060–2080 with lower forcing. While this ensemble only extends to 2080 (precluding a direct comparison of the RCP8.5 2080–2100 conditions), SST changes range from 0.92°C to 1.3°C by 2080. Despite the reduction in warming, this still constitutes changes leading to high risk of long-term degradation as defined by Frieler et al. (2013).

3.1.1. Degree Heating Months

We computed the cumulative number of months above the mean of maximum monthly SST climatology in each GoM

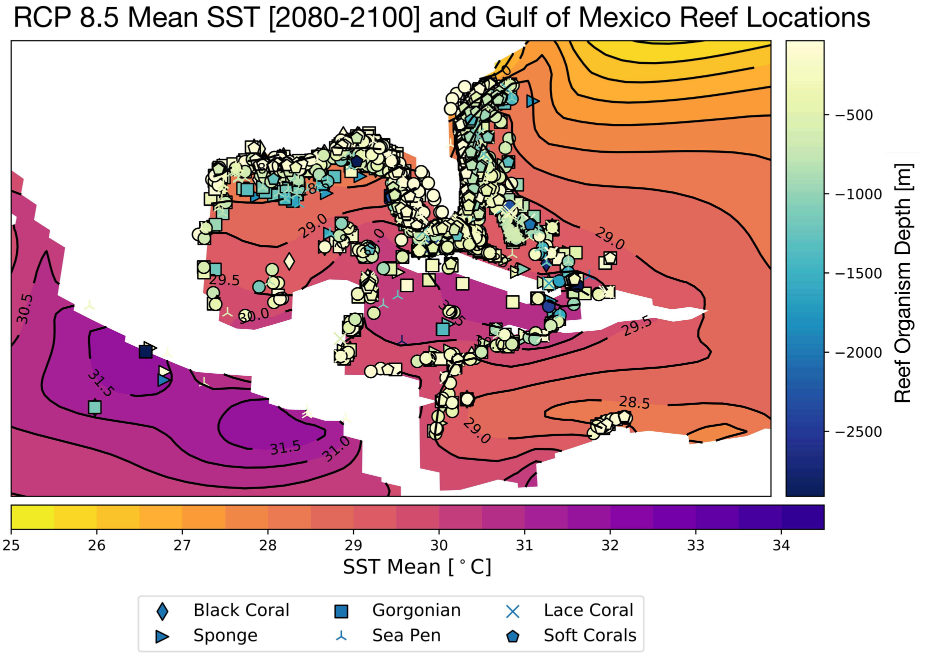

FIGURE 2 | Projected mean Gulf of Mexico SST for 2080–2100, RCP8.5 Large Ensemble, CESM1.2, with all reported Gulf of Mexico reef organism locations overlain. Colors of coral sites indicates reef organism depth [meters] and symbols denote type of reef builder, as in **Figure 1**. Continental regions are shown in white.

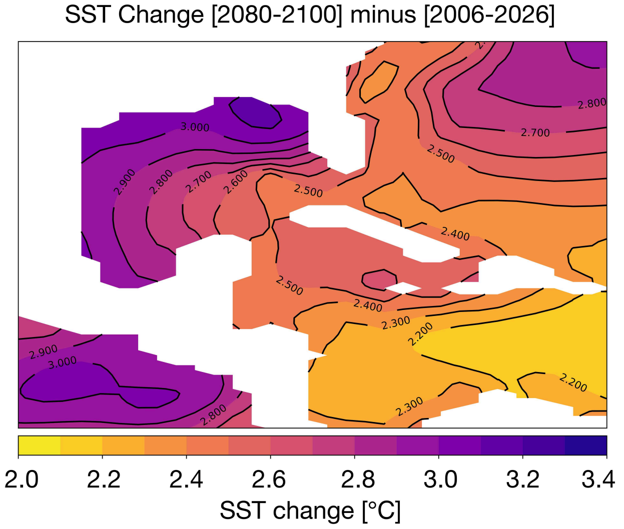

FIGURE 3 | Simulated changes in Gulf of Mexico SST [°C] in the RCP8.5 Large Ensemble, CESM1.2. (2080–2100 mean minus 2006–2026 mean). Continental regions are shown in white.

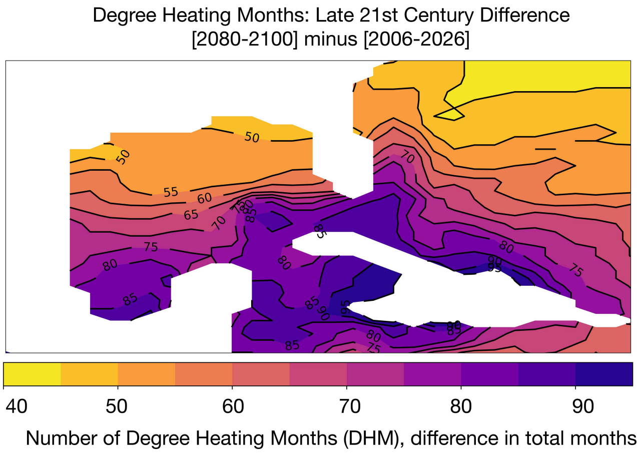

FIGURE 4 | Simulated changes in Degree Heating Months (DHM) in GoM SST [°C] in the RCP8.5 Large Ensemble. DHM climatology is based on the period 2006–2080. DHM are defined as months that exceed 1°C of the hottest month in the grid cell climatology. Continental regions are shown in white.

grid cell (following our definition of DHM, see section 2.2) (following Liu et al., 2003; Donner et al., 2005; Frieler et al., 2013). Multiple studies (Glynn and D'Croz, 1990; Hoegh-Guldberg, 1999; Sheppard, 2003; Donner et al., 2005) show that a SST exceedance threshold of 1°C in a given month will lead to bleaching; Donner et al. (2005) consider a higher temperature threshold to be anything exceeding 2°C above monthly climatologies, corresponding to a degree heating week (DHW) exceeding 8 weeks of high heating. **Figure 4** shows the difference in DHM between the beginning (2006–2026) and end of the twenty-first century. The number of DHM increases for the lower threshold of 1°C throughout the GoM, with the largest increases in DHM in the southern GoM and Caribbean (an increase of 75–90 DHM across the 20 year period). Along the Texas, Louisiana, and Florida coasts, DHM increases by 50–55 months total compared to the 2006–2026 base period. Put

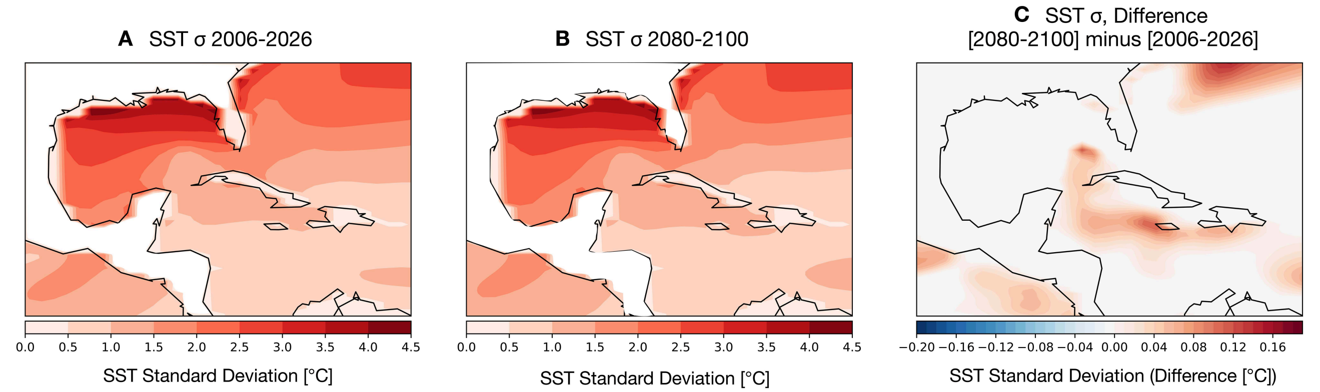

FIGURE 5 | Simulated changes in the standard deviation (1-σ) of GoM SST [°C] in the RCP8.5 Large Ensemble, CESM1.2. **(A)** 2006–2026 SST σ. **(B)** 2080–2100 SST σ. **(C)** (2080–2100 mean σ minus 2006–2026 mean σ). Continental regions are outlined in black contours.

another way, GoM corals are likely to experience thermal stress for approximately 2–4 more months of the year by 2080–2100.

3.1.2. SST Variance

Coral bleaching is less frequently observed in zones that experience high variance in SST anomalies (see Sully et al., 2019, for a review). To assess the potential for changes in SST variance to either dampen or amplify thermal stressors on GoM reefs, we computed the change in variance in the earlier part of the twenty-first century (**Figure 5A**) compared to the last 20 years (2080–2100) (**Figure 5B**). The overall spatial variance of SSTs remains largely unchanged throughout the twenty-first century: higher latitude GoM SSTs are highly variable, with more muted changes in the southern Gulf and Caribbean. The change in variance (**Figure 5C**) between the two time periods is close to zero degrees across much of the GoM with the exception of a few zones surrounding the Caribbean islands, which show an increase in overall variance. We note that these areas of higher SST variance correspond to main ocean currents driving GoM circulation, the Loop and Caribbean currents.

Given that increased variance is likely to help prevent bleaching, there is no modeling evidence that reductions in SST variance in the GoM will contribute to exacerbated coral bleaching.

3.2. Changes in Salinity and Carbonate Chemistry

While warming SSTs are expected to exert a primary influence on coral reefs over the coming decades, other hydrological and chemical changes in the ocean can also impact reef survival. Like SSTs, changes in variables such as salinity and pH exhibit spatial heterogeneity in simulations spanning the twenty-first century.

3.2.1. Salinity

GoM salinity is projected to increase; **Figure 6** shows the average salinity for 2080–2100 (a) and the change from 2006 to 2026 (b). Salinity in the GoM and Caribbean is quite high, 36–37 g/kg, and the CESM RCP8.5 ensemble exhibits a trend toward saltier water characterizing the twenty-first century. Salinity falling below 22 psu is thus unlikely to stress GoM coral reefs. High salinities can also be a stress on coral reef communities, but the maximum salinities predicted for the GoM in the 2080–2100 simulation are well within the range of naturally observed salinities near reefs, and far lower than some regions (e.g., the Red Sea) (Coles and Jokiel, 1992). That said, changes in community structure among reef dwellers are possible with projected salinity shifts.

3.2.2. Ocean Carbonate Chemistry

To measure the potential for ocean acidification to obstruct aragonite calcification and degrade coral skeleton growth, we examined changes in both pH and $\Omega_{aragonite}$ (see section 2). For the modern period, the model predictions under-predict $\Omega_{aragonite}$ relative to field observations (**Figure 7**). For the surface ocean (0–50 m), the offset between the model and data is relatively small with the exception of the highest latitude sites (**Figure 7**). At 100 m water depth, the model-observation offset is greater (due to higher model-predicted DIC at depth), but a general trend of decreasing $\Omega_{aragonite}$ with depth is present in both the field data and the model predictions. We note that the field data were collected in 2007 while the model predictions for the "modern" period span from 2006 to 2026. As a result, it is possible that the model-data discrepancy is due to the impacts of atmospheric CO_2 on carbonate chemistry that occurred after the field data were collected. Alternatively, the model predictions for deep-water reefs may be inaccurate in their absolute value.

Figure 8 shows the CESM results for changes in pH across the GoM for the end of twenty-first century. The surface ocean in the entire GoM regions is predicted to acidify by approximately −0.265 pH points on average, with the largest drop in pH along the northern Gulf coast (**Figure 8**). To assess the direct impacts of this change in ocean chemistry on coral growth, we computed $\Omega_{aragonite}$ in CESM's ensemble mean for the 2080–2100 period (**Figure 9**). Given potential model biases at depth (see above), we focus on the surface (0–50 m), though model predictions for 100 m depth are shown in **Figure S5**; additionally, the model prediction for alkalinity changes at the surface is given in **Figure S6**.

As shown in **Figure 9**, our results suggest that the surface ocean of the entire GoM region will drop below $\Omega_{aragonite} = 3$. This is notable as the modern scleractinian corals are largely

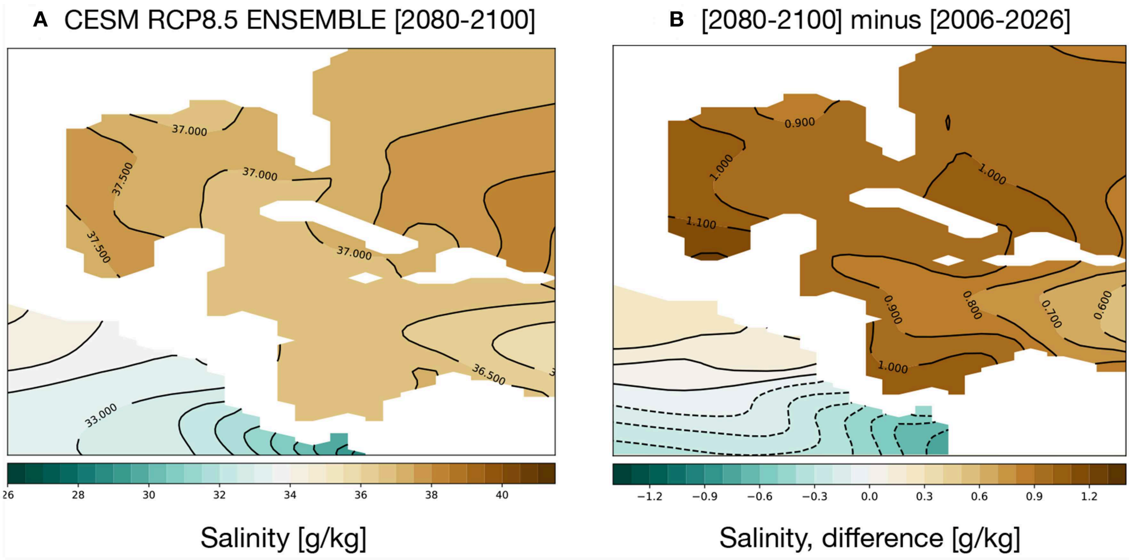

FIGURE 6 | Simulated changes in GoM salinity in the RCP8.5 Large Ensemble, CESM1.2. **(A)** 2080–2100 mean. **(B)** (2080–2100) mean minus (2006–2026) mean. Continental regions are shown in white.

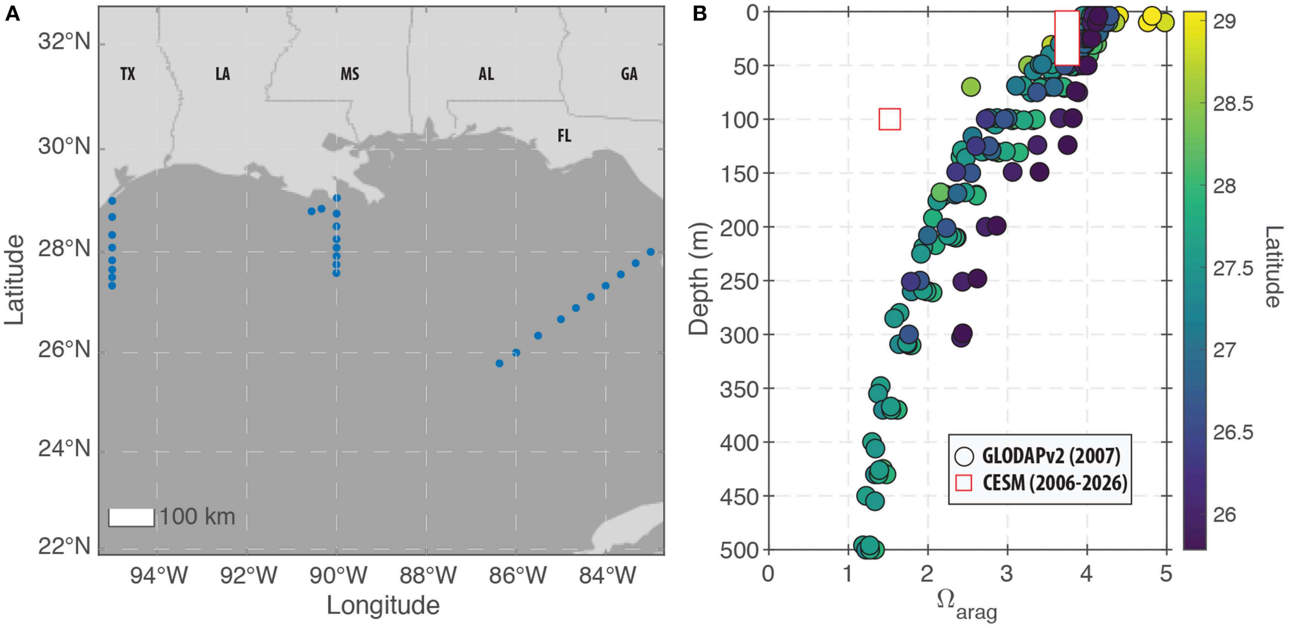

FIGURE 7 | Modern observations of carbonate chemistry in the GoM. **(A)** Map showing the locations of the GLODAPv2 stations within the GoM that are used for comparison to the CESM predictions. The displayed region (83°W to 95°W and 22°N to 33°N) defines the GoM region used for displaying the model predictions in **(B)** as well as **Figure 10**. **(B)** Field measurements (circles) and model predictions (squares) of changes in $\Omega_{aragonite}$ with depth in the GoM. For the surface ocean (0–50 m), the model reproduces most of the data with the exception of the highest latitude sites. However, at 100 m water depth, the model under-predicts $\Omega_{aragonite}$ relative to all of the field observations.

restricted to areas of the ocean where $\Omega_{aragonite}$ exceeds this value (Kleypas et al., 1999). No surface regions of the Gulf of Mexico are predicted go below the experimental calcification threshold of $\Omega_{aragonite}$ = 2 (Langdon et al., 2000; Albright et al., 2008) or to reach the thermodynamic limit for aragonite precipitation ($\Omega_{aragonite}$ = 1; **Figure 10**).

Compared to reefs in the upper 50 m of the water column, deeper water reefs would experience lower saturation states because aragonite has retrograde solubility (i.e., $\Omega_{aragonite}$ decreases with depth due decreased temperature and increased pressure). Modern field observations show that $\Omega_{aragonite}$ values at 100 m depth in the GoM are approximately 1 unit lower than

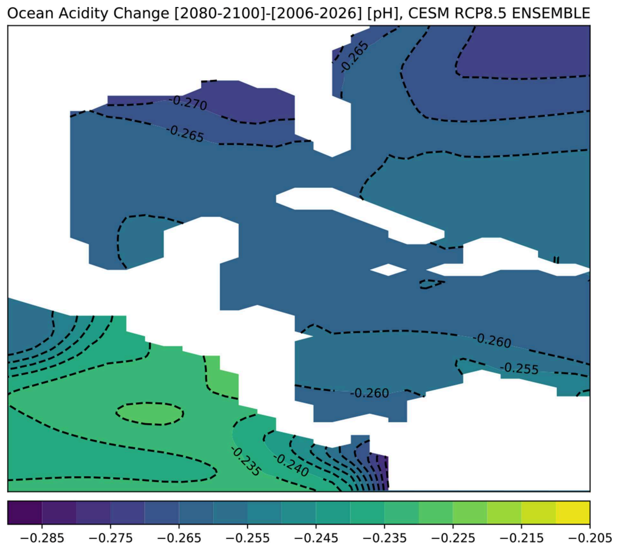

FIGURE 8 | Simulated changes in GoM pH in the RCP8.5 Large Ensemble, CESM1.2. (2080–2100 mean minus 2006–2026 mean). Continental regions are shown in white.

surface waters (**Figure 7**; Wanninkhof et al., 2015; Feely et al., 2018). This means that some of the deeper, mesophotic reefs (even those as shallow as 100 m) may already be experiencing stress due to low $\Omega_{aragonite}$ values. Alternatively, deeper-water reef builders (e.g., glass sponges, gorgonian corals, and sea pens) are likely adapted for those conditions.

The model predicted change in $\Omega_{aragonite}$ at 100 m depth is much less severe than at the surface; the CESM model estimates only a 0.3 unit change in $\Omega_{aragonite}$ at 100 m between the beginning and end of the century, with almost no change at the 500 m horizon (not shown). As mentioned above, the model predicted value for $\Omega_{aragonite}$ at 100 m water depth over the modern (2006–2026) period does not match existing field measurements (**Figure 7**) due to model-predicted DIC concentrations that are too high. While the model is inaccurate in terms of the absolute value for $\Omega_{aragonite}$ at depth, this does not necessarily mean that the magnitude of the change predicted by the model for 100 m water depth is also inaccurate. For example, the model prediction that changes in carbonate chemistry are greater in the surface ocean is consistent with the underlying driver being the addition of CO_2 to atmosphere, which exchanges more rapidly with the surface ocean relative to below the mixed layer.

The small change in $\Omega_{aragonite}$ predicted at depth may stress coral communities. That said, it is also possible that the predicted changes would not be as damaging as the changes predicted for shallow water reefs in that the deeper communities are already adapted/acclimatized to lower $\Omega_{aragonite}$ values (Farfan et al., 2018).

Due to the retrograde solubility of aragonite, the predicted increase in temperature acts to slightly increase $\Omega_{aragonite}$ (**Figure 10**); however, the effect of increasing atmospheric CO_2 and associated ocean acidification greatly exceeds the effect of temperature and leads to an overall decline in $\Omega_{aragonite}$ for the whole region (**Figure 10**). Similarly, the effect of increasing salinity on $\Omega_{aragonite}$ is negligible compared to the predicted pH changes. More importantly, the combination of heat and acidity stresses can often act synergistically (e.g., Rodolfo-Metalpa et al., 2011; Prada et al., 2017), meaning that even moderate heating and $\Omega_{aragonite}$ decreases can amplify each other leading to intolerable conditions for coral reefs. Furthermore, with surface oceans getting warmer and more acidic (low Ω) waters at depth, it is possible that surface-adapted reef communities in the GoM will have no suitable refuge by the end of the century (e.g., Pereira et al., 2018; Rocha et al., 2018).

4. CONTEXTUALIZING ANTHROPOGENIC CHANGES WITH HOT-HOUSE CLIMATES OF THE PAST

Scleractinian coral reefs have a long history extending back to the Middle Triassic (242–247 million years ago) (Martindale et al., 2019). Specifically, there are numerous records of reefs in the paleo-GoM, including microbial reefs from the Upper Jurassic (164–153 Ma) (Mancini and Parcell, 2001), coral and rudist bivalve reefs from the Cretaceous (145–90 Ma) (e.g., Enos, 1974; Scott, 1984; Höfling and Scott, 2002; Hattori et al., 2019), sponge and coral reefs from the Paleocene (66 to 59 Ma) (Bryan, 1991), as well as the drowned and living reef banks that initiated during the last deglacial period (∼14,500 years ago) (Khanna et al., 2017).

Ancient coral reefs that grew during (or were killed off by) hyperthermal (sudden, extreme heating) events can be seen as analog case studies for changes in reef communities today. When looking at the entire Phanerozoic (the last 541 million years), many of the worst reef collapses are coincident with evidence of thermal stress and ocean acidification (Kiessling and Simpson, 2011). When scleractinian reef systems are considered (the last 250 million years), this trend is even more concerning. Heat stress and acidification occur coincident with the last 3 greatest metazoan reef collapses: the Triassic/Jurassic mass extinction at 201 Ma (a 99.4% loss of reef volume), Pliensbachian/Toarcian extinction and Toarcian Oceanic Anoxic Event at ∼183 Ma (a 98.3% loss of reef volume), as well as the early Cenozoic Hyperthermal Events [e.g., Paleocene-Eocene Thermal Maximum at 56 Ma (a 99.6% loss of reef volume) and Early Eocene Climate Optimum (54 Ma)] [reef loss calculated from metazoan reef volumes reported in Kiessling and Simpson, 2011]. It should be noted that since acidification events are so geologically short-lived, it is often difficult to attribute this stress to long-term community change (Hönisch et al., 2012). Ancient reefs are imperfect analogs; modern fast growing coral species, such as *A. cervicornis*, generally evolved in the last half million years (Hoegh-Guldberg et al., 2007) and thus the reef communities are not identical. Nevertheless, many coral genera (from the Cenozoic in particular) are extant (not extinct), so reasonable comparisons can be made between groups (Weiss and Martindale, 2019). Further, many important reef forming corals were present in the GoM as far back as the early Eocene, including

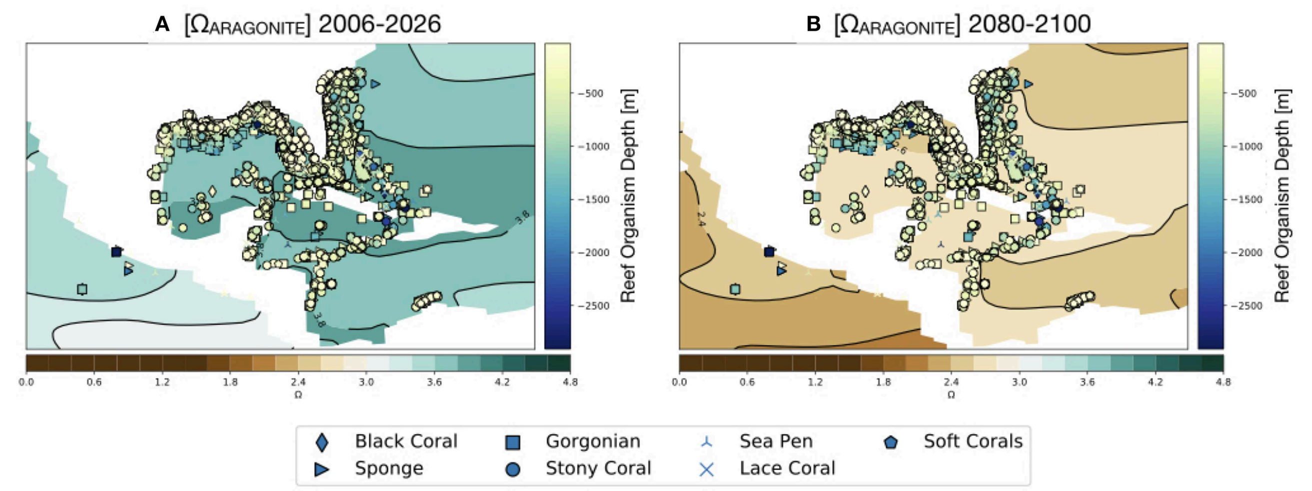

FIGURE 9 | Simulated values of $\Omega_{aragonite}$ for the GoMand northern Caribbean region in the RCP8.5 Large Ensemble (CESM1.2) in the surface ocean (0–50 m). Reef organisms and depth at which they occur [m] overlain (see **Figure 1**). **(A)** 2006–2026 mean, **(B)** 2080–2100 mean. Continental regions are shown in white.

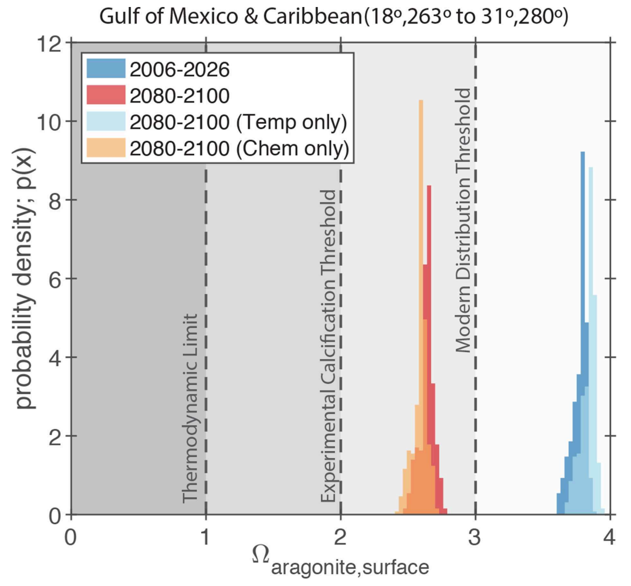

FIGURE 10 | Simulated values of $\Omega_{aragonite}$ for the GoM and northern Caribbean Region (i.e., the region shown in **Figure 7A**) in the RCP8.5 Large Ensemble, CESM1.2. The dark blue and dark red probability density functions (PDFs) show the model predictions for the 2006–2026 and 2080–2100 periods, respectively. The light blue and orange PDFs show the model predictions for the 2080–2100 period where either ocean chemistry or water temperature is held constant at the 2006–2026 values. The gray shading and dashed lines indicate the typical limits for the presence of scleractinian corals in the modern ocean ($\Omega > 3$; Kleypas et al., 1999), the experimentally measured limits for calcification by coral reef communities ($\Omega > 2$; Langdon et al., 2000; Albright et al., 2008), and the thermodynamic limit for aragonite precipitation ($\Omega = 1$).

Astrocoenia, *Favia*, *Goniopora*, *Montastraea*, *Siderastrea*, and *Stylophora* (Budd, 2000).

The Paleocene-Eocene Thermal Maximum in particular has been noted as one of the better analogs for modern climate change due to the similarities in the cause (i.e., greenhouse gas emissions) and its consequences (e.g., ocean acidification, increases in temperature) (Hönisch et al., 2012). In the Tethys Ocean, Paleocene coral reefs underwent a protracted, three-step collapse, from coral-dominated to foraminiferal or microbial reefs, before the complete demise of reef ecosystems near the Paleocene/Eocene boundary (Scheibner and Speijer, 2008; Zamagni et al., 2012). Nevertheless, these reef ecosystems were able to maintain a relatively high diversity (Zamagni et al., 2012). The main driver of the reef turnover is thought to be elevated temperature, but ocean acidification (Kiessling and Simpson, 2011), excessive sedimentation, and nutrification (Zamagni et al., 2012) are also implicated. In the GoM region, temperature, increased sedimentation, and nutrient input due to tectonism (Galloway et al., 2000) led to the development of sponge and coralline algae dominated reefs. Some zooxanthellate and apozooxanthellate massive and platy corals were also present (Bryan, 1991). Weiss and Martindale (2019) show that corals with particular traits, such as flexible photosymbiosis and feeding strategies and those that lived in siliciclastic environments, were better able to withstand change during the Cenozoic hyperthermal events. Because the GoM is largely siliciclastic, it is possible that GoM corals may prove more resilient than those in carbonate environments. Importantly, the rates of climate change in the modern are faster than during the Paleocene (Zeebe et al., 2016), barring direct comparison between the two time periods.

Finally, the Last Interglacial (LIG, ∼129–116 ka) was the last time the Earth was as warm as today with 11% warmer temperatures in the northern hemisphere, a greater loss of Arctic sea ice, and a partial loss of the Greenland ice sheet (Kukla et al., 2002; CAPE-Last Interglacial Project Members, 2006); these conditions are all possible in the near future under realistic carbon emissions scenarios. The Florida Keys in the southeastern GoM had extensive coral reef coverage during the LIG. These reefs contained many of the coral species we find in the Florida Keys today with branching *Acropora* and *Porites*, and boulder-shaped *Montastraea, Diploria,* and *Siderastrea* corals with ooid banks to the west and east of the reef (Stanley, 1966). Reconstructions from Tropical Atlantic locations find temperature and seasonality variability similar to present (Felis et al., 2015; Brocas et al., 2016, 2018). However, sea level was up to 6 m higher than today during the LIG, and likely exerted a dominant control on coral reef distributions. Evidence from Florida Keys, Bahamas, and Cayman Islands for the LIG found corals grew to about 3 m above current sea level, but not the peak 6 m (Blanchon, 2011). Evidence from the northern Yucatan peninsula suggest that a rapid depth change from 3 to 6 m induced a higher-energy wave environment that remobilized lagoonal sediments and buried or eroded adjacent reef framework resulting in marine sand bodies that prevented the submerged reefs from recovering (Blanchon et al., 2009). While the LIG is not a perfect analog for the current climate change, it provides some insights into coral response to quick pulses in sea level rise due to collapsing ice sheets and shifts in oceanic-atmospheric conditions. Coral reefs did exist and flourish in many locations during the LIG, but rapid changes in sea level given, for example, a partial collapse of the Greenland ice sheet could severely inhibit future growth.

These ancient events provide useful information regarding sensitivities, survival, and recovery during extreme stress events, as well as natural reef ecosystem responses to climate change in the absence of human-induced changes or interventions.

5. DISCUSSION: GULF CORALS IN THE ANTHROPOCENE

This study examines future projections for oceanic conditions in the GoM and the potential impacts of multiple stressors on coral reef ecosystems. Using CESM 1.2, a state-of-the-art coupled GCM, we compared two key 20-year periods: 2006–2026 (a base control) and 2080–2100 (end of twenty-first century). We find that GoM SSTs are likely to warm by 2.5–3°C, elevating mean temperatures to a range of 28–30.5°C in a high-CO_2 forcing scenario. While corals do show signs of an ability to evolve toward higher temperatures (e.g., Howells et al., 2012; Palumbi et al., 2014; Dixon et al., 2018), there are annual mean SST thresholds (e.g., 30°C, Wilkinson and Souter, 2008; Johnston et al., 2019b) beyond which corals simply bleach and die. By the end of the twenty-first century, the ensemble mean SST fields are spatially heterogeneous, but a great number of reefs, particularly off the coast of Belize, Florida, and Cuba, may experience mean annual temperatures closer to 30°C by 2100; further, these estimates potentially contain a cold bias (Liu L. et al., 2012), and in reality, GoM temperature observations are already hotter (Johnston et al., 2019b). Taken together, these results suggest that Gulf reef systems will experience frequent and severe thermal stresses by the end of the twenty-first century. Preventing such widespread and severe bleaching to the Earth's coral reef systems likely requires limiting global warming to 1.5°C, which is, at present, a lofty target (Frieler et al., 2013). To avoid widespread degradation of Gulf corals and reef communities, atmospheric CO_2 levels would likely need to be stabilized below measured 2005 levels (Donner et al., 2005).

The CESM1.2 RCP8.5 large ensemble provides no evidence that changes in GoM SST variance or salinity will adversely impact coral reef ecosystems. That said, an evaluation of relevant carbonate chemistry variables (i.e., pH and carbonate saturation state), suggest that a threshold may be crossed by the end of the century. Scleractinian coral reefs that are currently growing in supersaturated waters of $\Omega_{aragonite}$ greater than 3.4 (**Figures 9**, **10**) will experience significant pH and carbonate saturation state drops (**Figures 8**, **9**). These changes in carbonate chemistry will negatively impact GoM reef biomineralization. Today, scleractinian coral reefs that are found in low pH or $\Omega_{aragonite}$ waters have lower biodiversities and abundance of reef builders or dwellers than reefs in higher $\Omega_{aragonite}$ waters (Fabricius et al., 2011). Reefs in low $\Omega_{aragonite}$ regions are typically poorly cemented, have higher bioerosion, and have fewer structurally complex framework builders, which together result in lower structural integrity of the reef (Fabricius et al., 2011; DeCarlo et al., 2015). If the GoM becomes more acidic (lower $\Omega_{aragonite}$) we should expect the reef ecosystems to become less diverse and structurally weakened with a higher likelihood of significant coral bleaching. These issues are important on their own, but also lead to secondary issues; for example, lessened structural integrity can lead to more significant storm damage during hurricanes (Cheal et al., 2017), which will also increase in intensity and severity with rising temperatures (Molina et al., 2016; Murakami et al., 2018); reef species may also become more susceptible to disease or see a decline in fecundity.

The combination of thermal and chemical stress will make these environmental changes even more damaging (e.g., Donner et al., 2007, 2018; Rodolfo-Metalpa et al., 2011; Prada et al., 2017; Bahr et al., 2018). Deeper water, mesophotic reefs have distinct communities and ecosystems when compared to shallow water reefs (e.g., Bongaerts et al., 2010; Pereira et al., 2018; Rocha et al., 2018) but are, nevertheless, likely to experience severe thermal stress (Schramek et al., 2018). Given the issues of accuracy and resolution in predicting $\Omega_{aragonite}$ values at 100 m depth shown in this work, it is hard to make confident conclusions about the fate of mesophotic reefs. On the one hand, the predicted amount of $\Omega_{aragonite}$ change at 100 m depth is minimal (especially when compared to the surface), but on the other hand, these values are already below an important calcification threshold for scleractinian corals. If deep Mesophotic reefs are primarily inhabited by organisms that are well adapted to these lower $\Omega_{aragonite}$ conditions, the communities may not experience a catastrophic change. Future research should focus on the physiological limits of deep mesophotic reef communities as there is still very little known about these ecosystems (Bongaerts et al., 2010; Kahng et al., 2010).

We acknowledge several important caveats of this work. Coupled atmosphere-ocean GCMs contain significant cold temperature biases in the GoM and Caribbean (Liu L. et al., 2012; Martin and Schumacher, 2012; Ryu and Hayhoe, 2015; Exarchou et al., 2018; McGregor et al., 2018). Analysis of the Coupled Model Intercomparison Project (CMIP3) revealed that SST variability in the Intra-Americas Sea is less than observed in historical simulations (Liu L. et al., 2012); many GCMs produce large cold biases across the Intra-Americas Sea when assessed with gridded SST data products. This is crucially important for coral bleaching thresholds, likely leading to underestimated temperature maxima in the GCM predictions. In Key West, for example, summer water temperatures during 2019 were frequently observed above 32°C (National Data Buoy Center, NOAA). Coral bleaching may thus be underestimated in CESM 1.2 as well, and anthropogenic bleaching events may occur with greater severity than projected in this study.

Recent event-based evidence demonstrates that increases in upwelling from stronger winds, frequent during tropical storms, can lead to cold water events and anoxic conditions, promoting coral death and disease (Lirman et al., 2011). An anomalous cold event in 2010 killed numerous near-shore corals in the Florida Keys (Colella et al., 2012) and in the winter of 1969–1970 (Hudson et al., 1976). Cold coral bleaching events might also be altered by climate change, but the evaluation of changes in frequency in such events requires analysis of daily wind patterns, which is beyond the scope of this work.

Finally, the spatial resolution of CESM is 1 × 1°; reefs typically occupy spatial scales at tens to hundreds of meters (Donner et al., 2005). This discrepancy in scale creates uncertainties related to downscaling and microclimate affects. While GCM simulations afford important future mean state projections, an inability to resolve details at the reef scale and examine local circulation changes may inhibit our ability to make robust predictions about the future of GoM reef bleaching. Advances in regional ocean modeling and downscaling climate model outputs may facilitate the simulation of local upwelling and upper-ocean heating processes; such advances would refine projections of reef impacts (Donner et al., 2005, 2007, 2018). Further, recent work shows 1 × 1° IPCC-class GCMs contain biases in the simulation of the Loop Current, which largely moderates GoM temperatures (Liu Y. et al., 2012). The Loop Current carries warm waters into the central GoM; if this current slows, it could reduce the warming in the central GoM, mitigating the impacts of global warming. Adding embedded, online ecological models that explicitly simulate reef response to temperature and acidity changes would enhance the accuracy of the results presented here. These advances in model development are forthcoming (Bopp et al., 2013; Jones et al., 2019).

6. THE FUTURE OF THE GULF OF MEXICO'S CORAL REEFS

6.1. Climate Change and Biodiversity Loss

Coral reefs are critical ecosystem focal points in marine environments, supporting the world's fisheries, protecting coastlines, and promoting tourism. Through all of these structures, coral reefs generate hundreds of billions of dollars to the global economy each year (Mora et al., 2011; NOAA Ocean Service Education, 2017; Reef Relief, 2019). In the GoM alone, reef-related expenditures generate more than $4.4 billion annually in southeast Florida and reef recreation supports more than 70,000 jobs (Carnes, 2010). The many threats posed by climate change to coral reefs, including bleaching and acidification, motivates a pointed look toward reef systems lining GoM coastlines. The reefs that protect the coastline of the GoM are subject to unique regional ocean changes, warranting this geographically-focused study.

Multiple secondary impacts are likely to accompany rising temperatures and climate change in the GoM. Warm SSTs drive stronger tropical storms (Molina et al., 2016; Murakami et al., 2018). In recent decades, major hurricanes (e.g., Mitch, which decimated reefs in Belize) have wiped out coral reefs. During the 2005 hurricane season, coral reefs in the GoM (Flower Garden Banks, the Dry Tortugas, and the Florida Keys) experienced extensive damage; however, these reefs were spared from widespread bleaching event that occurred that year because the passing hurricanes reduced water temperatures (Stone et al., 2005; Gierach and Subrahmanyam, 2008; Wilkinson and Souter, 2008). Recovery timescales are on the order of multiple years to decades in a relatively healthy reef. In reefs that are already degraded or experience repeated storm events, recovery from physical disturbance can take even longer (Dollar and Tribble, 1993; Edmunds and Gray, 2014). Given consistent projections showing increases in the frequency and severity of tropical storms and Gulf hurricanes (Balaguru et al., 2018; Klotzbach et al., 2018; Trenberth et al., 2018; Ting et al., 2019), it is likely that high storm surge and wave impacts could further degrade GoM reefs, especially if they are less robust due to weakened cementation. This could initiate a positive feedback loop: coral reefs in the GoM protect local shorelines and infrastructure through wave energy dissipation, prevention of shoreline erosion, import of sediments, and via stabilizing mangrove and seagrass populations (NOAA Ocean Service Education, 2017; Reef Relief, 2019). Storm-driven losses of coral reefs may further reduce the resilience of the built environment along Gulf coastlines. Indeed, the economic damages imparted by hurricane activity in Texas and Florida in 2017 alone surpassed a staggering 125 billion dollars (Klotzbach et al., 2018). Some of these storms also cause unpredictable damages such as low salinity runoff or pollution (Rice University, 2019).

Additional anthropogenic stressors will interact to further degrade coral reefs in the GoM. These include increased sedimentation, fresh-water run-off and pollution due to development (Yeats et al., 1978; Nelsen et al., 1994; Osterman et al., 2008; Liu et al., 2013; Ren et al., 2015), and nutrification, particularly due to agricultural sources such as fertilizers (Nelsen et al., 1994; Osterman et al., 2008) and hydrocarbon extraction (Guzman and Jarvis, 1996). A combination of the above can lead to hypoxia (Justić et al., 2003; Osterman et al., 2008; Rabalais et al., 2010). Many of these effects favor the growth of coral competitors, such as macroalgae, that can further hamper reef development and growth (Gorgula and Connell, 2004; Vermeij et al., 2010). In a healthy ecosystem, herbivorous fishes and invertebrates can help to balance the overgrowth of algae (Williams and Poulnin, 2001; Bellwood et al., 2006; Smith et al., 2010); however, the physiology and reproductive capabilities of these organisms are also compromised by climate change and ocean acidification (Munday et al., 2008; Pankhurst and Munday, 2011). Further, because fish depend on the structural complexity of reefs (Graham and Nash, 2013), losing coral reefs can lead to a feedback where loss of fish leads to algae overgrowth, which then dampens reef development, leading to even fewer fish (Graham et al., 2007; Wilson et al., 2010; Nyström et al., 2012).

6.2. Adaptation and Mitigation

The ability of GoM reefs to adapt to the stressors outlined in section 3 is an open question. Corals may be able to survive in warmer temperatures through adaptation, epigenetic modification, or the utilization of thermal-tolerant symbionts (Howells et al., 2012; Palumbi et al., 2014; Dixon et al., 2018; Sully et al., 2019); however, acclimatization to acidification has not yet been demonstrated (Comeau et al., 2019). The adaptability of coral symbionts will likely play a key role in determining thermal resistance of GoM reefs. Reef structures may acclimate rather than completely dying off if symbiont species more tolerant to high temperatures and bleaching re-occupy coral tissues over time (Hughes et al., 2003) or if corals can acquire thermal tolerant symbionts (Howells et al., 2012). Coral reef generation times are on the order of several years and depend on favorable environmental conditions (Hughes et al., 2003), so if existing corals in a given community are stressed, they will not spawn. Bleaching onset research indicates adaptation via re-population of thermally tolerant symbionts occurs within 0–0.5° warming; given that most GoM SSTs warm by more than 2° in the CESM RCP8.5 ensemble mean, we must not discount the fact that zooxanthellate Gulf corals may disappear completely by 2100. Future reefs may shift toward populations typical of the late Cretaceous and early Cenozoic, when reefs were dominated by non-corals (i.e., rudists, sponges and red algae) and azooxanthellate coral types (Bryan, 1991; Kiessling and Baron-Szabo, 2004).

Coral communities could also migrate toward more favorable environments and regrow. The rate and direction of climatic shifts will likely drive coral species shifts across the GoM, and these changes in climate velocity (Pinsky et al., 2013) are crucial to robust predictions of reef survival (**Figure S7**). Projected climate velocities for the GoM in terms of SST changes indicate rapid shifts of up to 10 km/yr throughout the forthcoming twenty-first century (**Figure S7**). While some marine species can migrate rapidly, coral reefs are largely stationary and migrate over generations of new reefs established in new regions. The establishment process requires many factors to encourage reef growth, including the presence of crustose coralline algae (Morse et al., 1994, 1996; Heyward and Negri, 1996), low sediment input (Gilmour, 1999), lithified substrate (Jackson, 1977; Purkis et al., 2011), and precise water quality conditions (Negri and Hoogenboom, 2011). On evolutionary timescales, reefs often shift poleward to avoid thermal stress (e.g., Kiessling, 2001) and this has already been documented in geologically-recent and modern reefs (e.g., Greenstein and Pandolfi, 2008; Yamano et al., 2011; Pandolfi and Kiessling, 2014). Poleward migration may not be a feasible option since GoM corals are limited latitudinally and are already positioned at their northern limit (e.g., Kiessling, 2001; Jones et al., 2019).

It is also hypothesized that reefs may find refuge from thermal stress in the surface waters by migrating to deeper habitats where temperatures are lower (Riegl and Piller, 2003; Bongaerts et al., 2010; Bridge et al., 2013; Padilla-Gamiño et al., 2019); this has occurred to some extent in Pulley Ridge, though recent surveys have found that these deep water hermatypic corals are not surviving (Slattery et al., 2018). Deeper water, mesophotic reefs have distinct communities and ecosystems when compared to shallow water reefs (e.g., Bongaerts et al., 2010; Pereira et al., 2018; Rocha et al., 2018); thus these deeper habitats likely would make poor refuges for shallow-water reef species. Vertical migration in the water column is harder for the reef builders, which require clear water and sunlight for photosynthesis. With sea level rise, many deeper reefs that have narrow depth ranges will not be able to keep pace with increasing water depth. Furthermore, mesophotic reefs inhabit waters with lower $\Omega_{aragonite}$ values, leading to the possibility that GoM reef communities would experience an environmental pincer movement: thermal stress from above as well as acidification stress from below (which would also make pole-ward migration problematic). In general, there are myriad conditions that would prevent this from being a feasible adaptation for coral survival on a large scale (Smith et al., 2016; Bongaerts et al., 2017).

Even if corals adapt or acclimatize to some environmental stresses (e.g., temperature or salinity), they may not be able to adapt or acclimate to all of them (e.g., ocean acidification) (Okazaki et al., 2013; Comeau et al., 2019). A controversial solution involves geoengineering via reef-shading, covering large portions of reefs to reduce direct heating via solar radiation (Coelho et al., 2017). This is an expensive and precarious solution which cannot bolster coral resistance to thermal stress. Increasing coral tolerance through assisted evolution, such as selective breeding, assisted gene flow, transplanting of juveniles, epigenetic programming or conditioning, and coral microbiome manipulation may be viable within the next decade (Horoszowski-Fridman et al., 2011; van Oppen et al., 2015; Van Oppen et al., 2017), and would directly bolster reef resiliency to ecosystem collapse.

6.3. Looking Ahead

The marine organisms occupying the GoM evolved in the last 420,000 years; now, atmospheric ρCO_2 levels dramatically exceed ice core measurements of greenhouse gas concentrations spanning their entire evolutionary history (Hoegh-Guldberg et al., 2007). In an even broader geologic context, the rate of greenhouse gas emissions, and therefore the rate of climate change, during the Paleocene-Eocene Thermal Maximum was orders of magnitude slower than the modern warming trend, meaning modern climate change is unprecedented in geological history (Zeebe et al., 2016). Given the innumerable benefits that coral reefs in the GoM provide to coastal societies, it is our hope that this work sheds light on future risks specific to this highly vulnerable ecosystem. While reef systems can recover from bleaching events, reefs generally require decades to return to their pre-bleached state (Frieler et al., 2013). It is likely that the accelerating rate of global climate change will exceed the speed at which corals reefs and their symbionts can adapt (multiple decades), a defining feature of abrupt climate change (Hughes et al., 2003; Frieler et al., 2013).

Widespread degradation of GoM reefs is especially likely under the RCP8.5 "business-as-usual" scenario considered in this work. To avoid consequential environmental, social, and economic damages (e.g. Chen et al., 2015) and promote long-term conservation and recovery of GoM coral reefs, substantial, rapid reductions of anthropogenic greenhouse gas emissions are past-due.

DATA AVAILABILITY STATEMENT

The datasets analyzed for this study are housed in the Earth System Grid, a publicly available climate model output repository (https://www.earthsystemgrid.org/). Additional data information and our analysis code is available in the **Supplementary Material**.

AUTHOR CONTRIBUTIONS

SD, RM, and KD designed the study and formulated scientific questions. SD extracted, post-processed and analyzed climate model data, and formulated coral stressor conditions with assistance from RM and KD. MT modeled the ocean carbon changes and assisted in estimating drivers of acidification as a coral stressor with help from RM. RM, KD, and AW contextualized future GoM change with information surrounding coral communities in past climates. All authors contributed to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00691/full#supplementary-material

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REVIEW
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Coral Reefs in the Gulf of Mexico Large Marine Ecosystem: Conservation Status, Challenges, and Opportunities

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The importance of coral reefs (CR) within marine ecosystems has become widely recognized. Although shallow CR are not as abundant in the Gulf of Mexico (GoM) as in other areas such as the Caribbean, their uniqueness, singularity, isolation, and conservation status make their conservation highly important. Corals and CR, both shallow and deep, are more widely distributed throughout the GoM than previously thought, providing new venues of research but also new challenges for their sustainable management. They are widely present in the three countries circumscribing the GoM (Cuba, Mexico, and the United States). Corals are also distributed throughout different depths, from the keys of Florida and Cuba, to the mesophotic reefs in Flower Garden Banks, Pulley Ridge, and submerged banks in the southern GoM; additional coral presence occurs even beyond mesophotic depths (∼30–150 m). Like reefs around the world, they are subject to an increased threat from anthropogenic causes, including overfishing, pollution, and climate change. But there is also hope. Some reefs in the area, such as those in Flower Garden Banks National Marine Sanctuary are probably the best-preserved reefs in the region, with coral cover greater than 50%, which is unusual in the Wider Caribbean. Others are experiencing new protections through the work of government, and local communities. The objectives of this manuscript are to summarize the overall status of corals and CR in the GoM, analyze some of the current and future threats, and explore opportunities for their conservation in the region. Aside from the above mentioned anthropogenic threats bleaching, coral diseases, and hurricanes have been identified as main contributors for CR declines not only in the GoM but abroad; some nowadays present but likely to increase threats are invasion by alien species or by *Sargassum* spp. Among some of the opportunities identified are to capitalize on existing and emerging multilateral agreements, and initiatives (e.g., GoM Large Marine Ecosystem, trinational sanctuaries agreement); increase financial support for conservation through international initiatives and the private sector; and a need to comprehend the inherent interconnection among corals, CR, and deeper bank ecosystems as they do not function in isolation.

Keywords: corals, coral reefs, ecosystem management, Gulf of Mexico, mesophotic reefs, resilience, threats

INTRODUCTION

With a calculated area of > 1.5 million km^2 (Turner and Rabalais, 2018), the Gulf of Mexico (GoM) is considered one of the Large Marine Ecosystems (LMEs) in the World (Sherman, 1991) due to its distinctive hydrographic regimes, productivity, and biological population. Even though coral reefs (CR) are not the most abundant or representative ecosystems in the GoM, they constitute important habitats and provide significant ecosystem services for the three countries that share its waters (Mexico, Cuba, and the United States, US hereafter); among those services are commercial fisheries and recreation. Furthermore, CR protect shorelines from erosion, hurricanes, and tropical storms (Birkeland, 1997; Barbier et al., 2011). Ecologically CR provide structure that results in their high productivity; habitat contributed by corals yields a high diversity and density of marine species (Nellemann et al., 2008); while their association and interaction with other tropical marine ecosystems such as mangroves and seagrasses have shown to be of great importance for goods and services through functional linkages (Harborne et al., 2006), and their hydrological connectivity to those ecosystems is critical for completion of biological cycles (Ortiz-Lozano et al., 2013; Robertson et al., 2019), some of them remain scarcely quantified (Harborne et al., 2006).

Shallow reefs in the GoM are calculated to occupy 2,640 km^2 (<0.2%) (Tunnell et al., 2007) while the extent of mesophotic corals, defined as light-dependent corals living at depths between 30–150 m (Hinderstein et al., 2010), and deep-sea corals in the LME - by comparison - are largely unknown (Brooke and Schroeder, 2007), although recent studies are helping to close this gap[1]. The largest distribution of shallow corals happens on the Florida coast (Florida Keys and Dry Tortugas), and Cuba, with roughly 85% of shallow corals of the GoM (Tunnell et al., 2007), but the uniqueness and singularity of reefs throughout the gulf makes them particularly important for this LME (**Figure 1**). The reefs within the GoM are also highly variable, having both some of the lowest (Florida Keys, just above 10%), and the highest coral cover (Flower Garden Banks, almost 60%) (Schutte et al., 2010) in the Wider Caribbean region (GoM + Caribbean) (Tunnell et al., 2007).

Similar to CR all around the world, the shallow reefs of the GoM are experiencing significant declines in their overall health, expressed in loss of live coral cover due to pollution, habitat destruction, overfishing, diseases, bleaching, overgrowth by algae and sponges (Schutte et al., 2010), turbidity, and sedimentation (Jones et al., 2015) that are altering and impairing the overall function of these ecosystems, and decreasing their ecosystem services (Mumby and Steneck, 2008). The reefs of the Florida Keys have probably been one of the systems most affected by health degradation in the region, with a decrease in coral cover, and a reduction of species numbers, particularly after the bleaching event of 1997–1998, and these reefs are showing little to no recovery (Somerfield et al., 2008). In contrast, CR of the Flower Gardens Banks National Marine Sanctuary in the US have been historically relatively unaffected by coral diseases, bleaching [e.g., although corals bleaching occurred at the Flower Garden Banks every summer during 1989–1991 it was always minor (<5%), and yielded negligible mortality (Hagman and Gittings, 1992); Schmahl et al. (2008) indicated bleaching and diseases were 0–0.5% in 2004–2005], or other deleterious events, until 2016 when they were affected by a possible decrease in dissolved oxygen (DO) concentration affecting an estimated 2.6% of corals in East Flower Garden Bank, and up to 82% of corals in the area suffered partial or total mortality (Johnston et al., 2019). Moreover, and although shallow CR are by far the most affected, mesophotic and deep-sea corals have not been exempt to damages. White et al. (2012) found evidence of deterioration in one of 11 sites visited after the Deepwater Horizon oil spill in 2010, finding signs of stress that included “varying degrees of tissue loss, sclerite enlargement, excess mucous production, bleached commensal ophiuroids, and covering by brown flocculent material.”

Due to the importance of these ecosystems, several conservation initiatives are underway, from large-scale protection such as the creation and expansion of marine protected areas (MPAs), to the restoration of degraded reefs. This manuscript intends to show the current conservation status of the corals and CR of the GoM, analyze the actions taken in the three countries for their protection, and recommend future actions that managers and decision makers might need to take for their protection. Needless to say, but not surprising, the majority of the studies come from the US.

SHALLOW CORAL REEF DISTRIBUTION AND CONSERVATION STATUS

Coral reefs development within the ca. 360,000 km^2 shallow waters (<50 m deep) of the GoM continental shelf is minimal, with <1% covered by hermatypic CR. Several unfavorable conditions in the GoM for CR development include a great riverine influence, the presence of two tidal systems (one prevalent most of the year generated by trade winds, and the second one present during winter and associated with north winds), upwelling, and perhaps freshwater inflow from

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[1] https://portal.gulfcouncil.org/coralhapc.html

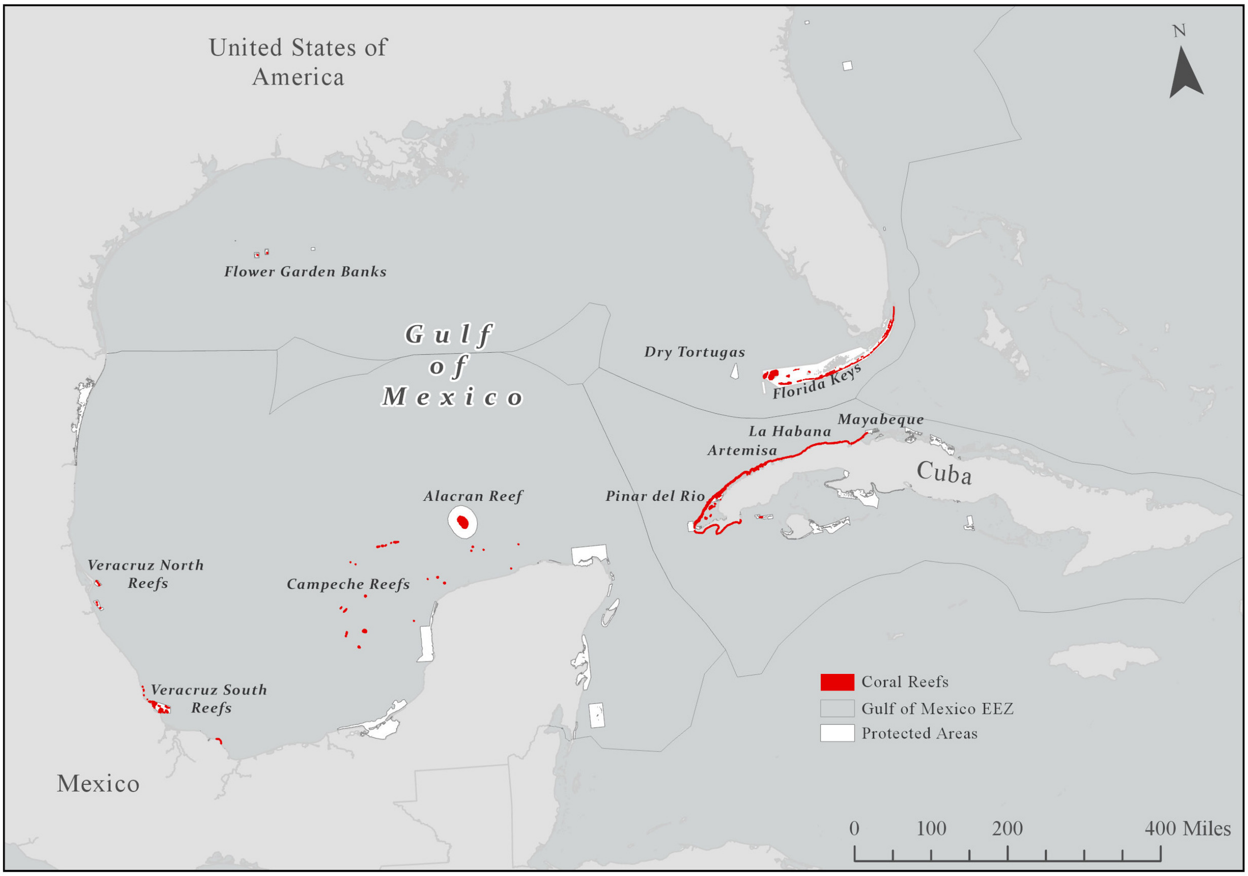

FIGURE 1 | Distribution of shallow coral reefs (red) in the Gulf of Mexico (GoM). Exclusive Economic Zone = EEZ. Also shown are managed areas within the GoM, which tend to be focused on fisheries management.

groundwater (Jordán-Dahlgren, 2004). Other well-known factors affecting their distribution and abundance are turbidity, thermal stress and, particularly for zooxanthellate corals, light availability, all of which have been covered elsewhere (e.g., Veron, 1995; Birkeland, 1997; Jones et al., 2015). These authors have indicated that corals are capable of building reefs by using sunlight, which happens to be key for the existence of all modern CR; their zonation is largely due to corals adaptation to different lights levels; and aside of controlling growth and indirectly formation of calcium carbonate, light is known to be responsible for changing corals shape from mounds to plates among polymorphic coral species. It is noteworthy that some reefs in the GoM developed in spite of temperature and organic inputs, turbidity, and sedimentation produced by human activities and natural disturbances (Salas-Pérez and Granados-Barba, 2008; Gutiérrez-Ruiz et al., 2011).

United States

Although corals and CR are not the most predominant ecosystems in the US GoM, different formations that include these rich coral-based ecosystems are present throughout the area. The eastern US GoM encompasses the most developed CR formations. Meanwhile, the western US GoM is characterized by three types of banks, the south Texas Banks grow on relic carbonates while the banks east off Texas and Louisiana have carbonate reef caps, and are either midshelf or shelf-edge/outer-shelf bedrocks (Rezak et al., 1990), most of them offering habitat for mesophotic and deep-sea corals, but limited habitat for shallow corals and CR due to their depth. Finally, the central GoM is the most impoverished US zone in natural reefs covering ca. 3.3% of its area (Parker et al., 1983), probably due to the large influence of discharges from the Mississippi River.

Fishery management plans for the US GoM includes 142 scleractinian coral species under the GoM Fishery Management Council (Gulf of Mexico Fishery Management Council [GMFMC], 2011). According to Simmons et al. (2014) there are 20 sites independent of their depth distribution subjected to current management efforts in the GoM, yielding two designated sanctuaries (Flower Garden Banks and Florida Keys), five fishery reserves (Madison-Swanson, Steamboat Lumps, the Edges, Tortugas North, Tortugas South), and 18 habitat areas of particular concern (Alderdice Bank, Bouma Banks, Fathom 29, Florida Middle Grounds, East Flower Garden, West Flower Garden, Geyer Bank, Jakkula Bank, McGrail Bank, MacNeil Bank, Madison-Swanson, Pulley Ridge, Rankin Bright Bank, Rezak-Sidner Bank, Stetson Bank, Sonnier, Tortugas North,

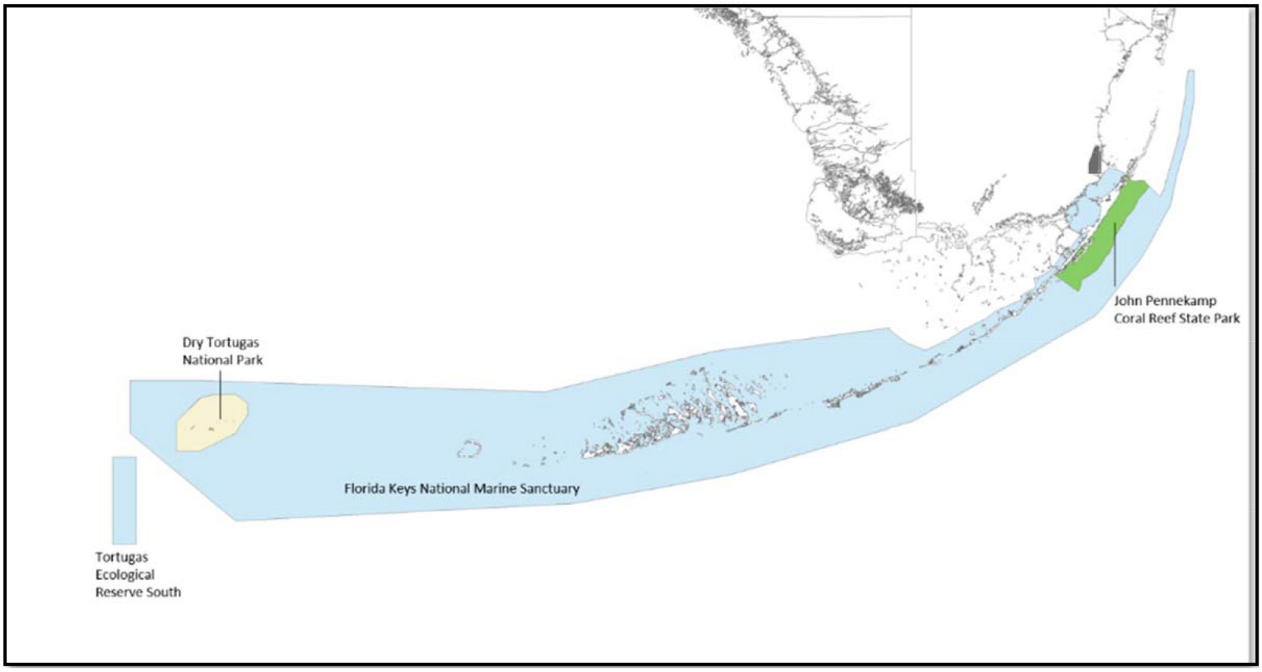

FIGURE 2 | Florida Keys reefs are offered varying levels of protection by the Florida Keys National Marine Sanctuary, Dry Tortugas National Park, and John Pennekamp Coral Reef State Park, see text for details.

Tortugas South). Note, some of these sites are designated as more than one category, and the Florida Keys National Marine Sanctuary was not listed as such in the above reference.

The Florida Reef Tract extends ~579.4 km (360 mi) from the St. Lucie Inlet in Martin County out to the Dry Tortugas. The most significant reef development occurs offshore of the Florida Keys, and in the Dry Tortugas, which fall within the GoM LME. Historically, the Florida Keys stands out because they host the first underwater national park or MPA (Dry Tortugas National Park, established in 1935), and the first underwater park (John Pennekamp Coral Reef State Park, established in 1963). This portion of the reef tract is also protected by the Florida Keys National Marine Sanctuary, established in 1990, which protects ~9,603.7 km^2 (2,800 nmi^2) of marine habitat within Florida Bay, the GoM, and the Atlantic Ocean (**Figure 2**). As an addition to the Florida Keys National Marine Sanctuary, in 2001 the Tortugas Ecological Reserve was established. It was considered the largest MPA within US waters at that time with ~514 km^2 (150 nmi^2), and is divided into diverse use zones (Jaap et al., 2008).

The Florida Keys reef system is a bank-barrier with shallow-water spur-and-groove formations that are connected by a linear transitional reef, and expanses that lack reef development due to the influence of Florida Bay (Shinn, 1963; Jaap, 1984). Over 6,000 patch reefs occur in the nearshore and offshore environments behind the forereef (Marszalek et al., 1977). Dry Tortugas National Park is characterized by a bank reef with spur and groove reefs, and large isolated formations, patch reefs or pinnacles, and *Acropora*-dominated shallow reefs (Haskell et al., 2000). To the west of the Park is Tortugas Bank, which is a deeper reef system, parts of which show very high coral cover. Just southwest of the Tortugas lies Riley's Hump, another bank reef system that is very important for fishes and other marine life. The Dry Tortugas reefs are located ~112.7 km (70 mi) from Key West, and at the confluence of a number of currents, so they benefit from relatively clean, clear water, and are protected from the same fishing and diving pressure experienced by reefs in the Keys both by their location, and through management actions. Moreover, throughout Florida take of any coral species is prohibited.

Zonation along the outer reef tract follows the typical Caribbean model (Goreau, 1959; Jaap, 1984), with a shallow *Acropora palmata* zone grading to a deeper *Montastraea* zone. Recent coring studies have shown that the reefs of the Florida Keys stopped accreting 3,000 years ago, and that the species assemblages have changed from the traditional reef-building species (*A. palmata* and *Orbicella* spp.) to weedier species such as *Porites astreoides* and *Siderastrea siderea* (Toth et al., 2018, 2019). Similar to elsewhere in the Caribbean, significant losses of the Acroporid species caused mainly by disease, and hurricanes in the 1980s led to a considerable reduction in coral cover on the shallow forereefs. As examples, at Carysfort Reef in the Upper Keys both species were completely lost between the summer of 1982 and April 1984, and at Looe Key in the Lower Keys snapshot monitoring revealed areal coral cover losses of ~93% for *A. palmata*, and ~98% for *Acropora cervicornis* (Szmant, 2005 in Acropora Biological Review Team, 2005). Similarly, the shallow reefs at Dry Tortugas once housed expansive thickets of both species but the *A. palmata* was almost completely lost between 1939 and 1982 based on maps published by Agassiz and Davis, and *A. cervicornis* declined by 95% in 1977 during a cold-water disturbance (Davis, 1982). Unfortunately, coral cover has continued to decline or remain depressed throughout the area.

The reefs of the Florida Keys support a healthy tourism economy, and both commercial and recreational fisheries. Visitors to the Keys and Dry Tortugas spend money on activities that are directly related to the reef (i.e., snorkeling and SCUBA diving), and on activities that are made possible or enjoyable because of the protection the reef provides (i.e., swimming at a beach and parasailing). Visitor expenditures on reef-related tourism range from $8,000 to 916,000 USD annually and expenditures on reef-adjacent tourism range from $8,000 to just over $2 million USD yearly for individual reefs throughout the Florida Keys (Spalding et al., 2017).

The submerged topographic features in the NW GoM supports spectacular CR communities (both shallow and mesophotic reefs) (**Figure 3**). Three of these features, East and West Flower Garden Banks, and Stetson Bank, are included in the National Marine Sanctuaries, and a number of other banks are under consideration to be added to the sanctuary at present[2]. What makes the CR of the Flower Garden Banks stand out among all the reefs in the GoM is their relative resistance to coral disease, bleaching, and other impacts that have dramatically disrupted CR communities throughout the Wider Caribbean, and the tropical world. Results of >25 years of monitoring within the sanctuary have shown that the Flower Garden Banks continue to support healthy amounts of coral cover (almost 60%), experienced few of the impacts that have been lethal to corals elsewhere (i.e., bleaching and diseases), and continue to support abundant fish assemblages (Johnston et al., 2016). As previously stated, <5% bleaching happened every summer from 1989–1991 (Hagman and Gittings, 1992), and neither bleaching nor disease were > 0.5% from 2004–2005 (Schmahl et al., 2008).

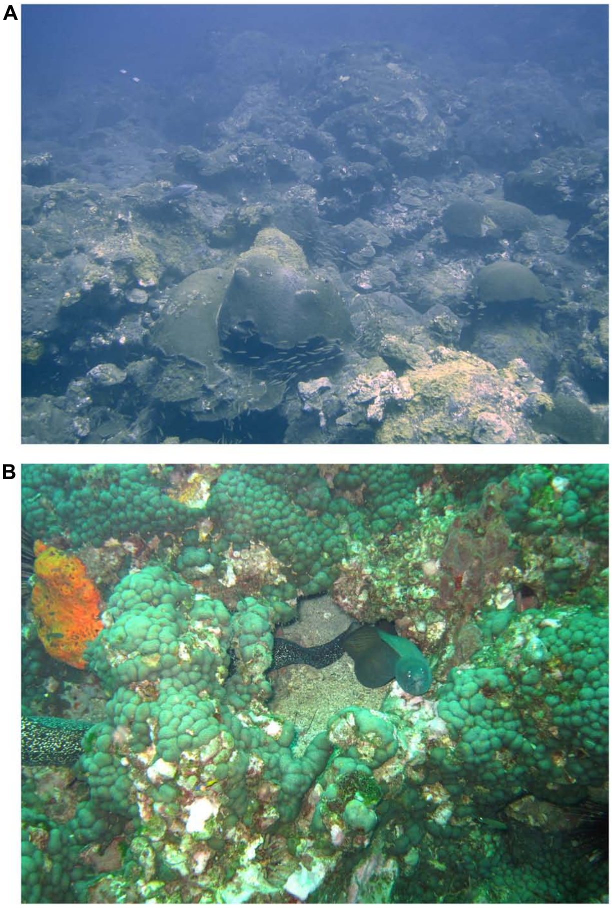

FIGURE 3 | Coral reefs and coral communities in the Flower Garden Banks National Marine Sanctuary. **(A)** East Flower Garden (–18 m), and **(B)** Stetson Bank (–20 m). Photos by DLG-A.

The features of the NW GoM create a mosaic of biological habitats that are home to distinct biological communities distributed within several recognized biological zones (Schmahl et al., 2008). Rezak et al. (1990) showed how variations in water depth, currents, temperature minima, salinity, and turbidity combine to determine the distribution, and character of the biological communities in the NW GoM. Among the environmental factors potentially influencing the distribution of biological zones are summarized (**Figure 4**) based on data from Rezak et al. (1990), and descriptions by Schmahl et al. (2008).

Considering these regional biological controls is an important framework for knowing how their changes may affect the distribution of biological communities on the banks in the future. Changes in the depth, and geography of water temperature, current patterns, turbidity, salinity, and nutrient levels in the region may alter the zonation patterns, and the composition of biological communities that make up the zones. These possible changes should trigger the design of monitoring programs seeking recognition of climate, and other impacts where and when they occur, and to develop resource protection strategies in response.

Mexico

When Angelo Heilprin visited Veracruz (SW GoM) in 1890, he was surprised to find a city constructed using corals (Heilprin, 1890), as scientists from that time assumed there were no CR in the western waters of the GoM. However, on its southern region the GoM presents two large zones with CR: Veracruz in the SW, and Campeche Bank to the south.

Veracruz has two well-known reefs systems: to the north, the Lobos-Tuxpan Reef System, composed of nine reefs (de la Cruz-Francisco et al., 2016), and in the south, the Veracruz Reef System, with 50 reefs (Liaño-Carrera et al., 2019), making it the largest reef system in this region (Jordán-Dahlgren, 2004). Recently, the Tuxtlas Coral Reef System, composed of 35 reef structures (**Table 1**) along the coast was described (Comisión Nacional de Áreas Naturales Protegidas [CONANP], 2018a). Each reef covers <10 km^2 with depths between 20–45 m (Jordán-Dahlgren, 2004).

The Campeche Bank Reef System, which extends >200 km from the Yucatan Peninsula, is composed of 11 named emergent

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[2] https://flowergarden.noaa.gov/management/expansiondeis.html

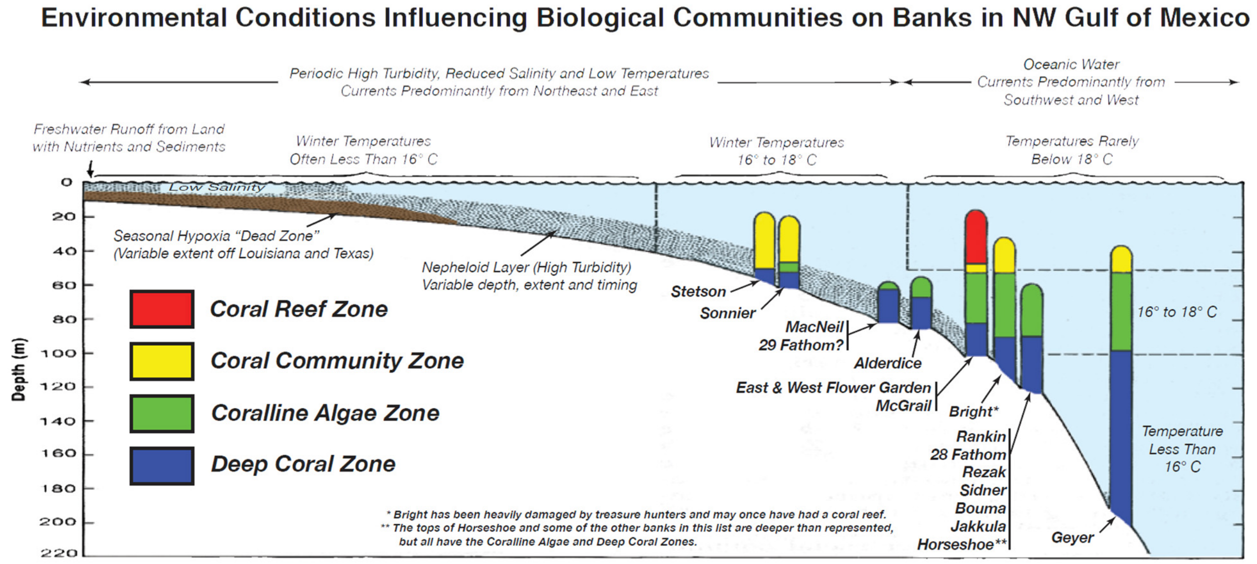

FIGURE 4 | Environmental controls on biological communities on NW Gulf of Mexico reefs and banks using data from Rezak et al. (1990), and Schmahl et al. (2008). Some of the zones of the mentioned banks have not been fully evaluated so this diagram is only a tool for predicting the distribution of the various community zones. Evaluating how changes in the factors that control these communities will be an important basis for assessing climate impacts, and developing management responses as possible changes in the distribution, and composition of biological communities on the banks occur.

reefs, and four named submerged banks (Tunnell, 2007), as well as many unnamed submerged reefs, most of them yet to be described. Many reefs are grouped into a common name (for example Triángulos, which includes Triángulo Este, Triángulo Sur, and Triángulo Oeste) (**Table 1**). Corals in the Campeche Bank cover areas varying from 3–20 km^2, except for the Alacranes Reef, which extends ∼650 km^2 (Jordán-Dahlgren, 2004).

TABLE 1 | Coral reefs in the south coast of the GoM.

Reef system	Reefs
Lobos-Tuxpan Reef System	Blanquilla, Medio, Lobos, Oro Verde, Tanhuijo, Enmedio, Pantepec, Tuxpan, Blake
Veracruz Reef System	Amarillo, Tía Juana, Juan Ángel, Rincón, Montenegro, Punta Brava, Ahogado Punta Gorda, Los Verdes, Las Holandesas 1, Punta Gorda, Las Holandesas 2, Las Holandesas 3, Galleguilla, La Blanquilla, Anegada de Adentro, La Gallega, Ahogado de Guilligan, Ahogado de Andrea, Ahogado Chico, Ahogado Grande, Ahogado del Jurel, Bajo Paduca, Isla Verde, Hornos, Pájaros, Ahogado del Caracol, Mersey, Ahogado Terranova, Isla Sacrificios, Anegada de Afuera, Ingeniero, Santiaguillo, Bajo Enmedio, Topatillo, Anegadilla, La Palma, Enmedio, Blanca, Ahogado Medio, Polo, Sargazo, Chopas, Giote, Ahogado Cabezo, Periférico, Ahogado de Rizo, Ahogado del Pez León, Cabezo, Rizo, Punta Coyol
Los Tuxtlas Coral Reefs	Punta Puntilla, Isla El Terrón-Arrecife, Playa Escondida, Poza de Roca Partida 1, Poza de Roca Partida 2, Ermita 1, Bahía Pirata, Punta Lagarto, Poza Montepío, Pedregal Borrego, Escollera Balzapote, Balzapote las Cruces, Pedregal Balzapote, Jicacal Poza, Pedrera de Playa Escondida, Jicacal 1, Jicacal 2, La Barra, La Playita, Los Morritos, El Salado, Los Mulatos, Barco Viejo, Gusinapan, Olapa, Perla del Golfo-Zapotitlan, Mezcalapan, Sochapan, Punta Tecuanapa, Peña Hermosa, Punta Peña Hermosa, El Terrón 1, El Terrón Poza, Punta San Juan, La Cuadrada
Campeche Bank	Alacranes, Cayo Arenas (Isla de la Ensenada), Bajo Nuevo, Bajos Ingleses, Triángulos (Triángulo Oeste, Triángulo Este, Triángulo Sur), Banco Pera, Bajos Obispos, Banco Nuevo, Cayo Arcas (Cayo Oeste, Cayo Centro, Cayo Este), Bajos de Sisal

In this region, the number of scleractinian coral and octocoral species decrease from east to west (Jordán-Dahlgren, 2002; Horta-Puga et al., 2007). The conservation status of these reefs is considered good, although the only places that have been assessed with relative frequency are the CR of the Veracruz Reef System (Arguelles et al., 2019). Nonetheless, Jackson et al. (2014) established that in 1965 the coral cover of these areas was 34.1%, decreasing to 17.2% by 1999, showing a potentially important decrease in coral cover similar to the one documented in the Caribbean. In other areas such as Alacranes Reef, coral cover has been reported at 11.2% which, although lower than in the Veracruz Reef System, is still higher than some of the coral cover registered in Mexican Caribbean Reefs at <10% (Suchley and Álvarez-Filip, 2018), and very similar to the cover in Florida mentioned previously.

Due to the large number of knowledge gaps on the distribution of CR in the southern GoM, there is an imminent need to describe these "new" coral formations, in aspects such as their size, depth, and species composition, as well as their related biota, and ecosystem services.

Mexico has designated over 90 million ha of natural protected areas, with ca. 650,000 km^2 of the marine coastal zones split over 37 MPAs; additionally 92% of the Mexican islands are included in the natural protected areas (CONANP, 2018b). The Lobos-Tuxpan Reef System has an area of >30,000 ha, the Veracruz-Reef System has an area of >60,000 ha, and Los Tuxtlas Reef System has an area of >177,000 ha. The first two are protected as National Parks, however the last one is not. Taking these into account, in Veracruz the protected area is roughly 30% of the reefs area, though Los Tuxtlas Reef System is under study to be included as a protected area. If this area reaches such status, all of the larger reef systems will be protected. In recent years, new reefs have been discovered in the region, and it is likely there are even more undiscovered reefs.

Close to the southwest GoM reefs there are mangroves and seagrass beds. Even when in Mexico mangroves are protected, these stands, and the coastal lagoons close to the reefs into the GoM do not form part of the same MPAs, creating management challenges. There are 10 MPAs into the GoM, three of them (Sistema Arrecifal Veracruzano, Sistema Arrecifal Lobos-Tuxpan, and Arrecife Alacranes) include CR but no mangroves; the remaining seven MPAs include mangroves but no reefs. Coastal lagoons in the GoM have an area of 5,767 km^2 (Contreras and Castañeda, 2004). All lagoons are closely related to mangroves, and most of them include seagrass, especially those from the Yucatan Peninsula, requiring an integrated management that considers their connectivity. According to Contreras and Castañeda (2004), by state, from northwest to southeast, the number and area of lagoons are as follow: Tamaulipas has six lagoons with a total area of 2,171 km^2, Veracruz has 20 lagoons with 1,213 km^2, Tabasco has five lagoons with 3,213 km^2, Campeche has three lagoons with 1,788 km^2, and finally Yucatan has five lagoons with a total area of 135 km^2. Tamaulipas and Tabasco, the states with the highest area of coastal lagoons, are the only states that have no CR on their continental platform. Nonetheless, it is noteworthy that in Mexico an adequate legal framework to establish networks of protected areas is lacking; mainly because connectivity is not considered an important factor in MPAs selection within the national legislation (Ortiz-Lozano et al., 2013).

Cuba

Corals and CR are distributed all around Cuba, with an estimated extension of ∼3,115 km (1,440 km of reefs in the north, and ∼1,675 km in the south). Four main reefs systems could be identified based on their geographic area: Archipiélago de Los Colorados, Archipiélago de Los Canarreos, Archipiélago Sabana-Camagüey, and Archipiélago de las Doce Leguas (Jardines de la Reina). Los Colorados, as well as the reefs of Artemisa, Havana, and Matanzas provinces, represent the southeastern portion of the GoM LME.

The biodiversity in Cuban CR has been studied for >60 years, focusing mainly in groups such as corals, algae, fishes, and mollusks (Alcolado et al., 2003; González-Ferrer, 2004; Claro, 2007; Suárez et al., 2015). Fifty-five scleractinian coral species have been identified in Cuban waters (González-Ferrer, 2004). *Acropora palmata*, *Pseudodiploria strigosa,* and *Pseudodiploria clivosa* are the most abundant species in healthy reef crests, while *Siderastrea siderea* is the most consistently-abundant coral species in all reef sites (González-Díaz et al., 2018). Other species that are abundant on Cuban reefs are *Agaricia agaricites*, *Agaricia humilis*, *Montastraea cavernosa*, *Siderastrea radians*, *Stephanocoenia intersepta*, *Porites astreoides*, *Porites porites*, and *Porites furcata*, while *Agaricia lamarcki* is very abundant in the fore reefs (González-Ferrer, 2004). In general, *Acropora cervicornis*, and *Orbicella* spp. are currently uncommon on Cuban CR, possibly indicating losses due to coral diseases or competition with macroalgae in recent decades (González-Díaz et al., 2018).

Between 2010 and 2013 Caballero Aragón et al. (2019) studied 199 reef sites covering 12 Cuban localities, and documented a similar number of coral species to those recorded in the 1980s; however, dominance has changed as opportunistic species (*Siderastrea siderea*, and *Agaricia agaricites*) substituted key ones (*Acropora palmata*, and *O. annularis*).

Lately, Cuban CR have been called "the crown jewels of the Caribbean Sea." Surveys on seven of the main Cuban CR systems (Havana, Artemisa, Los Colorados, Punta Francés, Los Canarreos Archipelago, Península Ancón, and Jardines de la Reina) between 2010 and 2016, suggest differences among communities. Offshore reefs along the south-central coast at Jardines de la Reina, and Península Ancón, exhibited higher coral density, and diversity of species than those closer to populated areas, suggesting their relatively good health (González-Díaz et al., 2018).

The connectivity of CR with other ecosystems such as mangroves, and seagrass beds has required the protection of extensive areas to include these ecosystems. In the northwestern shelf of Cuba (southern border of GoM), for example, seagrass beds extend between 17–40 km from the coast, and the reefs in Archipiélago de Los Colorados are on the shelf's border, far from the coastline. In Cuba, 105 MPAs have been proposed, covering 25% of the Cuban insular shelf; 57 of them have already been incorporated into the MPA system, and 13 more are being managed to its standards, for a total of 70 areas with some degree of implementation. About 30% of the Cuban CR, 24% of the seagrass beds, and 35% of mangroves are legally protected by the "Sistema Nacional de Areas Protegidas." The main challenges of these areas are insufficient financial resources, and the difficulty of reinvesting profits generated within them. Prohibited fishing practices, and capture of protected species are the principal issues affecting MPAs (Perera et al., 2018).

MESOPHOTIC AND DEEP-SEA CORALS

The presence of mesophotic corals and CR, has been recorded in the three countries of the GoM. Locker et al. (2010) identified the potential habitat distribution for mesophotic CR in the US, finding that the area of their possible distribution in depths between 30–100 m in the northern and eastern GoM, is 20 times greater than in other areas such as in the Hawaiian Islands, and the different US jurisdictions in the Caribbean. Nonetheless, the knowledge of occurrence, and distribution of these ecosystems remains scarce, but advances continue to move forward. Probably one of the most well-known deep reef areas in the region is Pulley Ridge, located ∼250 km west of Cape Sable, Florida. Although known for its diversity, and productivity since the 1800s, the presence of corals was only documented in the 1980s after an expedition from the Department of Interior's Mineral Management Service. Subsequent expeditions have further characterized the area, and determined the presence of coral formations composed of species such as *Helioseris* spp., *Agaricia* spp., *Madracis* spp., and *Montastraea cavernosa*. Area coverage by these corals was estimated at 1.5%, and these corals in mesophotic areas are often described as healthier than those observed on shallow reefs, although some signs of coral diseases were evident (Reed et al., 2019).

The eastern US GoM encompasses the most developed CR formations with seven offshore reefs or banks (see section "Shallow Coral Reef Distribution and Conservation Status") with a variable area of ∼41–645 km^2 (Simmons et al., 2014). The western US GoM is characterized by three types of banks, the south Texas Banks grow on relic carbonates while the banks east off Texas and Louisiana have carbonate reef caps, and are either midshelf or shelf-edge/outer-shelf bedrocks (Rezak et al., 1990). There are six midshelf banks: 32 Fathom, Claypile, Coffee Lump, Fishnet, and the two previously mentioned (Sonnier, Stetson) with areas varying from ∼0.4–18.9 km^2; 18 shelf-edge banks: Applebaum, Diaphus, Elvers, Ewing, Parker, Sacket, Sweet (only listed the seven not mentioned in section "Shallow Coral Reef Distribution and Conservation Status"), with areas ranging from 0.18–71.7 km^2; and 14 Texas Banks: Aransas, Baker, Big Adam, Blackfish Ridge, Dream, Harte, Hospital Rock, Mysterious, North Hospital, Seabree, Small Adam, South Baker, Southern Bank Test, Steamer covering from 0.07–∼2.4 km^2 (Simmons et al., 2014).

In an attempt to locate, and chart deep-sea corals in the GoM, Schroeder et al. (2005) compiled information from different sources (i.e., peer-reviewed and unpublished material, findings from a September–October 2003 cruise in the northern GoM, and the 2003 taxonomic database from the National Museum of Natural History), and identified the presence of at least 24 sites where assemblages of *Desmophyllum pertusum*, and *Madrepora oculata* were present. Subsequently, other studies have found new geological, and man-made features in the area, and identified the presence of these and other coral species (Brooks et al., 2012). The presence of oil platforms, and programs such as "Rigs to Reefs" have created substratum appropriate for the colonization of mesophotic corals along the northern GoM, increasing the expansion of these communities (Sammarco et al., 2004; Brooks et al., 2012).

Although mesophotic corals have been identified in the southern portion of the GoM, their extension, and composition are scarcely known, requiring an imminent effort to further study these ecosystems. Ortiz-Lozano et al. (2018) studied 22 emergent, and recorded 18 submerged CR, 16 within, and two outside the Veracruz Reef System National Park in order to identify the role of submerged reefs within protection policies (e.g., port and fishing activities); noting that ∼68.8% of those submerged reefs were not officially recognized, and thus are excluded in the protection decrees. A more recent study using high-resolution bathymetry updated the recorded reef number to 27 in the Veracruz Reef System, most of them submerged (below −30 m) yielding a total of 25 submerged, and 25 emergent reefs (Liaño-Carrera et al., 2019).

Mesophotic reefs in Cuba were characterized for the first time during the joint Cuba-US expedition in 2017. Benthic macrobiota yielded 491 taxa with 149 fishes identified, and 345 specimens of benthic macroinvertebrates, and macroalgae collected to verify taxonomy, and assess population structure. The deep fore-reef escarpment had the greatest diversity, and density of macrobiota; nearly all vertical surfaces were covered with diverse sponges, algae, gorgonians, and black corals. *Agaricia* spp. were the most abundant scleractinian corals, particularly from 40–75 m deep. Although corals were generally in good health, some colonies (mainly *Agaricia* spp.) showed signs of bleaching, and one *Agaricia* specimen had Black Band Disease. Sites outside of MPAs generally had lower fish abundances, a possible indicator of historical overfishing.

Recent events such as the Deepwater Horizon oil spill, show the particular vulnerability of mesophotic corals, and reef communities to human impacts. Different authors, including White et al. (2012), and Silva et al. (2016), documented damages to deep-sea coral communities in the proximity of the event's site. Characteristics of these ecosystems, such as their isolation, and slow growth, make them particularly vulnerable to long-term impacts (Fisher et al., 2016; Silva et al., 2016). Based on their importance for the ecosystem services they provide (e.g., refugia, food resources, and biological control, as well as useful biotechnological, and medicinal compounds) the study of mesophotic CR is a must.

THREATS TO GoM CORAL REEFS

Rising ocean temperatures, and global climatic changes are among the primary threats to CR around the world, and in the GoM (Anthony et al., 2015). Coral bleaching has likely been one of the most important factors that has affected CR in the Wider Caribbean region over the last 30 years; the 2005 bleaching was recorded as the most intense event of this type in the region. At some sites it affected over 80% of shallow corals, and killed 40% (Eakin et al., 2010). Also, as in many other parts of the world, overpopulation, coastal pollution, and overfishing are considered among the top anthropogenic stressors responsible for CR decline (Jackson et al., 2014).

United States

During the last three decades, the CR of the Florida Keys have suffered a significant loss in coral cover. In the 1970s for example, *Acropora palmata* dominated most of the outer reef, until a series of disease outbreaks, and hurricanes in the 1980s decimated its population; in some cases, up to 98% of their baseline abundance decreased as compared to the 1970s (Bruckner, 2002). Palandro et al. (2008) found a reduction in coral cover of 37% in eight reef sites monitored by the Coral Reef Evaluation and Monitoring Project between 1996 and 2002 using satellite data, however from direct evaluation the reduction was 52%; and when 1984 Landsat images were used coral cover loss was 61%. Furthermore, taxonomic losses of corals for virtually all habitat types were between 72–73%, with a consistent decline in overall taxonomic richness for all habitats (Jaap et al., 2008).

Bleaching, coral diseases, and hurricanes have been pointed out as the main contributors to coral decline on Florida Keys' reefs. At least six major bleaching events related to the increase in water temperature have affected the reefs of the Florida Keys since 1987 (Manzello, 2015), in some cases affecting >40% of coral colonies (Eakin et al., 2010; van Woesik and McCaffrey, 2017). In the bleaching event of 1997–1998, surface water temperatures were recorded peaking at 32°C, causing extensive bleaching to scleractinian corals, milleporids, and octocorals (Jaap et al., 2008). Similar to warm water, cold water events can cause rapid coral mortality in shallow reefs at large geographical scales (Lirman et al., 2011).

Since the first descriptions in the 1970s, coral diseases have become more widespread, and prevalent in CR throughout the region (Gil-Agudelo et al., 2009; Peters, 2015). The Wider Caribbean region seems to have been the hotspot of these threats to corals, with the Florida Keys being particularly affected. Many coral diseases known now were first identified in the Florida Keys, including White Band Disease, Yellow Band/Blotch Disease, and White Pox (Gil-Agudelo et al., 2009). A new coral disease known as Stony Coral Tissue Loss Disease was discovered in 2014, and described in the Miami area first (Precht et al., 2016). This disease has since spread to the northern limit of the reef tract, and was recently discovered on reefs west of Key West. It affects 22 species of corals, and can cause losses of as much as 30% of coral density, and 60% of living tissue area, probably becoming the most devastating coral disease to date (Walton et al., 2018) (**Figure 5**). Other reef organisms have also suffered disease that have decimated their population, such as gorgonian corals (Geiser et al., 1998), sea urchins (Ritchie et al., 2000).

Hurricanes have also been an important contributor to the decline of corals and CR of the Florida Keys. Although these events are part of the natural cycle of corals in the Caribbean, successive hurricane events in short periods of time over the Florida Keys, as well as the effect of other variables, seem to have had a deleterious effect on these reefs (Jaap et al., 2008). Gardner et al. (2005) showed that coral cover was reduced by ∼17%, on average after a hurricane in the Caribbean, followed by a slow recovery after; but CR have shown little recovery, particularly areas previously dominated by *A. palmata*, mainly due to the interaction of other stressors.

FIGURE 5 | Stony Coral Tissue Loss Disease on a *Colpophyllia natans* coral head in David Reed, Upper Florida Keys. Photo by Jennifer Stein (The Nature Conservancy) in 2017.

Pollution is also a determinant factor in the decline of CR in the Florida Keys. Maliao et al. (2008) found differences in the composition of the benthic biota of CR between the Lower and Upper-Middle Keys, explained by the higher nutrient concentration found in the Lower Keys, potentially due to patterns of human population, and water mixing. Furthermore, a phase shift occurred in these coral communities, changing from a coral to an algae and sponge dominated ecosystem (Maliao et al., 2008). More recently, LaPointe et al. (2019) showed correlations between increased nitrogen levels as a result of Everglades discharges, and coral stress, and decline at Looe Key reef. Over the study period (1984–2014), water temperatures exceeded the threshold for bleaching (30.5°C) repeatedly, but the three major bleaching events occurred only when nitrogen to phosphorus ratios were high following elevated rainfall or Everglades discharges (LaPointe et al., 2019).

In contrast to the Florida Keys, and other parts of the GoM and the Caribbean, corals in the Flower Garden Banks National Marine Sanctuary seems to be more protected from major bleaching events, and the mortality often associated with them (Hagman and Gittings, 1992; Precht et al., 2008; Johnston et al., 2013). The aforementioned (see section "Threats to GoM Coral Reefs") 2005 bleaching event affecting >80% of shallow corals in the Wider Caribbean, was minute in comparison, as its effect was <0.5% for the Flower Garden Banks. Nonetheless, in 2016, a strong bleaching event affected >40% of coral colonies at different degrees but with low mortality[3] (Davies et al., 2017; Kiene et al., 2017). Although most of the impacted corals have subsequently recovered from this event, its severity questions whether these CR can maintain their resistance, and resilience to changing conditions in the GoM.

Corals in the Flower Garden Banks National Marine Sanctuary also seem to be protected from coral diseases. Borneman and Wellington (2005) described the presence of several potential coral diseases in the area, finding limited incidence, and low coral mortalities, and the apparent absence of coral diseases usually present on Caribbean reefs such as Black Band Disease, and Yellow Blotch Disease. In 2019, unconfirmed signs of coral disease were found in East Garden Bank affecting diverse species, such as *Pseudodiploria strigosa*, and *Orbicella faveolata* (DLG-A personal observation; **Figure 6**).

The distance of these banks from the continent (∼185 km) limit the influence of land based pollution. Nonetheless, extreme events such as hurricanes can cause plumes of continental water to reach the Flower Garden Banks, potentially exposing the reef to pollutants (Schmahl et al., 2008). In 2016, an apparent decrease in DO concentration affected 5.6 ha of reef, and up to 82% of coral colonies of East Flower Garden Bank; besides corals, other organisms such as poriferans, crustaceans, mollusks, and echinoderms, also suffered extensive mortality (Johnston et al., 2019). Wright et al. (2019) also showed how the influence of runoff from storm events such as Hurricane Harvey, can produce sublethal stress in these reefs. It is unclear how these events will impact the corals in the future with the increase of nutrient pollution, and dead zones in the area.

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[3] https://flowergarden.noaa.gov/newsevents/2016bleachingarticle.html

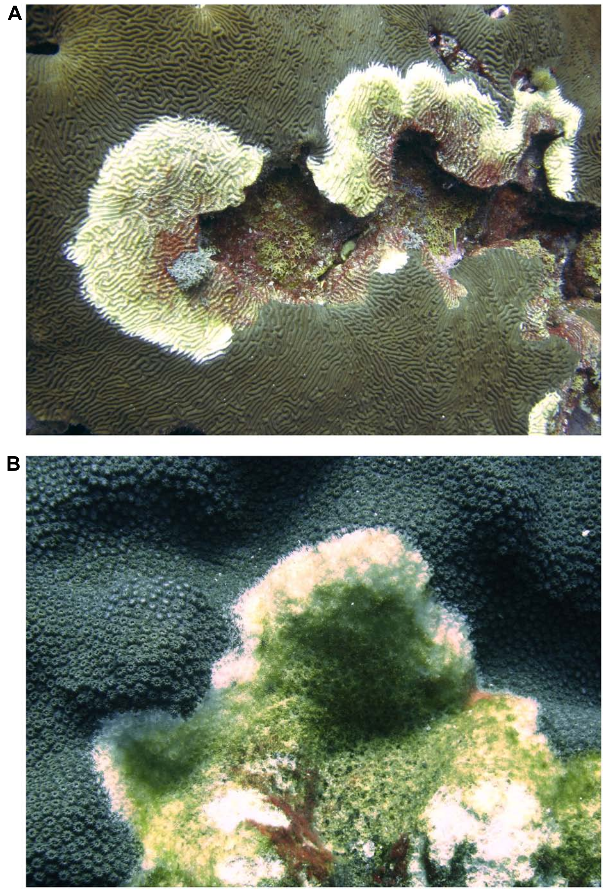

FIGURE 6 | Corals **(A)** *Pseudodiploria strigosa*, and **(B)** *Orbicella faveolata* with signs that resemble White Band Disease in East Flower Garden Bank at –18.3 m (–60 ft). Photos by DLG-A.

Some direct human activities are concerning for the ecosystems of the Flower Garden Banks. Anchoring, fishing, and diving are subject to regulations in the area to minimize potentially harmful effects on the reefs, including direct damage to corals, and release of pollutants and/or debris. All corals and benthic invertebrates in the Flower Garden Banks National Marine Sanctuary are protected from any take or harm through the National Oceanic and Atmospheric Administration (NOAA) regulations. Hurricanes have also been found to cause damage to the banks corals and CR, including due to the mass movement of sand, the movement, and overturning of coral structures, and damage to sponges and other sessile organisms (Schmahl et al., 2008).

Mexico

A diverse number of threats, natural and human-associated, are affecting the reefs of the GoM coast of Mexico. Tropical storms and hurricanes, and winter "Nortes" (cold fronts with high winds that decreases sea surface temperature) increase the potential damage to CR (Jordán-Dahlgren, 2004). Similar to other areas of the GoM and the Caribbean, bleaching events have been reported along the Mexican coast, and in the Veracruz Reef System National Park, particularly in species such as *Acropora* spp. (Ortiz-Lozano et al., 2018), *Colpophyllia natans*, *Orbicella* spp., *Siderastrea* spp. (Carricart-Ganivet et al., 2011), and *Porites* spp. (Carricart-Ganivet, 1993). A reduction of these key species might generate catastrophic collapses of coral communities, particularly when the reproductive capacity of such taxa is reduced or eliminated (Jordán-Dahlgren, 2004).

Similar to almost every reef in the Wider Caribbean, White Band Disease affected corals from the Veracruz Reef System and Campeche Banks in the 1980s, and was the main suspect for the decline in Acroporid corals on some of these reefs. Yellow Blotch Disease, and other diseases have further impacted reef-building corals such as *Orbicella* spp. in this region (Jordán-Dahlgren, 2004).

As a result of their geographic location, Veracruz reefs are the most impacted CR systems in the Mexican GoM. They are not only exposed to the impact of anthropogenic development, including urban, industrial, and agricultural, but also to large riverine discharges. Over-sedimentation, pollution, overfishing, habitat destruction, and coastal development are probably the most important human-made threats to these reefs (Toledo-Ocampo, 2005), noteworthy these impacts may result in deterioration of water column transparency, with its inherent light availability reduction, and their potential consequences on zooxanthellate corals. Currently, the construction of the "Nuevo Puerto de Veracruz" is under way in an area adjacent to the Veracruz Reef System National Park[4]; its northern breakwater has been recently built over a fringing reef, and the southern breakwater will be built next to another reef, impacting these important ecosystems. Adverse consequences are also expected due to dredging work, anchoring, and the increase in maritime traffic (e.g., Foster et al., 2010). Meanwhile, due to their oceanic location, the reefs in the Campeche Banks experience anchoring, and overfishing as their main stressors, although pollution associated with oil platform construction, and operation has also been identified (Hudson et al., 1982; Jordán-Dahlgren, 2004). The recent massive arrivals, and accumulation of algae to Mexican shores, particularly *Sargassum* spp., is a concern due to the potential nutrient upload, a consequence of the decomposition of these organisms. Moreover, little is known about the effect of climate regimes on the occurrence of *Sargassum* spp. pelagic taxa over interannual and decadal scales (Sanchez-Rubio et al., 2018), which might be enhanced with current global climatic changes.

Cuba

The main anthropogenic threats to Cuban CR are related to overfishing by subsistence fisheries (particularly in the northern coasts of Artemisa, Havana, and Matanzas provinces due to their accessibility). Nationally, it is estimated that 20% of fishery resources are fully exploited, 74% overexploited, and 5% collapsed. Other threats such as environmental degradation, and climate change are playing a role in fishes decline, also likely affecting reefs (Baisre, 2018).

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[4] https://www.gob.mx/semarnat/articulos/sistema-arrecifal-veracruzano-y-el-desarrollo-sustentable?idiom=es

TABLE 2 | Population density in coastal municipalities (directly related with coral reefs), and main anthropogenic stressors in the northwestern Cuban provinces facing the Gulf of Mexico.

Province	Municipality	Density of Habitants (Hab/km^2)	Urban Communities	Rural Communities	Main Source of Anthropogenic Stressors
Pinar del Río (8,883.74 km^2)	Sandino	21.7	6	24	Ilegal and sustainable fisheries
	Matua	26.9	3	16	
	Minas de Matahambre	38.3	3	11	
	Viñales	40.2	5	27	
	La Palma	54.2	4	32	
Artemisa (4,003.24 km^2)	Bahía Honda	55.5	6	46	
	Mariel	165.4	8	23	
	Caimito	167.8	10	24	Honda Bay
	Bauta	312.4	9	27	Mariel Bay
	Jaruco	89.5	4	12	Cabañas Bay
Mayabeque (3,743.81 km^2)	Sta. Cruz del Norte	91.0	8	21	Ilegal and sustainable fisheries
La Havana (728.26 km^2)	Playa	5, 030.5			Havana Bay
	Plaza de la Revolución	12, 050.3			Almendares River
	Centro Havana	40, 984.2			Quibú River
	Havana Vieja	20, 019.0			Jaimanitas River
	Regla	4, 184.5			Ilegal and sustainable fisheries Industries

Source: ONE (2016).

Land-based pollution is another important factor affecting the Cuban CR of the GoM. Based on their impact, three areas can be distinguished (**Table 2**). First, Los Colorados Reefs and Pinar del Rio Province, showing relatively healthy reefs, far from the coast, and with low population density living in small coastal communities. Second, Artemisa Province, with two bays as a major source of land based pollution, with easy accessibility to the reefs but with relatively low population density. Lastly, Havana City, with reefs highly impacted due to industrial activities, and acute and chronic land based pollution sources. Because Havana City is the capital of Cuba, it is also the most populated city.

OTHER IMPACTS

A particular area of concern in the GoM is the potential impact of oil and gas development in the region. The US GoM is one of the major areas of offshore oil and gas production in the world, producing 1.65 million barrels/day (b/d) in 2017. This is expected to rise to 1.8 million b/d by 2019[5]. At present, more than 3,600 production platforms are used to extract oil and gas from the US GoM (Sammarco, 2013). Mexico and Cuba are also seeking to expand their offshore oil production in the GoM, which increases the need to understand the ecological implications of potential changes to the benthic ecosystems, and associated nektonic organisms.

Production platforms and other structures required for the production of offshore oil and gas are known to serve important ecological functions, including increases in secondary biomass production (Cresson et al., 2014), provision of refuge or food for diverse fishes (Nelson and Bortone, 1996; Szedlmayer and Lee, 2004), and support for diverse assemblages of epibenthic invertebrates (Lewbel et al., 1987); they also serve as stepping stones (Sammarco, 2013), which might also have deleterious impacts in natural communities by allowing the expansion of non-native species. Programs such as "Rigs to Reefs" have been designed to increase the productivity by adding available substrates for reef formation (Macreadie et al., 2011; Stephan et al., 2013).

However, there are also very real risks involved with the installation of oil and gas platforms. The risk of oil spills became evident not only after the 2010 Deepwater Horizon event, but others such as the Ixtoc in Mexico in 1979 (Jernelöv and Lindén, 1981), and many minor spills that have resulted from both natural events (such as hurricanes), and human caused incidents[6]. They can also serve as stepping stones (Sammarco, 2013), which might have deleterious impacts on natural communities. Since the 1930s, *Tubastraea coccinea*, an invasive species originally from the Pacific arrived to the Caribbean, and has been transported throughout the GoM by colonizing oil and gas platforms (Sammarco et al., 2004). *Oculina patagonica* is another coral

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[5] www.eia.gov

[6] https://response.restoration.noaa.gov/oil-and-chemical-spills/oil-spills/largest-oil-spills-affecting-us-waters-1969.html

species found in the Veracruz reefs, whose origin appears to be the Mediterranean Sea (Colin-García et al., 2018). Similarly invasion by lionfishes (*Pterois volitans*, and *Pterois miles*) has happened, and have reached almost all environments of the GoM (Schofield, 2010) potentially helped by these platforms. In 2013, the fish *Neopomacentrus cyanomos* originally from the Indo-West Pacific was reported for the first time in the SW corner of the GoM (González-Gándara and de la Cruz-Francisco, 2014). In 2017, Bennett et al. (2019) registered this species for the first time in the coasts of Alabama, northern GoM, inhabiting natural gas platforms, showing the potential effect of these structures in the rapid spread of non-native species across the GoM.

Additionally, during the extraction of oil and gas, Produced Waters (PWs, complex mix of hydrocarbons, heavy metals, and other substances both present in the reservoir, and added during the production process) are also extracted. These PWs are usually treated on site, and released to the environment, carrying substances that have been shown to be deleterious to aquatic organisms during controlled laboratory toxicology tests (Kennicutt, 1994; Fleeger et al., 2001). It is estimated that the PW: oil production ratio in the US is 7:1 (Veil, 2011), meaning that more than 12 million barrels of PWs can be potentially entering the GoM on a daily basis. The effect that these effluents can cause to marine environments such as CR is still largely understudied (Lee and Neff, 2011; Brooks et al., 2012; Cordes et al., 2016), and deserves further attention not only in the US waters, but also throughout the GoM.

OPPORTUNITIES FOR CONSERVATION AND SUSTAINABILITY

Several opportunities exist to add momentum, and strengthen conservation of CR throughout the GoM. The first involves capitalizing on existing, and emerging multi-lateral agreements and initiatives, including the GoM LME Program (Global Environment Facility, 2016), and the trinational US-Mexico-Cuba sister sanctuaries agreement. The second involves bringing greater focus onto the GoM within existing global networks of conservation practitioners, including the Reef Resilience Network, and the Coral Restoration Consortium. There is an emerging opportunity for increased financial support for conservation through international initiatives, and the private sector, including insurance policies that focus on the risk-reduction function of reefs in coastal communities, and more broadly on the emergence of corporate sustainability initiatives that emphasize the business dependency on healthy CR, and other coastal habitats.

Governments from the three countries recognize the importance of corals and CR in the GoM, and continue their efforts to protect these delicate ecosystems. In the US, the Flower Garden Banks National Marine Sanctuary is in the process of expansion, seeking to include 14 additional reefs, and banks formations of the northern GoM. Cuba has also identified the need for expansion of their MPAs network, and is working toward the designation of new areas. The Mexican government has recently signed international agreements for the protection of the environment that will help in the conservation of CR. Protection of some species has taken place in the three countries of the GoM (**Table 3**).

It is important to recognize that corals, CR, and coral bank ecosystems do not function in isolation from other communities, and that their condition is dependent on their ecological connectivity throughout the entire GoM (Kiene, 2018). Ocean currents that flow from the Caribbean, and into the Atlantic physically connect coral species across the Wider Caribbean region (Schill et al., 2015). Fishes, marine mammals, sea turtles, and other organisms migrate among US, Cuban, and Mexican waters, and offspring from reef associated species are transported from one country to another by the currents of the GoM (Brenner et al., 2016). Recent modeling studies on virtual larvae have allowed detection of trajectories illustrating habitat connectivity. For example, Criales et al. (2019) studied blue crab (*Callinectes sapidus*) showing variable larval dispersal pathways between 2015 and 2016, which were driven by the interaction of winds, the Mississippi River plume, Loop Current intrusions in the northern GoM, Loop Current eddies, and their cyclonic counterparts. Their findings supported the homogeneous genetic population structure of *C. sapidus* among Mid-Atlantic and GoM populations, as the Mississippi River plume provided a conduit to transport virtual larvae to the South Atlantic Bight. Virtual larvae of red grouper (*Epinephelus morio*), lionfishes (*P. volitans*, and *P. miles*), and a "generic" marine organism showed physical connectivity among the Campeche Banks – particularly the NE perimeter – to the NE GoM defined as locations within the gulf, and western Atlantic explained by the position, and strength of the Loop Current (Johnston and Bernard, 2017). Garavelli et al. (2018) studied the connectivity along banks in the NW GoM using virtual larvae, concluding that *Montastraea cavernosa* larvae, a common reef-building coral species in CR and banks in the region, is exported to the northeastern, and southwestern GoM. This same species is a key element in shallow reefs in the region, making deep banks potentially important as refugia for the changing condition that shallow reefs are experiencing (Studivan and Voss, 2018). However, see Rocha et al. (2018) for an alternative view of the refuge hypothesis associated to mesophotic reefs (basically might work as long as reefs are far away from the wise monkey's reach), nonetheless the authors recognize inherent threats to, and prioritize protection of mesophotic reefs.

Other studies have also identified important connectivity in CR organisms that are protected or constitute commercially important resources. As an example, population dynamics of the Caribbean spiny lobster (*Panulirus argus*) showed the importance of reefs in Cuba and Florida for the larval export throughout the GoM, and the Caribbean (Kough et al., 2013). Similarly, Paris et al. (2005) found an important connectivity of snappers (Lutjanidae) living in CR in Cuba with other CR in the region, showing the importance, and need of transnational resource management strategies. These organisms are known to move considerable distances across shallow shelf areas to reach their spawning aggregations, and healthy habitats, particularly among those with "stepping-stone" patches of submerged reef habitats (Claro et al., 2001; Robertson et al., 2019). Organisms that use different habitats through ontogeny should benefit

TABLE 3 | Scleractinian coral species by reef system (Reef) in the Gulf of Mexico ordered alphabetically by Family name.

Taxa	Reef	Threaten/Protection
Acroporidae		
Acropora cervicornis (Lamarck, 1816)	*FK, DT*, TL[1], *SAVNP*[1,3,4,9], *TR*[1], *CB*[1,3], CCR[2]	Critically endangered (IUCN)/ Threatened (USESA)
Acropora palmata (Lamarck, 1816)	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,3,4,9], *TR*[1], *CB*[1,3]	Critically Endangered (IUCN)/ Threatened (USESA)
Acropora prolifera (Lamarck, 1816)*	*FK, DT*, *TL*[1], *SAVNP*[1,9], *CB*[1,3], CCR[8]	
Agariciidae		
Agaricia agaricites (Linnaeus, 1758)	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,4,9], TR[1], *CB*[1], CCR[2]	Least Concern (IUCN)
Agaricia fragilis Dana, 1848	FK, DT, PR, *FGBNMS*[1], MB[5], *TL*[1], *SAVNP*[1,4,9], TR[1], *CB*[1], CCR[8]	
Agaricia grahamae Wells, 1973	PR, SAVNP[9], CCR[8]	Least Concern (IUCN)
Agaricia humilis Verrill, 1902	FK, DT, TL[1], *SAVNP*[1,9], TR[1], *CB*[1], CCR[8]	Least Concern (IUCN)
Agaricia lamarcki Milne Edwards & Haime, 1851	*FK, DT*, PR, TL[1], *SAVNP*[1,4,9], TR[1], CB[1], CCR[8]	Vulnerable (IUCN)
Agaricia tenuifolia Dana, 1848	*CB*[1], CCR[8]	Near Threatened (IUCN)
Agaricia undata (Ellis & Solander, 1786)	PR, CCR[8]	
Helioseris cucullata (Ellis & Solander, 1786)	*FK, DT*, PR, *FGBNMS*[1], TL[1], *SAVNP*[1,9], TR[1], *CB*[1], CCR[8]	Least Concern (IUCN)
Astrocoeniidae		
Stephanocoenia intersepta (Lamarck, 1836)	*FK, DT*, *FGBNMS*[1], MGB[5], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[2]	Least Concern (IUCN)
Caryophyliidae		
Coenocyathus sp.	*FGBNMS*	
Colangia immersa Pourtalès, 1871	SAVNP[9]	
Oxysmilia sp.	*FGBNMS*	
Paracyathus pulchellus (Philippi, 1842)	*FGBNMS*, TR[6]	
Phyllangia americana Milne-Edwards & Haime, 1849	*SAVNP*[9]	
Polycyathus senegalensis Chevalier, 1966	*FGBNMS*	
Rhizosmilia maculata (Pourtalès, 1874)	*FGBNMS*	
Dendrophylliidae		
*Tubastraea coccinea*ˆ Lesson, 1829	*FGBNMS*, *TL*, *SAVNP*[9], *CB*	
Faviidae		
Colpophyllia natans (Houttuyn, 1772)	*FK, DT*, *FGBNMS*[1,5], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[8]	Least Concern (IUCN)
Diploria labyrinthiformis (Linnaeus, 1758)	*FK, DT*, TL[1], SAVNP[1,4], *CB*[1], CCR[8]	Least Concern (IUCN)
Favia fragum (Esper, 1795)	*FK, DT*, SAVNP[1,9], *CB*[1], CCR[8]	Least Concern (IUCN)
Favia gravida Verrill, 1868	FK, DT, SAVNP[1]	
Isophyllia rigida (Dana, 1846)	FK, DT, TL[1], SAVNP[1], CB[1], CCR[8]	
Isophyllia sinuosa (Ellis & Solander, 1786)	*FK, DT*, SAVNP[1], CB[1], CCR[8]	Least Concern (IUCN)
Manicina areolata (Linnaeus, 1758)	FK, DT, TL[1], *SAVNP*[1,4,9], CB[1], CCR[8]	Least Concern (IUCN)
Mussa angulosa (Pallas, 1766)	*FK, DT*, *FGBNMS*[1], TL[1], *SAVNP*[1,4,9], CB[1], CCR[8]	Least Concern (IUCN)
Mycetophyllia aliciae Wells, 1973	*FK, DT*, TL[1], CB[1], CCR[8]	Least Concern (IUCN)
Mycetophyllia danaana Milne Edwards & Haime, 1849	*FK, DT*, TL[1], *SAVNP*[1,9], CB[1], CCR[8]	Least Concern (IUCN)
Mycetophyllia ferox Wells, 1973	FK, *DT*, TL[1], *SAVNP*[9], *CB*[1], CCR[8]	Vulnerable (IUCN)/ Threatened (USESA)
Mycetophyllia lamarckiana Milne Edwards & Haime, 1849	FK, DT, TL[1], *SAVNP*[1,4,9], *CB*[1], CCR[8]	Least Concern (IUCN)
Mycetophyllia reesi Wells, 1973	CCR[8]	
Pseudodiploria clivosa (Ellis & Solander, 1786)	*FK, DT*, *FGBNMS*, *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[8]	
Pseudodiploria strigosa (Dana, 1846)	*FK, DT*, *FGBNMS*[1,5], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[8]	
Scolymia cubensis (Milne Edwards & Haime, 1848)	FK, *DT*, PR, *FGBNMS*[1], TL[1], *SAVNP*[1,9], CB[1], CCR[8]	Least Concern (IUCN)
Scolymia laceras (Pallas, 1766)	FK, DT, TL[1], *SAVNP*[1,4,9], CB[1], CCR[8]	
Scolymia wellsii Laborel, 1967	SAVNP[1], *CB*[1], CCR[8]	
Meandrinidae		
Dendrogyra cylindrus Ehrenberg, 1834	*FK,* DT, TL[1], *CB*[1], CCR[8]	Vulnerable (IUCN)/ Threatened (USESA)
Dichocoenia stokesii Milne Edwards & Haime, 1848	*FK, DT*, TL[1], *SAVNP*[1,9], *CB*[1], CCR[8]	Vulnerable (IUCN)
Eusmilia sp.	*FGBNMS*	
Eusmilia fastigiata (Pallas, 1766)	*FK, DT*, TL[1], SAVNP[1], *CB*[1], CCR[8]	Least Concern (IUCN)
Meandrina meandrites (Linnaeus, 1758)	*FK, DT*, TL[1], SAVNP[1,4], *CB*[1], CCR[8]	Least Concern (IUCN)

(Continued)

TABLE 3 | Continued

Taxa	Reef	Threaten/Protection
Merulinidae		
Orbicella annularis (Ellis & Solander, 1786)	*FK, DT*, *FGBNMS*[1,5], *TL*[1], *SAVNP*[1,4,9], TR[1], *CB*[1], CCR[8]	Endangered (IUCN)/ Threatened (USESA)
Orbicella faveolata (Ellis & Solander, 1786)	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,9], *CB*[1], CCR[2,8]	Endangered (IUCN)/ Threatened (USESA)
Orbicella franksi (Gregory, 1895)	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,9], *CB*[1], CCR[8]	Vulnerable (IUCN)/ Threatened (USESA)
Montastraeidae		
Montastraea cavernosa (Linnaeus, 1767)	*FK, DT*, PR, *FGBNMS*[1,5], MB[5,7], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[2,8]	Least Concern (IUCN)
Oculinidae		
Madrepora carolina (Pourtalès, 1871)	*FGBNMS*	
Oculina diffusa Lamarck, 1816	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,4,9], TR[1], CB[1], CCR[8]	Least Concern (IUCN)
Oculina patagonica de Angelis, 1908	*SAVNP*[9], TR[6]	Least Concern (IUCN)
Oculina robusta Pourtalès, 1871	FK, DT, TL[1], SAVNP[9], TR[1,6]	
Oculina tenella Pourtalès, 1871	FK, DT, PR, *FGBNMS*, TR[6]	
Oculina valenciennesi Milne Edwards & Haime, 1850	SAVNP[1,9]	
Oculina varicosa Le Sueur, 1820	TL[1], *SAVNP*[1,9], TR[1]	Vulnerable (IUCN)
Pocilloporidae		
Madracis asperula Milne Edwards & Haime, 1849	FK, DT, *FGBNMS*	
Madracis auretenra Locke, Weil & Coates, 2007	*FK, DT*, *FGBNMS*, MB[5,7], *SAVNP*[4,9]	Least Concern (IUCN)
Madracis carmabi Vermeij, Diekmann & Bak, 2003	*SAVNP*	
Madracis decactis (Lyman, 1859)	*FK, DT*, *PR*, *FGBNMS*, MB[5,7], *SAVNP*[4,9], *CB*, CCR[8]	Least Concern (IUCN)
Madracis formosa Wells, 1973	*FK,* DT, PR, *FGBNMS*, CB, CCR[8]	Least Concern (IUCN)
Madracis pharensis (Heller, 1868)	FK, DT, PR, MB[5,7], *SAVNP*[9]	Least Concern (IUCN)
Poritidae		
Porites astreoides Lamarck, 1816	*FK, DT*, *FGBNMS*[1,5], *TL*[1], *SAVNP*[1,4,9], TR[1], *CB*[1], CCR[2,8]	Least Concern (IUCN)
Porites branneri Rathbun, 1888	FK, DT, TL[1], SAVNP[1,9], CB[1], CCR[8]	Near Threatened (IUCN)
Porites colonensis Zlatarski, 1990	TL[1], SAVNP[1,9], TR[1], *CB*	
Porites divaricata Le Sueur, 1820	*FK, DT*, PR, TL[1], SAVNP[1,9], CB[1], CCR[8]	Least Concern (IUCN)
Porites furcata Lamarck, 1816	*FK, DT*, *FGBNMS*[1], TL[1], SAVNP[1,9], CB[1], CCR[8]	Least Concern (IUCN)
Porites porites (Pallas, 1766)	*FK, DT*, *FGBNMS*, TL[1], *SAVNP*[1,4,9], TR[1], *CB*[1], CCR[2]	Least Concern (IUCN)
Rhizangiidae		
Astrangia solitaria (Le Sueur, 1818)	*SAVNP*	
Scleractinia *incertae sedis*		
Cladocora arbuscula (Le Sueur, 1820)	FK, DT, TR[6], CCR[8]	Least Concern (IUCN)
Solenastrea bournoni Milne Edwards & Haime, 1849	*FK, DT*, *FGBNMS*, SAVNP[1], CB[1], CCR[8]	Least Concern (IUCN)
Solenastrea hyades (Dana, 1846)	*FK, DT*, CB[1], CCR[8]	Least Concern (IUCN)
Siderastreidae		
Siderastrea radians (Pallas, 1766)	*FK, DT*, FGBNMS[1], MB[5,7], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[8]	Least Concern (IUCN)
Siderastrea siderea (Ellis & Solander, 1786)	*FK, DT*, *FGBNMS*[1], *TL*[1], *SAVNP*[1,4,9], *TR*[1], *CB*[1], CCR[2,8]	Least Concern (IUCN)

Valid family and species names from World Register of Marine Species [WORMS] (2019). Florida Keys = FK; Dry Tortugas = DT; Pulley Ridge = PR; Flower Garden Banks National Marine Sanctuary = FGBNMS; McGrail Bank = MGB; Midshelf Banks = MB, includes Claypile, Sonnier, Stetson, Fishnet, Coffee Lump, and 32 Fathom; Tuxpan-Lobos Reefs = TL; Sistema Arrecifal Veracruzano National Park = SAVNP; Los Tuxtlas Reefs = TR; Campeche Banks = CB; Cuban Reefs = CCR. Species observed by at least one of the authors of this manuscript are italicized under reef abbreviation. Species status is from International Union for Conservation of Nature (IUCN, 2019); United States (US) Endangered Species Act = USESA (2019), any species under the latter is protected anywhere it occurs. See text for further details about regulation on an specific reef system. *Reported as a hybrid species (e.g., Liaño-Carrera et al., 2019); ^only observed on artificial reefs within Mexico. [1]Berumen Solórzano (2018), [2]Caballero Aragón et al. (2019), [3]Jordán-Dahlgren (2004), [4]Lara et al. (1992), [5]Simmons et al. (2014), [6]Jordán-Garza et al. (2017), [7]Weaver et al. (2006), [8]González-Ferrer (2004), [9]Liaño-Carrera et al. (2019).

by provisions of proper habitat that facilitates their migration among isolated reefs.

However, the scale, and intensity of the disturbances in the GoM is threatening the biodiversity, and connectivity of the CR network among populations. For instance, new pollution or hypoxia-induced events continue to appear around the gulf, and the Caribbean. If such network fragmentation continues to increase, any given species' ability to cope with regional extinction threats will largely depend on its dispersive capabilities (e.g., pelagic larval duration length; Cowen and Sponaugle, 2009). It is imperative then to identify, and implement "ecological corridors", and conservation actions in order to mitigate habitat destruction, and barriers for dispersal to maintain ecological connectivity. Thus, international cooperation in ocean conservation issues is an essential part of protecting the ecological integrity of CR to preserve populations of reef-dependent species that are commercially important, and threatened throughout the GoM. Studies like those conducted by Schill et al. (2015) can help inform international collaborations like these by using connectivity mapping to inform MPA design, and siting across jurisdictional boundaries.

Recognizing the strong biophysical, and economic connectivity within the GoM, the US executed conservation agreements with Mexico (in 2012), and Cuba (in 2015) to collaborate in the creation of an international network of MPAs to conserve CR resources. This initiative was one of the first formal intergovernmental cooperative plans that came from the normalization of relations between the US, and Cuba (Wenzel et al., 2019), yielding the 2015 Memorandum of Understanding between Cuba's Ministry of Science Technology and Environment, and the US NOAA, allowing scientific, and management cooperation between their MPAs (NOAA, 2015).

To continue benefiting marine conservation in the region, the US-Cuba relationship has been recently integrated to the ongoing transboundary GoM LME Program. This sister sanctuary initiative has provided MPA site managers in Mexico, Cuba, and the US an opportunity to share the understanding of the ecosystem protection strategies, and trends in the condition, and management of all the sites (**Figure 7**). Termed "RedGolfo," the goal is to provide managers of the sites with tools to identify strengths, and weaknesses in how they address key conservation issues, and inform local, and collective decisions on how technical, and management resources can best be applied in the GoM. The ultimate goal is to make the function of the MPA network equal more than the sum of the conservation efforts at each individual site. Through this network of MPAs, and with the cooperation of resources users, Non-Government Organizations, and other stakeholders, Mexico, Cuba, and the US have the opportunity to form valuable joint marine conservation, and research programs to support the long-term management of GoM resources[7].

There are several existing international communities of practice through which GoM reef managers, and scientists could collaborate more closely, and bring the attention to these important habitats. The Reef Resilience Network brings together some 1,500 members from across the globe, and is supported by over 100 experts in CR, fisheries, climate change, and science communication who act as trainers, and advisors. The network distributes pertinent information about the science, and management of CR, develops, and supports both online, and in-person training on a variety of issues, and hosts webinars on key issues, including new management techniques, current events, and publications.

The Coral Restoration Consortium is a community of practice consisting of scientists, managers, and coral restoration practitioners with the goal of encouraging collaboration, and the sharing of lessons learned to help increase the scale, and efficiency of coral restoration efforts worldwide. Working groups of the consortium are currently developing best management practices, and action plans for different types of restoration and/or issues to consider when planning, and conducting restoration (i.e., genetic diversity, how to appropriately monitor success, etc.). The consortium co-hosts webinars with the Reef Resilience Network to disseminate relevant, and timely information to practitioners.

In some places of the Wider Caribbean region, the loss of coral cover has been devastating during the last decades, followed by a slow, and sometimes null recovery. In response, active coral restoration programs have developed around the world with the goal of propagating and/or breeding corals within in-water, and land-based nurseries, and reintroducing them to degraded reef sites to help support natural recovery. Since 2012, over 60 restoration programs have focused on the Acroporid species in the Caribbean basin alone (Young et al., 2012). Coral gardening, pioneered by Rinkevich (1995), has traditionally been the most widely used method of restoration because it involves harvesting a very small amount of coral fragments from the wild, and propagating it to create a sustainable source for future transplantation efforts. More recent advances include the ability to settle sexual recruits in land-based facilities for future restoration efforts (Peterson and Tollrian, 2001), and the ability to induce spawning in corals held in land-based facilities (Craggs et al., 2017) to produce larvae more frequently. Although the restoration work began with a focus on *A. cervicornis*, programs have since expanded to target other branching, and boulder corals of a wide suite of species.

Finally, an effort to increase the characterization, and protection of the deeper part of the CR or mesophotic reefs in the GoM, is urgently needed. For example, in Mexico the National Commission of Protected Areas recognized only 28% of the 18 submerged reefs associated to the Sistema Arrecifal Veracruzano National Park in the management plan, but these CR were identified during consultation with reef users, and academic mapping efforts rather than through a systematic governmental effort, highlighting the need to identify, and characterize these ecosystems (Ortiz-Lozano et al., 2018). In Cuba, the Cooperative Institute for Ocean Exploration, Research and Technology of the US, and the Marine Science Institute of the University of Habana, completed in 2017 a systematic survey to characterize the extent, and health of reefs from depths of 30 to approximately 150 m (Reed et al., 2018), but there are still important gaps of information to address.

Coral reef ecosystems across the GoM have been nationally protected, and new initiatives have brought international attention to their conservation, and future. However, their sustainability is still far from being secured, as governmental, and societal commitment to their conservation still depends in the identification, and implementation of long-term strategies based in agreements in social-economic tradeoffs. Managing the large diversity, and productivity of CR in a heavily used region such as the GoM requires a shared vision that supports the provisioning of benefits to communities, but also maintains the multiple natural functions that make CR the most productive marine systems. The needed management actions to enhance the condition of CR must include punctual actions such as limiting carrying capacity, and reef visitation, as well as additional

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[7] http://blueoceanproductions.com/blog/gulf-mexico-marine-protected-area-network/

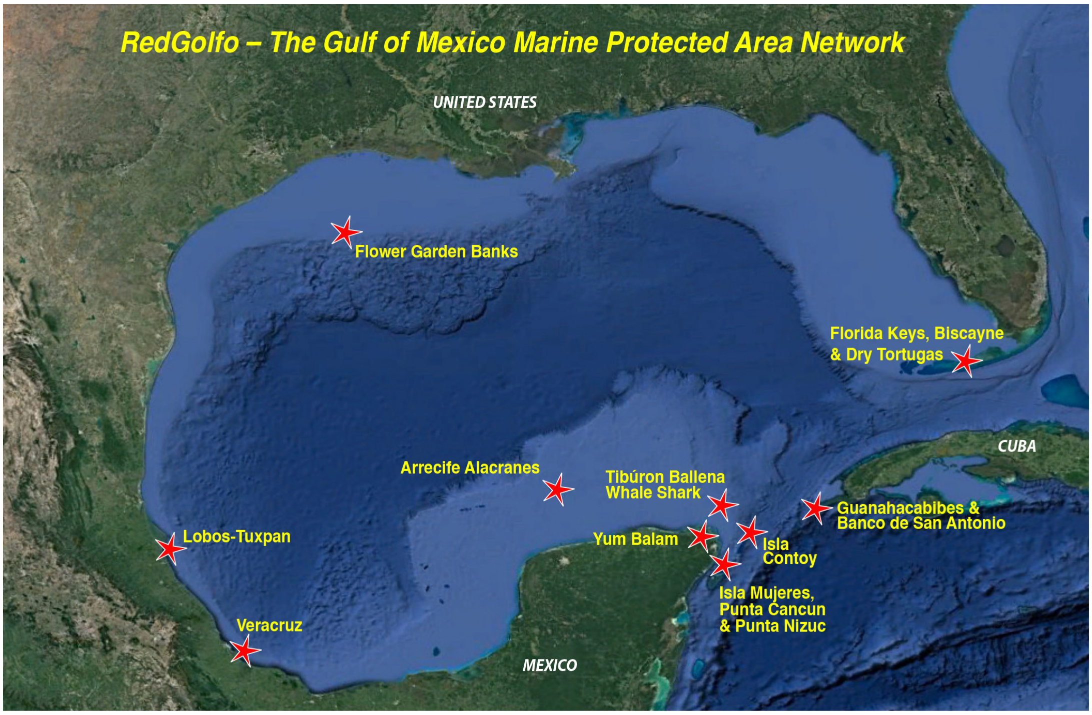

FIGURE 7 | RedGolfo, the Gulf of Mexico Marine Protected Area Network (Source: http://www.cubamar.org).

regulations that enhance fisheries, and transboundary resource management to promote the ecological connectivity beyond individual jurisdictions. At a larger scale, it is imperative to cut down on land-based pollution entering the GoM, requiring an integrative approach by the three countries that share its waters. For instance, a key management action needed is the implementation of water treatment of all anthropogenic water discharges throughout the GoM.

The present study highlights the urgent need to develop criteria that can identify impacts caused by climate factors vs. those caused by other locally produced stresses, which will provide guidance for management responses to ecosystem changes. As a starting point, the condition of the reefs needs to be characterized, mapped, and monitored in a common way across jurisdictions as a basis for comparing ecosystem responses to environmental change. On the same token, a reconstruction of the microbial communities is imperative, which will allow identification of main viral or bacterial coral diseases experienced in the region. Establishment of baseline measurements on corals, and other organisms to compare when disease or mortality events occur are also needed, thus microbial, and molecular times series on GoM reefs would be advantageous whenever disease outbreaks happen. Ideally properly designed innovative ways to identify the degree of connectivity or isolation (physical, and biological) among coral populations, and how it may threaten or sustain their persistence should be launched. Moreover, endangered, charismatic or commercially exploited species associated with any of these reefs, and preferentially inhabiting through their ontogeny more than one needs further study or verification of their migration patterns. It is important to understand how human activity can impact connectivity or create connectivity that otherwise would not exist, as this can modify the way invasive species, and disease pathogens are spread throughout the region. Thus, as suggested by Garavelli et al. (2018), future connectivity research among all mesophotic coral ecosystems, and beyond to include other important coral habitats in the region using multiple species models to assess the possibility of establishing a regional conservation plan are needed. Using large-scale mapping might help with prioritizing areas for protection and/or restoration to get a higher return on investment not just locally but regionally as well. Bearing in mind that modeling connectivity – although appealing – is always limited to source data, subjected to logical flaws, and parameterization ambiguities (Johnston and Bernard, 2017). Predictive likelihood of habitats are also an option with their own inherent data restrictions.

Coral reefs are, as stated throughout this review, relevant, structural, and functionally diverse ecosystems of the natural realm of the GoM LME. Their long-term viability is threatened by an increasing number of factors, from natural to anthropogenic. Efforts must continue not only to increase our knowledge of these ecosystems but also to implement coordinated transboundary management actions that protect them, and build the resilience needed to assure their survival in decades to come. Such efforts should not be unilateral, and require an integrative approach by Mexico, Cuba, and US to not only address and/or implement the suggested criteria, and measurements but also to foster collaborative research among the three countries sharing the GoM waters, which likely will identify further needs (e.g., response plans for disease outbreaks), and priorities.

AUTHOR CONTRIBUTIONS

DG-A and CC-B worked equally on the manuscript and first authorship and corresponding authorship were agreed upon them upon recommendation by JB, alphabetical order was followed after the aforementioned contributors. DG-A, CC-B, and JB conceptualized the idea and provided the framework for the document. JB put together the final co-author team. All authors wrote the manuscript with major contributions by region/country as follows: PG-D (Cuba), WK (Texas), CL (Florida), and HP-E (Mexico). All authors reviewed the drafts, provided comments and suggestions, and approved the final manuscript. DG-A, CC-B, and JB wrote the final manuscript.

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First Report of Endolithic Members of *Rhodosorus marinus* (Stylonematales, Rhodophyta) Growing Inside Rhodoliths Offshore Louisiana, Northwestern Gulf of Mexico

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Endolithic, red unicells residing in the interior of *Lithothamnion* rhodoliths, collected offshore the NW Gulf of Mexico in mesophotic rhodolith beds at ∼54–55 m depth and maintained in closed microcosms, were used to establish cultures following their isolation. These endolithic unicells subsequently developed into amorphous blobs of palmelloid cell colonies. Each cell contains unstacked, 2–5 lobed parietal chloroplasts, one prominent central pyrenoid, and have a thin or thick cell wall. Single cells, or cell clusters (in pairs, tetrads, or up to 12) are embedded inside an extracellular matrix whose boundaries remain closely appressed to neighboring cell clusters. Cell division by concavo-convex division resulted in hemispherical cells subsequently expanding in size. Plastid *tuf*A, *psb*A and 16S rDNA sequence analyses confirmed that the colonies are *Rhodosorus marinus* Geitler. This is the first report of a unicellular red alga spending part of its life history endolithically inside biogenic rhodoliths.

Keywords: CCA, coralline algae, Gulf of Mexico, mesophotic, metabarcoding, rhodoliths, Rhodophyta, *Rhodosorus*

INTRODUCTION

The unicellular marine coccoid red algal genus *Rhodosorus* was described by Geitler (1930, p. 633, Figure 15) from seawater cultures originating from Las Palmas, Canary Islands. *Rhodosorus marinus* Geitler was the only species in the genus until Fresnel and Billard (1995) described a second species, *Rhodosorus magnei*, isolated from the French West Indies (Isle de St Barthélemy). The current distribution of *Rhodosorus* (Guiry and Guiry, 2019) indicates that these unicellular red algae predominantly inhabit warm and coastal waters worldwide (West and Calumpong, 1990; Fresnel and Billard, 1995; Zuccarello et al., 2008).

The two species are distinguished by their color, cell size and number of chloroplast lobes (Fresnel and Billard, 1995). Pickett-Heaps et al. (2001) reported that the four strains of *Rhodosorus* investigated displayed continuous cytoplasmic rotation within the wall, and Wilson et al. (2002) documented chloroplast rotation and morphological plasticity in *R. marinus*. Previously placed in the Porphyridiales (e.g., West and Calumpong, 1990), the genus currently belongs in the family Stylonemataceae, order Stylonematales, in the class Stylonematophyceae (Yoon et al., 2006, 2010; Yang et al., 2010, 2016).

Whereas *R. marinus* and *R. magnei* typically grow epiphytically on the surface of seaweeds (Fresnel and Billard, 1995), we recently found a member of *Rhodosorus* growing inside (endolithically) calcified *Lithothamnion* (Hapalidiaceae, Hapalidiales) rhodoliths collected in mesophotic rhodolith beds in the northwestern Gulf of Mexico. Rhodoliths are free-living marine benthic spheroidal nodules predominantly accreted by crustose coralline red algae (CCA) precipitating $CaCO_3$ within their organic cell walls (Foster, 2001; Krayesky-Self et al., 2016, 2017; Fredericq et al., 2019; Spalding et al., 2019). Two major rhodolith categories can be found in the northwestern Gulf of Mexico (NWGMx), i.e., *biogenic* and *autogenic* rhodoliths. *Biogenic* rhodoliths (**Figure 1a**) are formed by the non-geniculate CCA themselves, e.g., *Lithothamnion* sp. In contrast, *autogenic* rhodoliths are derived from already existing calcium carbonate rubble established by differential erosion processes of the caprock (Gore, 1992), with the rubble becoming secondarily covered by various encrusting and fleshy algae (Felder et al., 2014; Fredericq et al., 2014; Richards et al., 2016; Krayesky-Self et al., 2017; Schmidt et al., 2017). Autogenic rhodoliths are viewed as a specific type of nucleated rhodoliths (*sensu* Freiwald and Henrich, 1994) in which the core derives from calcium carbonate rubble as opposed to other materials. These two categories of rhodoliths co-inhabit the same rhodolith beds but the internal (endolithic) microbiome of each category may differ with regard to the diversity of taxa (biogenic: Krayesky-Self et al., 2017, and autogenic: Sauvage et al., 2016a; Fredericq et al., 2019).

This endolithic taxon retrieved from a biogenic rhodolith is herein characterized on the basis of anatomical evidence via light, phase contrast, fluorescent and TEM microscopy, and also on the basis of DNA sequence analyses of plastid *tuf*A (plastid-encoded protein chain elongation factor EF-Tu), *rbc*L (encodes the large subunit of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase), *psb*A (photosystem II reaction center protein D1 gene), and 16S rDNA.

MATERIALS AND METHODS

Study Area and Sample Collection

Mesophotic rhodolith collections representing *Lithothamnion* sp., a currently undescribed species of CCA (**Figure 1a**) (Hapalidiaceae, Hapalidiales, Rhodophyta) (J. Richards, unpublished data), were collected at Ewing Bank (27°57.08N, 92°01.03.′W, coll. S. Fredericq, depth 54–55 m, 26.viii.2012, LAF6573b) offshore Louisiana in the northwestern Gulf of Mexico aboard the *R/V* Pelican, a UNOLS research vessel operated out of LUMCON, Cocodrie, LA. Rhodoliths were retrieved using a Hourglass-design box dredge (Joyce and Williams, 1969) with minimum tows (usually 8 min or less) (Felder et al., 2014; Fredericq et al., 2014, 2019). Rhodoliths were initially stored on-site by location in containers filled with seawater collected *in situ* from the same depth and site of the sampled rhodoliths using the onboard CTD water-sampling rozette. Samples were kept aerated on board ship for the duration of the trip (4 days) and immediately transferred into microcosms, filled with *in situ* collected seawater, located in our laboratory at UL Lafayette 2–5 h upon return to the laboratory. The *Lithothamnion* rhodolith investigated in the present study is part of the same voucher that included endolithic *Ochrosphaera* (haptophyte) cellular inclusions housed within the rhodolith's interior (Krayesky-Self et al., 2017).

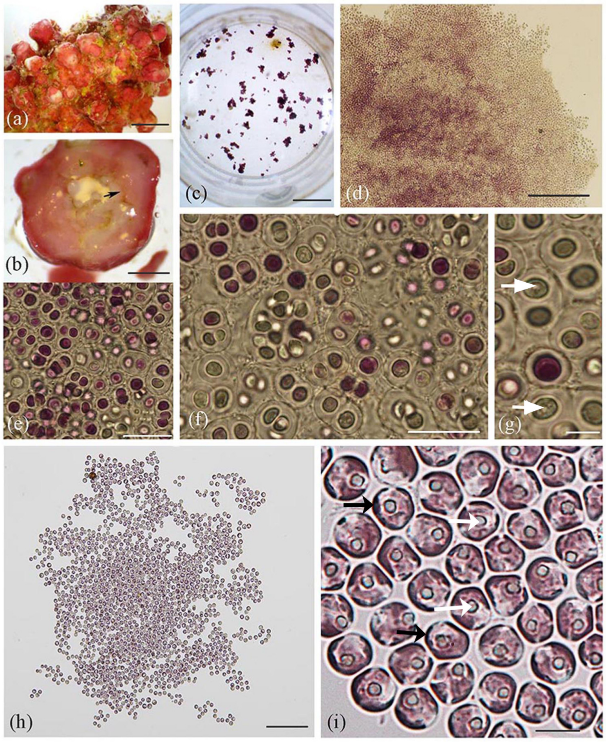

FIGURE 1 | *Lithothamnion* sp. rhodolith collected from Ewing Bank, northwestern Gulf of Mexico, and light microscopy images of *Rhodosorus marinus* cells. **(a)** Surface view of habit of *Lithothamnion* (LAF6573b); **(b)** cross section through rhodolith protuberance displaying internal area where endolithic *Rhodosorus* cells were found (arrow); **(c)** culture well plate viewed under dissecting scope, with cultured *Rhodosorus* cells and *Ochrosphaera* haptophyte cells (brown clusters); **(d)** magnified view of cell clusters seen in **Figure 3c**); **(e–g)** light micrographs of single cells or cell clusters (in pairs, tetrads, or up to 12 cells). Cell division by concavo-convex division resulted in hemispherical cells subsequently expanding in size, each with a prominent central pyrenoid (white arrows); **(h)** *Rhodosorus* subculture; **(i)** close-up of cells shown in (3 h) showing parietal chloroplast lobes (black arrows) and pyrenoid (white arrows). Scale bars: **(a)** = 0.5 mm, **(b)** = 2 mm, **(c)** = 15.5 mm, **(d)** = 200 μm, **(e)** = 20 μm, **(f)** = 20 μm, **(g)** = 5 μm, **(h)** = 150 μm, **(i)** = 6 μm.

Establishment of Microcosm

A 75-L closed microcosm tank, established from a subset of samples from Ewing Bank, was equipped with a SeaClone 100 protein skimmer (Instant Ocean, Blacksburg, VA, United States), water jet (MJ2000) and 600 lumen light (FugeRay Unibody). The protein skimmer provided filtration and a flow of 1,200 L/h (Krayesky-Self et al., 2017; Fredericq et al., 2019). The LED photosynthetically available radiation (PAR) in the microcosm was about 30 μmol photons m^{-2} s^{-1}, a measurement approximating *in situ* light PAR or irradiance levels measured with a LI-COR Biosciences (Lincoln, NE, United States) biospherical PAR sensor incorporated in a CTD (for conductivity, temperature, and depth) rosette and water sampler. The closed microcosm was filled with *in situ* collected water with CTD rosette Niskin bottles and the systems was maintained at approximately 10 h light/14 h dark cycle at 24°C, the same temperature measured in the field at 55 m depth in late summer. Deionized water was used to counteract evaporation within the microcosm. Rhodolith vouchers are deposited in the Algal Herbarium of the University of Louisiana at Lafayette (LAF).

Light Microscopy and Phase Contrast Microscopy

Rhodoliths were cross-sectioned with straight-edged razor blades, and cultured cells were viewed under a Zeiss Stemi 2000-C (Oberkochen, Germany), Olympus SZ61 stereomicroscope (Waltham, MA, United States), and with phase contrast using a Motic BA300 microscope (Carlsbad, CA, United States).

Fluorescence Microscopy

Specimens from the culture wells were pipetted onto microscope slides following the protocol of Krayesky-Self et al. (2017). A Nikon E600FN epifluorescence microscope (Melville, NY, United States) was used to visualize autofluorescing cells with blue light. Photographs were taken with an Olympus digital camera.

Transmission Electron Microscopy

A subsample of the *Rhodosorus* cells was fixed in Trumps fixative (Electron Microscopy Science) for 1 h at ~22°C, then fixed in 2% OsO_4 for 15 min, dehydrated, embedded in Spurr's resin, cut into 1 nm sections, stained using uranyl acetate and lead citrate and viewed on a Hitachi 7600 TEM microscope (Dallas, TX, United States) following the procedure in Krayesky-Self et al. (2017).

Establishment of Cell Cultures

With a sterile razor blade, a rhodolith nodule was sectioned into thin pieces and examined under an Olympus BX60 compound microscope with a SLMPlan 50X/0.45 M-plain objective attached to a Canon PowerShot A330 camera (Melville, NY, United States). A Sutter Ultra-micropipette puller produced fine ultra-micropipette tips that were used with a mechanical manipulator to remove single cells from within the coralline cells. The pipettes were controlled using a micro-manipulator and suction was controlled using a one-way valve and a transfer pipette. Following the procedure of Krayesky-Self et al. (2017), cells retrieved from the inside of the rhodoliths were cultured, and subcultured into 24-well culture plates. The isolated cells grew within the well-plates which contained 50% filtered seawater with 50% K-Media nutrients at room temperature, following the procedure of Krayesky-Self et al. (2017). Cells were placed in filtered microwaved-sterilized natural seawater for 5–7 days and this seawater was refreshed with modified K-media every 2 weeks after 7 days. The cultures have been maintained since 2012. Larger cultures were then established in Corning 25 cm^2 tissue culture flasks at 19°C and periodically checked for growth.

Single Cell DNA Amplification

Single cells were isolated from the inside of *Lithothamnion* sp. (LAF6573b) and transferred into culture plates. The DNA of the isolated cells was then amplified by whole genome amplification using a *Phi29* REPLI-g single cell kit (Qiagen, Valencia, CA, United States) to produce sufficient DNA for subsequent polymerase chain reaction (PCR) with primers for genes of interest. The manufacturer's REPLI-g protocol was modified by adding a 5-min incubation period at 95°C to lyse the cells before the denaturing buffer incubation step (65°C for 10 min). All other steps occurred following the manufacturer's protocol.

DNA Amplification and Sequencing

The genomic DNA from the individual cells was PCR-amplified and sequenced using four different molecular markers. Plastid *tuf*A was amplified and sequenced using the methods and primer combination designed by Sauvage et al. (2016a), plastid *rbc*L using primers listed in Schmidt et al. (2016), plastid *psb*A using primers designed by Yoon et al. (2002), and 16S rDNA using primers listed in Olsen et al. (2004). The resulting PCR products of the four genes were gel-purified and cycle sequenced using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Life Technologies, Grand Island, NY, United States). The cycle sequencing reactions were then purified using Ethanol/EDTA precipitation. The resulting dried precipitated DNA was then resuspended in HiDi™ formamide (Life Technologies, Grand Island, NY, United States), heat-denatured and sequenced on the ABI 3130xl Genetic Analyzer at UL Lafayette. Chromatograms were assembled in Sequencher v5.1 (GeneCodes®, Ann Arbor, MI, United States).

Metabarcode Database

A *tuf*A Illumina-metabarcoding (amplicon-based environmental sequencing) framework on environmental samples of various limestone fragments established by Sauvage et al. (2016a,b), provided us with reference *tuf*A metabarcodes of cryptic (hidden) phototrophs retrieved from four small $CaCO_3$ substrata collected from the Ryukyu archipelago, Japan; the NW Gulf of Mexico; and the Florida Keys. The Sanger *tuf*A sequence of the endolithic *tuf*A sequence from Ewing Bank, NW Gulf of Mexico, was approximately 900 bp long and was BLASTed against Sauvage et al.'s (2016b) *tuf*A barcode reference dataset (with each barcode approximately 375 bp long) and against available *tuf*A GenBank sequences. This was done in order to possibly link the taxonomic identity of any of the *tuf*A metabarcodes with that of the *tuf*A Sanger sequence.

Tree Building

The assembled sequences were run through BLASTn on GenBank[1] and the nearest hits were downloaded from the public NCBI database and used to establish the data sets. The available resulting *tuf*A dataset of *Rhodosorus* sequences consisted of a GenBank-downloaded *R. marinus* sequence from Venice, Italy (AF545599), Core OTU 374 retrieved within endolithic samples (reef rubble) originating from Japan (Ryukyus archipelago)[2] (Sauvage et al., 2016a,b) and a newly generated *R. marinus* (LAF7199 S13) sequence from offshore LA, NW Gulf of Mexico (MN808825), and of a *R. magnei* sequence from Guadeloupe, F.W. I. (EF660206). The *psb*A sequence of the endolithic taxon (MN808824) was compared to that of *R. marinus* from Venice, Italy (AY119744), the Florida Keys (EF660237) and the Maldives (EF660236), and to *R. magnei* from Guadeloupe F.W.I. (EF660268). The 16S (MN808823) and *rbc*L sequence of the endolithic taxon (MN808826) was compared to *R. marinus* from Italy (AF170719, AY119778, respectively).

The sequences of each gene dataset were then aligned manually in Mega v5.2.2 (Tamura et al., 2011). The resulting alignments were analyzed using PartitionFinder2 (Lanfear et al., 2016) to determine the best fitting model of evolution and the optimum data partition. The analyses resulted in the selection of the General Time Reversible model with a proportion of invariable sites and a gamma distribution applied separately to each codon position of the three protein-encoding genes, and as a single partition for the non-protein-coding gene (16S) on the basis of the three information criteria, i.e., Akaike information criterion corrected (AICc), Akaike information criterion (AIC), and Bayesian information criterion (BIC). The alignments were analyzed by Maximum likelihood (ML) as implemented by RAXML (Stamatakis, 2014) with the above model and partition scheme with 1000 restarts to find the tree with the lowest likelihood score and 1000 Bootstrap (BS) replications.

RESULTS

Non-flagellated unicells were captured from the rhodolith's (**Figure 1a**) interior (**Figure 1b**) using a micromanipulator and microscope and used to establish cell cultures (**Figure 1c**) following their isolation. These cells subsequently developed into free-living amorphous blobs of palmelloid cell colonies (**Figures 1c–i**) that consistently grew along with brown cell clusters (**Figure 1c**). Unicells were either purple, pink or greenish and appeared to divide by vegetative cell division to produce two-to-four cells in compact (**Figures 1e–g**) or loose (**Figures 1h,i**, **2a**) cell clusters (in pairs, groups of three, tetrads, or up to 12 cells) that were embedded inside a cell wall whose boundaries remain closely appressed to neighboring clusters (**Figures 1e–g**, **2b**) or more spatially isolated from one another (**Figure 1h**). Cell walls were either thick (**Figures 1e,g**, **2a**) or thin (**Figure 1i**). Vegetative concavo-convex cell division resulted in hemispherical cells (**Figure 1f**) subsequently expanding in size. Each cell contained one prominent central or off-centric pyrenoid (**Figures 1g,i**), parietal chloroplasts with 2–5 peripheral plastid lobes barely extending from the cell surface and visible using different focus levels (**Figure 1i**). Other cellular details were not perceptible with conventional brightfield microscopy.

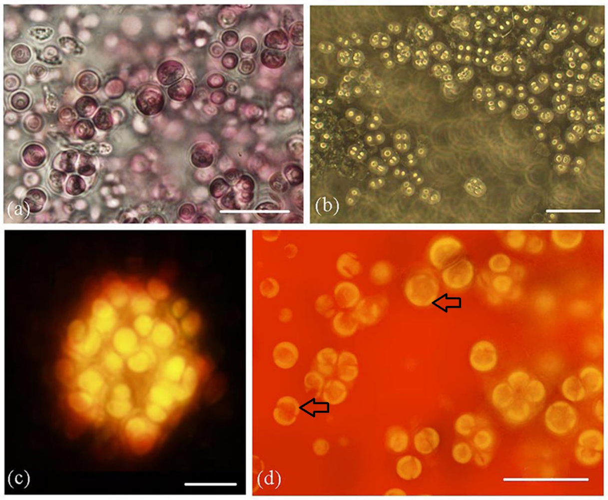

FIGURE 2 | *Rhodosorus marinus* cultures. **(a)** light photomicrograph; **(b)** phase-contrast photomicrograph; **(c)** auto-fluorescence of cluster of cells shown from above in (2a); **(d)** autofluorescence of cells, showing 2–5 chloroplast lobes (black arrows). Scale bars: **(a)** = 20 μm, **(b)** = 35 μm, **(c)** = 10 μm, **(d)** = 20 μm.

Phase contrast (**Figure 2a**) and autofluorescence (**Figure 2b**) also showed the palmelloid organization of cultured cells. Autofluorescence micrographs (**Figure 2c**) clearly documented 2–5 plastid lobes per cell (**Figure 2d**).

Transmission electron microscopy (TEM) observations confirmed that the *Rhodosorus* cells contained crescent-shaped to oval plastids and one prominent pyrenoid (**Figures 3a–c**). The pyrenoid extends toward the interior of the cell and depending on the plane of the section are shown to be connected to a plastid lobe appearing stalked (**Figure 3a**). One-to-five plastid lobes per cell were seen in various planes of sectioning (**Figures 3a–c**) and follow the contour of the cells. Each plastid lobe contains parallel, evenly spaced, unstacked thylakoids (**Figures 3a–c**) and does not abut the cell wall but remains separated from it by an evenly distributed intracellular space immediately below the cell wall. Phycobilisomes were not seen on the thylakoids. Floridean starch was not abundant in young, actively growing cultured cells (**Figure 3a**) but formed extensive floridean starch sheaths (**Figures 3b,c**) surrounding the pyrenoid in cells from mature cultures, i.e., in non-actively growing cells that were maintained

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[1] http://blast.ncbi.nlm.nih.gov/Blast.cgi

[2] https://doi.org/10.5061/dryad.6cj8h

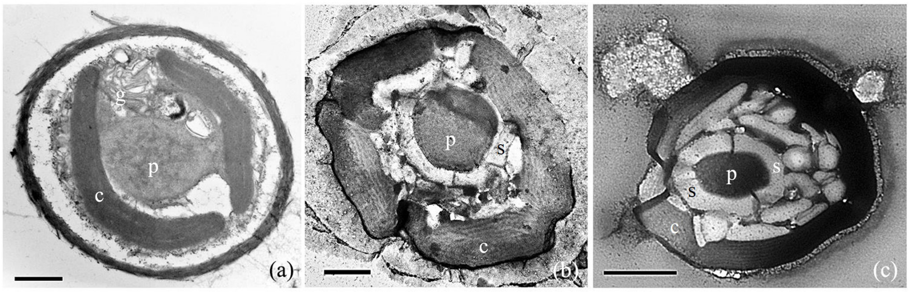

FIGURE 3 | TEM photomicrographs of *Rhodosorus marinus* cells taken from cultures established from individual cells removed from *Lithothamnion* sp. rhodolith. **(a)** Two crescent-shaped chloroplast lobes (c), a stalked pyrenoid (p), and golgi apparatus (g); **(b)** five chloroplast lobes (c) and a central pyrenoid (p) surrounded by floridean starch (s); **(c)** copious amounts of floridean starch granules (s) surrounding the pyrenoid (p), and chloroplast lobes (c). Scale bars: **(a)** = 1 μm, **(b)** = 0.5 μm, **(c)** = 1 μm.

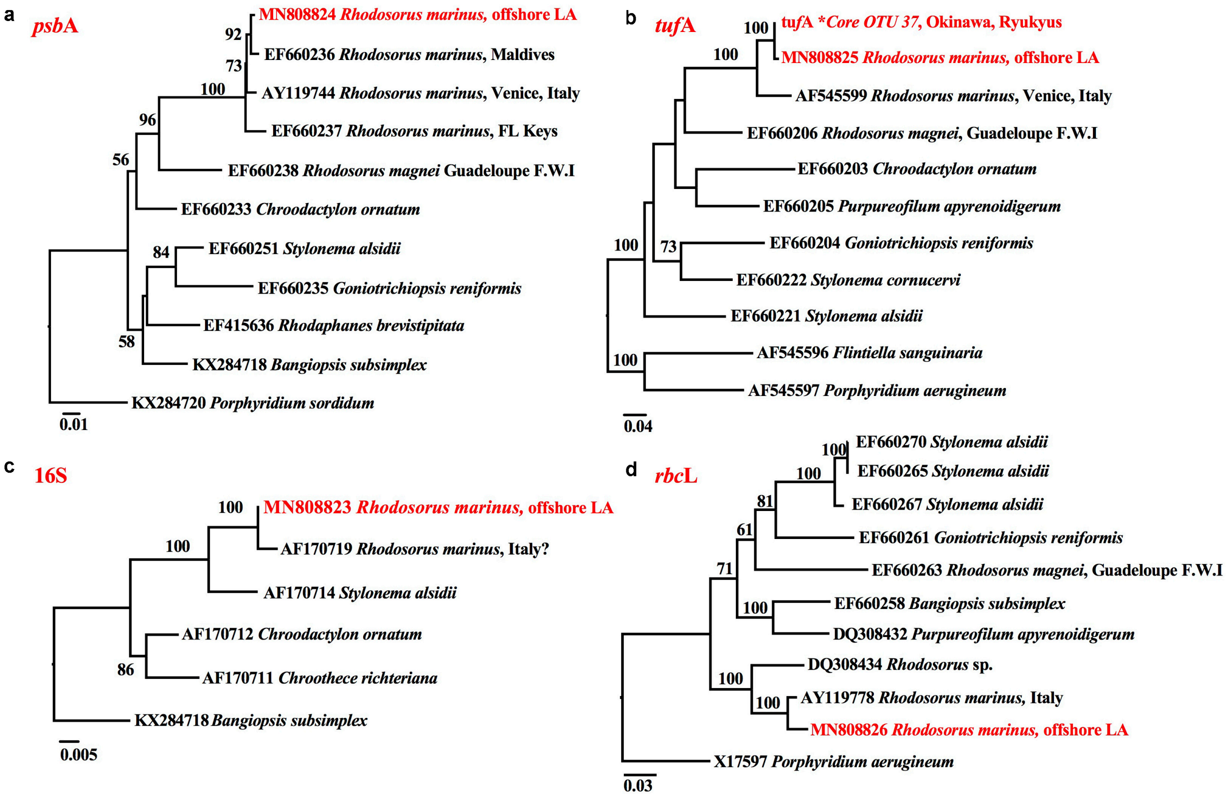

FIGURE 4 | RaxML phylograms of **(a)** *psb*A, **(b)** *tuf*A, **(c)** 16S, and **(d)** *rbc*L sequences showing that the endolithic *Rhodosorus* species from offshore Louisiana (highlighted in red) corresponds to the *R. marinus* from **(a)** the Maldives, Venice, Italy, and the Florida Keys, **(b)** Venice, Italy, and a Core OTU* from Okinawa, Ryukyus, Japan, **(c)** Italy? (SAG.116.79), and **(d)** Italy.

in culture for a period of 2 months (**Figure 3b**) and 2 years (**Figure 3c**), respectively.

The small branch length between *the psb*A (**Figure 4a**), *tuf*A (**Figure 4b**), 16S (**Figure 4c**) and *rbc*L (**Figure 4d**) sequences of the endolithic *Rhodosorus* taxon from the NW Gulf of Mexico and downloaded GenBank sequences of *R. marinus* worldwide indicate that they do not represent separate species. *tuf*A metabarcoding enabled us to link the taxonomic identity of a hidden (cryptic) ∼375 *tuf*A metabarcode from reef rubble from Okinawa, Ryukyu archipelago, Japan with the ∼900 bp *tuf*A sequence of the endolithic Louisiana taxon (**Figure 4b**).

DISCUSSION

Morphologically, each of the cultured cells originating from endolithic cells inhabiting NW Gulf of Mexico *Lithothamnion* rhodoliths conforms to the concept of *R. marinus* Geitler, a species that has fewer chloroplast lobes (∼2–5) than *R. magnei* (8–11) (Fresnel and Billard, 1995); however, it should be noted that these characteristics were found to be quite variable and dependent on culture conditions and that they cannot be used to differentiate these two species (Wilson et al., 2002). Our observations coincide with those by Giraud (1976) who noted that the width of the cell wall in *R. marinus* varies greatly depending on culture conditions. Our observations of the NW Gulf of Mexico cultured cells also resemble aspects of cultures of *R. marinus* from Hawaii in that they may form loose cell packets enclosed in a poorly defined mucilage (West, 1969). Pyrenoids encased by prominent cytoplasmic starch as shown in *R. marinus* by Giraud (1976), Lee (1974), and Fresnel and Billard (1995) were not observed in the actively dividing Louisiana vouchers but were prominent in cultures that were maintained for up to 2 years. Perhaps the fact that such prominent starch cells were not found in young cultures may indicate that cells were still actively growing and not storing energy in the form of floridean starch. Molecularly, comparative plastid *tuf*A, *psb*A and 16S sequence analysis also confirmed that the endolithic *Rhodosorus* taxon from the NW Gulf of Mexico is *R. marinus*.

Rhodosorus marinus may be more ubiquitous than the present records indicate. It may be overlooked in collections because of its very small size and because the distribution record of the genus is patchy (West and Calumpong, 1990). *Rhodosorus* was originally described from the Canary Islands (Geitler, 1930) and subsequently recorded in France (Giraud, 1958), Italy, and the Florida Keys (Ott, 1967), and Hawaii (West, 1969). More recent reports, listed in Guiry and Guiry (2019) include a European distribution for France (Billard and Gayral, 1972; Anon, 2017), Spain (incl. Canary Is., Gallardo et al., 2016), the Canary Islands (John et al., 1979; Gil-Rodríguez and Afonso-Carrillo, 1980; Haroun et al., 2002; Gil-Rodríguez et al., 2003; John et al., 2004; Afonso-Carrillo, 2014), in addition to being distributed in British Columbia (Scagel et al., 1989), the tropical and subtropical western Atlantic (Wynne, 2017), Japan (Yoshida et al., 1990, 2015; Yoshida, 1998), and the Philippines (Ang et al., 2014).

Rhodosorus marinus typically grows epiphytically on macroalgae, mostly siphonous green algae, and co-occurs with chrysophytes and haptophytes (e.g., *Ochrosphaera*) (West and Calumpong, 1990; Fresnel and Billard, 1995). West (1969) isolated *R. marinus* and *Ochrosphaera verrucosa* from *Porite*s coral fragments which he maintained for 7 years in aerated seawater cultures from Coconut Island, Kaneohe Bay, Oahu, Hawaii. Just as *O. verrucosa* endolithic life history stages were detected by *tuf*A metabarcoding in calcium carbonate substrata from geographically isolated reef habitats in southern Japan, the Florida Keys, and the NWGMx (Sauvage et al., 2016a,b), so too is the *O. verrucosa* metabarcode a perfect match to the *tuf*A sequence retrieved from cells in cultures co-occurring with *Rhodosorus* and isolated from *Lithothamnion* rhodoliths. Besides *O. verrucosa,* we have previously documented the presence of other microalgal cells growing endolithically within biogenic *Lithothamnion* rhodoliths from the NW Gulf of Mexico, i.e., the dinoflagellate *Prorocentrum lima* (Krayesky-Self et al., 2017).

This is the first report of a unicellular species of red algae, i.e., *R. marinus*, that grows inside biogenic rhodoliths indicating that this species spends part of its life history endolithically inside mesophotic rhodoliths, co-habiting with the haptophyte *Ochrosphaera* (Coccolithales, Prymnesiophycidae Coccolithophyceae) a taxon occasionally referred to as *Hymenomonas globosa* (Magne) Gayral and Fresnel, a common coastal haptophyte (Fresnel and Probert, 2005). Both taxa thus appear to have a wide distribution in the $CaCO_3$ endolithic niche worldwide. *R. marinus* was not observed growing as free-living cells in our laboratory microcosms.

This study adds to our previous discovery that the interior of rhodoliths are marine biodiversity hotspots (Sauvage et al., 2016a; Krayesky-Self et al., 2017; Fredericq et al., 2019) for previously unknown endolithic stages in the life history of ecologically important and diverse microalgae encompassing phyla as diverse as dinoflagellates (i.e., *Prorocentrum*), haptophytes (i.e., *Ochrosphaera*), and, as noted herein, red algae (i.e., *Rhodosorus*) as well. The metabarcoding approach may reveal additional unknown biodiversity that can form the basis for species description through careful culturing efforts and anatomical observations, as was performed here.

DATA AVAILABILITY STATEMENT

This manuscript contains previously unpublished data. The repository of the *tuf*A metabarcode (part of the Core OTU 374) is DRYAD, doi: 10.5061/dryad.6cj8h (Sauvage et al., 2016b). All DNA sequences are available from GenBank, and newly generated DNA sequences represent GenBank numbers MN808824 (*psb*A), MN808825 (*tuf*A), MN808823 (16S), and MN808826 (*rbc*L).

AUTHOR CONTRIBUTIONS

SF, SK-S, TS, and WS conceived the study and collected the samples. SK-S, DP, TS, LB, and WS conducted the laboratory work. WS, TS, and SK-S conducted the data analyses. SF, SK-S, and WS wrote the manuscript with contributions from TS. All authors edited the manuscript before submission.

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Insights on Bloom Forming Jellyfish (Class: Scyphozoa) in the Gulf of Mexico: Environmental Tolerance Ranges and Limits Suggest Differences in Habitat Preference and Resistance to Climate Change Among Congeners

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Jellyfish are important components of marine food webs and form problematic blooms that negatively impact human enterprise. Jellyfish of the genus *Aurelia* (Class Scyphozoa) are common bloom-formers in the Gulf of Mexico (GoM). *Aurelia* have a multi-modal life cycle where the perennial polyp produces seasonal medusae. Abiotic tolerance ranges and limits strongly influence the distribution of marine species but are unknown for most jellyfish species. Tolerance limits for survival are crucial to understanding present polyp distribution and how distribution may change in climate change scenarios. We sampled and barcoded two *Aurelia* species from the GoM, namely *Aurelia* sp. 9 and a possible new species found offshore (*Aurelia* sp. new). Planulae obtained from one medusa of *Aurelia* sp. new, and five medusae of *Aurelia* sp. 9 were used to establish laboratory cultures. Polyps of *Aurelia coerulea*, a species native to Japan but introduced in North America, Australia, and Europe, were obtained from a local aquarium, barcoded, and used to establish laboratory cultures. Using controlled laboratory experiments, we determined the temperature and salinity limits for polyp survival of the two GoM species and *A. coerulea*. We find that *A.* sp. 9 and *A. coerulea* were tolerant of a broad range of temperatures and salinities, but differed in tolerance limits, suggesting potential differences in habitat and resistance to climate change. *A.* sp. 9 was most tolerant of high temperatures and low salinities, such as those found in the estuaries of the GoM. Summer high temperatures in the coastal GoM exceed the upper thermal tolerance limit of *A.* sp. new and *A. coerulea*, suggesting that *A.* sp. new is an offshore species and that the coastal GoM waters may not be a suitable environment for *A. coerulea*. Based on the upper thermal limits identified in this study, the 4°C ocean temperature increase projected for the GoM by the next century may negatively impact *Aurelia* sp. 9 and *Aurelia* sp. new populations and is expected to deter *A. coerulea* from invading the GoM. This is the first account of *Aurelia* sp. new and the first report of temperature and salinity ranges and tolerance limits for *Aurelia* species.

Keywords: jellyfish, Scyphozoa, Cnidaria, Gulf of Mexico, temperature tolerance, salinity tolerance, climate change, *Aurelia*

INTRODUCTION

Jellyfish are important components of marine food webs. They feed on zooplankton and fish larvae (Möller, 1984; Purcell and Sturdevant, 2000; Riascos et al., 2014) and are food for a variety of marine animals such as penguins, turtles, and tuna (Hays et al., 2018). Large aggregations of jellyfish, also known as "blooms," are associated with numerous negative socio-economic impacts. Jellyfish clog fishing nets (Nagata et al., 2009), reduce catch quality (Quiñones et al., 2013), obstruct power plant cooling intakes (Abdul Azis et al., 2000), and sting beachgoers (De Donno et al., 2014). Blooms also cause problems for aquaculture by fouling net pens and jellyfish nematocyst-rich mucus is responsible for fish gill disorders (Purcell et al., 2013).

In the Gulf of Mexico (GoM), problematic jellyfish blooms in coastal areas are often caused by medusae of the Class Scyphozoa, Phylum Cnidaria. Scyphozoan jellyfish have a multi-modal life cycle (Ceh et al., 2015) where the perennial benthic polyp produces seasonal jellyfish. Young medusae (ephyrae) are produced by polyps via an asexual transverse fission process called "strobilation." In the GoM, there are 20 reported species of Scyphozoa, representing three orders and eleven families (Segura-Puertas et al., 2009). The predominant bloom-forming jellyfish genera in coastal and shelf ecosystems are *Aurelia*, *Chrysaora*, and *Stomolophus* (Larson, 1991), which bloom mostly in the summer months (Graham, 2001; Robinson and Graham, 2013).

Polyps have a key role in maintaining and expanding Scyphozoan populations (Lucas et al., 2012). Each polyp releases multiple medusae per strobilation event. Medusae production is controlled by the number of strobilating polyps and the rate and duration of jellyfish release (Lucas et al., 2012), therefore the size of jellyfish blooms is in part determined by the size of the polyp population. Polyps also reproduce asexually, increasing their benthic population size and thus contributing to the magnitude of jellyfish blooms (Lucas et al., 2012).

Current knowledge on the location, size, and dynamics of natural polyps in the GoM is lacking. Polyps are tiny, and found in sheltered, poorly visible places, making detection difficult. Polyps are known to inhabit hard substrates including biofouling benthic organisms, floating platforms and manmade structures (Duarte et al., 2013). Most of the GoM has a soft sandy or muddy bottom, so settlement surfaces are likely limited. However, despite the conspicuous blooms, polyps of even the most common Scyphozoan species have not been found in the GoM. The inability to locate polyp populations in nature hinders the study of jellyfish population dynamics and blooms. For example, triggers of strobilation and jellyfish production cannot be studied *in situ*, and the geographic origins of jellyfish blooms are unknown. Moreover, without knowledge of the current geographical ranges of polyp populations, it is difficult to predict how jellyfish will respond to climate change.

Scyphozoans' response to climate change is not well understood. Medusae presence and abundance in ecosystems is generally highly variable. The timing, location, and number of individuals observed can vary significantly within and between years and locations (Purcell, 2005; Heim-Ballew and Olsen, 2019). The variability in the frequency and magnitude of jellyfish blooms is due in part to global multi-decadal climate oscillations (Condon et al., 2014). However, evidence from some ecosystems suggests that anthropogenic perturbations to ecosystems may facilitate bloom-formation (Purcell et al., 2007; Purcell, 2011). Jellyfish have been shown to increase in abundance in heavily fished ecosystems (Lynam et al., 2006) in areas with benthic hypoxia (Shoji et al., 2010; Miller and Graham, 2012) and in areas experiencing eutrophication (Purcell et al., 1999a; Haraldsson et al., 2012).

In the GoM, climate change is expected to affect temperatures, precipitation patterns, tropical storm activity, and sea levels (Biasutti et al., 2012). Bottom temperature increase may impact benthic polyps, their survival capabilities and their strobilation rates, thus influencing bloom magnitude and frequency. Bottom-water temperatures have increased 2°C over a 30 year period on the northern GoM continental shelf (Turner et al., 2017), which is 1.9 times faster than the local increase in air temperatures during the summer months and 6.4 times faster than the global annual sea temperature increase (Turner et al., 2017). Also, the average temperature of GoM water is projected to increase by 4°C by the end of the century (Muhling et al., 2011; Biasutti et al., 2012). How this increase in temperature will affect Scyphozoan populations and bloom frequency is unclear. It has been shown that temperature affects growth rate, asexual reproduction, and strobilation of polyps of *Aurelia* spp. (Purcell, 2007; Willcox et al., 2007; Hubot et al., 2017). Thermal tolerance limits constrain the biogeographical range where Scyphozoan species can survive. The ability to tolerate regional or local thermal conditions may also impact the potential for a species to become an exotic invader. The invasive Scyphozoan *Aurelia coerulea*, for example, has so far become established in habitats that possess similar seasonal maxima and minima to its native latitudinal range of 30°N to 45°N (Dawson et al., 2005; Scorrano et al., 2017).

Salinity is another important environmental factor that can impact the development and survival of Scyphozoan jellyfish polyps (Rippingale and Kelly, 1995; Purcell et al., 1999b, 2009; Pitt and Kingsford, 2003). Jellyfish outbreaks frequently occur in coastal environments that experience variable salinity, such as bays, estuaries and partially enclosed marine waters worldwide (Purcell et al., 1999b). Furthermore, changes in precipitation are predicted to alter the salinity of coastal areas, including the GoM (Biasutti et al., 2012), motivating studies on the salinity preferences and limits of jellyfish species. Only a few natural polyp habitats of *Aurelia* spp. have been studied (Gröndahl, 1988; Purcell et al., 2009; Malej et al., 2012; Marques et al., 2015, 2019; Hoèvar et al., 2018), thus information on the diversity of salinity tolerances within the genus is limited. Many past studies were also confounded by the presence of multiple cryptic species within the *Aurelia* genus (Dawson and Martin, 2001; Scorrano et al., 2017). Field and laboratory studies demonstrate *Aurelia* congeners to have differing responses to salinity variation (Spangenberg, 1964; Purcell et al., 2009; Marques et al., 2019). The size of wild populations of *A. coerulea* polyps appeared to be negatively impacted by high salinities especially in combination with high temperatures (Marques et al., 2019). Low salinity retarded growth of wild *A. labiata* (Purcell et al., 2009), while varying the salinity within the range of local environmental fluctuation was found to have no significant effect on polyp growth in *Aurelia* sp. from Tasmania (Willcox et al., 2007).

Temperature and salinity tolerance ranges, limits, and capacity for acclimatization strongly influence the distribution of marine species (Pörtner, 2002; Stillman, 2003; Somero, 2005, 2010), but are unknown for most jellyfish species. Yet, tolerance limits are crucial to understanding present jellyfish polyp distribution in the GoM and how distribution may change in climate change scenarios. In this study, using laboratory experiments, we assessed the temperature and salinity tolerance of the polyps of two species of *Aurelia* collected from the GoM and an invasive *Aurelia* species native to the South and East China Seas (Dawson et al., 2005). Namely, we focus on *Aurelia* sp. 9 and a new *Aurelia* species reported for the first time in this paper and found offshore in the GoM, as well as *Aurelia coerulea,* a species native to Japan that has invaded the Pacific coast of the United States and other locations around the world (Dawson et al., 2005; Scorrano et al., 2017). Our aims are to 1) determine the range and limits of temperatures that each species can likely tolerate in nature, 2) investigate whether the three species have the same or different upper thermal limits and 3) resolve the salinity tolerance ranges and limits for each species. This study aims to identify the temperature and salinity tolerance limits of three *Aurelia* species, predict their biogeographical distribution in the GoM, and to provide insight into how jellyfish populations may fare as ocean temperatures increase.

MATERIALS AND METHODS

Organism Sources and Culture Establishment

Five female medusae of *Aurelia* sp. 9 were collected in Galveston Bay in October 2017. Medusae were carrying planulae. Soon after collection of the specimens, planulae were isolated and placed into 700 ml containers with filtered sea water of ambient bay salinity. Planulae were transported to the Texas A&M University at Galveston Sea Life Facility, where they were pooled into a single culture and allowed to metamorphose into polyps. Approximately 50 polyps belonging to the species *A. coerulea* were provided by the Moody Gardens Aquarium and used to start cultures. A single live adult female *Aurelia* jellyfish carrying planulae was collected by dip net on July 1, 2017 during a research cruise aboard the R/V *Pelican*. Collection took place approximately 80 miles south of the coast of Louisiana in the GoM (28° 0′ 0″N, −89° 4′ 8″W). Instruments onboard the research vessel measured water parameters to be 37 ppt salinity and 28.8°C. Tissue from the medusa was preserved in 100% ethanol. The planulae were collected from the medusa and transported to the Texas A&M University at Galveston where they settled into polyps. Polyps of all three species were maintained at the Sea Life Facility at Texas A&M University at Galveston in aerated aquaria at a salinity of 33–35 ppt, ambient temperature of 15–23°C, minimal lighting and were fed once or twice a week with a combination of freshly hatched *Artemia salina* nauplii and algae-enriched rotifers. Seawater of appropriate salinity was made by adding Instant Ocean aquarium salt to filtered seawater of ambient bay salinity until the target salinity was reached. Water in aquaria was changed once a week. A second partial *Aurelia* medusa was collected on July 3rd, 2017 in a neuston net and preserved in 100% ethanol. Both medusae specimens were used for molecular analyses.

Molecular Barcoding for Species Identification

Total genomic DNA was purified from individual polyps taken from the established polyp cultures of each species and from the tissues of two ethanol-preserved medusae samples collected aboard the R/V *Pelican*. Mitochondrial cytochrome c oxidase subunit I (COI) and nuclear internal transcribed spacer 1 (ITS1) were used for species-level characterization. COI was amplified using the primers LCOjf (Dawson et al., 2005) and HCO2198 (Folmer et al., 1994) using the thermal cycling protocol described by Piraino et al. (2014). ITS1 was amplified using the primers KMBN-8 and KMBN-84 from Chiaverano et al. (2016), using the thermal cycling protocol described by the authors. All polymerase chain reactions (PCR) were performed in a BioRad thermocycler. To check the quality and size of amplicons, PCR products were visualized on a 1.5% agarose gel stained with SYBR Safe. PCR products were purified using ExoSAP-IT^{TM} (Applied Biosystems) or GeneJET Gel Extraction Kit (Thermo Scientific). COI amplicons were bi-directionally sequenced by the Texas A&M University Corpus Christi Genomics Core Lab using the PCR primers. Sequences were viewed and assembled in Geneious 9.1.8. To identify species, each consensus sequence was queried, using the BLASTn search algorithm, against the nucleotide collection (nr/nt) database of the National Center for Biotechnology (NCBI, http://www.ncbi.nlm.nih.gov).

Thermal Tolerance Ranges and Limits

We assessed temperature tolerances using two different approaches, the Chronic Lethal Thermal Method (CLM) and the Critical Thermal Method (CTM). Both methods utilize a dynamic approach to thermal tolerance determination where temperature is gradually changed until a predefined endpoint is reached. However, the methods differ in the rate of temperature change and the endpoint used (Beitinger et al., 2000) and therefore evaluate different aspects of thermal tolerance. Maximum and minimum limits in both the CTM and the CLM are determined by calculating the arithmetic mean of the endpoint temperatures among biological replicates (Vinagre et al., 2018).

The CLM utilizes a rate of temperature change that is slow enough to allow organisms to reacclimate at each new temperature and uses death as the endpoint (Beitinger et al., 2000). Temperature change rates are usually set at 1°C/day or slower (Beitinger et al., 2000; Eme and Bennett, 2009). By incorporating acclimation, the CLM has the advantage over the CTM of producing a more accurate estimate of a species' actual thermal limits in nature (Beitinger et al., 2000). We used the CLM approach to estimate the maximum and minimum temperatures that each *Aurelia* species can tolerate in the wild, in the forms of the Chronic Lethal Thermal Maximum (CLMax) and Chronic Lethal Thermal Minimum (CLMin) for each species. In order to acquire a more detailed understanding of how each species responds to temperature change, we monitored polyps for signs of stress at regular intervals during temperature increase and decrease during the CLM trials. We used tentacle morphology and polyp response to tactile stimuli (prodding with a metal probe) to monitor stress, and created a ranking system, that we termed "response score" (**Table 1**). This score is based on observations that under standard culture conditions, polyps respond to external stimuli with immediate muscle contractions and maintain tentacles in an extended position ready to feed. The response score was used to track each species' ability to acclimate to thermal increase or decrease and to track the onset of thermal stress leading to death.

The CTM is a common method for defining species' thermal tolerance limits (Bennett et al., 2018) that has also been used to evaluate invertebrate response to climate change (Madeira et al., 2012; Vinagre et al., 2016, 2018, 2019). CTM is particularly useful for more precisely distinguishing tolerances between species (Beitinger et al., 2000) and was used in this study to resolve differences in upper thermal tolerance limits between *Aurelia* congeners. In the CTM, temperature is changed at a constant rate until a predefined sublethal critical endpoint is reached. The critical endpoint is generally specified as a non-lethal but incapacitating point (Lutterschmidt and Hutchison, 1997). CTM rates of temperature change are set fast enough so that acclimation does not occur, but slow enough for temperature to be tracked and should be standardized to allow comparison between species (Eme and Bennett, 2009; Bennett et al., 2018). We used the commonly chosen rate of temperature change of 1°C/15 min (Bennett et al., 2018; Vinagre et al., 2018, 2019).

TABLE 1 | Response scores with corresponding polyp morphology and degree of tentacle and body response.

Response score	Polyp morphology characteristics	Tentacle/body response to stimuli
5	Tentacles open as in feeding. Polyp is well-formed.	Immediate retraction, followed by re-elongation
4	Tentacles remain partially retracted. OR stomach is inverted.	Immediate retraction, no re-elongation.
3	Tentacles remain significantly retracted, shrunken or closed. OR significant morphological abnormalities present.	Greater than 1 s delay in retraction after a stimulus is applied. Retraction slow.
2	Mouth may be fixed agape. Tissue recoil is maintained.	Tentacles not responsive to touch.
1	Loss of tissue recoil.	Tentacles not responsive to touch.

To estimate the salinities that *Aurelia* polyps can tolerate in the wild, we used a chronic salinity change approach similar in concept to the CLM, which we call the Chronic Lethal Salinity Method (CLSM). We tracked individual polyps over gradual increase or decrease in salinity and monitored their apparent stress level at regular intervals using response scores, until the endpoint. The response score data was used to track each species' ability to acclimate to salinity change and to track the onset of salinity stress leading to death. Death was designated as the endpoint. Slow rates of change in environmental variables allow polyps to physiologically acclimate, such that tolerance limits approximate what species would tolerate in the wild. We selected a rate of salinity change of 1 ppt per day to maximize acclimation time within practical limits for the investigators. Using this approach, salinity limits were calculated by taking the arithmetic mean of the lethal endpoint salinities among biological replicates (CLSMin and CLSMax).

Chronic Thermal Acclimation Range and CLM

For each *Aurelia* species, three non-asexually reproducing polyps were placed and allowed to settle in each well of a 12-well culture plate with 7 ml of seawater at a salinity of 33 ppt. Polyps were selected from random locations within the parent culture in an effort to maximize genetic diversity and prevent selection of polyps belonging to the same clonal line. After 3 days, polyps were checked for attachment, and one healthy, attached polyp was retained in the dish; all others were removed. Three replicate culture plates were used for each species for a total of 36 biological replicates (polyps) per species. The experimental culture plates were placed in an incubator with the lights off. Temperature was gradually increased starting from 21°C and increasing at 1°C per day. 21°C was the average temperature of the culture conditions in the facility where long-term cultures were kept. This acclimation temperature was selected to minimize baseline physiological stress of the polyps prior to the start of chronic temperature acclimation experiments. One 12-well culture plate populated with 12 polyps/species was used as the control and maintained in an incubator at 21°C with the lights off for the duration of the experiment. Polyps were fed approximately 10 *A. salina* nauplii and 15 rotifers per well every third morning (every 2°C increase) for 2–3 h. Complete water changes were performed after feeding. Water for all cultures was made using natural filtered seawater adjusted to the target salinity of 33 ppt using Instant Ocean sea salt. Water was pre-warmed in the incubators to the target temperatures before each water change.

Water parameters were checked with a YSI to maintain accuracy. Temperature inside the incubators was logged using HOBO Onset temperature and light loggers. Polyps were observed under a Leica dissecting microscope every 2°C increment until their response scores reached 3, then they were observed at every 1°C increment. Polyps were scored for signs of stress according to a 5-point scale based on their tentacle morphology and response to stimuli (**Table 1**). A metal probe or plastic pipette tip was touched to the tentacles and body of each polyp to evaluate response to stimuli (**Figure 1**). The temperature, response score of each polyp, and number of polyps in each well was recorded. Any independent child polyps or free-swimming ephyra were removed. Polyps were considered to have reached the lethal endpoint when they lost tissue integrity at a response score of 1, which was defined as the absence of recoil by the tissue upon prodding the polyp body with a probe. The experiment was then repeated, but with decreasing temperature. Temperature was gradually decreased starting from 21°C at 1°C per day. Polyps were cultured, fed, and monitored in the manner described for increasing temperature.

Calculating Chronic Lethal Thermal Limits (CLMax and CLMin)

The CLMax for each species was determined by averaging the temperatures at which each polyp reached the lethal endpoint using the equation:

$$\mathrm{CLMax}_{\mathrm{species}} = \Sigma(\mathrm{T}_{\mathrm{endpoint}})/\mathrm{n}$$

Where $\mathrm{T}_{\mathrm{endpoint}}$ is the temperature at which polyps had a response score of 1 during the CLMax trials, and n is the sample size. The CLMin for each species was calculated using the same equation but using data from the CLMin trials.

Critical Thermal Maximum (CTMax)

Fifty to one hundred healthy polyps of each *Aurelia* species were transferred from different locations in the master cultures to 700 ml containers with 33 ppt water and aeration. Each species was placed in an incubator and kept at 21°C for 2 weeks for acclimation. 21°C was used as the acclimation temperature to approximate the average winter sea temperature along the shelf of the northern GoM (Boyer et al., 2011) where natural polyp populations may be located. Polyps were fed *ad libitum* with newly hatched *A. salina* nauplii twice a week for 24 h. Lights were off in the incubator. Water was changed in the containers on the day following feeding. Polyps were starved for 24 h before CTMax experiments. 5 polyps per well and 10 polyps per species were placed into 24.1 mm diameter propylene wells with 420 μm mesh bottoms (TedPella). Wells were inserted into foam so that they would float and placed into a thermostable water bath with vigorous aeration. Salinity and temperature parameters were maintained the same as during acclimation. Polyps were allowed to settle for 24 h at 21°C. Temperature was increased at a rate of 1°C/15 min. Each polyp's response to stimuli was evaluated at every 1°C by touching the tentacles with a metal probe. If no response was observed, the polyp body was touched with the metal probe. Response to stimuli was observed under a Leica dissecting microscope due to polyps' small size. Water bath temperature was measured using a digital thermometer immediately prior to removing the polyps from the water bath for observation. Individual wells were carefully scooped with the surrounding water from the water bath using a plastic container and placed under the microscope. When no response to the stimuli from either tentacles or polyp body was observed, the polyp was considered to have reached its endpoint and the temperature of the water bath was recorded as the thermal maximum of the polyp. Salinity was maintained at 33 ppt for the duration of the experiment, while dissolved oxygen concentration and pH were both monitored to ensure consistent levels.

Calculating Critical Thermal Maximum (CTMax)

The CTMax for each species was calculated by averaging the temperatures at which polyps lost response to stimuli using the equation:

$$\mathrm{CTMax}_{\mathrm{species}} = \Sigma(\mathrm{T}_{\mathrm{endpoint}})/\mathrm{n}$$

Where $\mathrm{T}_{\mathrm{endpoint}}$ is the temperature where polyps lost response to stimuli and n is the sample size. Intraspecific variability of the CTMax was determined by calculating the coefficient of variation given as a percentage for each species, using the equation: (standard deviation/mean)*100.

Chronic Salinity Acclimation Range and CLSMin

For each *Aurelia* species, three non-asexually reproducing polyps were placed in each well of a 12-well culture plate with 7 ml

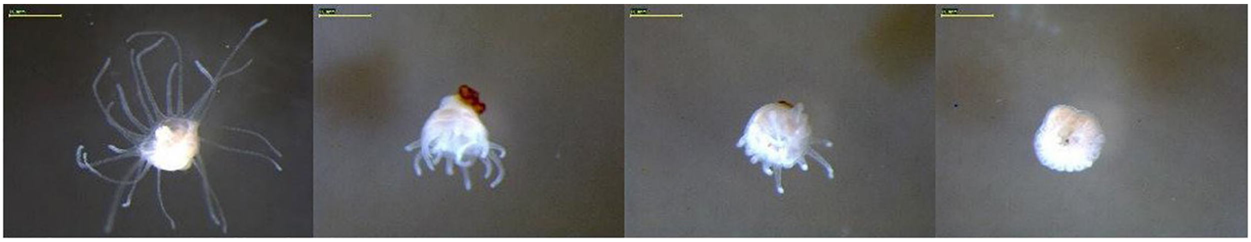

FIGURE 1 | Examples of response scores of *Aurelia* sp.1 polyps. Response to stimuli is in decreasing order from left to right 5-1. A response score of 5 indicates optimal polyp response; a response score of 1 indicates compromised tissue integrity (refer to **Table 1** for a complete definition of response scores).

of seawater at a salinity of 33 ppt and allowed to attach. After three days, polyps were checked for attachment. One healthy attached polyp was retained in the dish, while the others were removed. Two replicate culture plates were used for each species, with a total of 24 polyps per species. Culture plates were placed in incubators at 19°C, which is the winter average ocean temperature of the northern GoM coast (Boyer et al., 2011). The specific temperature approximates winter thermal conditions of estuaries, bays, and the coastline of the region, where potential habitats for coastal polyps are likely located. Lights were off in the incubators. Salinity was increased by 1 ppt a day, by completing a water change with water of the appropriate salinity. Eight polyps of each species were used for the control and maintained in an incubator at 19°C and salinity of 33 ppt. Water for all cultures was made using natural filtered seawater adjusted to the target salinities using Instant Ocean sea salt. Water was pre-warmed in the incubator to 19°C and water parameters were verified with a YSI prior to water changes. Temperature inside the incubator was logged using HOBO Onset temperature and light loggers. Polyps were fed approximately 10 *A. salina* nauplii and 15 rotifers per well once a week for 2–3 h. Complete water changes were performed after feeding. Polyps were observed for data collection under a Leica dissecting microscope at every 2 ppt increment until their response scores reached 3, then they were observed at every 1 ppt increment. Polyps were scored for visible stress level according to the 5-point response score scale defined above (**Table 1**). A metal probe or plastic pipette tip was used to touch tentacles and body of each polyp to evaluate response to stimuli. The salinity, response score of each polyp, and number of polyps in each well were recorded. Any independent child polyps or free-swimming ephyra were removed. Polyps were considered deceased when they lost tissue integrity, defined as the absence of recoil by the tissue upon prodding the polyp body with a probe, at a response score of 1. The experiment continued until all polyps reached a response score of 1. The experiment was then repeated, but with decreasing salinity. Salinity was gradually decreased by 1 ppt per day starting from 33 ppt. Water of target salinity was made by adjusting natural filtered seawater to target salinities using deionized water. Water quality monitoring, feedings and data collection were performed as described for increasing salinity.

Calculating Chronic Lethal Salinity Limits (CLSMin)

The CLSMax could not be determined because polyps' tolerance exceeded the range of the YSI (42 ppt). The CLSMin for each species was calculated by averaging the lethal endpoint salinities for each species from the decreasing salinity trial using the equation:

$$\mathrm{CLSMin}_{\mathrm{species}} = \Sigma(\mathrm{S}_{\mathrm{endpoint}})/\mathrm{n}$$

Where $\mathrm{S}_{\mathrm{endpoint}}$ is the salinity where polyps lost tissue integrity at a response score of 1, and n is the sample size.

RESULTS

Identification Through Molecular Barcoding

Cytochrome c oxidase subunit I sequences were approximately 650 bp in length, which is a standard length for *Aurelia* COI. ITS1 sequences were around 600 bp. Polyps from coastal medusae collected in Galveston Bay were confirmed to be *Aurelia* sp. 9 according to COI with a Percent Identity of 99.83% and an *E*-value of 0. Polyps that had been provided by the Moody Gardens Aquarium belonged to *A. coerulea* based on COI with a Percent Identity of 100% and *E*-value of 0. For the offshore *Aurelia* species, top BLASTn matches for mitochondrial COI were to *A. relicta* (Accession number KX691571), with a Percent Identity of 91.33% and an *E*-value of 0. The top match for nuclear ITS1 was *Aureli*a sp. Incheon with a Percent Identity of 84.70% and *E*-value of 1e-158. *Aurelia* sp.5 (*A. relicta*) was also among the top 5 database matches and had a higher Percent Identity of 88.65% and an *E*-value of 5e-122. Since we are unable to identify the offshore *Aurelia* to any known *Aurelia* species, we refer to this strain as *Aurelia* sp. new. A multigene phylogenetic analysis to clarify the phylogenetic position of *A.* sp. new within the genus is in progress, but outside the scope of this paper.

Chronic Thermal Acclimation Limits (CLMin and CLMax)

Polyps of *A. coerulea* maintained an average response score of 5 from 8°C to 27°C. At temperatures above 27°C, the response scores decreased from 5 to 1 over a span of 3°C. Below 8°C, the response scores of *A. coerulea* polyps decreased to 3 at 5°C. *A. coerulea* polyps did not show visible changes in stress level from 5°C down to 0°C, but response scores fell from 3 to 1 when temperatures decreased from 0°C to –2°C. Loss of response to stimuli occurred at about –1°C (**Figure 2**). For *A. coerulea* polyps, the CLMax was 30.9°C and the CLMin was –2°C; all polyps of this species reached the endpoint at the same temperature during the experiment with decreasing temperature (**Table 2**). The thermal range for *A. coerulea* spanned 32.9°C.

Polyps of *Aurelia* sp. new maintained an average response score of 5 from 13°C to 27°C. At temperatures above 27°C, the response scores decreased from 5 to 1 over a span of 2°C. Below 13°C, response scores decreased to 4 by 10°C, and steadily to 1 at 6°C. Loss of response to stimuli occurred at about 7°C (**Figure 2**). For *Aurelia* sp. new polyps, the CLMax was 30°C and the CLMin was 6°C; all polyps of this species were observed to reach their endpoints at the same temperatures (**Table 2**). The thermal range for *A.* sp. new spanned 24°C.

Polyps of *Aurelia* sp. 9 maintained an average response score of 5 from 14°C to 30°C. At temperatures above 14°C, polyps' response scores decreased from 5 to 1 over a span of 5°C. Below 14°C, response scores decreased to 4 by 10°C, and to 1 at 3°C. Loss of response to stimuli occurred at about 5°C (**Figure 2**). For *Aurelia* sp. 9 polyps, the CLMax was 34.7°C and the CLMin was 3.1°C (**Table 2**). The thermal range for *A.* sp. 9 spanned 31.6°C.

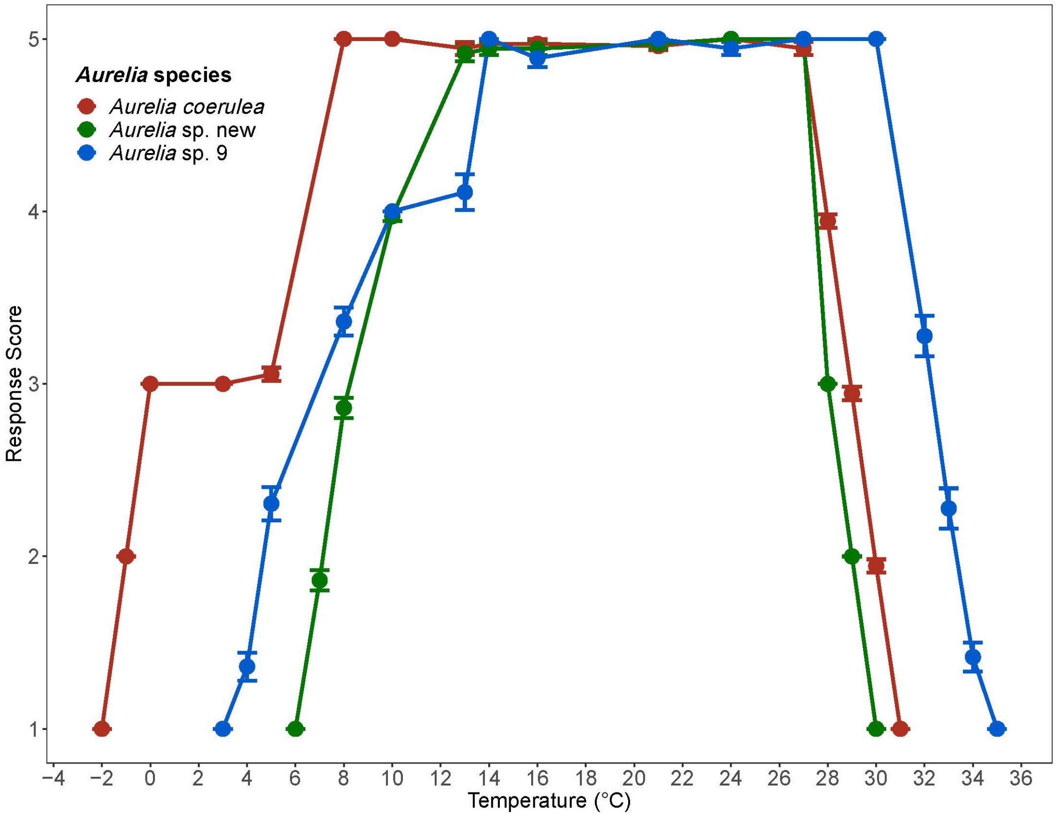

FIGURE 2 | Response scores of *Aurelia* species during 1°C/day temperature change. Response scores 1-5 are described in **Table 1**. Temperature is in degrees Celsius (°C). Error bars display standard error. Colors correspond to *Aurelia* species: red is *Aurelia coerulea*, green is *A.* sp. new, and blue is *A.* sp. 9.

Polyps in the control groups maintained response scores of 4 or above throughout the experiment. Results for the control polyps can be found in **Supplementary Material S1**.

Critical Thermal Maximum (CTMax)

Polyps of *Aurelia* sp. 9 had the highest thermal tolerance with a CTMax of 37.2°C. The first polyp lost response to stimuli at 34°C, but most polyps lost their response to stimuli above 37°C with the most tolerant polyps retaining response until 38.4°C. Intraspecific variation for *Aurelia* sp. 9 was 4.0%. *Aurelia* sp. new polyps had a CTMax of 32.1°C with 0% intraspecific variation (all lost response to stimuli at the same time and at the same temperature). *A. coerulea* polyps were the least tolerant to high temperatures with a CTMax of 29.6°C. The first polyps lost response to stimuli at 28.7°C. One polyp tolerated temperatures up to 31.8°C. Intraspecific variability for *A. coerulea* was 4.1%. Results for CTMax experiments are summarized in **Table 3**.

Salinity Acclimation Range and CLSMin

Aurelia coerulea polyps maintained an average response score of 5 down to about 12 ppt, with response scores falling below 4 at approximately 11 ppt. Polyps lost response to stimuli at about 7 ppt and tissue integrity at 6 ppt. CLSMin for *A. coerulea* was 6.2 ppt. *Aurelia* sp. new maintained response scores of 5, with no signs of visible stress, down to a salinity of 18 ppt, and response scores of 4 or above to 15 ppt. Polyps lost response to stimuli at about 12 ppt and tissue integrity at 10 ppt. The CLSMin for *Aurelia* sp. new was 10 ppt. *Aurelia* sp. 9 polyps maintained

TABLE 2 | Chronic lethal temperature limits for three *Aurelia* species: Chronic Lethal Minimum (CLMin) and Chronic Lethal Maximum (CLMax).

Species	CLMin (°C)	*n*	*SD*	CLMax (°C)	*n*	*SD*	Range (°C)
Aurelia sp. 9	3.1	36	0.5	34.7	36	0.7	31.6
Aurelia sp. new	6	36	0	30	36	0	24
Aurelia coerulea	−2	36	0	30.9	36	0.2	32.9

Sample size, standard deviations, and range (CTMax-CTMin) are shown. CLMin and CLMax values are in degrees Celsius (°C).

TABLE 3 | Critical Thermal Maximum (CTMax) values for three *Aurelia* species.

Species	CTMax (°C)	*n*	*SD*	Intraspecific variability (%)
Aurelia sp. 9	37.2	8	1.5	4.1
Aurelia sp. new	32.1	6	0	0
Aurelia coerulea	29.6	6	1.2	4.0

Sample size, standard deviations, and intraspecific variability are shown. CTMax values are in degrees Celsius (°C). Intraspecific variability is shown as a percentage.

response scores of 5 at 10 ppt, and response scores of 4 or above to approximately 7 ppt. Polyps lost response to stimuli at about 4 ppt and lost tissue integrity at 2 ppt. The CLSMin for *Aurelia* sp. 9 was 2.2 ppt. CLSMin values are summarized in **Table 4**. In the chronic salinity acclimation experiment with increasing salinities, polyps of all three species maintained optimal response scores to a salinity of 42 ppt, which was the measurement limit for the YSI salinity meter. The upper acclimation limit for salinity and the CLSMax could not be determined but exceeds ecologically relevant values for the GoM. Polyps in the control groups maintained average response scores of 4 or above for the duration of the experiment. Results for the control polyps can be found in **Supplementary Material S1**.

DISCUSSION

Environmental changes associated with climate change drive species range shifts. General trends across the globe reveal that species respond to warming ocean temperatures by shifting pole-ward (Thomas, 2010). However, in the GoM, the North American continent forms a physical barrier limiting species' northward movement. Due to their complex life cycle, the success of jellyfish species depends on the ability of the polyp, ephyra, and jellyfish life-stages to tolerate future conditions. Since it is the polyp stage that is responsible for maintaining and expanding jellyfish populations between seasons and years, species' success is influenced by the ability of the polyp to tolerate temperature increases.

The offshore *Aurelia* species may be a new species as it was not represented among GenBank COI or ITS1 sequences. Additional molecular and morphological analyses are required to confirm the identity of *Aurelia* sp. new as a distinct species. Only two *Aurelia* species have been previously reported in the GoM: *A.* sp. 9 and *A.* c.f. sp. 2 (Chiaverano et al., 2016).

Aurelia coerulea, *Aurelia* sp. new, and *Aurelia* sp. 9 possess distinct thermal tolerance ranges and thermal limits (**Table 2**). More specifically, the thermal ranges of the invasive species *A. coerulea* and *Aurelia* sp. 9 are of similar size, differing only by 1.3°C based on lethal limits. The response scores of both species show a similar trend, as both maintained response scores of 5 over a 21°C span (**Figure 2**). However, *A. coerulea* has a lower thermal tolerance with its experimental thermal tolerance range shifted by about 4°C relative to that of *Aurelia* sp. 9, suggesting a preference for cooler temperature. This is also reflected in the climate of its native geographical origin in the South and East China Seas. The thermal range of *Aurelia* sp. new is approximately 8°C narrower than that of *A. coerulea* and *A.* sp. 9 (**Figure 2**), suggesting that polyps of this species may prefer thermally stable conditions. CLMax values and visible stress as measured by response scores suggest that *A. coerulea* and *A.* sp. *new* may have similar upper thermal limits. Control polyps that were kept at a constant temperature but otherwise treated in an identical manner, maintained high response scores for the duration of trials, indicating that the observed lethal limits were due to thermal stress.

Unlike *Aurelia* sp. 9 and sp. new, polyps of *A. coerulea* have been found in the wild (Ishii and Katsukoshi, 2010; Marques et al., 2019). Interestingly, the experimentally resolved temperature range where polyps of *A. coerulea* maintained minimal signs of stress (response scores of 4 or above) determined in this study align well with published reports of the habitat temperatures for this species derived from field surveys of wild populations. According to our experiments, *A. coerulea* polyps experienced minimal stress from 6.5°C to 27°C, whereas natural polyp habitats in the Thau Lagoon (northwestern Mediterranean) range from 7.6°C to 25.8°C (Marques et al., 2019), 6°C to 30°C for polyps in Lake Verano, Italy (Belmonte et al., 2011), and 9°C to 29°C for *A. coerulea* in Tokyo Bay, Japan (Ishii and Katsukoshi, 2010). These are the minimum and maximum recorded water temperatures of wild populations surveyed over the span of approximately 1 year (Ishii and Katsukoshi, 2010; Marques et al., 2019).

The thermal range of *A. coerulea* suggests that it is unlikely to develop a resident population within the coastal GoM. Winter low temperatures along the northwestern and northeastern coasts of the GoM average 13–20°C (averaged from https://www.nodc.noaa.gov/dsdt/cwtg/all_meanT.html), which is well above the lower thermal tolerance limit of –2°C (CLMin) for *A. coerulea.* However, with a CLMax of 30.9°C, this species may be restricted by the summer water temperatures along parts of the northwestern and northeastern GoM coasts, which average 28–31°C (averaged from https://www.nodc.noaa.gov/dsdt/cwtg/all_meanT.html). Summer average temperatures in the coastal GoM are thus likely to be lethal to *A. coerulea* whose response scores indicated damaging levels of thermal stress at temperatures above 27°C.

Aurelia sp. 9, the common-bloom forming *Aurelia* species in the GoM, had a thermal tolerance range of 3.1°C to 34.7°C based on lethal limits and displayed minimal signs of stress between 10°C and 31°C. Monthly annual averages for coastal western and eastern GoM range from 13°C to 31°C suggesting that, from a thermal perspective, the conditions of bays, marinas, and coastlines are suitable habitats for *Aurelia* sp. 9 polyps. Out of the three species evaluated, *Aurelia* sp. 9 was tolerant of temperatures at least 3°C higher than the other two species. *Aurelia* sp. new had the narrowest thermal range of 24°C, and displayed signs of stress outside of the range of 10°C to 27°C. The upper lethal thermal limit of *Aurelia* sp. new (CLMax = 30°C) suggests that it may also not be able to tolerate the summer high temperatures observed along the northern GoM coast. However, the temperatures in the deeper waters along the continental shelf in the GoM where the medusa of this species was collected, are generally lower than the coastal

TABLE 4 | Chronic Lethal Salinity Minimum (CLSMin) for three *Aurelia* species.

Species	CLSMin (ppt)	*n*	*SD*
Aurelia sp. 9	2.2	25	0.6
Aurelia sp. new	10	24	0
Aurelia coerulea	6.2	22	0.9

CLSMin values are in parts per thousand (ppt). Sample size and standard deviations are shown.

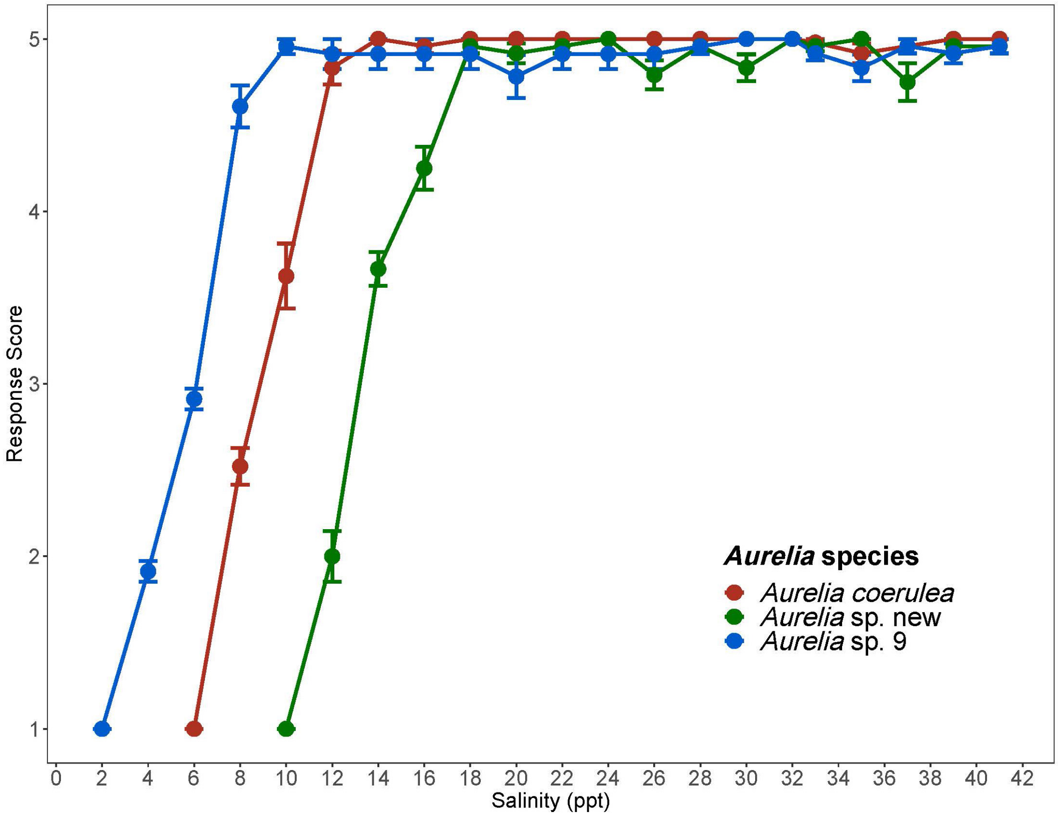

FIGURE 3 | Response scores of *Aurelia* species in response to 1 ppt/day salinity change. Response scores 1-5 are described in **Table 1**. Salinity is in parts per thousand (ppt). Error bars display standard error. Colors correspond to *Aurelia* species: red is *Aurelia coerulea*, green is *A.* sp. new, and blue is *A.* sp. 9.

summer averages, so it is possible that *Aurelia* sp. new is restricted to offshore areas.

We used the CTM to identify CTMax for each species to resolve the relative upper thermal limits of the *Aurelia* congeners (**Table 3**). CTMax values confirm that *Aurelia* sp. 9 is more tolerant of high temperatures than both *A. coerulea* and *Aurelia* sp. new. *A. coerulea* had the lowest CTMax among the congeners, indicating this species to be the least tolerant of high temperatures, which is reasonable considering the generally lower temperatures of its native range as compared to the GoM. Fast rates of warming, such as the 1°C/15 min rate used in this study to determine CTMax, may overestimate the actual upper thermal tolerance limits of organisms in nature (Peck et al., 2009). CTMax values are usually greater than CLMax values, because slower rates of warming in the chronic experiment allow more time at each temperature for lethal physiological effects to accumulate and set in. This relationship was observed for *Aurelia* sp. 9 and *Aurelia* sp. new, where CTMax values were about 2°C greater than CLMax values, but not for *A. coerulea*, where the CTMax was approximately 1°C lower than the CLMax (**Figure 4**). The lower CTMax may indicate that *A. coerulea* polyps are sensitive to rapid temperature changes.

Chronic salinity experiments show that polyps of all three species are generally able to withstand a wide range of salinities and are not sensitive to hypersaline conditions (**Figure 3**). Of the three species, *Aurelia* sp. 9, had the lowest CLSMin value of 2.2 ppt. Additionally, polyps of this species had no visible signs of stress during the 1 ppt/day salinity decrease until salinity dropped below 10 ppt, suggesting that *A.* sp. 9 polyps are tolerant of low salinities and salinity change. When considered together with the high thermal tolerance of this species, salinity tolerance results suggest that coastal areas of the GoM as well as some bays and estuaries in this region, are suitable habitats for polyps of *A.* sp. 9. *A. coerulea* polyps had a CLSMin of 6.2 ppt with no visible signs of stress until salinity decreased below 14 ppt. Most wild populations of *A. coerulea* have been recorded at salinities above 20 ppt (Belmonte et al., 2011; Marques et al., 2019). *Aurelia* sp. new had a CLSMin of 10 ppt and was therefore the least tolerant of low salinities among the three species. Visible signs of stress were observed for polyps of this species at salinities below 18 ppt, suggesting possible low resilience to salinity change (**Table 4**). Compared to the two coastal species, *Aurelia* sp. new has a considerably more limited ability to withstand both temperature and salinity change, indicating that *A.* sp. new is an offshore species in the GoM.

Because of the difficulties in finding polyps in the wild, we acknowledge that we could not control or assess patterns of relatedness within the polyps used in our experiments. Additional molecular, morphological, and physiological studies

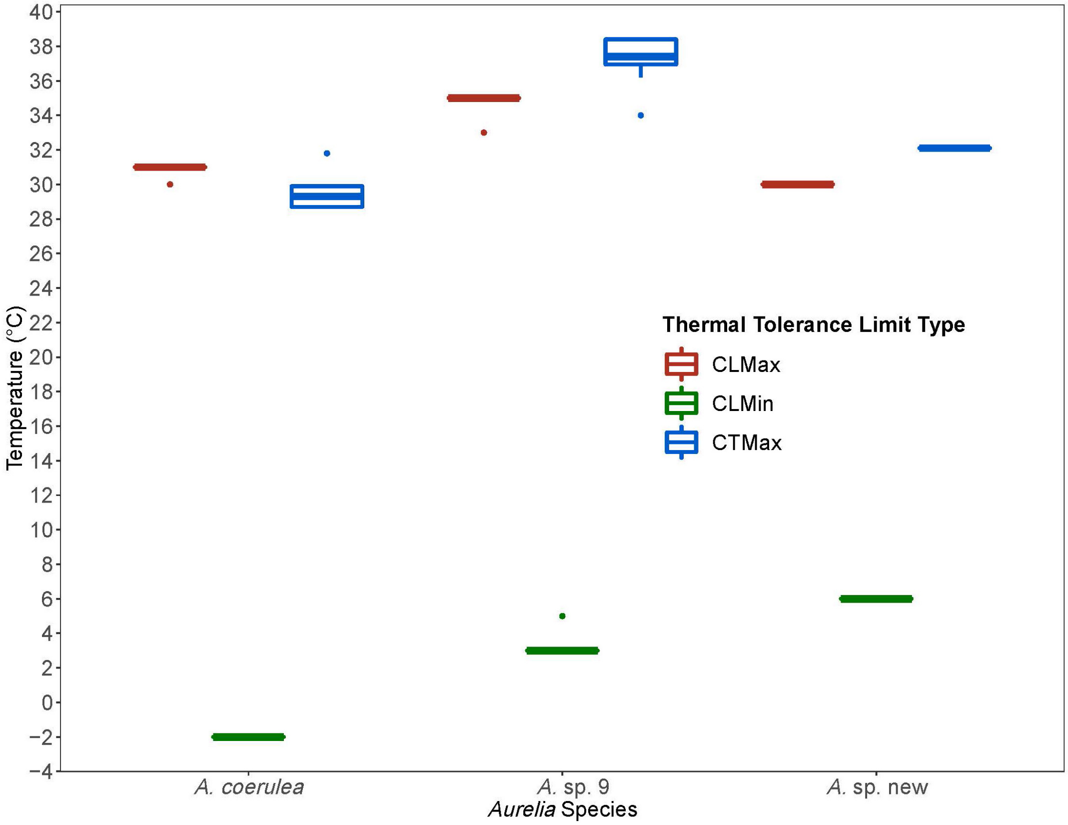

FIGURE 4 | Comparison of thermal tolerance values from Chronic Lethal Maximum and Minimum and Critical Thermal Maximum experiments for *Aurelia coerulea, A.* sp. new, and *A.* sp. 9. Thermal limits are in degrees Celsius (°C). Colors designate thermal limit type: red is Chronic Lethal Maximum (CLMax), green is Chronic Lethal Minimum (CLMin), and blue is Critical Thermal Maximum (CTMax). Boxplots displays the median with the lower and upper hinges corresponding to the 25th and 75th percentiles and whiskers extending to 1.5 times the inter-quartile range. Single points indicate outliers.

are necessary to confirm the environmental tolerance results found here, especially for *A.* sp. new, where polyps were sourced from a single medusa and may not adequately reflect the genetic variation of the species.

The temperature and salinity tolerance ranges and limits of *Aurelia* congeners can be used to predict species' responses to future conditions. Ocean surface temperatures are projected to increase by up to 4°C by the year 2100 (Biasutti et al., 2012), with benthic habitats becoming even warmer (Turner et al., 2017). A temperature increase of this magnitude may deter *A. coerulea* from invading or becoming established in the coastal GoM, as the upper thermal limit of this species is already at or below current summer average water temperatures. The temperature highs in the South and East China Seas (26–29°C) suggest that *A. coerulea* is currently living fairly close to its thermal limits in its native range, and may be especially at risk in enclosed habitats, which it is known to inhabit. Due to its similar upper thermal limits, *Aurelia* sp. new may also be negatively impacted overall. The Chronic Lethal Thermal upper limit (34.7°C) and Critical Thermal Maximum (37.2°C) of *Aurelia* sp. 9 suggest that it can withstand some increase in environmental temperatures. However, an increase of 4°C would bring water temperatures near the upper thermal limit for this species, which would potentially negatively impact *Aurelia* sp. 9 in the warmest extremes of its biogeographical range. Temperature increases are also expected to be greatest in coastal areas (Biasutti et al., 2012), indicating that coastal *Aurelia* sp. 9 populations would not benefit and may decline due to habitat temperature increase by the next century.

DATA AVAILABILITY STATEMENT

The DNA sequence datasets for this study are deposited in GenBank, Accession Numbers MN531714 to MN531721 for COI and MN527964 to MN527966 for ITS1. Genetic data will be available through the Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC). Thermal and salinity tolerance data is available in the **Supplementary Material S2**.

AUTHOR CONTRIBUTIONS

AF and MM designed the experiments and wrote the manuscript. AF carried out the experiments.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00093/full#supplementary-material

MATERIAL S1 | Daily averaged response scores for Chronic Lethal Maximum and Minimum experiments for control and experimental polyps. CLM_controls tab contains daily averaged response score for controls of each species maintained at 21°C.

MATERIAL S2 | Raw and processed data for thermal and salinity tolerance experiments. CLMin and CLMax tab contains Chronic Lethal Minimum (CLMin) and Chronic Lethal Maximum (CLMax) values for the three species with sample size, standard deviation, and sample size (CLMax – CLMin) shown. CLMax and CLMin values are in degrees Celsius (°C). CTMax tab contains CTMax values for the three species with sample size, standard deviation, and intraspecific variability shown. CTMax values are in degree Celsius (°C). Intraspecific variability is shown as a percent value. CLSMin tab contains Chronic Lethal Minimum Salinity values for the three species with sample size and standard deviation shown. CLSMin values are in parts per thousand (ppt). Response Score (temperature) tab contains the raw data for the Chronic lethal temperature experiments. Date, temperature in degrees Celsius (°C), species, plate number, well number, response score, and total number of polyps in well is shown. Response Score (salinity) tab contains the raw data for the Chronic lethal salinity experiments. Date, temperature in degrees Celsius (°C), species, plate number, well number, response score, and total number of polyps in well is shown.

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frontiers in Marine Science

ORIGINAL RESEARCH
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Community Dynamics of Fish Assemblages on Mid-Shelf and Outer-Shelf Coral Reefs in the Northwestern Gulf of Mexico

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Offshore coral reefs in the Gulf of Mexico (GOM) are unique model systems for examining the mechanisms structuring reef fish communities due to their substantial geographic isolation, and the presence of replicate experimental units of both low (mid-shelf) and high coral diversity (shelf-edge) reefs. Here, we examined the species assemblage structure of juvenile and adult fishes at two mid-shelf reefs (Sonnier and Stetson Bank) and two shelf-edge reefs (East and West Flower Garden Banks) in the northwestern GOM to evaluate the relative importance of habitat (i.e., coral diversity) vs. recruitment in structuring resident fish assemblages. Visual reef fish surveys ($n = 400$) were conducted at the four coral reefs during two seasons, spring-early summer and late summer-fall in 2009 and 2010. Two depth zones were surveyed at each reef, representing the reef crest (15–23 m depth) and upper slope (23–30 m depth) habitats. Seasonal variability in recruitment to both mid-shelf and shelf-edge reefs was observed, with higher mean juvenile density and diversity (H') observed during the late season at all reefs in 2009 and all but Stetson in 2010, supporting an early fall recruitment peak. Likewise, considerable inter-annual variability in juvenile recruitment was observed, with significantly lower juvenile density and H' observed at mid-shelf reefs in 2010 relative to 2009. Species diversity was strongly linked to coral diversity, with greater reef fish diversity consistently observed at shelf-edge relative to mid-shelf reefs. Observed differences in the composition of juvenile and adult assemblages at mid-shelf reefs suggest that reef fish communities at these reefs were more strongly influenced by post-settlement processes (e.g., juvenile mortality) than shelf-edge reefs, which may be a function of several limiting factors (e.g., predation, coral diversity, water quality). Results indicate that reef fish assemblages associated with mid-shelf and shelf-edge reefs in the northwestern GOM may have sufficient stabilizing mechanisms in place to facilitate recovery from anomalous recruitment events. The strong, reef type-specific differences in assemblage composition observed throughout the study indicate that mid-shelf and shelf-edge coral reefs may fill different functional roles for demersal fishes in the northwestern GOM.

Keywords: reef fish, Flower Garden Banks, Stetson Bank, Sonnier Bank, assemblage structure, recruitment, coral reef, biodiversity

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INTRODUCTION

An extensive body of community-level research conducted in numerous coral reef ecosystems reveals substantial variability in the species composition, spatial distribution, and temporal stability of resident fish assemblages (e.g., Sale, 2004; Mellin et al., 2016). As a result, it has been widely suggested that the primary mechanisms regulating reef fish community structure may vary considerably as a function of reef type, reef context, and geographic region (e.g., Beukers and Jones, 1998; Friedlander et al., 2003; Darling et al., 2017). A comprehensive understanding of local community dynamics is necessary for the development of effective and spatially explicit management strategies (Bohnsack and Ault, 1996; Sale, 2004). Thus, identifying processes responsible for maintaining community structure and biodiversity within reef-associated fish assemblages is critical as coral reef ecosystems worldwide are threatened by overfishing and habitat degradation (Newman et al., 2006; MacNeil et al., 2015).

Patterns of fish recruitment to coral reefs typically show a large degree of spatiotemporal variability (Doherty and Williams, 1988; Sale, 2004), and the relative importance of pre- and post-recruitment mechanisms in structuring reef fish communities has been widely debated in the literature (Armsworth, 2002; Smallhorn-West et al., 2017). Multiple small-scale studies on patch reefs have indicated that the community structure of adult fishes may be determined almost entirely by the initial species composition of juveniles recruiting from the plankton, with little evidence of post-settlement population regulation (reviewed in Doherty, 2002; Shima et al., 2018). Several larger-scale studies have also suggested that cross-shelf gradients in the species composition of reef-associated fish communities (e.g., Williams, 1983) appear to be structured primarily by offshore-inshore gradients in the delivery or survival of planktonic recruits, rather than subsequent movement or differential mortality of juvenile and adult fishes between offshore and inshore reef habitats (Roberts, 1991; see Wismer et al., 2009; Burgess et al., 2010). However, other long-term studies have found the distribution and abundance of adult reef fish populations to be largely independent of spatiotemporal fluctuations in recruitment and relatively consistent within a given reef type, suggesting that habitat characteristics and biotic interactions may ultimately determine the community structure and persistence of coral reef-associated fish assemblages in some systems (e.g., Robertson et al., 1988; Yeager et al., 2017).

Biotic interactions such as competition and predation are inherently density dependent (Carr et al., 2002; Hixon, 2015), and therefore the relative importance of post-recruitment processes in structuring a fish assemblage will be strongly influenced by the local quality, composition, and structural complexity of available habitat (e.g., Grober-Dunsmore et al., 2007, 2008). Newly settled reef fishes typically experience high predator-induced mortality during the first few weeks of life (Almany and Webster, 2006), and the availability of appropriately sized refuges within the reef structure can greatly influence the survival rates of new recruits as well as the species composition of individuals reaching maturity from a given cohort (Jones, 1988; Beukers and Jones, 1998; Syms and Jones, 2000). Refuge availability may be limiting even on a relatively large reef complex if the structured habitat varies greatly in quality, and numerous studies on coral reefs have found positive correlations between topographic complexity and the local density and diversity of resident fishes (Almany, 2004; Bejarano et al., 2015). Similar positive relationships between reef fish abundance and live coral cover have also been documented (Roberts and Ormond, 1987; Holbrook et al., 2008), and recent research has demonstrated that in certain coral reef systems, the diversity and species composition of corals within a given reef habitat may directly determine the diversity and community structure of the resident fish assemblage (Messmer et al., 2011).

The aim of the current study was to characterize the community structure of fish assemblages associated with mid-shelf and shelf-edge coral reefs in the northwestern Gulf of Mexico (GOM). Offshore coral reefs in the GOM represent a unique model system for examining the mechanisms structuring reef fish communities because they show an unusual degree of geographic isolation, but also contain replicate experimental units of both low coral diversity (mid-shelf) and high coral diversity (shelf-edge) reef habitats. Additionally, these coral reefs represent much of the hard-bottom habitat available to demersal fishes in the northern GOM, and they may be critical to the maintenance of reef fish populations throughout this region (Dennis and Bright, 1988; Schmahl et al., 2008; Hickerson et al., 2012; Voss et al., 2014). Here, we examined the species composition of juvenile and adult fishes at two low diversity coral reefs (located on the mid shelf) and two high diversity coral reefs (located on the shelf edge) in the northwestern GOM to evaluate the relative importance of habitat (i.e., coral diversity, depth) vs. recruitment in structuring resident fish assemblages. We also compared large-scale settlement patterns between reef types in an attempt to characterize the functional roles of mid-shelf and shelf-edge reef habitats within this continental shelf system.

MATERIALS AND METHODS

Study Area

Four coral reefs were included in the study: two mid-shelf reefs [Sonnier Bank (SONN), Stetson Bank (STET)] and two shelf-edge reefs [East Flower Garden Bank (EFGB), West Flower Garden Bank (WFGB)]. Based on the species richness of scleractinian corals, both mid-shelf reefs were considered to be low coral diversity (<12 species), while both shelf-edge reefs were classified as high coral diversity (>20 species).

The two mid-shelf reefs (SONN, STET) are located approximately 110 km offshore, cresting at depths of 18–20 m (**Figure 1**). Both reefs consist of relatively bare siltstone-claystone outcroppings characterized in limited areas of the reef crest and upper slope by *Millepora*-Sponge benthic communities (Rezak et al., 1990). Apart from the encrusting hydrozoan *Millepora* spp., which represents approximately 30% of benthic coverage on the crests of SONN and STET, the majority of scleractinian corals species occur only in small numbers as isolated colonies (Schmahl et al., 2008; Hickerson et al., 2012). The establishment of more extensive hermatypic coral communities within this reef

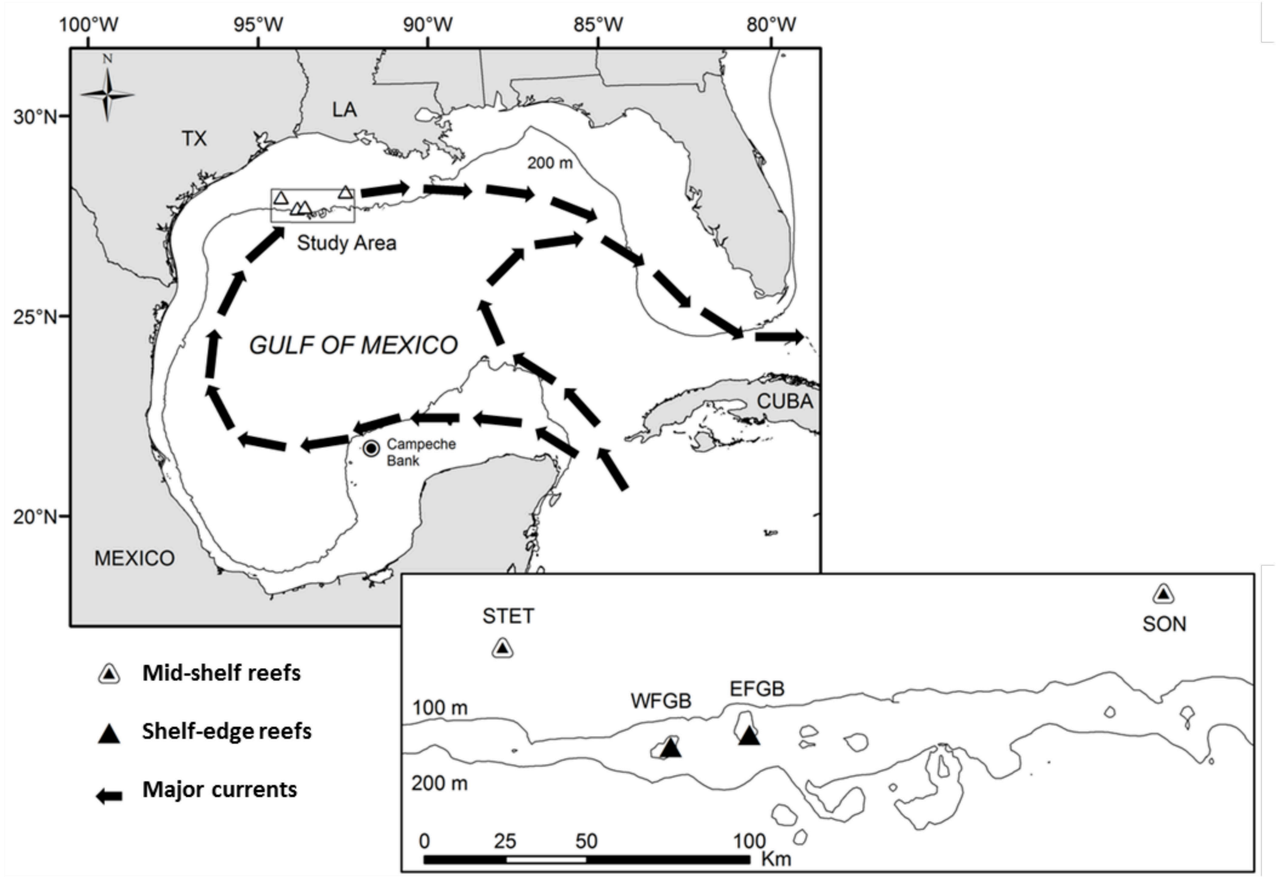

FIGURE 1 | Regional context of study reefs in the Gulf of Mexico (GOM). Arrows denote the directional flow of major basin-wide currents, and a rectangle delineates the study area (and location of map inset) along the northern continental shelf. Map inset illustrates the bathymetry of the study area in greater detail and shows the spatial arrangement of mid-shelf (Sonnier, SON; Stetson, STET) and shelf-edge (East Flower Garden Bank, EFGB; West Flower Garden Bank, WFGB) reef sites.

type is precluded by the high levels of turbidity and low winter temperatures (<16°C) associated with mid-shelf waters in the GOM (Rezak et al., 1990).

The two shelf-edge reefs (EFGB, WFGB) are complex carbonate reef caps located approximately 185 km offshore on the outer continental shelf, where oceanic water and a more stable temperature regime facilitate the development of extensive *Diploria-Montastrea-Porites* coral communities throughout the reef crest (≈ 20 m) and upper slope habitat zones (Rezak et al., 1990; Johnston et al., 2016). Both EFGB and WFGB are largely dominated by colonies of the hermatypic brain corals *Montastrea franski* and *Montastrea faveolata* and the star coral *Diploria strigosa*, although several other species (particularly *Porites* spp.) are also present in fairly extensive colonies (Schmahl et al., 2008). The benthic coral communities at shelf-edge reefs in the northwestern GOM are less diverse but similar in species composition to coral communities in the Caribbean (Schmahl et al., 2008), and coral coverage at both EFGB and WFGB is high (45–52%) (Johnston et al., 2016).

Three of the reefs represented in this study (EFGB, WFGB, and STET) are located within the boundaries of the Flower Garden Banks National Marine Sanctuary (FGBNMS), where federal regulations prohibit anchoring of vessels, commercial fishing, and spearfishing, although recreational hook-and-line angling is still permitted. Only SONN is located outside of the sanctuary boundaries, and thus this reef is vulnerable to habitat damage as a result of vessel anchorage and commercial fishing activities, as well as selective removal of large, upper-trophic level fishes by recreational spearfishers (Schmahl et al., 2008). Recent sanctuary expansion has been proposed which would result in the future inclusion of SONN in the FGBNMS.

Reef Fish Surveys

Fish surveys were conducted from May to October in 2009 and 2010. This sampling period was chosen to correspond with potential periods of high recruitment for juvenile reef fishes, based on documented peaks in larval abundance that occur from spring to early fall in the FGBNMS when water temperatures are the warmest (McGowan, 1985). The sampling period was divided into spring-early summer (May 15–July 15) and late summer-fall (August 1–October 1) sampling seasons, and all reefs in the study were surveyed at least once during each sampling season (**Table 1**). Two depth zones were surveyed at each reef,

TABLE 1 | Summary of survey effort in 2009 and 2010, with the number of transects (*n*) conducted at East Flower Garden Bank (EFGB), West Flower Garden Bank (WFGB), Sonnier Bank (SONN), and Stetson Bank (STET) during each sampling period.

Year	Season	Site	*n*	S_{Juv}	S_{Adult}	S_{Total}	% Juv
2009	Early	SONN	21	16	18	25	75.9
		STET	25	24	19	29	91.7
		EFGB	39	20	27	31	72.8
		WFGB	39	19	31	33	75.9
	Late	SONN	22	20	27	36	78.5
		STET	36	28	27	39	90.4
		EFGB	36	19	29	34	82.3
		WFGB	33	19	30	35	83.3
2010	Early	SONN	23	16	21	25	35.2
		STET	24	21	26	32	53.8
		EFGB	12	11	27	29	23.6
		WFGB	12	12	23	25	34.2
	Late	SONN	24	17	27	33	76.7
		STET	12	12	13	19	56.0
		EFGB	18	16	27	27	34.0
		WFGB	24	17	28	30	52.4

Species richness of juveniles (S_{Juv}), adults (S_{Adult}), and pooled (S_{Total}) are reported, as well as the proportion of total fishes observed as juveniles (% Juv).

representing the reef crest (15–23 m depth) and upper slope (23–30 m depth) habitats.

Visual fish counts were conducted with SCUBA on line transects 5-m in length and 2-m in width. All fish within a given transect area were identified to the lowest possible taxa and assigned an age class based on body size and coloration, either juvenile (for juveniles and young-of-the year) or adult (for sub-adult and adult individuals). Fish were enumerated in order of encounter to minimize diver bias or double counting, and transect locations were designated using a stratified random sampling design, with divers assigned randomly generated compass headings and numbers of fin-kick cycles within each depth zone prior to every dive (approximately 2–3 transects were conducted per dive). Sampling surveys took place at multiple mooring locations at each reef in order to facilitate representative sampling across the reef crest.

In 2009, measurements of rugosity (defined here as the ratio between substrate contour and straight-line distance) were taken along each transect to serve as an indicator of habitat complexity. Rugosity was measured by draping a weighted chain along the contour of the reef and measuring the length of chain needed to cover a 1-m linear distance. Three measurements of rugosity were taken at regular intervals along each transect, and the rugosity estimate was reported as the mean value of these three measurements. In 2010, vessel limitations resulting from the Deepwater Horizon oil spill limited our sampling effort and rugosity measurements were not conducted during this survey year.

Data Analysis

Density was calculated for each transect as the total number of fishes (all species combined) encountered per square meter. The assumptions of normality and homogeneity of variance were tested and values were *ln*-transformed before analysis to correct for heteroscedasticity of variance among transects. Diversity was also calculated for each transect using the Shannon diversity index (H'):

$$H' = -\Sigma p_i ln p_i$$

where p_i is the proportion of the total number of individuals encountered on the transect represented by species i. Seasonal, within-reef, and among-reef trends in fish density and diversity for each year of the study were analyzed using multivariate analysis of variance (MANOVA), with season, depth zone, and reef as the main effects. *Post hoc* differences in mean density and diversity were examined using Tukey's honestly significant difference (HSD) method (α = 0.05). Because juvenile recruitment patterns are often influenced by different mechanisms than those structuring mature reef fish assemblages (Sale, 1991), juvenile and adult age classes were analyzed separately. The effects of rugosity on overall fish density and diversity were analyzed using linear regression.

Comparisons of assemblage structure among reefs for each year, sampling period, and age class were conducted in PRIMER v5 (Clarke and Warwick, 2001) using non-metric multidimensional scaling (MDS) models of *ln*-transformed density data. Data ordination was based on a Bray–Curtis similarity matrix and stress coefficients (residual modeling error) of 0.2 were treated as critical values to evaluate goodness-of-fit for each MDS model in two dimensions (Clarke and Warwick, 2001). Pairwise analysis of similarity (ANOSIM) permutation procedures were used to analyze the degree of overlap and test for differences in juvenile and adult assemblage structure among reefs for each sampling season and year of the study (999 permutations, α = 0.05). Pairwise ANOSIM procedures were also performed on untransformed juvenile and adult presence absence data within each reef in order to compare the species present in the mature fish assemblage with the species composition of newly settled recruits.

RESULTS

Assemblage Composition

In total, 11,234 fishes representing 70 species from 24 families were observed in 2009, and 7,027 fishes representing 64 species from 23 families were observed in 2010 (**Supplementary Table S1**). Overall species richness (all transects pooled) was fairly similar among reefs during both survey years, ranging from 40 to 43 species observed at each reef in 2009 (43–72 transects surveyed per reef in 2009) and 34–39 species observed at each reef in 2010 (30–47 transects surveyed per reef in 2010). Pomacentrids and labrids were the dominant families at both mid-shelf and shelf-edge reefs in 2009, together accounting for 88–92% of the total fish assemblage at each reef (**Figures 2A,B**). In 2010, these two families remained numerically dominant (75–85%) at both shelf-edge reefs (EFGB, WFGB); however, at the mid-shelf reefs (SONN, STET), blenniids (primarily the seaweed blenny *Parablennius marmoreus*) also made up a significant

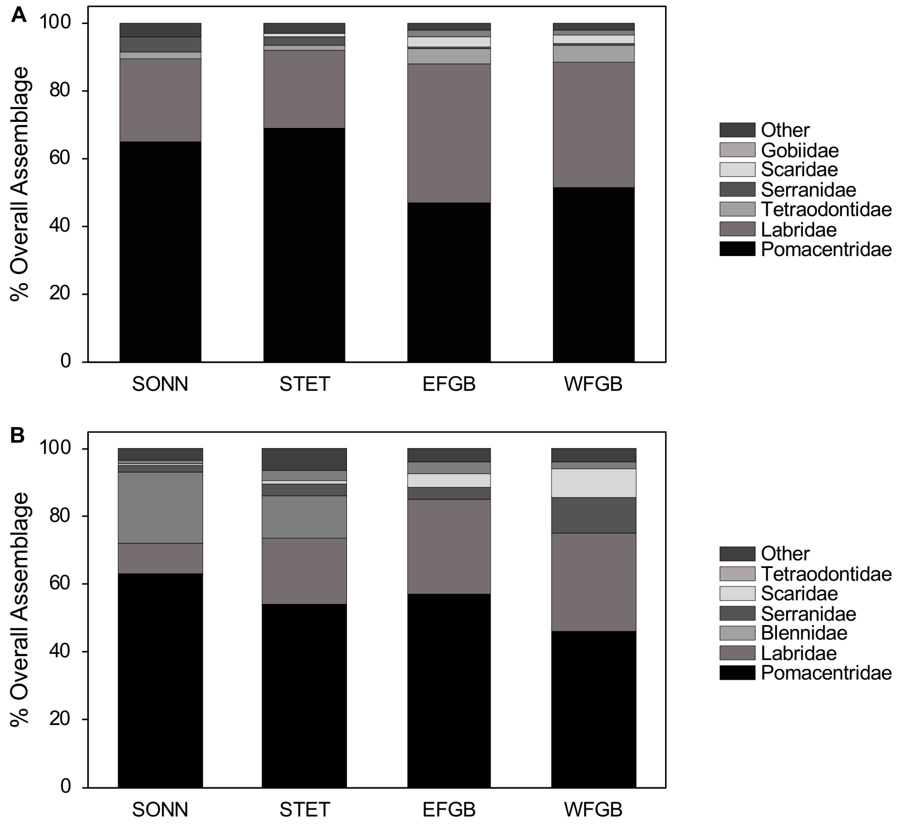

FIGURE 2 | Percent composition of the six numerically dominant reef fish families present at each reef for 2009 **(A)** and 2010 **(B)**. Both juveniles and adults were included in the analysis, and figures represent the pooled values from all transects conducted within each reef during a given year.

proportion of the fish assemblage, representing 21% of all fish observed at SONN and 12% at STET. Relative abundances of pomacentrids and labrids were fairly equal at the two shelf-edge reefs in 2009, while pomacentrids (65–69%) were notably more abundant than labrids at the two mid-shelf reefs. In 2010, pomacentrids were more abundant (46–63%) than labrids at all four reefs.

Spatiotemporal Trends in Abundance and Diversity

Mean densities of juvenile reef fishes (all species pooled) varied significantly by reef, season, and depth zone for both years of the study (ANOVAs, $P < 0.01$; **Figures 3A–D**). In 2009, mean juvenile fish density was significantly higher at STET than at the other mid-shelf reef (SONN) or either of the shelf-edge reefs (EFGB, WFGB) (Tukey HSD, $P < 0.05$). Mean density was also significantly higher during the late season surveys and in the shallow depth zone. There was a significant interaction between reef and depth zone (ANOVA, $P < 0.001$); juvenile fish densities were relatively similar between shallow and deep habitats at EFGB and WFGB, but were significantly higher on the shallow reef crest at both mid-shelf reefs (SONN and STET). Mean densities of juvenile fishes were generally lower in 2010 than 2009 (**Figures 3C,D**), although significant differences were again detected among study sites (ANOVA, $P < 0.001$). Patterns of seasonality and depth distribution in 2010 were similar to those observed in 2009, with significantly higher densities during the late sampling season and in the shallow depth zone. The one notable exception was STET, showing an opposite trend with lower densities of juveniles during the late sampling season and no apparent difference in juvenile densities between depth zones. The lowest mean densities of juvenile fishes were observed at the two shelf-edge reefs (EFGB, WFGB) for both years of the study.

Mean densities of adult fishes showed less consistent patterns with respect to reef, season, and depth but all three factors were found to be significant (ANOVAs, $P < 0.01$; **Figures 4A–D**). In 2009, mean densities of adult fishes were significantly higher at the mid-shelf reef SONN than at the other three reefs (Tukey HSD, $P < 0.05$). There were also significant differences between seasons and depth zones, with higher densities of adults recorded in the shallow depth zone and the late sampling season. Again, these differences were apparent only at the two mid-shelf reefs. In 2010, densities of adult reef fishes were highly variable within all reefs surveyed, largely due to an increased presence of schooling planktivorous fishes on transects, and there were no significant differences among study sites, sampling seasons, or depth zones.

Shannon diversity (H') for juvenile fishes differed markedly between the two survey years (**Figures 5A–D**). This was

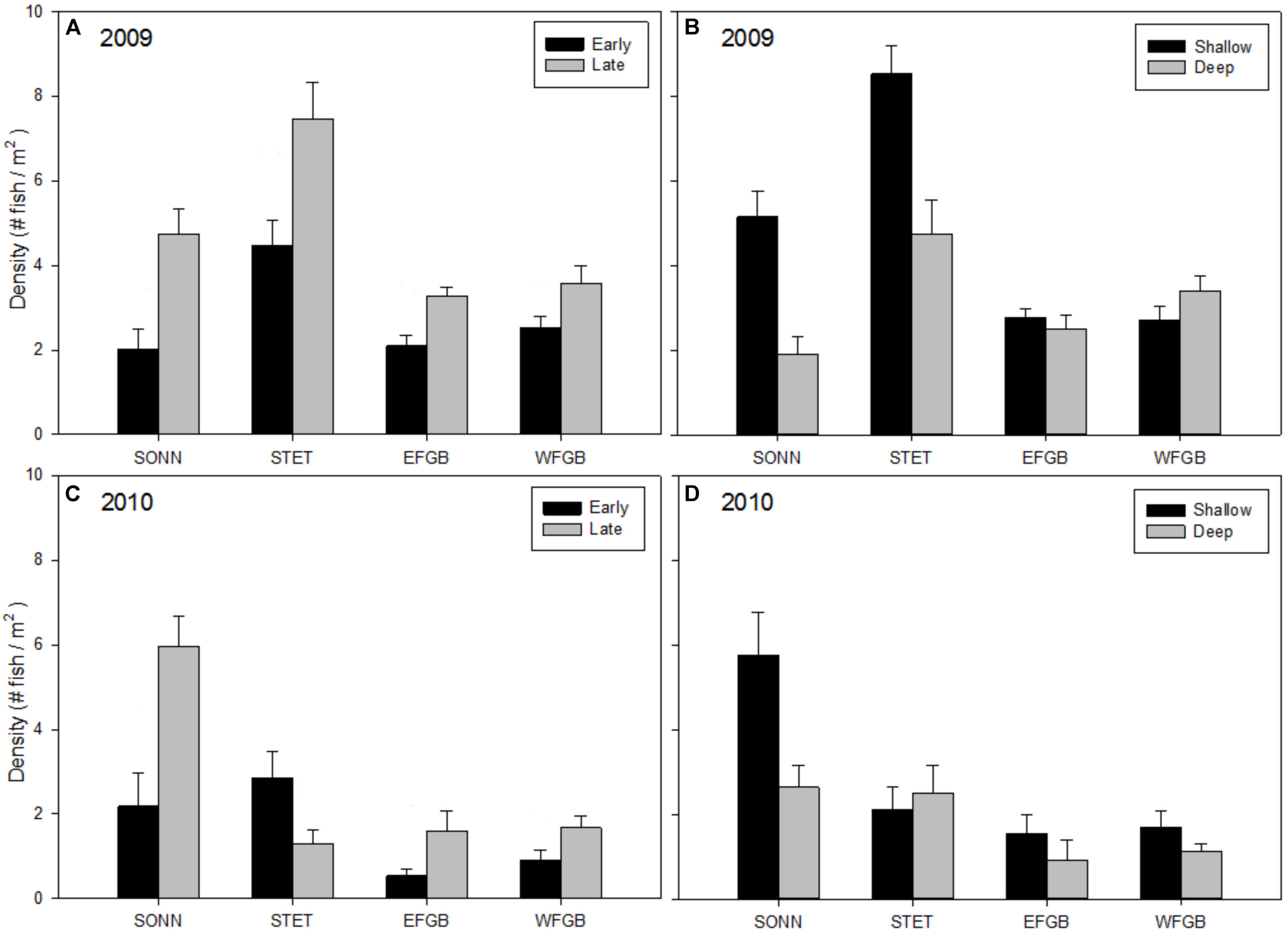

FIGURE 3 | Mean densities of juvenile reef fish (all species pooled) observed at each reef for 2009 **(A,B)** and 2010 **(C,D)**. Results were compared across seasons **(A,C)** and depth zones **(B,D)** for each year of the study, and error bars represent one standard error of the mean. Significant differences among study sites (if applicable) are denoted by uppercase letters in panel **(A)** for 2009 and **(C)** for 2010.

particularly evident at the mid-shelf reefs (SONN, STET) where certain tropical species observed as juveniles in 2009 were either absent (e.g., blue chromis *Chromis cyanea*, ocean surgeon *Acanthurus bahianus*, queen angelfish *Holacanthus ciliaris*) or present at markedly lower densities (e.g., bluehead wrasse, dusky damselfish *Stegastes adustus*, French angelfish *Pomacanthus paru*). A notable shift was also observed in juvenile species composition toward sub-tropical/temperate recruits, in particular, the cocoa damselfish (*Stegastes variabilis*), which represented a combined 29% of the juvenile fishes enumerated at the mid-shelf reefs in 2009 but accounted for nearly 60% of all juveniles observed in 2010 (and over 74% at SONN). In 2009, no significant difference in mean H' was detected for juvenile fishes among study reefs, although mean H' was significantly higher during the late sampling season (ANOVA, $P < 0.001$) and in the shallow depth zone (ANOVA, $P < 0.01$). In 2010, mean H' differed among reefs (ANOVA, $P < 0.001$), and diversity of juvenile fishes was significantly lower at SONN than at the other three reefs surveyed (Tukey's HSD, $P < 0.05$). However, no significant seasonal or depth-related effects on mean H' were detected in 2010. For adult fishes, H' remained fairly consistent between years (**Figures 6A–D**). Significant differences in H' were found among reefs in both 2009 and 2010, and H' of adult fishes at the two shelf-edge reefs (EFGB, WFGB) was significantly higher than at the two mid-shelf reefs (SONN, STET) for both years of the study (Tukey's HSD, $P < 0.05$). In 2009, H' was also significantly higher in the shallow depth zone at SONN and STET (ANOVA, $P < 0.01$), but was relatively similar between depth zones at EFGB and WFGB. For adult fishes, H' was also statistically similar between depth zones on both mid-shelf and shelf-edge reefs in 2010.

Microhabitat Selection

The effects of habitat complexity (i.e., rugosity) on overall reef fish density and H' were examined during the first year of surveys (2009) and the influence of rugosity on fish distribution differed between mid-shelf and shelf-edge reefs (**Figures 7A,B**). At the mid-shelf reefs (SONN, STET), there was a positive relationship between rugosity and fish distribution; linear regressions of rugosity against density and diversity (H') were both significant

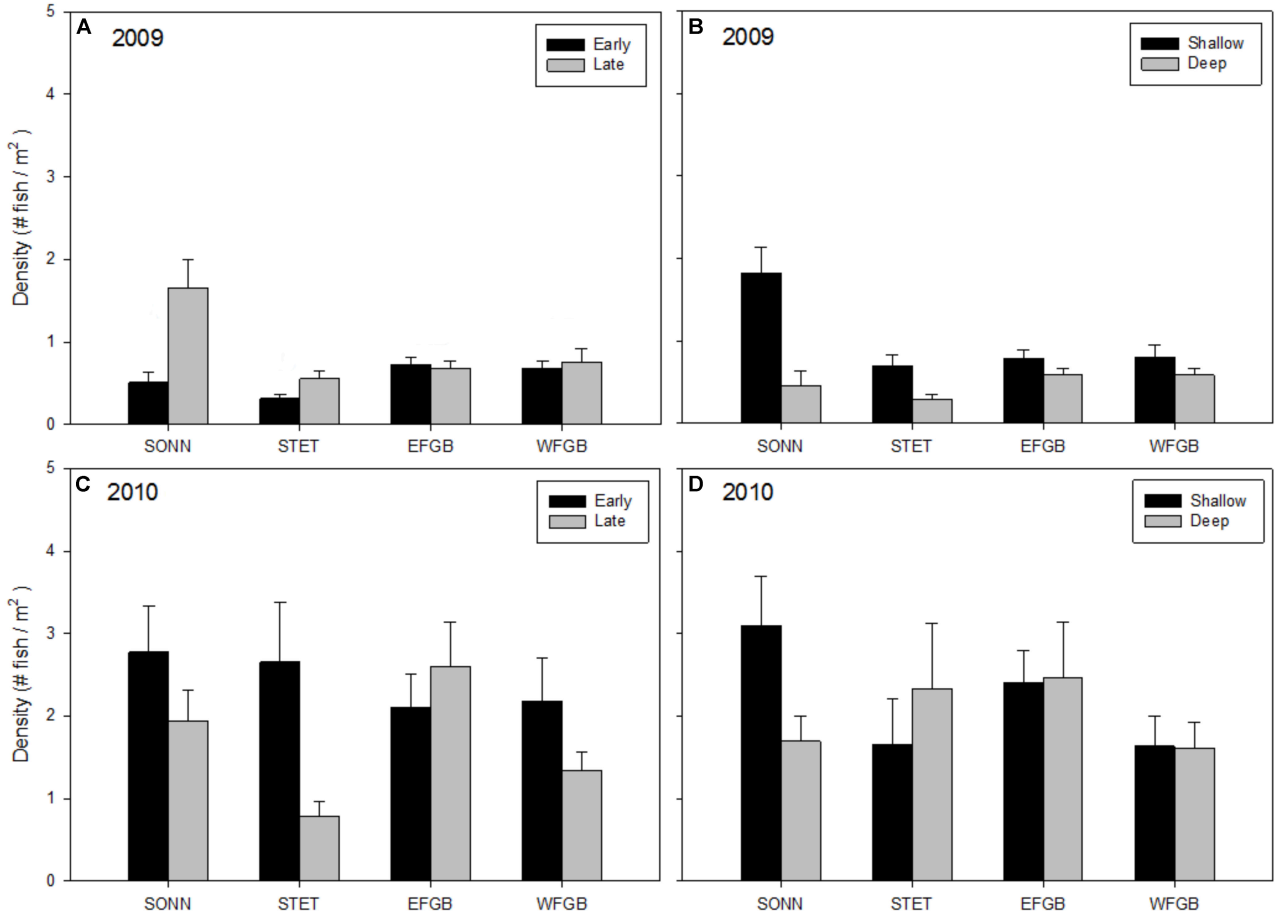

FIGURE 4 | Mean densities of adult reef fish (all species pooled) observed at each reef for 2009 **(A,B)** and 2010 **(C,D)**. Results were compared across seasons **(A,C)** and depth zones **(B,D)** for each year of the study, and error bars represent one standard error of the mean. Significant differences among study sites are denoted by uppercase letters in panel **(A)** for 2009. No significant differences among study sites were detected in 2010.

($P < 0.001$). No significant relationships between rugosity and reef fish density or diversity were detected within the shelf-edge reefs ($P = 0.524, 0.361$).

Comparison of Assemblage Structure Among Reefs

Density data for juvenile and adult reef fishes were analyzed separately both by survey year and by sampling season within each year using non-metric MDS ordination (**Figure 8**). Stress coefficients for all MDS models were below the experimental cutoff of 0.20 with the exception of the two juvenile models from 2009, which showed slightly higher values (0.22 for both sampling seasons). In general, MDS models with stress coefficients ranging from 0.20 to 0.30 are considered marginal for interpretation, particularly for ordinations based on a small to moderate sample size (<50 data points) (Clarke and Warwick, 2001). However, because both MDS models in 2009 were based on relatively large samples (124 and 127 transects, respectively), the juvenile models from this year were considered acceptable for analysis.

Overall, MDS plots of both juvenile and adult data revealed remarkably consistent distinctions in species composition between the mid-shelf reefs (SONN, STET) and the shelf-edge reefs (EFGB, WFGB), but considerable overlap between the two sites within a given reef type (**Figure 8**). Pairwise ANOSIM permutation procedures were used to test the significance of these apparent groupings, and results from these pairwise tests were largely in agreement with the spatial ordinations observed in our MDS models. For both juvenile and adult fishes over the two years of surveys, all pairwise comparisons between different (i.e., mid-shelf vs. shelf-edge) reef types revealed significant differences in the community structure of fishes associated with each reef type (ANOSIM, $P < 0.001$). In contrast, few significant differences in community structure were found in pairwise comparisons within a given reef type (e.g., between two mid-shelf reefs), particularly for adult fishes.

In 2009, no significant differences in juvenile community composition were detected between the two shelf-edge reefs (EFGB, WFGB) for either sampling season (ANOSIM, $P > 0.05$). Community composition of juvenile fishes at the two mid-shelf reefs (SONN, STET) differed significantly during the early

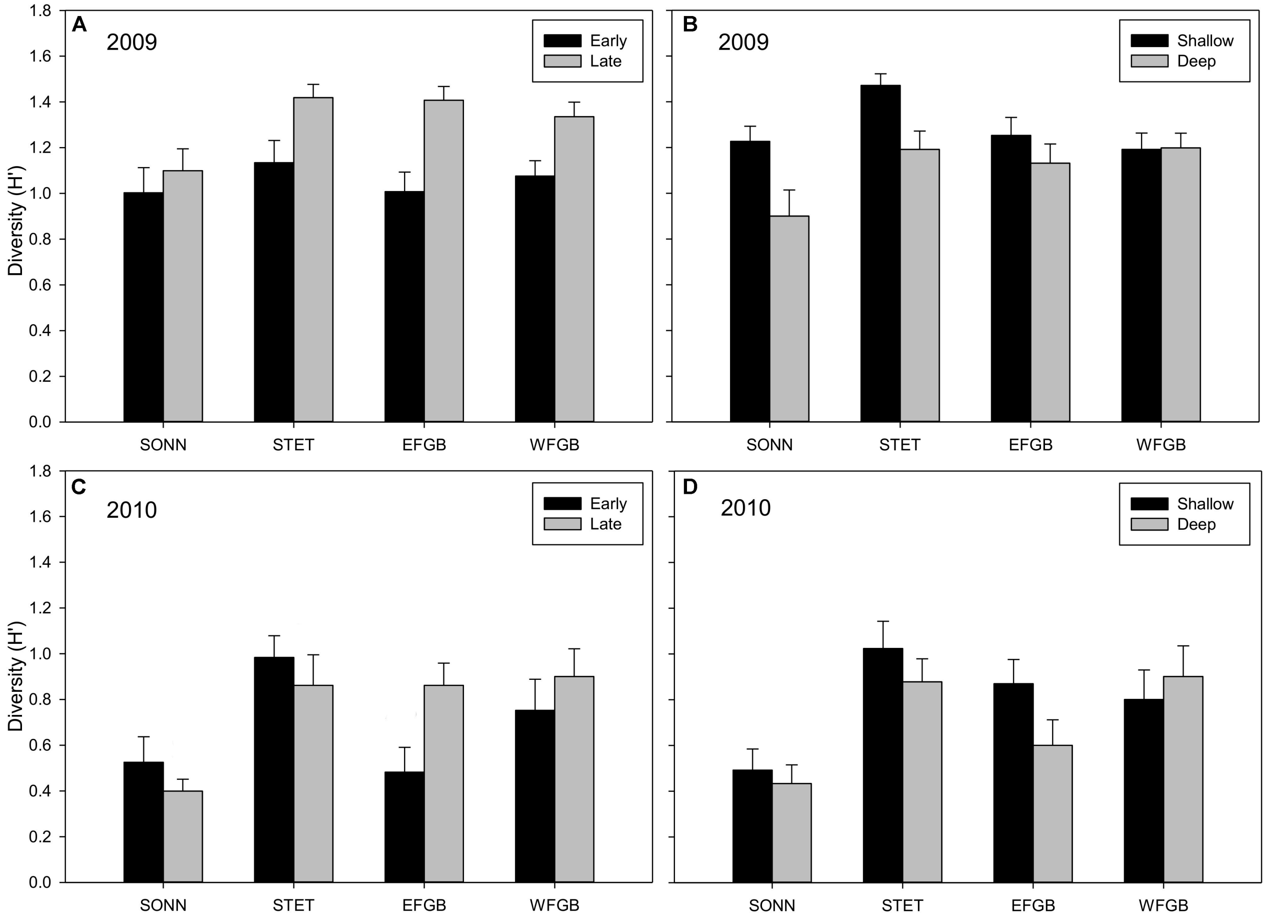

FIGURE 5 | Mean Shannon–Wiener diversity estimates (*H′*) for juvenile reef fish observed at each reef in 2009 **(A,B)** and 2010 **(C,D)**. Results were compared across seasons **(A,C)** and depth zones **(B,D)** for each year of the study, and error bars represent one standard error of the mean. Significant differences among study sites are denoted by uppercase letters in panel **(C)** for 2010. No significant differences among study sites were detected in 2009.

sampling season (ANOSIM, $R = 0.242$, $P < 0.001$) but was similar during the late sampling season ($P > 0.05$). Juvenile assemblages at both mid-shelf reefs during the early season were numerically dominated by three species; bluehead wrasse *Thalassoma bifasciatum*, cocoa damselfish, and purple reef fish *Chromis scotti*, and differences in the relative abundances of these species at SONN and STET were responsible for structuring the majority (61%) of the dissimilarity in juvenile assemblage structure within the mid-shelf reef type during early season surveys (SIMPER). No significant within-reef type differences were found for adult fishes in 2009; pairwise comparisons of adult assemblage structure showed similar species compositions between the two mid-shelf reefs (SONN, STET) and between the two shelf-edge reefs (EFGB, WFGB) during both early and late sampling seasons (ANOSIM, $P > 0.05$). In 2010, findings closely resembled those from 2009, with one notable difference. While both age classes at the two shelf-edge reefs (EFGB, WFGB) were again similar in species composition for each sampling season (ANOSIM, $P > 0.05$), significant differences in assemblage structure between the two mid-shelf reefs (SONN, STET) were observed for both juveniles and adults during the early sampling season in 2010 (ANOSIM, $R_{Juv} = 0.170$, $P < 0.001$; $R_{Adult} = 0.212$, $P < 0.01$). The majority (53%) of early season dissimilarity in adult assemblage structure between SONN and STET was attributed to differences in the relative abundance of the seaweed blenny *P. marmoreus* (SIMPER). The effects of this event were short-lived and by the late 2010 sampling season, seaweed blenny densities had returned to 2009 levels and adult assemblages within the low-diversity reef type (i.e., SONN, STET) were once again similar ($P > 0.05$).

Juvenile and Adult Species Presence Within Each Reef

For both survey years, 85–100% of fish species observed as juveniles at the two shelf-edge reefs (EFGB, WFGB) were also represented in the adult assemblages (**Figures 9A,B**). In 2009, just three species at EFGB and two at WFGB were present only as juveniles, and in 2010, there were no such species at EFGB and only one at WFGB. However, at the two mid-shelf reefs, the number of species observed only as juveniles was markedly higher (9 species at SONN and 12

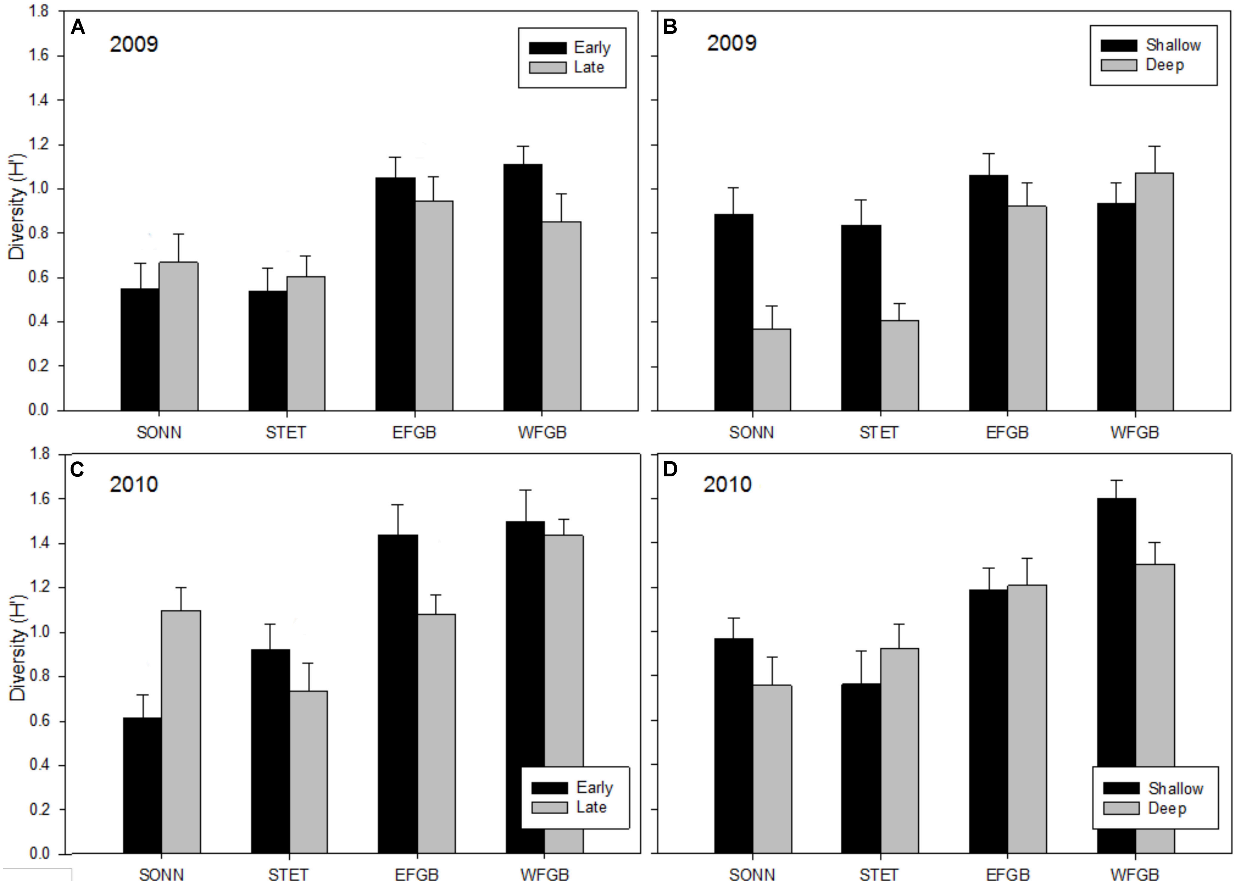

FIGURE 6 | Mean Shannon–Wiener diversity estimates (H') for adult reef fish observed at each reef in 2009 **(A,B)** and 2010 **(C,D)**. Results were compared across seasons **(A,C)** and depth zones **(B,D)** for each year of the study, and error bars represent one standard error of the mean. Significant differences among study sites are denoted by uppercase letters in panel **(A)** for 2009 and **(C)** for 2010.

at STET in 2009; 14 species at SONN and 7 at STET in 2010) (**Figure 9**). During each year of surveys, 27–61% of all juvenile fish species recruiting to each mid-shelf reef were never observed as adults, and pairwise comparisons between age classes at both mid-shelf reefs (SONN, STET) revealed significant differences in species presence between the adult fish assemblage and juvenile recruits (ANOSIM, $P > 0.05$). Examples of taxa observed at mid-shelf reefs as juveniles but not adults included cherubfish *Centropyge argi*, painted wrasse *Halichoeres caudalis*, sailfin blenny *Emblemaria pandionis*, yellowtail damselfish *Microspathodon chrysurus*, and *Sparisoma* spp. In contrast, only 0–13% of juvenile fish species recruiting to shelf-edge reefs over each survey year were never observed as adults, and pairwise within-reef comparisons revealed similar juvenile and adult species presence at both EFGB and WFGB (ANOSIM, $P < 0.05$).

DISCUSSION

Recruitment to both mid-shelf and shelf-edge reefs showed a strong seasonal component, with higher juvenile density and assemblage diversity (H') observed during the late (August 1–October 1) season at all reefs in 2009 and all but STET in 2010, supporting the early fall recruitment peak previously suggested for coral reef fishes in the northwestern GOM (Rooker et al., 1997). The period of increased juvenile density observed in our study corresponds with a period of elevated mean sea surface temperature and annual peak eddy activity in the region (Limer et al., in review), and similar increases in recruitment have been widely observed in other coral reef systems during the summer months when oceanographic conditions are optimal for larval growth and survival (e.g., Doherty and Williams, 1988; Adjeroud et al., 1998; Chittaro and Sale, 2003). Seasonality in recruitment is generally most pronounced on high-latitude reefs occupying tropical-temperate transition zones (Doherty, 1991; Beck, 2015; Komyakova and Swearer, 2019), which is the case for both the mid-shelf and shelf-edge reefs in our study. However, the most pronounced late-season increases in juvenile density for both survey years occurred at the two mid-shelf reefs (SONN, STET), where oceanographic conditions are influenced by seasonal coastal processes [e.g., freshwater input from the Mississippi-Atchafalaya River System (MARS) is higher during late spring/early summer] and water temperatures are cooler

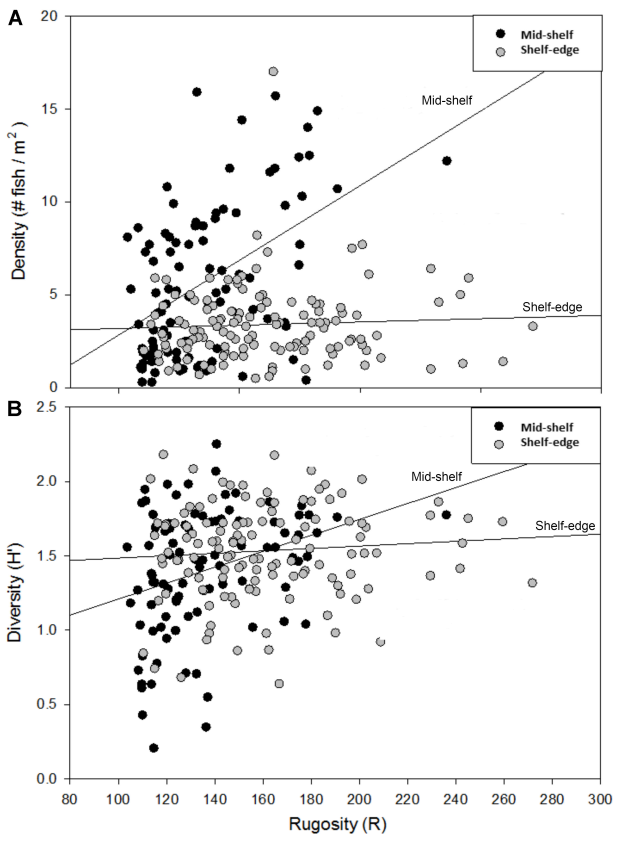

FIGURE 7 | Relationship between habitat rugosity and the density **(A)** and diversity **(B)** of reef fishes (both age classes pooled) observed at mid-shelf and shelf-edge reefs during the 2009 study year. Trend lines represent the linear regression of transect density and diversity (*H′*) against transect rugosity within each bank type (mid-shelf vs. shelf edge). Relationships were statistically significant for both density (r^2 = 0.23) and diversity (r^2 = 0.10) at mid-shelf reefs, while neither relationship was significant at shelf-edge reefs.

during the winter months, potentially restricting the time frame of successful recruitment (see Rezak et al., 1990).

Vertical zonation of coral and reef fish community structure is well documented (Edmunds and Leichter, 2016; MacDonald et al., 2016). Still, depth-related differences in reef fish density and diversity were primarily observed at the mid-shelf (low coral diversity) reefs, with greater juvenile and adult densities observed at shallow depths near the reef crest. Perhaps this is not surprising due to the fact that hermatypic corals are primarily restricted to the shallower portions of the reef crest at both SONN and STET, with deeper areas characterized by less complex bedrock outcroppings and benthic algae. In contrast, coral coverage was high and more ubiquitous across both depth zones at the two shelf edge reefs (EFGB, WFGB), which may explain the relative similarity in reef fish density and diversity across the two depth zones sampled at these reefs. Still, our surveys were limited to the upper 30 m of the water column and it is likely that shifts in reef fish community structure may have been more evident at mesophotic depths (>30 m).

Juvenile density on both reef types displayed considerable inter-annual variability, with significantly reduced density and *H′* observed in 2010. Previous studies on coral reef fishes have documented declines in the density and condition of newly settled recruits in response to cooler water temperatures (e.g., Sponaugle et al., 2006), and it is possible that poor recruitment in 2010 may have been influenced by the exceptionally cold preceding winter, which caused regional sea surface temperatures to remain 2–4°C below 2009 values until mid-May (Texas Automated Buoy System; TABS, Buoy V). Although reef fish assemblages in the northern GOM are composed of both tropical and sub-tropical/temperate taxa, decreased recruitment in 2010 appeared to be driven primarily by poor representation of tropical recruits, which may be particularly sensitive to sub-optimal thermal conditions (Sponaugle et al., 2006). The greatest inter-annual differences in recruitment occurred at the two mid-shelf reefs (SONN, STET) where winter water temperatures are lowest, and at each of these reefs in 2010, several tropical species observed as juveniles in 2009 were either absent or present at markedly lower densities. This was accompanied by a notable shift in juvenile species composition toward sub-tropical/temperate recruits, in particular, the cocoa damselfish, which dominated juvenile assemblages at mid-shelf reefs in 2010 relative to 2009 (60% of all juveniles observed in 2010). Considering that congeneric juveniles (*Stegastes* spp.) have been shown to aggressively inhibit recruitment of other tropical reef fish species (Risk, 1998), the exceptional success of cocoa damselfish at SONN in 2010 may have contributed to the seemingly anomalous increase in juvenile density, but significantly lower juvenile diversity, observed at this reef. Nevertheless, natural variability in recruitment is common in reef fishes (Sponaugle, 2015) and observed inter-annual differences may simply be a function of inherent stochasticity in the remote production and planktonic delivery of larval recruits. Indeed, oceanographic conditions in 2009 were likely more favorable for larval subsidy from Campeche Bank and Yucatan Shelf reefs to reach the northern GoM as the Loop Current pushed further northward, with eddies produced from this mesoscale feature crossing over the study reefs with greater frequency in 2009 relative to 2010 (Limer et al., in review). It is also important to note that the Deepwater Horizon oil spill occurred in the northern GOM in May of 2010, potentially explaining the decrease in juvenile densities observed in that year. However, given the lack of geographical overlap between the study reefs and the oil spill footprint, it is likely that the impact of the spill on fish density and community structure at the study sites was minimal (Johnston et al., 2013). Invasive Indo-Pacific lionfish (*Pterois* sp.) were also first observed at Sonnier Bank in fall of 2010; however, individuals were not documented at the other reefs until 2011 (Johnston et al., 2013). While potential negative effects of lionfish on reef fish community structure are well documented, it is unclear to what extent lionfish may have affected juvenile community structure and/or densities at our study reefs in 2010.

The assemblage structure of adult reef fishes in our study appeared to be fairly resilient to short-term fluctuations in recruitment, remaining consistent within and distinct between the two reef types. *H′* of adult fishes was consistently highest

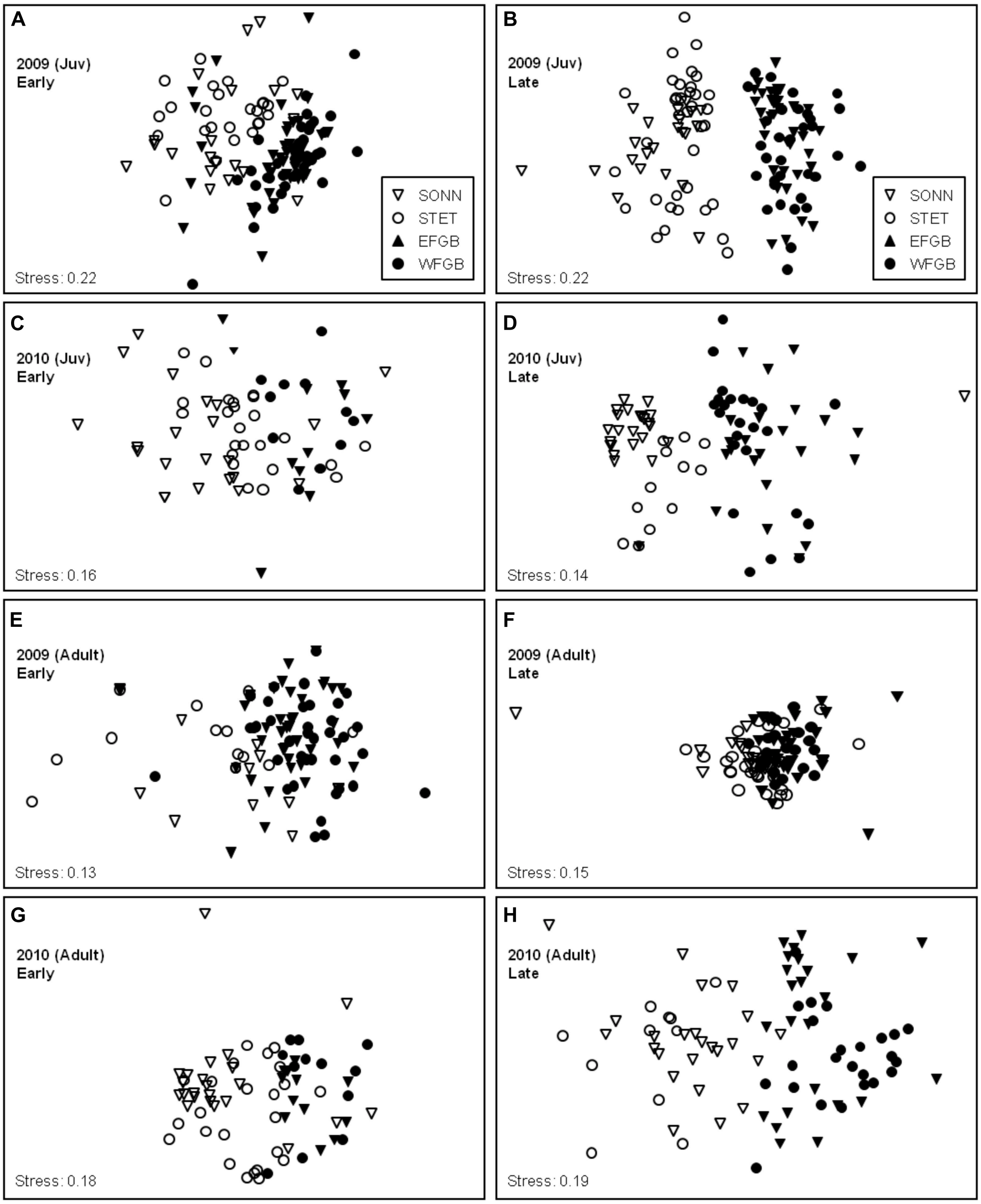

FIGURE 8 | Non-metric multidimensional scaling (MDS) ordinations of juvenile **(A–D)** and adult **(E–H)** species density data for all four study reefs for 2009 **(A,B,E,F)** and 2010 **(C,D,G,H)**. Early and late sampling seasons were analyzed separately within each study year for both age classes. Symbol legends are shown in panels **(A)** and **(B)**. Replicates from low diversity (mid-shelf) study sites (SON and STET) are represented by open symbols (▽, ∘, respectively) and high diversity (shelf edge) study sites (EFGB and WFGB) are represented by filled symbols (▼, •, respectively).

at the two shelf-edge reefs (EFGB, WFGB) over both years of surveys, and MDS ordination revealed distinct differences in species composition between mid-shelf and shelf-edge reefs, but little to no separation within either reef type. Similar inshore-offshore gradients in diversity and species composition have been widely reported for reef fishes inhabiting tropical-temperate transition zones (e.g., Cheal et al., 2012), and cross-shelf gradients in diversity are often accompanied (or driven) by clear shifts from sub-tropical/temperate reef fish communities inshore (i.e., SONN, STET) to primarily tropical, coral reef-associated assemblages near the shelf edge (i.e., EFGB, WFGB), where the effects of winter cold fronts and terrigenous influences (e.g., sedimentation, nutrient enrichment) are buffered by deeper water and exposure to warm oceanographic currents (Dennis and Bright, 1988; Malcolm et al., 2010). These conditions also promote coral growth, and similar patterns of diversity between corals and fishes (higher fish diversity associated with higher coral diversity) consistent with those observed in the current study

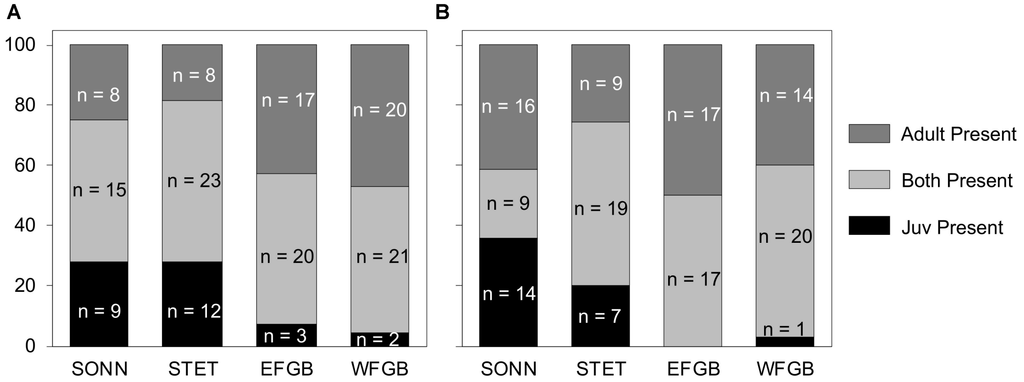

FIGURE 9 | Percentage of reef fish species present only as juveniles (black), only as adults (dark gray), and as both adults and juveniles (light gray) within the two low diversity (mid-shelf) reef sites (SONN, STET) and the two high diversity (shelf edge) reef sites (EFGB, WFGB) for 2009 **(A)** and 2010 **(B)**. The raw species counts (*n*) within each category at each reef type are also given.

have been noted in multiple geographic regions (Bellwood and Hughes, 2001; Connolly, 2005; Burgess et al., 2010). Still, it has been widely debated whether cross-shelf gradients in reef fish community structure are established post-settlement as a direct result of changes in the benthic coral community (e.g., Adjeroud et al., 1998) or whether they are simply produced by cross-shelf gradients in recruitment (James et al., 2002; Burgess et al., 2010).

Similar to studies conducted in other regions (reviewed Burgess et al., 2010), natural correlations between reef type and distance offshore prevent us from definitively separating the effects of shelf position and coral diversity; however, the current study is also unique from many previous efforts (see James et al., 2002) in that our life stage-specific data allowed for the direct comparison of juvenile settlement patterns with mature fish assemblages at reefs occupying different shelf positions. Distinct differences in the composition of juveniles observed between the mid-shelf reefs (SONN, STET) and the shelf-edge reefs (EFGB, WFGB) indicates that an inshore-offshore recruitment gradient may exist for reef-dependent fishes in the northern GOM, likely established by decreased larval delivery or survivorship closer to the coast (see Roberts, 1991), where pelagic conditions are often strongly influenced by cold, low-salinity, nutrient-rich input from MARS (Rezak et al., 1990; reviewed in D'Sa and Dimarco, 2009). It is also possible that regional patterns of fish diversity are influenced by increased exposure of the shelf-edge reefs (EFGB, WFGB) to tropical larvae originating from the southern GOM or Caribbean Sea (Rezak et al., 1990; Schmahl et al., 2008; Kitchens et al., 2017). However, the notable distinction between juvenile and adult assemblages observed within both mid-shelf reefs (SONN, STET) also suggests that the species composition of mature fish communities associated with this reef type may not directly resemble the initial species composition of settlers. Therefore, while the supply of larval recruits to reefs in the northern GOM is likely influenced to some extent by shelf position, recruitment limitation may not be the primary determinant of adult community structure throughout this system, and initial patterns of settlement may be modified to a considerable extent by intrinsic characteristics of the reefs.

Habitat characteristics have been widely implicated in determining the local abundance and diversity of coral reef fishes in other regions (e.g., Grober-Dunsmore et al., 2008; Bejarano et al., 2015), and the relative influence of habitat-mediated interactions on juvenile survivorship and distribution is generally strongest when densities of recruits are at or near carrying capacity (see Beukers and Jones, 1998; Almany, 2003). Several studies have reported that while pre-settlement processes (i.e., larval supply and dispersal) appear to be the primary determinants of community structure on reef types characterized by high rugosity and extensive coral coverage (e.g., EFGB, WFGB), post-settlement processes (e.g., competition, predation) may be more critical on reef types where habitat complexity is low and refuge spaces are limited (e.g., SONN, STET) (Benfield et al., 2008). Predation is the primary agent of post-settlement mortality for reef fishes (Almany and Webster, 2006; Hixon, 2015), and at both SONN and STET, the large proportion (20–36%) of species observed as juveniles but not adults indicates that mortality rates of new recruits to these mid-shelf reefs may be substantial. Intense local predation on coral reefs can significantly reduce assemblage diversity by eliminating rarer species of recruits from persisting into the adult assemblage (e.g., Heinlein et al., 2010), and this may explain the consistently lower diversity of adult fishes observed at the two mid-shelf reefs (SONN, STET), as well as the strong associations between fish distribution and habitat rugosity (i.e., prey refuges). It is also possible that suboptimal physicochemical conditions (e.g., temperature, salinity) on mid-shelf reefs during cooler months contribute to greater overwinter mortality and vulnerability to predation for tropical species. In contrast, little evidence of post-settlement regulation was detected on the shelf-edge reefs (EFGB, WFGB), where the low densities and even spatial distribution (i.e., weak habitat associations) observed for juvenile fishes indicate levels of recruitment well below saturation. Adult reef fish assemblages at both EFGB and WFGB showed strong resemblance to the species composition of juvenile assemblage and well over 90% of all species recruiting to each reef over the course of the study appeared to successfully persist as mature populations, suggesting that community structure on these reefs is determined largely at time of settlement.

Both shelf-edge reefs in the current study (EFGB, WFGB) appeared to maintain stable resident fish assemblages that were more consistent and predictable in community structure than those observed at the mid-shelf reefs (SONN, STET). One possible explanation for this incongruity is a high rate of self-recruitment at EFGB and WFGB due to the extreme biogeographic isolation and regional oceanographic conditions along the outer continental shelf (Cowen et al., 2006; Schmahl et al., 2008; Hickerson et al., 2012). The closest coral reef-associated fish assemblages upstream from EFGB and WFGB occur on the offshore reefs of Campeche Bank (approximately 700 km to the south; **Figure 1**). Under ideal oceanographic conditions, predicted transport time (Lugo-Fernández, 2006) from this region would be expected to exceed the reported planktonic larval duration (PLD) for many of the dominant species in our surveys of the EFGB and WFGB (Victor, 1986; Wellington and Victor, 1989), and considering that ecologically relevant scales of connectivity for reef fish populations in the region are typically on the order of 10 to 100 km (Cowen et al., 2006), the contribution of larvae derived from the Caribbean is likely to be minimal. Nevertheless, the degree to which larval contribution from the southern GoM or Caribbean Sea affects juvenile recruitment (density and assemblage structure) at northern GOM reefs is likely temporally variable and dependent on the position of the Loop Current and associated eddies (see Kitchens et al., 2017; Limer et al., in review). This may explain the greater density and diversity of juvenile recruits observed in 2009 compared to 2010 across all reefs, as the Loop Current penetrated farther northward in 2009 (Rooker et al., 2013; Limer et al., in review).

The only other potential source of larval contribution to EFGB and WFGB is the extensive network of petroleum platforms spanning the northern GOM, but because the major currents approaching the edge of the continental shelf are oceanic in origin, the majority of these platforms are hydrologically downstream from EFGB and WFGB (Lugo-Fernández et al., 2001). Furthermore, surveys conducted on both mid-shelf and shelf-edge platforms have indicated that the diversity of reef fishes recruiting to these structures is markedly depleted relative to natural reefs in the region (Sonnier et al., 1976; Rooker et al., 1997; Voss et al., 2014), and therefore, it is likely that petroleum platforms generally act as a sink rather than a source of tropical recruits (see Lugo-Fernández et al., 2001). Given the low likelihood of EFGB or WFGB receiving significant subsidies of larval recruits from remote source locations, fish communities at these two shelf-edge reefs must be largely replenished through local production, which is possible given that oceanographic conditions in this region are generally favorable for larval retention (Lugo-Fernández et al., 2001).

If resident fish assemblages at our two shelf-edge coral reefs (EFGB, WFGB) are primarily self-replenishing, it is likely that larval subsidies originating from these reefs may also be largely responsible for the replenishment and regional persistence of many tropical species across the continental shelf (Dennis and Bright, 1988; see Malcolm et al., 2010). However, the magnitude and inshore extent of larval export from the EFGB and WFGB can be expected to vary from year to year as a function of regional oceanographic conditions in the GOM (Lugo-Fernández et al., 2001), and this may have contributed to observed interannual variability in the composition of newly recruited juveniles at our two mid-shelf reefs (SONN, STET). By chance, our surveys appeared to occur over one "good" recruitment year (2009) with favorable oceanographic conditions and one "poor" recruitment year (2010) where lower sea surface temperatures and increased freshwater inflow likely had a negative impact on the delivery and survivorship of pelagic larvae closer to the coast. Both mid-shelf reefs in 2010 showed decreased juvenile diversity and a marked shift in recruitment composition toward species commonly observed on platforms and nearshore reefs (e.g., cocoa damselfish, seaweed blennies) (Rooker et al., 1997; Dance et al., 2011), suggesting that in years or seasons when conditions are unfavorable, tropical recruits originating from shelf-edge coral reefs may be poorly represented across the continental shelf, and our mid-shelf reefs (SONN, STET) may receive a greater proportion of sub-tropical/temperate recruits from other mid-shelf reefs or production platforms. Such spatiotemporal variability in both the magnitude and source of recruitment is typical of coral-reef associated fishes and fluctuations in recruitment of tropical reef fishes have been widely attributed to stochastic oceanographic and climatic conditions in other regions (e.g., Victor, 1986; Doherty and Williams, 1988; Fontes et al., 2016; Shulzitski et al., 2016). However, results from the current study also suggest that the reef fish assemblages associated with mid-shelf and shelf-edge reefs in the northwestern GOM may have sufficient stabilizing mechanisms in place to facilitate recovery from anomalous recruitment events. The strong, reef type-specific differences in community composition observed throughout the study indicate that mid-shelf and shelf-edge coral reefs may fill different functional roles for demersal fishes in the northwestern GOM.

DATA AVAILABILITY STATEMENT

Data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

Ethical review and approval was not required for this animal study in accordance with the local legislation and institutional requirements. No animals were sampled or handled as part of this project.

AUTHOR CONTRIBUTIONS

All authors designed the study and contributed to the final version of the manuscript. LW, MD, and JR performed the sampling surveys and wrote the manuscript. LW analyzed the data.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00152/full#supplementary-material

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frontiers in Marine Science

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Will the Florida Big Bend Area Become the Next Gulf of Mexico Reef Tract?

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INTRODUCTION

Today, the best-developed coral reefs in the continental United States occur in the Florida Reef tract along some 580 km from the Dry Tortugas to the southeast coast of Florida between 24° and 26° N (**Figure 1A**; Morey et al., 2017; Cummings et al., 2018). These long-lived communities encrust and have built upon earlier structures deposited during the Pleistocene and Holocene epochs (Shinn and Lidz, 2018). Together, they represent the only barrier reef system in North America, and as such, have received management protection as part of the Florida Keys National Marine Sanctuary (FKNMS) since 1990. Along Florida's west coast, however, examples of actively accreting reef communities are comparatively rare, being restricted to the mesophotic reefs (40–150 m depth) of Pulley Ridge, located to the west-northwest of the FKNMS (Reed et al., 2019), and the shallower, euphotic reefs of the Florida Middle Grounds (25–45 m depth), located further north along the West Florida Shelf (WFS) at 28° N (Jaap, 2015). To a large extent, these west coast Florida ecosystems occur where they do because of warm-water delivery by the Loop Current, which brings oligotrophic water from the Caribbean into the Gulf of Mexico (GoM) (Cummings et al., 2018). Outside of this influence, actively accreting reef communities give way to more sparsely populated live bottom, characterized by cold-tolerant scleractinian and soft corals, sponges, hydrozoans, barnacles, seagrasses, and macroalgae (Jaap, 2015; Morey et al., 2017).

In the region of the WFS known as "The Big Bend," the carbonate platform is covered by a thin veneer of shifting sand, expansive seagrass meadows and abundant hard bottom (Continental Shelf Associates, Inc. and Martel Laboratories, Inc., 1985). Here, low relief rocky outcrops ($\sim$1 m) support cold-hardy corals in the genera *Oculina*, *Siderastrea*, *Solenastrea,* and *Cladocora* (**Figure 1B**). These non-accreting species achieve limited densities, tend to recruit and grow slowly, and are limited by cold winter temperatures, sand burial, and competition with benthic macroalgae (i.e., *Sargassum*; Beger et al., 2014; Tuckett et al., 2017; **Figure 1C**).

TROPICALIZATION

Regional environmental conditions in the Big Bend are dominated by atmospheric forcing and watershed input, as the wide continental shelf tends to limit oceanic upwelling, waves and tides, and seasonal discharge from the Apalachicola and other rivers delivers vast freshwater plumes high in chromophoric dissolved organic matter (CDOM), nutrients, tannins and chlorophyll a (Morey et al., 2017). Presently, the subtropical latitude and frequency of winter cold fronts appear to be keeping winter minimum temperatures below the 18°C threshold critical to coral

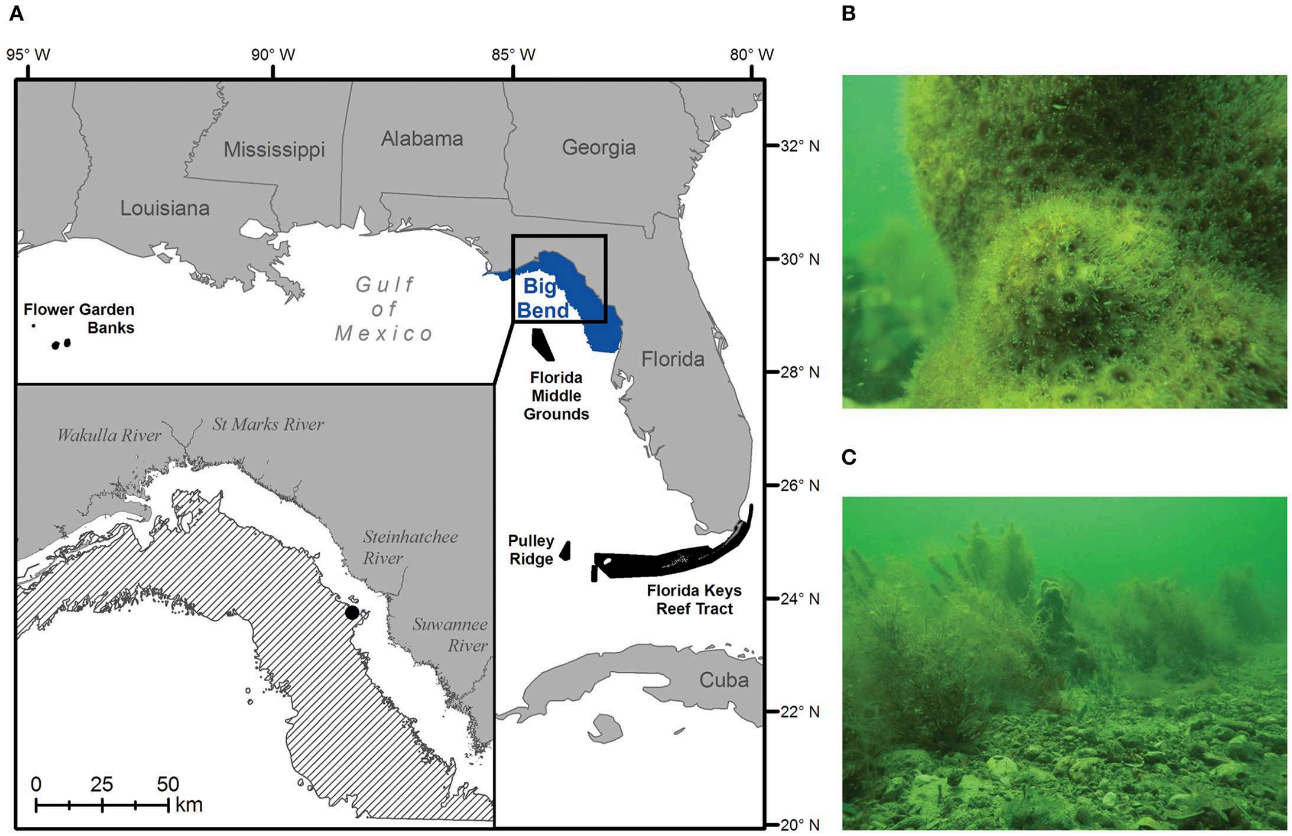

FIGURE 1 | The 0–20 m (**A**: blue polygon) and 5.5–18 m (**A** inset: black diagonal bars) depth bands of Big Bend region of Florida, USA in the northern Gulf of Mexico. Black polygons denote potential larval sources of hermatypic coral species to the area—in decreasing order of importance: the Florida Middle Grounds, Pulley Ridge, Florida Keys Reef Tract, and the Flower Garden Banks. Scenes of current hard-bottom communities dominated by **(B)** cold-tolerant scleractinian corals (shown: *Solenastrea* sp.), and **(C)** soft corals and attached macroalgae (shown: *Sargassum* sp. and *Caulerpa* spp.), were taken at 6.7 m depth off Steinhatchee, Florida on April 13, 2018 (**A** inset; black circle).

reef development (Buddemeier et al., 2004; Precht and Aronson, 2004). However, temperature minimums are becoming less severe along the northern coast of the GoM as reflected by the expansion of black mangroves into salt marsh habitats of the northern Gulf (Osland et al., 2013). Similarly, formerly rare species of tropical snappers (Lutjanidae) and parrot fishes (Labridae) are now commonly found in shallow seagrass meadows of the northern Gulf (Fodrie et al., 2010). In addition, coral species, such as *Acropora palmata,* have been recorded in the Flower Gardens reefs of the northwestern GoM (Precht and Aronson, 2004) at a latitude and depth previously unknown. Together, the occurrence of these taxa reflects the tropicalization of the GoM (Vergés et al., 2014; Heck et al., 2015). Tropicalization, a process by which species formerly restricted to tropical waters expand their ranges and become resident in temperate waters is a global phenomenon that follows the warming of the world's oceans (Vergés et al., 2014; Hyndes et al., 2016). This phenomenon is exemplified by global changes in coral distributions, in which coral recruitment is shifting poleward at the same time it is declining in equatorial regions (Price et al., 2019).

GoM CLIMATE CHANGE PREDICTIONS

Gulf surface water temperatures are predicted to rise by more than 2°C by the end of this century—this despite a 20–25% reduction in the Loop Current (Liu et al., 2015; Morey et al., 2017). In the Big Bend Area, where the shallow shelf restricts ocean mixing, the warming is expected to be particularly severe, with SST increases of nearly 4°C during the summer and fall (Liu et al., 2015). Moreover, increased frequency of drought conditions in the American Southeast (Pederson et al., 2012) coupled with groundwater withdrawal by growing human populations in the Suwannee River and adjacent basins will likely lead to reduced discharge of relatively cold water from springs and rivers (Hensley and Cohen, 2017), further alleviating cold stress to nearshore environments.

OUR PREDICTION

It now seems reasonable to expect that the extensive hard bottom habitats in the Big Bend region of Florida will come to support the development of coral reefs in the near future. We make this assertion for a number of reasons: (1) abundant substrate is available in the form of the largest carbonate platform in the region (Morey et al., 2017), (2) low-relief outcroppings are particularly abundant in the 10–20 m isobath (Phillips et al., 1990) where light and temperature will likely be conducive for reef accretion, (3) areas of the WFS influenced by the warm Loop Current waters currently support hermatypic reefs, and (4) extant reef systems offer a supply of potential recruits. Seasonal wind patterns (Morey et al., 2003, 2017; Todd et al., 2014) and simulated drifter experiments (Johnson et al., 2017) suggest periodic connectivity to the Florida Middle Grounds, FKNMS and to a lesser extent the Flower Garden Banks, a luxuriant reef system in the northwestern GoM (**Figure 1A**). Thus, reefs should be seeded by a supply of coral larvae spawned by the massive and plating corals (genera: *Orbicella*, *Agaricia,* and *Leptoseris*) and the branching species (*Acropora* spp.). The extent to which these species are presently delivering ill-fated propagules to the Big Bend Area is unknown, representing a critical knowledge gap in our understanding of potential range expansion in the region.

SPECIES INTERACTIONS, LANDSCAPE ECOLOGY, AND THE CHALLENGES OF CLIMATE CHANGE

Dispersal and autecology, however, are not the only factors constraining tropicalization of high-latitude reefs (Hoey et al., 2011; Beger et al., 2014; Tuckett et al., 2017). As recruits of tropical species begin to colonize the benthic seascape, their success will be influenced by competitive interactions among biogenic engineers and associated top-down controls. Temperate reefs dominated by persistent or ephemeral attached macroalgae and predominantly invertebrate (e.g., urchin) grazer guilds need to give way to low-algal, high-coral assemblages grazed by fishes (Beger et al., 2014). We argue that as temperature-mediated physiological constraints yield to climate change, urchin grazing rates will increase, recruiting herbivorous tropical fishes will facilitate coral settlement by grazing on resident seaweeds (Munday et al., 2008) and coral-dependent fishes will readily emigrate to nascent reefs as structural complexity increases. This succession will be aided by a number of mitigating factors, including: (1) macroalgal susceptibility to marine heat waves, which should become more common under future climate scenarios (Tuckett et al., 2017), (2) current overwintering populations of tropical herbivorous fishes (Fodrie et al., 2010; Prado and Heck, 2011), and (3) proximity of Big Bend outcroppings to typical nursery habitat, including seagrasses and mangroves. Indeed, the re-assembly of tropical seascapes in the Big Bend Area has been underway for some time, with accreting coral reefs representing possibly the last component of a migrating landscape.

We acknowledge that climate change will bring with it more than ameliorated thermal regimes. As others have noted, predictions of range expansion based on simple habitat projections can be flawed as they fail to consider the interactive effects of acidification, disease and unprecedented rate of environmental change (Pandolfi, 2011). Here, we argue that the Big Bend seascape may facilitate coral range expansion in the face of multiple stressors. For example, regarding acidification, which has been shown to be a significant threat to reef accretion, we anticipate the immense seagrass meadows surrounding the ledges and outcrops of hard substrate in the Big Bend (Continental Shelf Associates and Martel Laboratories, 1985; Iverson and Bittaker, 1986; Carlson et al., 2016; Yarbro et al., 2016) will provide a useful buffering capacity reducing the threat of acidification to coral larvae and recently settled coral recruits. These vast seagrass meadows will become increasingly autotrophic (Zimmerman et al., 1997; Palacios and Zimmerman, 2007) and that net carbon uptake within seagrass canopies will result in a localized drawdown of DIC, increasing oxygen levels, pH and the aragonite saturation state ($\Omega_{\text{aragonite}}$), while reducing the total CO_2, effectively buffering against acidification (Manzello et al., 2012; Unsworth et al., 2012; Hendriks et al., 2013). Analyzing the effect of this seagrass mediated drawdown, Unsworth et al. (2012) determined an 18% increase in calcification of corals in the presence of seagrass. Climate fluctuations are frequently associated with disease outbreaks, either due to increased virulence of existing pathogens or the emergence and spread of novel strains to naïve populations. The degree to which climate change has underlain the recent pandemic of Stony Coral Tissue Loss (SCTL) disease in the FKNMS is unclear (Walton et al., 2018), but the prediction that future coral range expansion will need to overcome population losses due to disease appears sound. Here again, the Big Bend Area is unique, as its primary larval sources (Florida Middle Grounds) have not yet been impacted by the pandemic and its geographic isolation from the FKMS might impede transmission via a water-borne pathogen.

MODERN EXAMPLES

While we are not alone in our prediction that corals will move poleward in response to climate change (Precht and Aronson, 2004; Greenstein and Pandolfi, 2008; Beger et al., 2014, but see Hoegh-Guldberg, 2005), we are the first to suggest a refuge for reef building species in the Big Bend Area of Florida, USA. This assertion is not without modern example as others have reported range shifts for corals during the most recent period of warming (i.e., 20–100 ybp). Precht and Aronson (2004) described species of *Acropora* beyond its historical northern limit in GoM in 2002 and Vargas-Ángel et al. (2003) found thickets of *A. palmata* along Florida's Atlantic coast in 1998 as far north as Ft. Lauderdale (26° N). We know that corals can proliferate and spread when conditions are conducive, as was seen following the introduction of the Indo-Pacific coral, *Tubastrea coccinea,* to the western Atlantic in the 1940s (Fenner, 2001) and *Oculina patagonica* to the Mediterranean Sea in 1966 (Serrano et al., 2013; Tuckett et al., 2017). Poleward shifts in native species also have been noted from Australia's east coast and South Korea (Tuckett et al., 2017). Importantly, there is mounting evidence that range extensions can be associated with phase shifts from temperate macroalgal communities to tropical coral reefs. Strong evidence for this has recently emerged from Australia's west coast (Tuckett et al., 2017) and from Japan (Yamano et al., 2011).

PALEO EXAMPLES

Modern examples mirror evidence from the paleo-record, which largely supports the controlling role that temperature plays in setting geographic limits on coral reef development (Kiessling et al., 2012). Notable range expansions, variously associated with equatorial contractions, are believed to have occurred during the Pleistocene (Pandolfi, 2011), Holocene (Kiessling et al., 2012), and Last Interglacial (Fields et al., 1993). From these, it is clear that subtropical reefs have repeatedly served as thermal refugia, and that range expansion and community reassembly has occurred repeatedly in response to climate change (Beger et al., 2014).

MANAGEMENT IMPLICATIONS

Will coral reef development occur along the WFS? As described above there are a number of factors that make coral reef development in the Big Bend Area of Florida possible over the next 30–100 years. At present, benthic monitoring programs in the region are insufficient and unable to capture such changes. To do so, more intensive work will be needed at the 5–15 m depth contours where coral recruitment will likely first be seen. Therefore, to better understand the interplay between thermal regime, larval supply and range expansions we recommend that monitoring of coral settlement (by deploying settlement tiles) and adult colonies (by benthic surveys) be coupled with detailed physicochemical monitoring of bottom-water conditions.

Throughout their geologic history coral reefs have proven to be resilient. Despite the substantial challenges of human-mediated climate change, we expect coral communities to reorganize and reassemble in a number of locations globally. Each occurrence of this process offers an opportunity to better understand how such iconic ecosystems achieved their complexity. Beyond academic inquiry, we argue that conversation should begin now regarding what active management measures could be implemented in tandem with coral reef range expansion in the GoM. For example, current paradigms do not yet include provisions for pro-active Marine Protected Area designation to secure locations for thermal refugia, or for "assisted migration," where connectivity constraints would be overcome by active transplant of corals; however, such measures could prove essential to the long-term viability of Florida coral reefs (cf. Vergés et al., 2019).

AUTHOR CONTRIBUTIONS

KH conceived, and BF and BP helped to develop, the central argument. BF prepared the figure. BF, BP, and KH contributed sections to the manuscript. All authors have revised, read, and approved the submitted version.

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The Influence of Eddies on Coral Larval Retention in the Flower Garden Banks

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While coral larval exchange among reef patches is crucial to the persistence of coral metapopulations, larval retention within patches is critical for local population maintenance. In isolated systems such as the Flower Garden Banks (FGB) of the northwest Gulf of Mexico (NW GoM), local retention is thought to play an important role in maintaining high levels of coral cover. Numerous mesoscale cyclonic and anticyclonic features (eddies) are known to spin off from the GoM's Loop Current, many of which pass over the FGB. We developed a biophysical model of coral larval dispersal (2004–2018) to investigate the extent to which eddies may facilitate coral larval exchange between and within the east and west FGB. Virtual larvae of the broadcast spawning *Orbicella faveolata* and the brooding *Porites astreoides* were released and tracked with species-specific reproductive and larval behaviors to investigate differences in retention and connectivity in corals with contrasting life histories. Eddies were detected and tracked using sea surface altimetry and compared with larval trajectories to assess the retentive characteristics of these features. Results suggest consistently high, but species-specific, levels of local retention and cross-bank connectivity in both coral species. High local retention is possible early in the dispersal of *P. astreoides*, and both species routinely experience retention due to recirculation in eddy features as late as 30 days after planulation or spawning. Eddies passing over the FGB were associated with pulses of between- and within-bank retention, indicating that larvae are capable of dispersing from and returning to coral reefs in the NW GoM. Although opportunities for retention are inherently ephemeral and stochastic due to the nature of Loop Current Eddy (LCE) shedding, eddy propagation should serve as a reliable reseeding mechanism for FGB coral populations. In particular, peaks in late summer eddy propagation correspond with mass coral spawning and may enhance larval retention. These findings support the assertions that healthy FGB reefs may be largely self-sustaining, and that persistent, self-sustaining populations at the FGB may supply downstream reefs with larvae and behave as a remote climate change refugium.

Keywords: coral reefs, eddies, local retention, biophysical models, larval ecology

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INTRODUCTION

The Flower Garden Banks (FGB) is an isolated reef system located in the northwest Gulf of Mexico (NW GoM) with two primary submerged coral reefs between 16 and 150 m in depth (Johnston et al., 2019). Other than a localized mortality event in 2016 (Johnston et al., 2019), these reefs have sustained high levels of coral cover (>50%) over the last several decades (Schmahl et al., 2008; Johnston et al., 2016). Researchers attribute their health to their depth, which provides thermal refuge (Muir et al., 2017), and their distance from shore, which provides a buffer from a variety of coastal, anthropogenic stressors (McLaughlin et al., 2003; Smith et al., 2008). Despite facing low levels of disturbance, the FGB require sufficient levels of recruitment to remain persistent. With the nearest reefs located over 600 km away along the Yucatan peninsula, it is thought that the FGB are largely self-sustaining (Gittings et al., 1992; Brazeau et al., 2005; Sammarco et al., 2012). Coral larvae produced at the FGB are subject to highly variable flow, that is thought to be largely dispersive to early life-stage propagules (e.g., Lugo-Fernández et al., 2001). Here we investigate the biophysical conditions that facilitate local retention at the FGB in two coral species.

Eddies—mesoscale cyclonic or anticyclonic features—regularly spin off from the GoM's Loop Current (Vukovich, 2012; Lindo-Atichati et al., 2013). The Loop Current is a prominent GoM current, forced by warm water entering the GoM between the Yucatan Peninsula and Cuba (Oey et al., 2005) (**Figure 1**). It can intrude as far north as the Mississippi River Delta and as far east as the Florida continental shelf before feeding into the Florida Current (Alvera-Azcárate et al., 2008). FGB coral larvae may be entrained in Loop Current Eddies (LCEs) when they pass over or near the FGB, which may enhance local settlement. Here we utilize a biophysical model of coral larval dispersal to investigate FGB coral larval retention in relation to the spatiotemporal propagation and persistence of eddies in the NW GoM. We also examine the influence of contrasting life histories and reproductive seasonality on local retention and between-bank connectivity across 15 years of hydrodynamic forcing (2004–2018).

The reef caps at the FGB are some of the few Caribbean reef systems still dominated by large, boulder and brain coral colonies (Schmahl et al., 2008; Clark et al., 2014). These include slow-growing, broadcast spawning species such as *Montastraea cavernosa*, *Pseudodiploria strigosa*, and the *Orbicella* species complex. The FGB National Marine Sanctuary (FGBNMS) monitors the mass spawning events at these reefs, which occur annually in the weeks following late summer full moons (Vize et al., 2005, 2008; Schmahl et al., 2008). Broadcast spawning corals will simultaneously release gametes, which fertilize in the water column or near the sea surface. Most larvae of broadcast spawning species are competent to settle in 3–6 days, and some species' larvae are viable for as long as 4 months (Harrison and Wallace, 1990; Graham et al., 2008; Porto-Hannes et al., 2015). Estimations for the maximum pelagic larval duration (PLD) for orbicellids ranges from 10 to 120 days (Porto-Hannes et al., 2015; Davies et al., 2017). The FGB also support populations of brooding corals including *Porites* spp. and *Agaricia* spp. Brooders tend to have an extended reproductive season, and *Porites astreoides* populations release planula larvae throughout late spring and summer (April–September), with peaks centered on new moons (Chornesky and Peters, 1987; McGuire, 1998; Edmunds et al., 2001). These weedy, opportunistic corals experience higher recruitment rates throughout the Caribbean than broadcasting species (Green et al., 2008), possibly due to early larval competency and shorter distance dispersal. *P. astreoides* larvae may settle in as little as 3 h, but the maximum PLD for this species remains unclear (Edmunds et al., 2001; Harii et al., 2002; Olsen et al., 2016). PLD is a crucial parameter influencing the dispersal potential of coral and other planktonic larvae (Shanks, 2009). Typically, longer PLDs are associated with greater dispersal potential, but the increased distance of larval transport may be associated with higher larval mortality and displacement from suitable habitat (Connolly and Baird, 2010; Buston et al., 2012). In this study, we selected *P. astreoides* as a model for brooding corals, and *Orbicella faveolata* as a model for broadcasting orbicellids.

Biophysical modeling and satellite drifter studies in the GoM suggest that a long dispersal window is necessary for export from the FGB to distant reefs (Davies et al., 2017; Olascoaga et al., 2018), but retention potential is approximately equal with a short or long PLD (Davies et al., 2017). Recent studies also show *M. cavernosa* populations are genetically well-mixed between east FGB (EFGB) and west FGB (WFGB) and with the nearby McGrail, Geyer, and Bright Bank populations. These coupled studies utilized an evolutionary genetics framework (Studivan and Voss, 2018a) and local hydrographic conditions over ecological time scales to infer population connectivity (Garavelli et al., 2018). Broadcast coral populations at the FGB may experience recruitment from populations throughout the wider Caribbean, as the FGB *O. faveolata* population genetic signature shows a relatively equal proportion of genets from extraneous Caribbean populations (Rippe et al., 2017). These studies suggest that there is an apparent lack of barriers to long distance gene flow from distant coral populations to the FGB. Though this body of work has collectively increased our insight into connectivity among the FGB and throughout the GoM, demographic population maintenance is likely driven by local retention. We have, however, little understanding of the biophysical mechanisms that would support this retention, nor of the temporal scale over which they operate.

Due to the isolation and relative health of coral reefs at the FGB, their potential as a climate change refugium is of particular interest (Hickerson et al., 2012; Davies et al., 2017). Western Atlantic reefs are experiencing severe declines due to disease (Precht et al., 2016; Wilson et al., 2016), elevated sea surface temperatures (SST) (LaJeunesse et al., 2015), and ocean acidification (Hughes et al., 2017; Langdon et al., 2018). The availability of larval recruits is thought to limit population recovery at many reefs (Hughes and Tanner, 2000; Williams et al., 2008; Ritson-Williams et al., 2009). FGB reef persistence and potential as a reef refugium depend heavily on the degree to which the FGB are self-sustaining through larval retention. While eddies have been proposed to aid in local retention in the FGB (Lugo-Fernández et al., 2001; Johnson et al., 2017), a systematic understanding of how coral reproductive and larval biology interact with the physical environment to enhance settlement in the FGB remains limited.

This study is the first to investigate the influence of LCEs on FGB coral larval local retention. Our biophysical models show that for two species of reef-building corals, pulses of reproductive output contemporaneous with mesoscale features can recirculate coral larvae over the FGB early in the dispersal window. Smaller pulses of larvae may return to the reefs between 2 weeks to 1 month into the dispersal window. Our models suggest that although inherently stochastic, over sufficient timescales eddies are a consistent and reliable mechanism for coral larval reseeding at the FGB.

MATERIALS AND METHODS

Study Site

Dispersal was simulated from EFGB and WFGB coral populations. The EFGB and WFGB have been under sanctuary designation since January 1992 (Schmahl et al., 2008). These coral communities are the most prominent and well-studied in the NW GoM region. While Stetson Bank is also included under the protection of the FGBNMS, it has considerably lower coral cover (DeBose et al., 2013) and low abundances of our target species, and thus was not used in the study. The reef caps on EFGB and WFGB support coral from ∼15 to 60 m (Hickerson et al., 2008).

Hydrodynamics

Fifteen years of hydrodynamic forcing were utilized from the HYbrid Coordinate Ocean Model (HYCOM, Bleck, 2002) GoM regional analysis (Chassignet et al., 2007). This hydrodynamic model has a resolution of 1/25° per grid cell (∼3.5 km). The first 5 years of hydrodynamics (2004–2008) and January–April 2009 were obtained from the HYCOM GOMl0.04 experiment 20.1. Hydrodynamics for the remainder of 2009 through April 2014 were obtained from HYCOM GOMl0.04 experiment 30.1, and the remainder of 2014 through 2018 were obtained from HYCOM GOMl0.04 experiment 32.5. Hydrodynamic fields were downloaded as daily NetCDF files each containing: eastward, northward, and vertical velocities; sea surface height (SSH or altimetry); temperature; salinity; and density. Velocities and density fields were utilized in biophysical simulations of the dispersal of *P. astreoides* and *O. faveolata.* SSH was used to identify daily eddy fields in the GoM, using "EddyScan," an automated algorithm for the detection of eddies (Faghmous et al., 2012) (described below).

Larval Dispersal Model

Larvae were tracked within the model domain using the Connectivity Modeling System (CMS), an open-source individual-based Lagrangian particle tracking software (Paris et al., 2013). Virtual larvae (particles) of each species were simulated and tracked in three dimensions throughout their PLD. Larval position was calculated every 10 min and recorded every 3 h. Horizontal and vertical diffusivity coefficients (2.45 and 0.01 m^2/s^2, respectively) were used to estimate sub-grid dynamics, following the methods of Okubo (1971). Because the reef caps of each bank were contained within a single (separate) grid cell of the hydrodynamic model, one release location on each bank was used for all simulations.

When available, the timing of virtual spawning for *O. faveolata* was based on FGBNMS field observations (Schmahl et al., 2008; Flower Garden Banks National Marine Sanctuary-Spawning Observations, 2018). For years without field observations, spawning was simulated after the full moon in August and following full moons in late July or early September, when predicted by sanctuary researchers (**Supplementary Table S1**). Throughout the 15 modeled years (2004–2018), 25 *O. faveolata* spawning events were simulated. Each simulated spawn occurred over 3 days, 7–9 days after the full moon; 5000 virtual larvae were released per spawning day per bank, for a total of 750,000 tracked virtual *O. faveolata* larvae throughout the model duration.

Simulated *P. astreoides* larvae were released every day throughout its reproductive season from April to September. The number of particles released each day from each bank was in proportion to an adjusted moon fraction:

$$\#\ particles\ per\ day\ =\ (1-Moon\ Fraction)\times 1000$$

Moon Fraction refers to the percentage of the moon visible to the observer, and values were obtained from the US Naval Observatory (U.S. Naval Observatory, 2017). Peaks in larval releases occurred during new moons, and troughs occurred during full moons (**Figure 6A**). Approximately 90,000 particles were released from each bank per year, with over 2,700,000 simulated *P. astreoides* larvae in total.

The buoyancy module of the CMS was implemented to simulate biological processes affecting the depth of larvae throughout dispersal. During dispersal, larvae may change in size, specific gravity, or in vertical swimming behaviors, which can all affect buoyant velocity and vertical position (Szmant and Meadows, 2006). Ontogenetic changes were approximated by simulating species-specific changes in particle size and specific gravity as larvae dispersed. Orbicellids undergo size and specific gravity changes when spawned egg bundles break apart, fertilize, and develop into planulae (Wellington and Fitt, 2003; Szmant and Meadows, 2006). *P. astreoides* release fully developed larvae (planulae; Chornesky and Peters, 1987), and thus, changes in larval size and specific gravity were modeled during dispersal to simulate the depletion of larval lipid stores and downward swimming behaviors. A sensitivity analysis was performed to determine the appropriate ranges for specific gravity and particle size, and to determine the intervals over which these parameters should change to produce a realistic series of depth-changes throughout the dispersal window (**Supplementary Figures S6, S7**). Buoyancy tables were modified from Holstein et al. (2015) (**Supplementary Table S2**).

Virtual *O. faveolata* larvae were given a pre-competency period of 3 days (Porto-Hannes et al., 2015), but a maximum PLD was set to 120 days to allow the model to represent dispersal for additional broadcast coral species (Graham et al., 2008; Davies et al., 2017). *P. astreoides* larvae were given a pre-competency

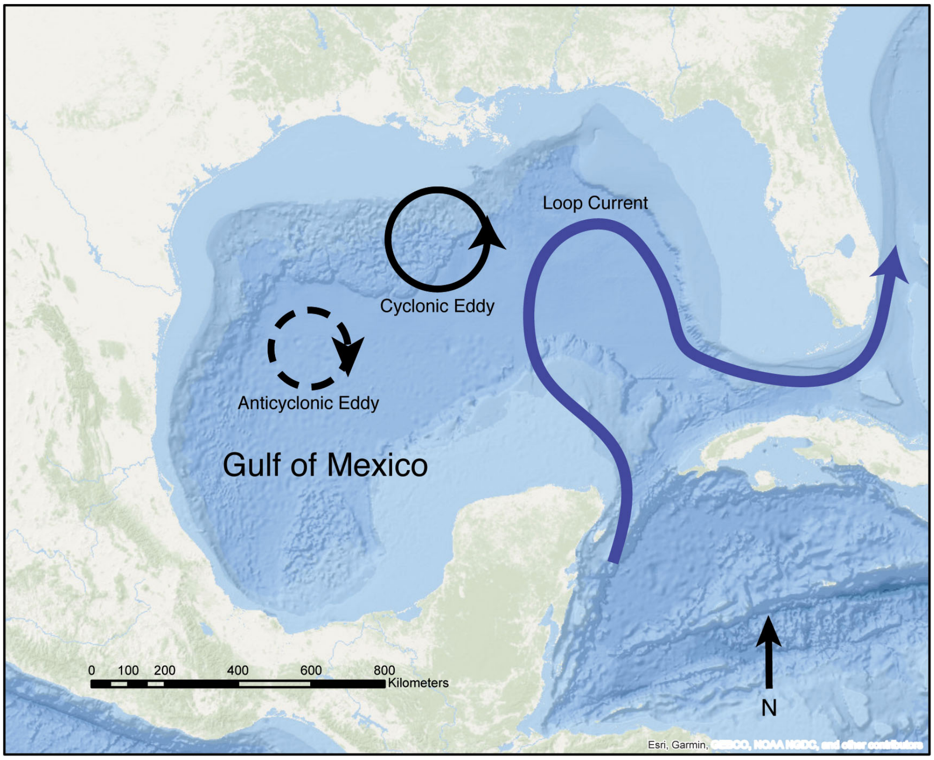

FIGURE 1 | Schematic of the GoM showing the Loop Current (blue) the FGB, and cyclonic and anticyclonic LCEs. The FGB are located on the Texas-Louisiana continental shelf in the NW GoM (Esri, 2019).

TABLE 1 | Definitions of modes of larval retention at FGB.

Term	Definition
Within-bank retention	Retention of larvae at the natal bank (EFGB or WFGB)
Between-bank retention (or connectivity)	Retention of larvae at FGB that involves larval exchange between EFGB and WFGB
Pre-advection retention	Early retention of larvae that occurs before larvae leave their natal bank
Recirculating retention	Retention of larvae that involves first leaving the boundaries of the natal bank, and then returning to the natal bank (due to eddies and other advection)
FGB total recirculating retention	Retention of larvae that involves first leaving the boundaries of the natal bank, and then returning to either the natal bank or another bank within FGB (recirculating retention + between-bank retention)

period of 3 h (Harrison and Wallace, 1990) and a maximum PLD of 30 days (Edmunds et al., 2001; Harii et al., 2002).

Eddy Tracking

EddyScan (Faghmous et al., 2012) was implemented to obtain tracks and contours for all eddies in the GoM detected from 2004 to 2018. The MATLAB algorithm implemented an iterative-thresholding approach to identify connected component features based on SSH. The features were then filtered based on a minimum feature size of four pixels. EddyScan generated a series of pixels corresponding to the contours of all eddies for each day of the year, as well as tracks for eddy centroids and the direction of spin (cyclonic or anticyclonic). The current software implements a parameter-free approach, preventing eddies from being unnecessarily discarded, an advantage over previous detection schemes. Some limitations include a higher misidentification rate for spin direction in eddies with shorter lifetimes, as well as an overestimation of eddy size (Faghmous et al., 2015). Based on the resolution of the hydrodynamic models, the minimum size of eddies detected is on the order of tens of kilometers, daily. The short timescale over which larval settlement occurs demands this daily, fine-scale approach. To investigate potential interactions between the larval trajectories and the eddies, the latitude and longitude of the eddy contours were extracted. This allowed for a record of monthly variation in the number of eddies passing over or near the FGB. For each month in each year, we calculated "Eddy Days," a metric we define as the cumulative number of eddies intersecting a 25 km buffer of the FGBNMS boundaries per day in a given month. For example, a single eddy interacting with the FGB for 3 days would contribute 3 Eddy Days, as would three separate eddies over 1 day. The number of cyclonic and anticyclonic Eddy Days experienced by the FGB were further summarized

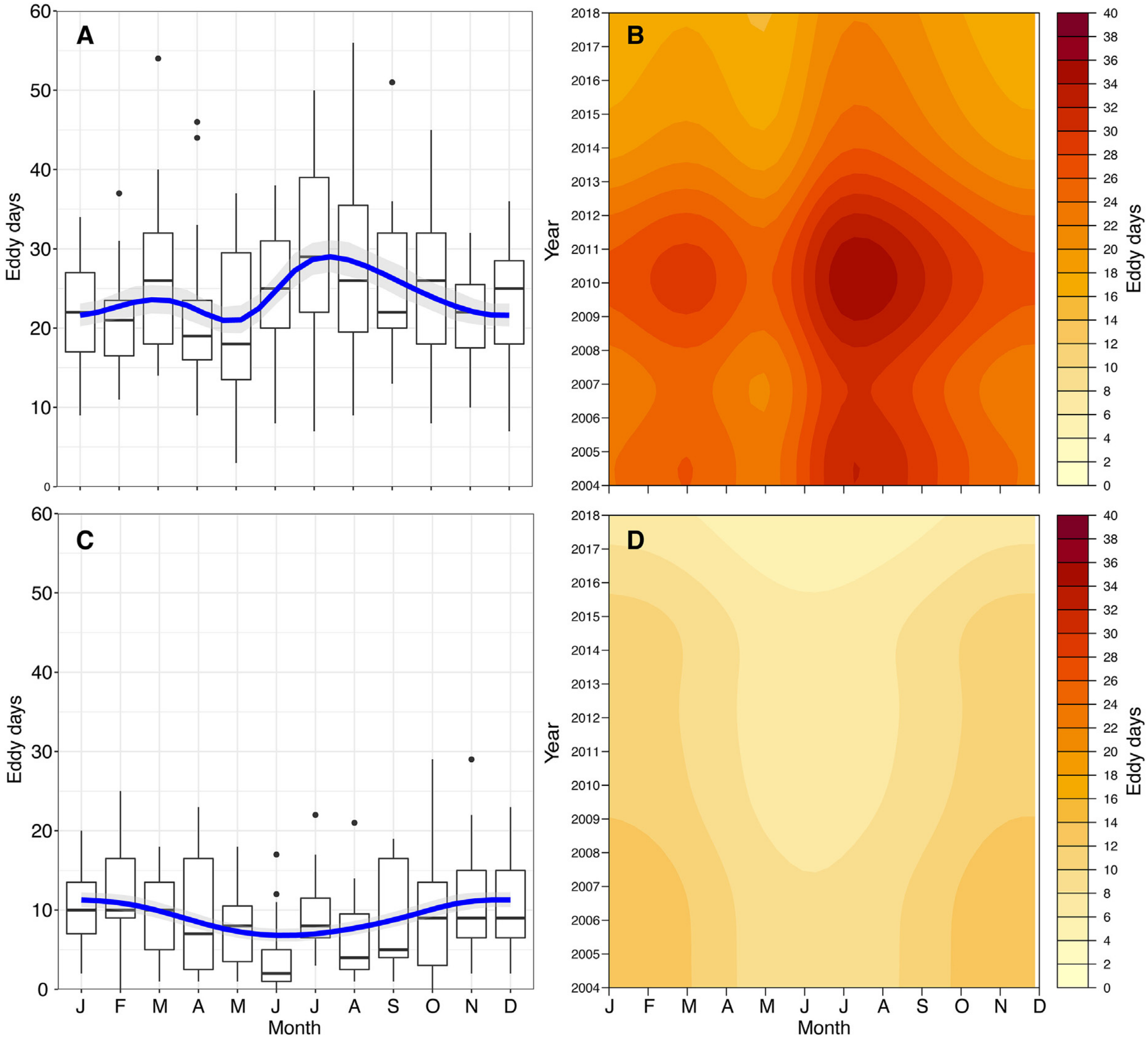

FIGURE 2 | Interactions of mesoscale features with the FGB. Interactions are described as Eddy Days, and shown by eddy spin direction (cyclonic, **A,B**; anticyclonic, **C,D**). Monthly summaries are shown in boxplots **(A,C)** with Poisson GAM predictions with cyclic cubic regression splines. GAM predictions across year and month are shown as heat maps **(B,D)** to demonstrate broad trends in the physical environment of the FGB.

using Poisson general additive models (GAMs) with cyclic cubic regression splines to describe long-term interactions of LCEs with the FGB (**Figure 2**).

Biophysical and Retention Analysis

In order to relate this simulation study to empirical studies of larval–mesoscale structure interactions (e.g., Lindo-Atichati et al., 2012) and to understand the interactions of simulated larval dispersal with temporally and spatially dynamic mesoscale oceanographic features, the number of simulated larvae entrained within any cyclonic or anticyclonic eddy within the model domain was assessed over every day of dispersal throughout the 15-year simulation. Note that virtual larval dispersal may have been influenced by an eddy without being in the eddy core.

A binary matrix was used to determine the presence or absence of every particle within the sanctuary boundaries of both banks every 3 h. Five modes of retention were then assessed: between bank retention (or connectivity) (1) from EFGB to WFGB, and (2) from WFGB to EFGB; within-bank local retention (3) at EFGB and (4) at WFGB; and (5) total FGB retention, which sums all modes of retention (1–4) (**Table 1**). Every intersection within the sanctuary boundary was considered to be an opportunity for potential settlement, but a larva's trajectory did not end after making a potential connection. Thus, the potential for multiple settlement opportunities and settlement opportunities late in dispersal were assessed. The total number of connections for each mode was determined throughout the dispersal window, as was the percentage of particles with at least one (or multiple) connection(s) (**Table 2**). Because the potential for retention and connectivity were being assessed, larval mortality was not considered.

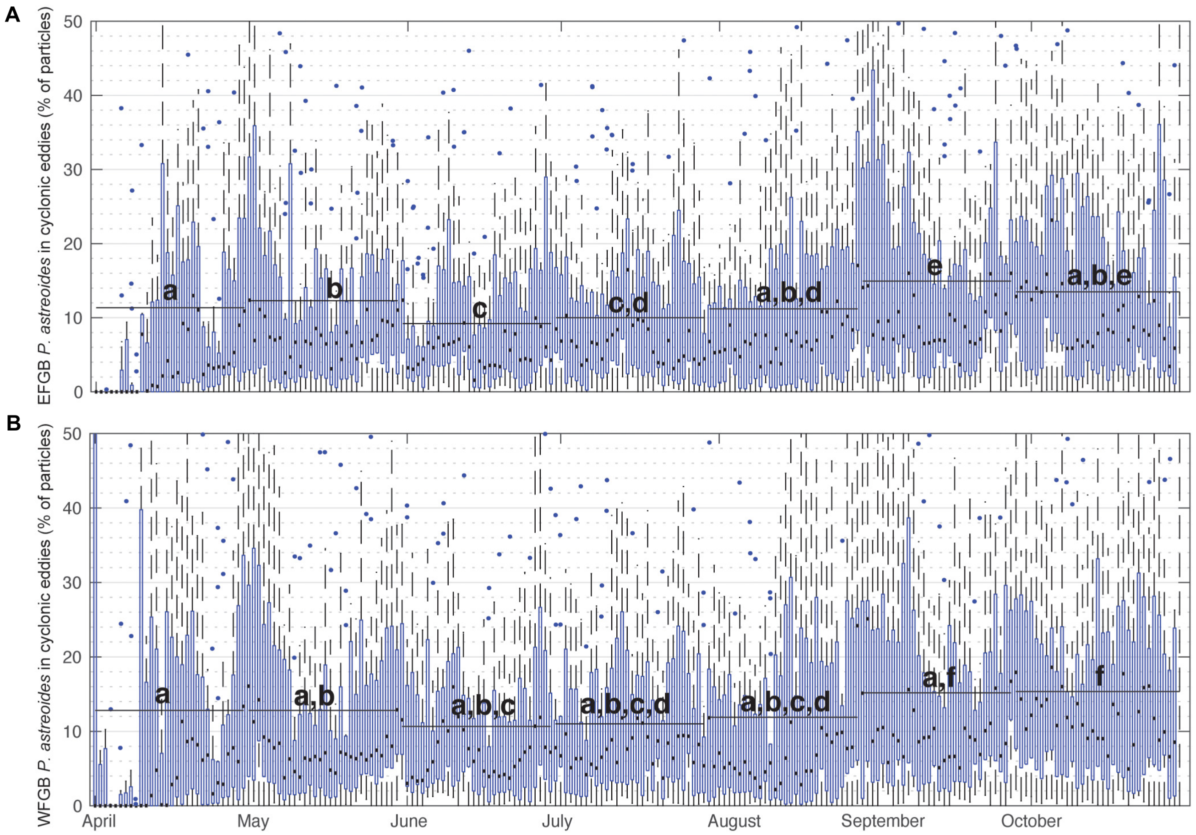

FIGURE 3 | Percentage of *P. astreoides* virtual larvae entrained in cyclonic eddies over time. Box plots show annual distributions across the 15 years of seasonal planulation (2004–2018) of the percentage of **(A)** EFGB and **(B)** WFGB *P. astreoides* larvae entrained in any GoM cyclonic eddy feature on that day of the year. Boxes are interquartile ranges, black lines are median values, blue circles are outliers, and whiskers represent the first and fourth quartiles. Black bars represent means taken over 30-day windows and letters correspond to significantly different pairwise comparisons (all significant differences $p < 0.05$, pairwise Wilcoxen tests with Benjamini and Hochberg adjusted *p*-values).

RESULTS

Virtual larvae of both species rapidly dispersed away from the FGB, and the trajectories they followed varied greatly both intra- and inter-annually. Particles were often entrained within the Loop Current to the east, and, in the case of *O. faveolata*, were at times advected through the Florida Strait and entrained further into the Gulf Stream. However, variable directional flow and stochastic eddy features resulted in advection of virtual larvae to the north, west, and south of FGB, both over open ocean and over the continental shelf of the northern and western GoM.

Eddies and Larval Trajectories

Between 80 and 120 eddies were detected per day throughout the GoM, many of which occurred near the FGB during the 15 modeled years. Over this time span, the number of FGB cyclonic Eddy Days was significantly elevated during the late summer months (Poisson GAM with cyclic cubic regression spline, deviance explained = 22.9%, $p < 0.0001$; **Figures 2A,B**). Anticyclonic Eddy Days showed the opposite trend, with fewer late summer anticyclonic eddy–FGB interactions (Poisson GAM with cyclic cubic regression spline, deviance explained = 14%, $p < 0.0001$; **Figures 2C,D**). In both cases, there was a significant effect of year ($p < 0.0001$), indicating considerable interannual variation in mesoscale features over the FGB. It is important to note that the GAM models smooth intra-annual variation (**Figures 2B,D**), which was high (**Supplementary Figures S1, S2**). For example, the GAM predicts highest cyclonic Eddy Days in late summer of 2010; while there were peaks in July and September of 2010, August had considerably fewer cyclonic Eddy Days (**Supplementary Figure S1**).

When summarized for all years, the percentage of *P. astreoides* virtual larvae entrained within cyclonic eddies remained relatively consistent, with daily medians consistently ranging between 2 and 15% (**Figure 3**). In late summer, particularly late August and September, a significantly greater percentage of *P. astreoides* larvae were entrained in cyclonic eddies than in other months (Kruskal–Wallis rank sum test, $p < 0.0001$; and pairwise Wilcoxen rank sum tests with Benjamini and Hochberg adjusted *p*-values). These trends were not seen in virtual *P. astreoides* larvae entrained in anticyclonic eddies (**Supplementary Figure S3**). The percentage of *O. faveolata* virtual larvae entrained in cyclonic eddies also significantly peaked in late summer (**Figure 4**), with daily medians ranging

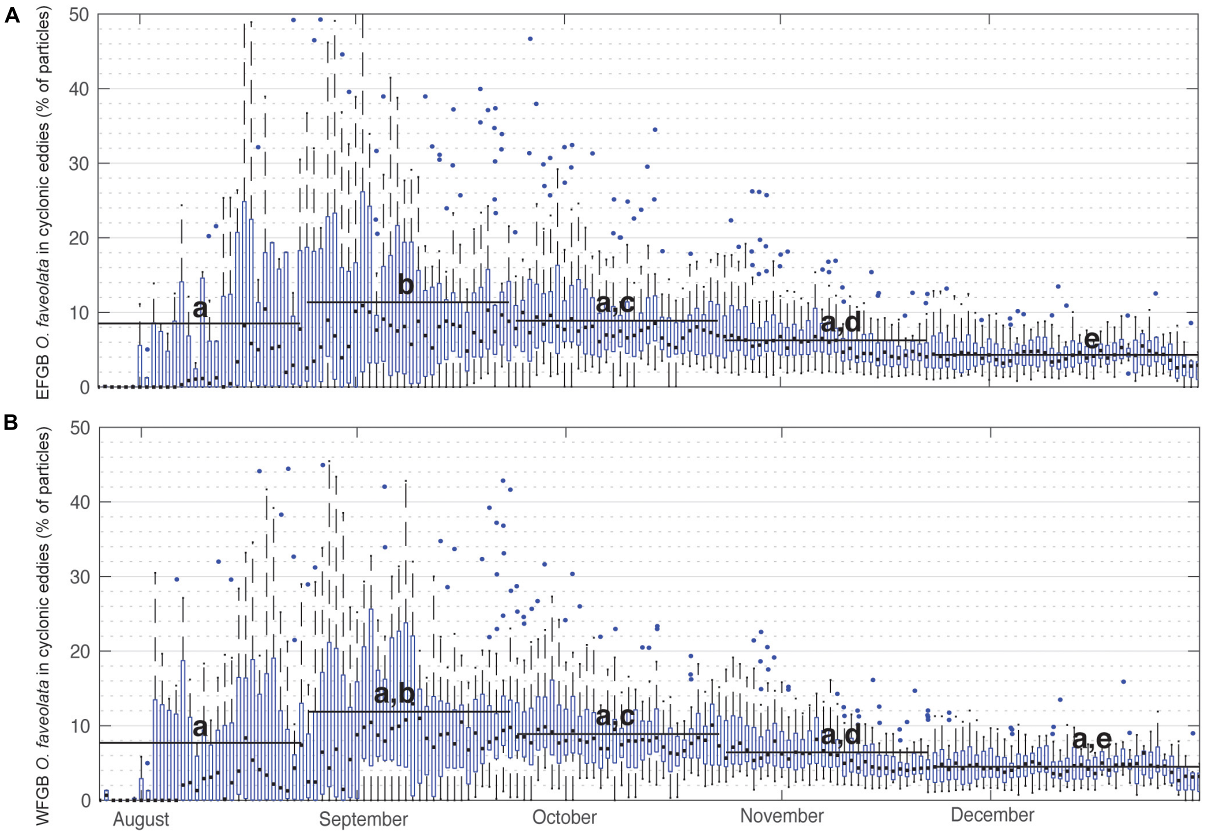

FIGURE 4 | Percentage of *O. faveolata* virtual larvae entrained in cyclonic eddies over time. Box plots show annual distributions across the 25 modeled spawn events (2004–2018) of the percentage of **(A)** EFGB and **(B)** WFGB *O. faveolata* larvae entrained in any GoM cyclonic eddy feature on that day of the year. Boxes are interquartile ranges, black lines are median values, blue circles are outliers, and whiskers represent the first and fourth quartiles. Black bars represent means taken over 30-day windows and letters correspond to significantly different pairwise comparisons (all significant differences $p < 0.05$, pairwise Wilcoxen tests with Benjamini and Hochberg adjusted p-values).

as high as 13% (Kruskal–Wallis rank sum test, $p < 0.0001$; and pairwise Wilcoxen rank sum tests with Benjamini and Hochberg adjusted p-values). This trend was not observed for anticyclonic eddies (**Supplementary Figure S4**).

Patterns in Simulated Larval Retention at FGB

Porites astreoides

The dispersal of *P. astreoides* virtual larvae was highly variable throughout its extended reproductive seasons. In extremely rare events (0.004% of planulae), entrainment in the Loop Current advected particles as far as the Florida Keys. High local retention occurred immediately following planulation and prior to larvae advecting from the sanctuary boundaries over the course of the first ~3 days of dispersal (pre-advection retention) (**Figure 5A**); 55–95% of all virtual larvae in a given year were competent to settle before leaving the sanctuary boundaries across all reproductive events. Larvae also recirculated over the FGB frequently, potentially due to entrainment within, as well as advection influenced by LCEs; 9.75% of all virtual *P. astreoides* larvae left and returned to the FGB at least once (**Table 2**). Nearly 80% of this recirculating retention occurred after 3 days of dispersal, while ~20% was due to very brief advection and rapid reintroduction to the sanctuary boundaries due to advective processes, some related to LCEs. Between-bank connectivity peaked 1 day into the dispersal window with an annual median of ~2.0% and range of 0.5–4.0% of all particles released making between-bank connections in a given year (**Figure 5B**). Every year, between-bank exchange occurred in under 2.5 days, but connectivity declined precipitously after 1 day of dispersal. Eastward transport was slightly higher as WFGB to EFGB connections made up 56% of all *P. astreoides* between-bank connections (**Table 2**). Total retention after 3 days gradually declined over the length of the PLD, falling to a median of <0.05% beyond 2 weeks of dispersal (**Figure 5C**).

Within-bank *P. astreoides* retention was consistently highest during new moons, following peaks in planulation (**Figures 6A,B,D**). Most of this was due to early retention, whereas recirculating local retention did not consistently follow this same trend. However, outlier years did follow this trend, and high reproductive output was associated with pulses of recirculating local retention when physical conditions were favorable (**Figures 6C,E**). *P. astreoides* between-bank

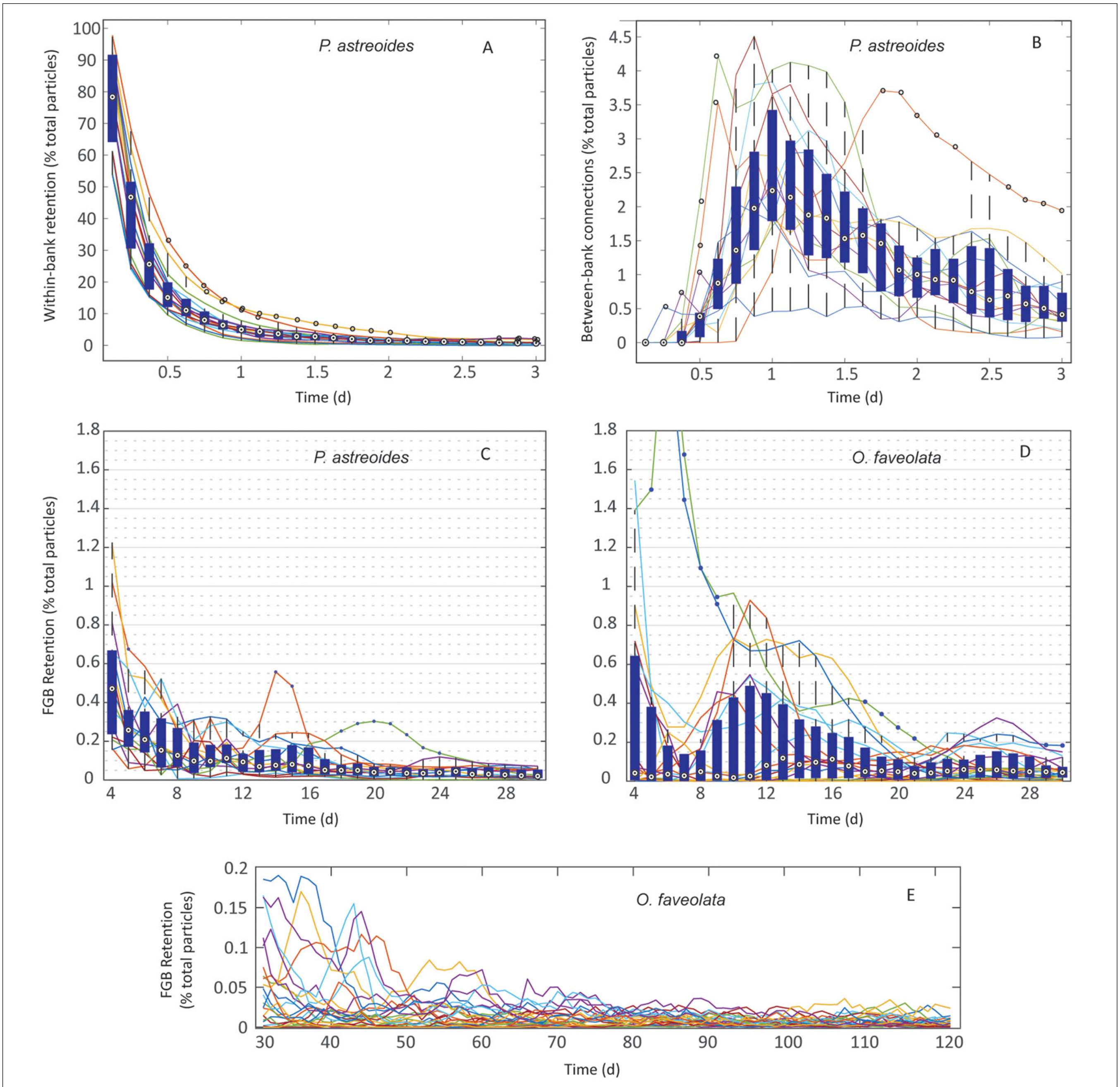

FIGURE 5 | Retention in *P. astreoides* and *O. faveolata* at FGB: **(A)** *P. astreoides*: 3 h–3 days of within-bank local retention. **(B)** *P. astreoides*: 3 h–3 days of between-bank retention. **(C)** *P. astreoides*: 3–30 days of dispersal – total FGB retention. **(D)** *O. faveolata*: 3–30 days of dispersal – total FGB retention. **(E)** *O. faveolata*: 30–120 days of dispersal – total FGB retention. Values represent retention per day as a percentage of total particles released per year. Boxes are interquartile ranges, targets are median values, blue circles are outliers, and whiskers represent the first and fourth quartiles. Lines represent individual years for *P. astreoides* and individual spawning events for *O. faveolata.* Note different *y*-axes scales.

exchange was also loosely associated with peaks in planulation (**Supplementary Figure S5**), particularly so in outlier years.

Larval distributions became more diffuse with time, and these distributions varied considerably between years (**Figure 7**). The effects of LCEs passing over the FGB in shaping the distribution of larval positions, and affecting recirculating retention, can be seen early in the competency window (**Figure 7G**), and as late as 4 weeks after planulation (**Figure 7C**).

Orbicella faveolata

Flower Garden Banks *O. faveolata* virtual larvae entrained in the Western Boundary Current and Loop Current had the potential to reach the Florida Keys and advect further to the northeastern boundary of the hydrodynamic model, near the mid-Atlantic Bight. Other dispersal pathways included westward transport along the Texas shelf and variable dispersal associated both with entrainment within LCEs and advection otherwise influenced by LCEs. Particles interacting with LCEs had the potential to return to the sanctuary boundaries, and 6.96% of all *O. faveolata* virtual larvae released throughout the simulation left and then returned to the FGB at least once (inclusive of between-bank exchange) (**Table 2**).

Orbicella faveolata retention peaked in magnitude at 3 days of dispersal, just after larvae became competent, and peaked again just after the first week of dispersal, which suggests recirculating interactions with LCEs (**Figure 5D**). Retention across years was highest later in the competency window at 1.5–2 weeks, reaching a median of >0.1%. While retention occurred in every year, it was highly variable throughout the PLD. The highest peaks in *O. faveolata* retention occurred stochastically, following only six of the 25 modeled spawning events from 2004 to 2018 (**Figure 5D**). Smaller magnitude, more frequent, and longer duration peaks in retention occurred as late as 26 days into the PLD (**Figure 5D**). Beyond 30 days of dispersal, retention became unlikely, and little to no retention occurred after 60–70 days of dispersal (**Figure 5E**).

Examples of how LCEs affected *O. faveolata* larval distributions over time can be seen in **Figure 8**. In some spawning events (August, 2006), substantial retention occurred throughout an entire month of dispersal (**Figures 8A–C**). On other occasions, advective forces dominated at the onset of competence (**Figures 8D,G**) and later in the dispersal window (**Figures 8E,F,H**), leading to negligible retention.

TABLE 2 | Percentage of all larvae released making at least one or multiple connections in different modes and directions.

Species	Mode of retention	≥ One connection (%)	≥ Two connections (%)
P. astreoides	EFGB-WFGB connectivity	11.24	0.58
	WFGB-EFGB connectivity	14.11	1.34
	EFGB within-bank retention before advection (>3 h)	79.06	–*
	WFGB within-bank retention before advection (>3 h)	80.30	–*
	EFGB within-bank recirculating retention	6.37	0.67
	WFGB within-bank recirculating retention	7.39	0.83
	FGB total recirculating retention	9.75	0.86
O. faveolata	EFGB-WFGB connectivity	7.55	1.02
	WFGB-EFGB connectivity	7.69	1.93
	EFGB within-bank recirculating retention	6.72	1.34
	WFGB within-bank recirculating retention	5.88	0.81
	FGB total recirculating retention	6.96	1.28

*≥ One connection indicates that particles had at least one opportunity to make a given connection. ≥ Two connections indicates a particle made a given connection multiple times, which may indicate a greater probability of occurrence. *Within-bank retention before advection in particles making at least two connections and within-bank recirculating retention making at least one connection are measurements of the same retentive phenomena.*

Eddies, Larval Trajectories, and Peaks in Retention

In general, LCEs were associated in retention that occurred later in larval PLDs. Thus, LCEs were more associated with *O. faveolata* retention, whereas pre-advection retention was the dominant mechanism for *P. astreoides*. Most individual *P. astreoides* planulation events did not result in recirculating retention, but advective processes associated with LCEs passing near the FGB resulted in stochastic pulses of recirculating retention.

Over the thousands of planulation and spawning events simulated, most did not involve significant recirculating retention associated with LCEs. However, these events were consistent throughout the 15 model years, resulting in heavily skewed distributions of annual retention (**Figure 5**). Although relatively rare, obvious entrainment within—or advection associated with LCEs and subsequent redelivery to the FGB—was observed in the dispersal of both species. For example, numerous LCEs passed over or near the FGB during and following the September 2018 *O. faveolata* spawning event (**Supplementary Figure S8**). Larval trajectories were influenced by the outer circulation of cyclonic eddies passing near or over the FGB throughout the first 5 days of their PLD. Nearly 2% of particles released from the EFGB during this spawning event passed over the WFGB during their eighth day of dispersal.

In another example, between 40 and 75% of virtual *P. astreoides* larvae planulated on August 24 2006 and August 25 2006 were predicted to return to the FGB between 5 and 8 days into their PLD (**Supplementary Figure S9**); each of the four modes of retention had a distinguishable peak in the PLD. 100% of EFGB larvae dispersed through WFGB's boundaries during the 5–8 day window. In addition, 100% of WFGB larvae recirculated after advection, and returned to WFGB by day 10. These larval trajectories were heavily influenced by an LCE passing over the FGB (**Supplementary Figures S9**, **S10**).

DISCUSSION

The biophysical models of larval dispersal developed for *P. astreoides* and *O. faveolata* emphasize that multiple biophysical mechanisms enhance local retention of larvae in isolated coral populations in the NW GoM. Differential life-histories in the modeled species—notably species-specific reproductive timing and larval traits—determined the relative influence of these mechanisms, including the role of LCEs in recirculating larvae over natal habitat or between submerged banks. The extended duration of this biophysical model, utilizing 15 years of regional hydrodynamics, has highlighted potential ecological trends in otherwise complex and stochastic biophysical phenomena.

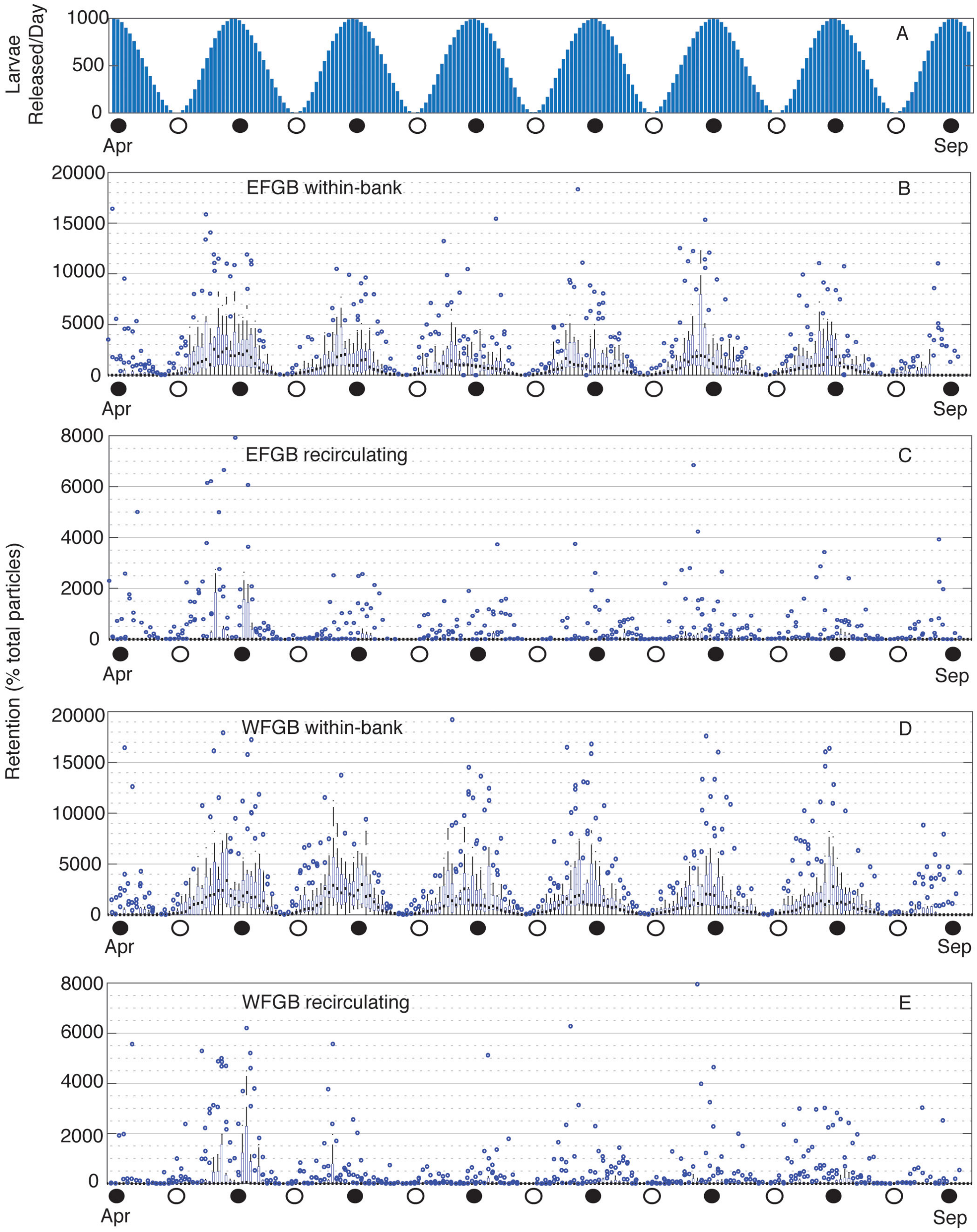

FIGURE 6 | Particles released per lunar day and daily EFGB and WFGB *P. astreoides* local retention. **(A)** Number of particles released per lunar day from April to September. **(B)** EFGB total within-bank retention, and **(C)** total recirculating retention, followed by **(D)** WFGB total within-bank retention, and **(E)** total recirculating retention. Box plots show the annual distribution of the number of particles locally retained at WFGB per lunar day across 15 years of seasonal planulation (2004–2018). Boxes represent interquartile ranges, black squares are median values, blue circles are outliers, and whiskers represent the first and fourth quartiles. Note different y-axis scales.

Biophysical models of larval dispersal, and assessments of larval retention, are limited by the resolutions (spatial, temporal, etc.) of their hydrodynamic datasets (Briton et al., 2018). Sub-grid dynamics, here approximated by diffusion, certainly affect the movement, retention, and dispersal of larvae as they move over or near highly rugose coral reefs and complex coastlines (Koehl and Hadfield, 2010; Nickols et al., 2012; Hata et al., 2017). Additionally, eddy features that influence retention on the FGB may be smaller than the minimum detection size in this study. For these reasons, we have likely underestimated the potential for larval retention at the FGB, particularly in the first several days of dispersal.

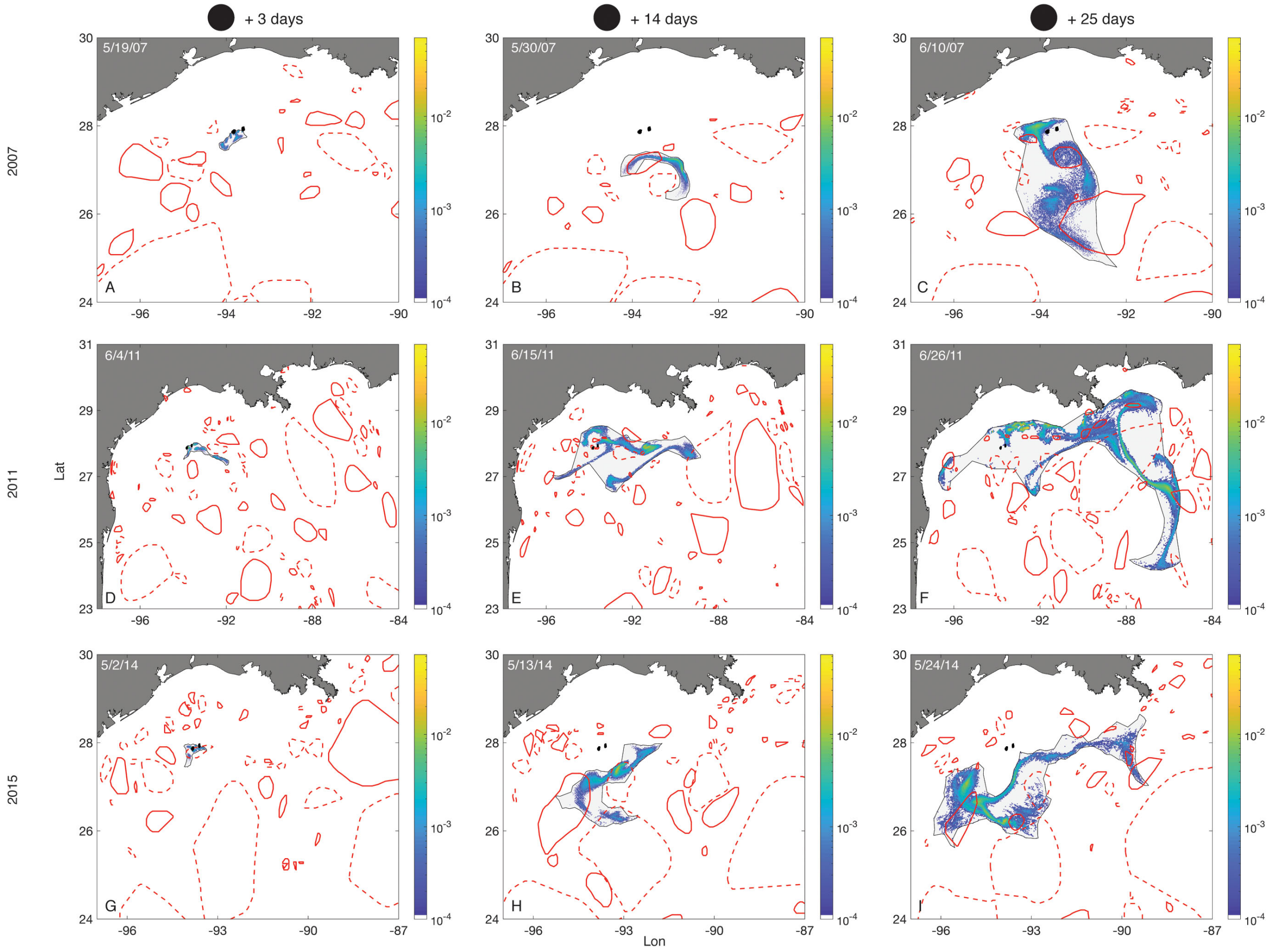

FIGURE 7 | Larval distributions–*Porites astreoides*. Plots show larval distributions as probability density surfaces bounded by non-convex hulls following seven days of planulation in each of three different months (rows) (larvae released from 3 days before to 3 days after the new moon of that month). The first column shows the distribution of larvae on the third day after the new moon. The next two columns show larval distributions 14 and 25 days after the new moon, respectively. Density is scaled to the maximum single cell value within a planulation event. The FGB sanctuary boundaries are shown as black filled polygons. Eddies are represented by red empty polygons. Solid lines are cyclonic eddies and dashed lines are anticyclonic eddies.

In general, the five modes of potential FGB coral larval circulation discussed by Lugo-Fernández et al. (2001) and further investigated by Davies et al. (2017) and Garavelli et al. (2018) were well-represented in our simulations. At times virtual coral larvae dispersed (1) cyclonically to the west, (2) continually to the east where they would be influenced by the Mississippi River plume, (3) across the GoM basin, or were entrained in eddies either (4) oceanically or (5) over the continental shelf. Larval retention at FGB is theoretically possible in each of these modes of circulation, depending on the interplay between larval traits and the physical environment.

Time to larval competency following planulation or spawning strongly determined within-bank retention, and whether larvae would have the chance to settle on natal reefs before advection. Thus, for brooders like *P. astreoides*, larval retention could occur in nearly any velocity field and within-bank retention would be expected to be far greater than for spawners. Broadcast spawner larvae, which are more likely to advect from the FGB before becoming competent, may be more reliant on interactions with LCEs and recirculation to settle over natal reefs.

Brooders often display high settlement success (Szmant, 1986), and high seascape genetic structure (Underwood et al., 2009), which suggests that local retention and recruitment of larvae is a feature of their life-histories. However, in the FGB, both brooders (Brazeau et al., 2005) and broadcast spawners (Goodbody-Gringley et al., 2012; Studivan and Voss, 2018a,b) demonstrated reduced genetic structure, implying substantial gene flow among well-mixed populations. With high levels of between-bank exchange, especially within the first several days of dispersal, our model corroborates this hypothesis, suggesting that these populations may be well mixed. This early between-bank exchange was driven by directional currents and by short-distance interactions with LCEs, and was predominantly in the west-east direction, with frequent reversals. FGB coral populations likely experience recruitment from

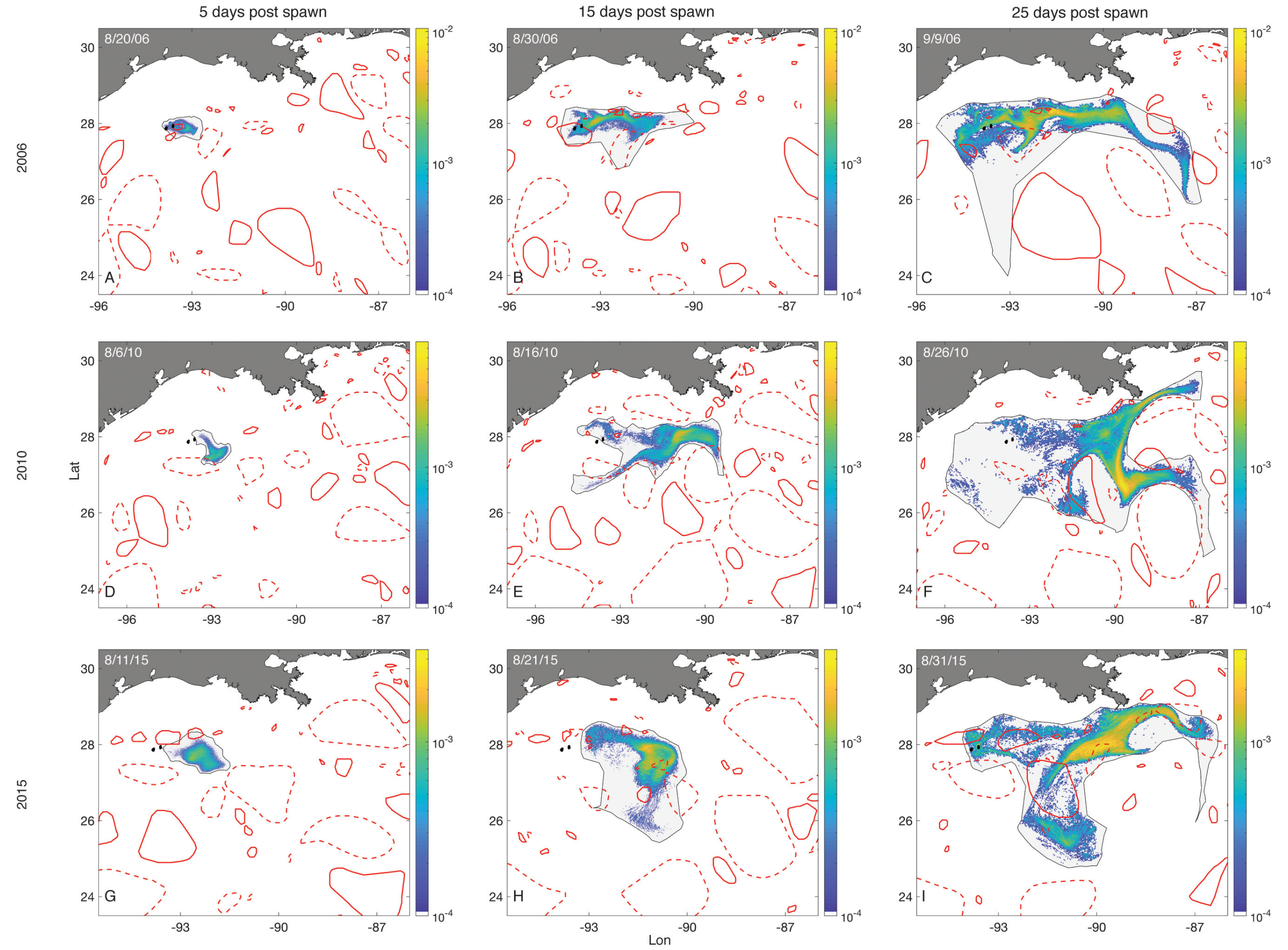

FIGURE 8 | Larval distributions–*O. faveolata*. Plots show larval distributions as probability density surfaces bounded by non-convex hulls following three 3-day spawning events (rows). The first column shows the distribution of larvae on the fifth day after the start of spawning, representative of the first full day in which all larvae were competent. The next two columns show distributions of those larvae 15 and 25 days into their dispersal windows. Density is scaled to the maximum single cell value within a spawning event. The FGB sanctuary boundaries are shown as black filled polygons. Eddies are represented by red empty polygons. Solid lines are cyclonic eddies and dashed lines are anticyclonic eddies.

localized retentive events and exchanges across banks and subpopulations.

With a longer reproductive season, *P. astreoides* larvae are exposed to a wider variety of hydrodynamic conditions than are the gametes and larvae of *O. faveolata*. It would be natural to assume that this would result in greater opportunities for retention due to favorable oceanography. Interestingly, while retention at FGB was more consistent inter-annually in *P. astreoides*, the exposure to a wider variety of hydrodynamic conditions did not necessarily lead to greater magnitudes of retention across the PLD as compared to *O. faveolata*. One explanation is that retentive LCEs move over the FGB seasonally, and are more contemporaneous with late summer orbicellid spawning than with the extended *P. astreoides* reproductive season. Our findings corroborate studies which suggest that the Loop Current sheds the greatest number of eddies in late summer and winter due to the interactions of seasonal winds in the GoM and Caribbean (Chang and Oey, 2012), with the greatest peak in eddy formation occurring in September. In our analysis, peaks in eddy formation, eddy interactions with the FGB, and orbicellid retention are all contemporaneous in late summer. Despite September being the end of its reproductive season, *P. astreoides* larvae eddy entrainment also peaked in September.

Van Woesik (2010) asserts that mass coral spawning synchrony and timing is associated with calm periods in local wind fields, and that the tightest spawning synchrony occurs when there are brief and pronounced summer doldrums. These doldrums, it is thought, should enhance fertilization success and local retention, due to reduced water movement. Interestingly, at the FGB, these summer wind doldrums are contemporaneous with maximum LCE shedding in late summer (Chang and Oey, 2012), which suggests an additional physical mechanism of retention associated with the timing of coral spawning. While we have not investigated the occurrence of summer doldrums in the years simulated, this would be an interesting area for further study of coral spawning and larval retention in the GoM.

Coral mass spawning is tightly synchronous and consistent at the FGB (Vize et al., 2005). Thus, it appears that late summer may be the biophysical optimum for the retention of coral larvae over the FGB, and the positive feedback of favorable biological and physical conditions may help in explaining the health and persistence of these isolated reefs.

Lugo-Fernández et al. (2001) predicted that cyclonic motion and eddy features could lead to larval retention within 24–30 days of coral spawning at the FGB. We found that after 30 days of dispersal, retention in both modeled species became vanishingly unlikely. However, we also found that an extended PLD lent itself to intra-annually rare, but inter-annually consistent late-duration larval retention. Small fractions of *O. faveolata* virtual larvae returned to the FGB throughout the 120 days of their PLD. Given a large reproductive event in a favorable year, this model predicts that *Orbicella faveolata* larvae—or larvae of other broadcast spawning species with extended maximum PLDs—could feasibly return to the FGB months after spawning. However, these long larval pathways back to FGB are less plausible due to increased mortality and involve many difficult-to-predict transitions between regional currents and mesoscale features. Longer PLDs are generally associated with longer distance dispersal in fishes (with notable exceptions) (Lester and Ruttenberg, 2005; Treml et al., 2012), but here we show that long PLDs can provide opportunities for recirculating retention late in the pelagic duration in corals, and that individual cohorts of larvae may experience multiple "chances" to settle on natal reefs.

Interactions with LCEs—both entrainment in the eddy core, and advection around its edges—have important implications for multiple chances at local retention for dispersing coral larvae. Because larvae are largely passive and at the mercy of hydrodynamics, the fact that LCEs may deliver the same larvae over the same reef multiple times may compound the probability of larval success. This is a particularly interesting phenomenon given the isolation and depth of the FGB. While shallow benthic and coastal features may influence local hydrodynamics and encourage reef-scale retention (Cetina-Heredia and Connolly, 2011), LCEs are regional mesoscale features. Mesoscale eddies have been associated with larval fish recruitment pulses and the entrainment of larvae near coastal habitats (Paris et al., 1997; Sponaugle et al., 2005; Lindo-Atichati et al., 2016; Shulzitski et al., 2016; Vaz et al., 2016), but the "second chances" potentially afforded by LCEs at the FGB may be unique due to their isolation. Because they are relatively deep and distant from shore, FGB reefs do not experience the complex coastal or barrier reef flows most typical coral reefs experience as a result of the interactions of waves, alongshore currents, and complex shallow bathymetry. As high-resolution hydrodynamics improve and become more widely available, the role of mesoscale and sub-mesoscale features in marine larval retention in a variety of habitats is becoming increasingly recognized and studied (Briton et al., 2018).

Coral larvae are expected to experience reduced fitness and high mortality as they disperse, and second chances at retention may be rarer than assumed here. We have not modeled the dynamics of recruitment or post-settlement, which may be affected, positively or negatively, by prolonged dispersal and changing seasonal environmental conditions. The overwhelming bulk of dispersal in this model, including interactions with LCEs, resulted in advection of virtual coral larvae away from the FGB and into deep or inhospitable waters. This corroborates previous modeling of corals (Davies et al., 2017; Garavelli et al., 2018) and fish (Johnson et al., 2017) in the region. Advection, rather than retention, is likely the defining feature of larval dispersal from FGB (Johnson et al., 2017).

Due to their relative geographic isolation and greater health compared to other western Atlantic reefs, the FGB have been proposed as a potential climate change refuge habitat (Hickerson et al., 2012; Davies et al., 2017; Studivan and Voss, 2018b). Climate refuges are thought to provide ecological or even evolutionary protection for a species or community during times of environmental change or instability. In general, in order for a coral reef to be an effective refuge, it should: (1) have relatively greater resistance or resilience to stress; (2) be capable of providing larvae to downstream habitats; and (3) be self-sustaining (Bongaerts et al., 2010; Davies et al., 2017; Kavousi and Keppel, 2018; Bongaerts and Smith, 2019). The stability of the coral reef community and isolation of the FGB satisfies the first criterion (Johnston et al., 2016), and several studies have suggested that the FGB provide coral recruits to downstream submerged banks (Garavelli et al., 2018; Studivan and Voss, 2018a,b), to Pulley Ridge (Olascoaga et al., 2018), to the Dry Tortugas (Studivan and Voss, 2018b), and to the Florida Keys (Lugo-Fernández et al., 2001; Davies et al., 2017), which would satisfy the second criterion. Here we have demonstrated several biophysical mechanisms thought to enhance retention of coral larvae at the FGB for species with considerably different life history traits. Due to their isolation, this local retention of larvae at the FGB may be a predominant source of coral recruitment, and these reefs may be largely self-sustaining. Assuming that conditions remain favorable for coral reefs at the FGB, the current study supports the hypothesis that these reefs could function as a refuge for Western Atlantic coral metapopulations experiencing disturbance. Our finding that LCEs play an important role in the retention of coral larvae at the FGB suggest that understanding how these ephemeral mesoscale features interact with micro- or habitat-scale oceanography and bathymetry is essential to understanding the persistence and resilience of these unique coral reefs.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available at https://github.com/seascapelab/FGB-eddies and by reasonable request to the corresponding author.

AUTHOR CONTRIBUTIONS

BL and DH conceived of and designed the experiments and analysis. BL performed all simulations and data analysis. All authors contributed to the interpretation of the results, writing the manuscript, and the manuscript revision, and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00372/full#supplementary-material

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REVIEW
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Artificial Reefs in the Northern Gulf of Mexico: Community Ecology Amid the "Ocean Sprawl"

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The northern Gulf of Mexico has been an important source for crude oil and natural gas extraction since the 1930s. Thousands of fixed platforms and associated equipment have been installed on the Gulf of Mexico continental shelf, leading to a pervasive 'ocean sprawl.' After decommissioning, 100s of these structures have been converted to artificial reefs under the federal 'Rigs-to-Reefs' program, in addition to artificial reefs specifically designed to enhance fisheries and/or benefit the recreational diving industry. Apart from a few natural banks, which reach to approximately 55 ft below the surface, artificial reefs provide the only shallow-water hard substrate for benthic organisms in the deeper waters of the northern Gulf of Mexico. This vast expansion in available habitat has almost exclusively occurred over a relatively short span of time (~50 years). The ecological interactions of artificial and natural reefs in the northern Gulf of Mexico are complex. Artificial reefs in general, and oil and gas structures in particular, have often been invoked as stepping stones for non-native and invasive species (e.g., *Tubastrea* cup corals, lionfish). The pilings are covered with fouling communities which remain largely unstudied. While the risks of these fouling organisms for invading natural reefs are being broadly discussed, other impacts on the ecological and economic health of the Gulf of Mexico, such as the potential to facilitate jellyfish blooms or increase the incidence of ciguatera fish poisoning, have received less attention. Artificial reefs also provide ecosystem services, particularly as habitat for economically important fish species like red snapper. Here we revisit the potential role of artificial reefs as 'stepping stones' for species invasions and for fisheries enhancement. Beyond concerns about ecological effects, some of these topics also raise public health concerns. We point out gaps in current knowledge and propose future research directions.

Keywords: oil and gas platforms, red snapper, lionfish, regal demoiselle, *Tubastrea*, jellyfish blooms, ciguatera, fouling communities

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INTRODUCTION

The northern Gulf of Mexico (nGoM) is home to nearly 2,200 active oil and gas platforms (BSEE/BOEM Data Center, 2019). In addition, there are almost as many artificial structures not currently used for oil or gas extraction, including 'reefed' oil and gas platforms, submerged vessels, reef balls and others (**Figure 1**; Broughton, 2012). These-human made structures create so-called 'ocean sprawl' (Duarte et al., 2013; Firth et al., 2016), altering the habitat by creating hard substrate, forming barriers to movement for some organisms and changing predator-prey interactions (Bishop et al., 2017). In 2016, the total number of artificial reefs in the nGoM (including active and inactive) amounted to 4,176 (NOAA, 2016).

Before oil and gas exploration, the seafloor was mostly sedimented, although the bathymetry of the continental slope is complex and frequently marked by domes, pockmarks, canyons, faults, and channels. The nGoM is additionally home to some of the best studied cold seep communities in the world (e.g., Fisher et al., 2007; Cordes et al., 2009) as well as coral banks and reefs. Known coral assemblages in the GoM range from phototrophic in the shallower portions to mesophotic and deep coral communities, down to more than 2,500 m in De Soto Canyon (Doughty et al., 2014). Shallower coral assemblages are often present on artificial structures (Bright et al., 1991; Sammarco et al., 2014a).

Near the edge of the continental slope off the coasts of Texas and Louisiana, multiple banks formed by underlying salt diapirs support natural reefs. The best known of these are the East and West Flower Garden Banks, which constitute the core of the Flower Garden Banks National Marine Sanctuary (FGBNMS). The Flower Garden Banks are not only the northernmost coral reefs of the greater Caribbean but also the most isolated and among the healthiest with regard to coral cover (Hickerson et al., 2012; Johnston et al., 2016a). Located within the sanctuary boundaries, High Island 389A (HI-389A) is a decommissioned platform installed in 1981 located on a 20-acre artificial reef site in a water depth of 410 feet (**Figure 2**). The structure has recently (July 2018) been reefed by removal of the top 65 ft below the water line. The FGBNMS further includes Stetson Bank, located closer to the shore. The FGBNMS Advisory Board recently voted to expand the sanctuary boundaries to include 14 additional banks. Approximately 150 platforms are located within 25 miles of the current sanctuary borders (US Department of Commerce, 2012). The proposed new boundaries as set out in the Sanctuary Expansion DEIS will incorporate three additional oil and gas production structures.

Natural and artificial reefs are interspersed with each other in the nGoM. This network of habitable 'islands' separated by stretches of uninhabitable (or less preferred) ground, provides unprecedented opportunities for organismal movement between these two habitat types. In this context, the geographic isolation of the FGB is a double-edged sword. On the one hand, it may provide relative protection from some dangers that threaten other Caribbean reefs, such as coral pathogens, nearshore anthropogenic impacts, and invasive species. On the other hand, isolation may hinder recruitment and adult replacement, especially after cases of local coral mortality. Despite isolation, some invasive species, most notably lionfish, have become established at the FGB (Johnston et al., 2016b). Oil and gas structures and other artificial reefs are often regarded as 'stepping stones' for invasives (Fenner, 2001; Sammarco et al., 2004, 2012a). However, this stepping-stone theory is ecologically complex, as much of the fauna on platforms is a typical 'fouling community' as opposed to a true reef community (Page et al., 2010). For example, artificial structures are more often dominated by small, flexible hydroid colonies rather than reef building corals. However, some species overlap between the two habitat types does exist. Utilization of these different habitat types by organisms with different life histories and ecological characteristics has far-reaching implications for marine conservation as well as commercial and recreational fisheries.

Previous reviews on the ecological roles of artificial reefs either had a national (Broughton, 2012) or global (Bull and Love, 2019) scope. The purpose of this review is to focus on the nGoM and summarize our current state of knowledge of the habitat preferences of different organismal groups inhabiting artificial reefs as well as functional connectivity between artificial and natural reefs. We will discuss the implications of the existing knowledge for ecosystem health and society, and identify knowledge gaps and future research directions.

Functional connectivity is here defined as the movement of organisms or particles among different locations or habitats (Bishop et al., 2017). When focusing on populations of individual species, the term population connectivity is used; multiple connected populations form a metapopulation (Cowen and Spunaugle, 2009). We consider the area offshore from the coasts of Texas, Louisiana, Mississippi, Alabama and Florida between approximately longitude 97° and 81° W and latitude 24° and 30° N (**Figure 1**). This area mostly encompasses the coastal areas to the continental slope, with a maximum depth of about 3,000 m. The review does not cover the effects of platform installation, operation and removal on soft sediment benthic communities, or the toxicological impacts of accidental spills or produced water, as these aspects have been reviewed elsewhere (e.g., Broughton, 2012; Cordes et al., 2016).

Prior reviews on connectivity between natural and artificial reefs in the nGoM were generally focused on particular taxonomic groups, such as corals (e.g., Sammarco et al., 2004) or commercially important fish (e.g., Shipp and Bortone, 2009; Cowan et al., 2011). This review has a wider taxonomic scope and broader view of ecological implications, in particular highlighting emerging concerns for which we lack sufficient knowledge. In light of the continuing proliferation of artificial reefs in the region, ongoing fisheries trends and the recent detection of previously unreported species (e.g., Bennett et al., 2019; Figueroa et al., 2019), this review is timely and can serve as a baseline to evaluate future developments. It is our hope that the information provided will guide future research efforts and management decisions.

CONNECTIVITY: STEPPING STONES, METAPOPULATIONS, RESILIENCE, AND REPLACEMENT

Connectivity and resilience in dispersal networks are generally correlated, as more densely connected habitats are more likely

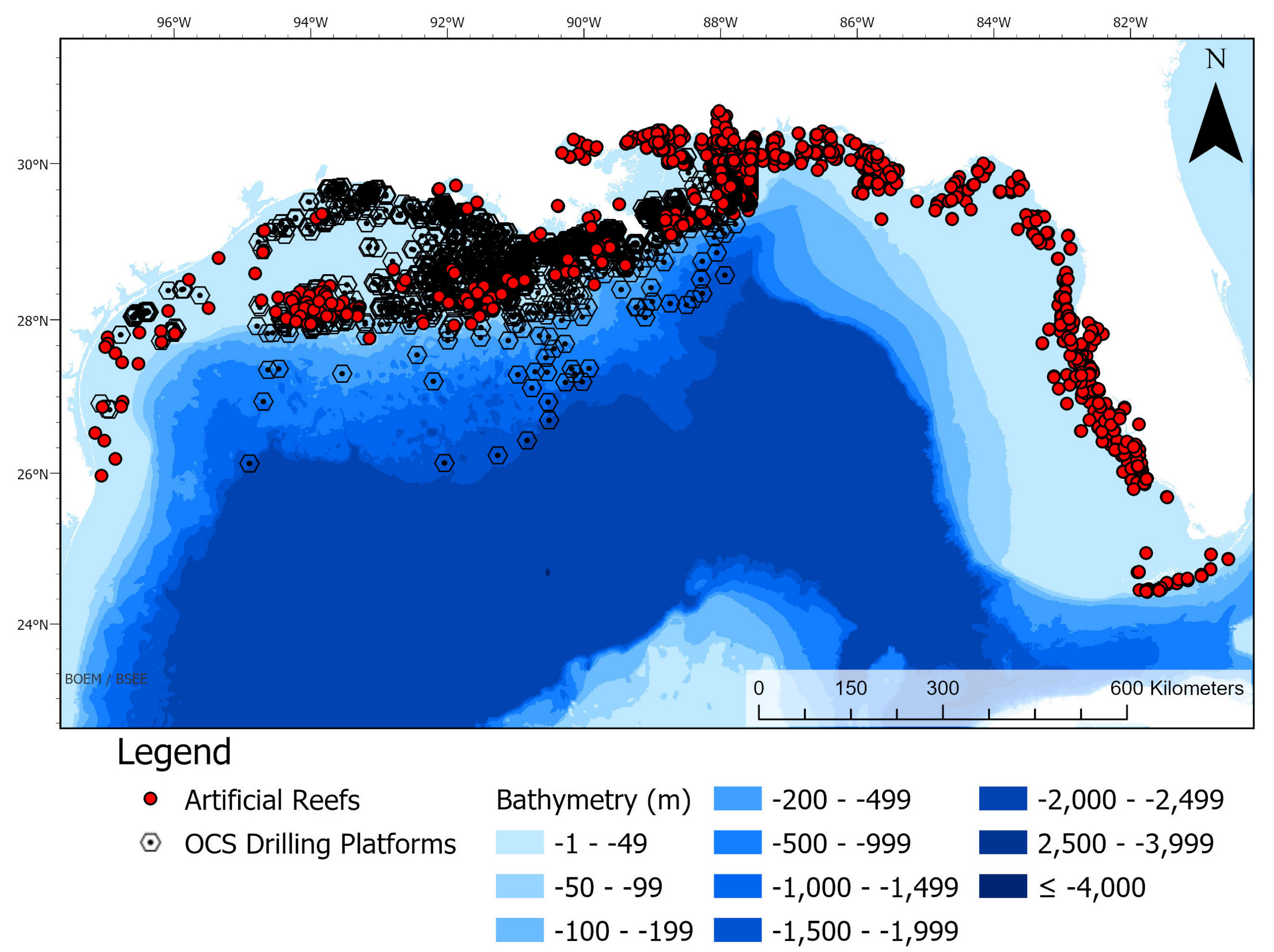

FIGURE 1 | Total artificial reefs of nGoM (red) and outer continental shelf drilling platforms (black) shown with bathymetry in meters. Data from NOAA (2016) and BSEE/BOEM Data Center (2019).

to avoid recruitment failures. The 1000s of artificial structures in the GoM expand the habitats for naturally occurring (Sammarco et al., 2004, 2012b; Kolian et al., 2017), invasive (Fenner and Banks, 2004; Sammarco et al., 2012b; Dahl and Patterson, 2014), and fouling communities in the region, and simultaneously increase the density of the dispersal networks of these communities.

The metapopulation effects of artificial structures have been investigated in other coastal oceans, and support the notion that these structures support benthic, epibenthic, and migratory communities in complex ways. Paxton et al. (2019) found that artificial reefs on the subtropical US Atlantic continental shelf disproportionately support highly mobile tropical planktivorous and piscivorous fishes when compared to natural reefs, and they expand the biogeographic ranges of those species into higher latitudes. In the North Sea, artificial structures can increase the resilience of threatened coral species, both within the connected communities on artificial structures, as well as in nearby naturally occurring communities (Henry et al., 2018). It is reasonable to assume that artificial structures in the GoM increase metapopulation resilience for a diverse set of species – including historical natives, native and non-native invaders, and those species unique to fouling communities.

However, artificial structures are inherently more ephemeral than most naturally occurring comparable habitats in the nGoM. These structures are routinely decommissioned and subsequently removed, or reefed. Even when reefed, artificial structures and associated communities may undergo physical degradation and/or community succession (Sammarco et al., 2014a), which suggests the populations found on artificial structures are dynamic in both space and time. Metapopulation resilience is sensitive not only to the density of the dispersal network, but also to the rates of colonization and extinction at individual patches (Hanski and Ovaskainen, 2000). Thus, the assumed density of connectivity among artificial structures must be weighed against these rates when assessing the persistence of metapopulations supported by artificial structures. To date,

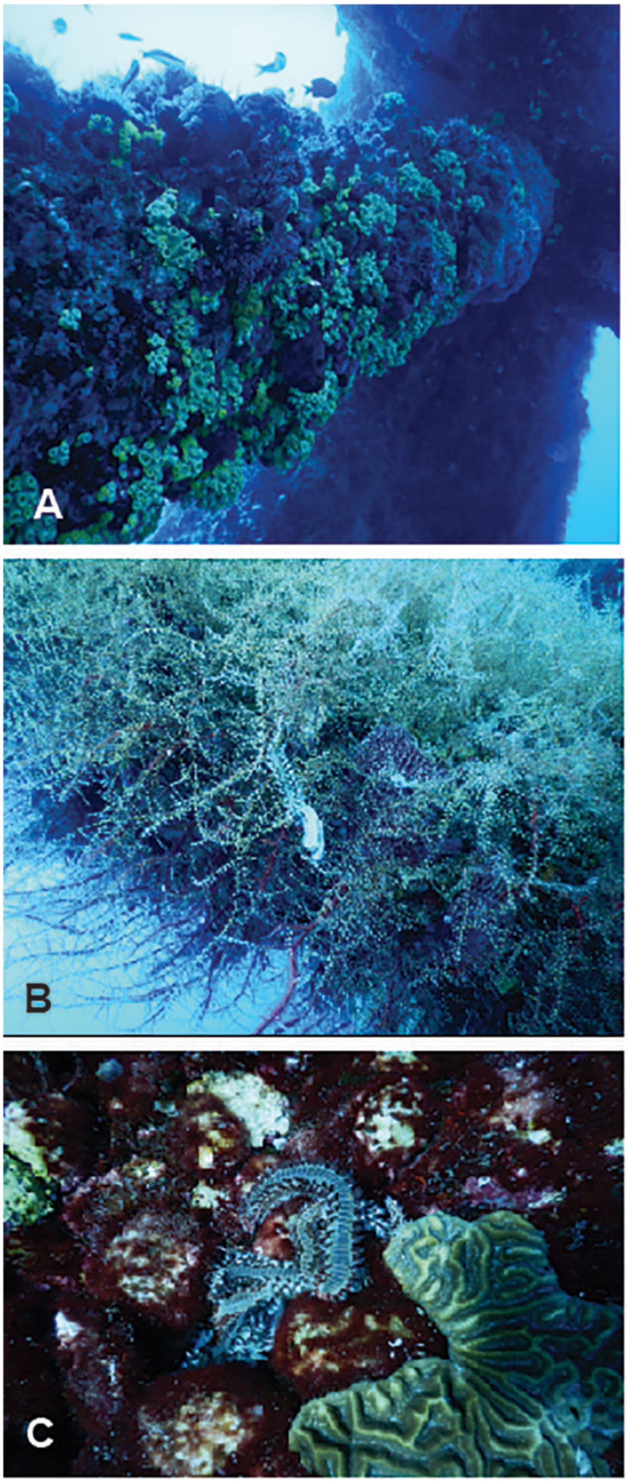

FIGURE 2 | Examples of the fouling community and associated motile fauna on High Island 389A (HI-389A). **(A)** Numerous colonies of *Tubastrea coccinea* shown on the underside of a horizontal beam of at 37 m. **(B)** The hydroid, *Thyroscyphus* sp., with a bearded fireworm, *Hermodice carunculata*, on top on a diagonal structure support beam on HI389-A at 20 m. **(C)** Five bearded fireworms, *H. carunculata*, in close proximity to a scleractinian coral (*Pseudodiploria strigosa*) on a horizontal beam of HI389-A at 9 m.

rates of colonization, extinction, and larval connectivity among artificial structures in the GoM are not well-understood; however, data are available on the rates of decommissioning of artificial structures, which could help to inform the persistence of these unique communities.

As noted elsewhere in this review and in previous studies, the artificial structure communities in the GoM are not identical to, and not entirely different from, adjacent natural habitats. The hypotheses are usually that, following local extinctions on natural habitats, recolonization may occur with larvae from nearby artificial structures (Sammarco et al., 2012b), or that fouling communities will not establish on naturally occurring hard substrates. Although invasives that occupy artificial structures are routinely found on the FGB (e.g., *Tubastrea coccinea*, Fenner and Banks, 2004), a possibility that has not been fully addressed to date is that invasive or competitive species that occupy artificial structures could supplant naturally occurring species on natural habitats following perturbation or local extinction. A specific example may be the potential for alternative stable states between coral and sponge communities (reviewed in Norström et al., 2009). Sponges of the genera *Cliona* and *Chondrilla* have been shown to supplant hard corals following coral mortality events and prevent the recolonization of coral. Sponge communities on artificial structures in the GoM can be diverse (Rützler et al., 2009), but the distributions of sponges in those genera on artificial structures is not currently known. Following a perturbation to the coral communities on the FGB, colonization from sponge communities on nearby artificial structures may be more likely than colonization of hard corals from reefs that are further away.

Fouling Communities

Fouling communities, defined as assemblages of sessile organisms and associated species with limited mobility growing on human-made structures, are vastly understudied on offshore artificial structures in the GoM. The term 'fouling community' has a negative connotation, implying that these organisms are unwanted and destructive. On vessel hulls, sessile organisms increase drag and thereby reduce vessel speed and fuel efficiency. On oil and gas platforms, fouling communities can greatly increase the weight of the structure, as well as the diameter and surface roughness of the platform members (Page et al., 2010) (**Figure 2**), affecting the hydrodynamic loading of the platform and interfering with visual inspection. However, fouling communities on platforms provide ecosystem services, as prey items and ecosystem engineers of complex habitat for other sessile and motile organisms (Daigle et al., 2013), including commercially important fish species. The establishment of fouling communities is largely driven by the relative concentrations of propagule stages present in the water column but varies depending on many physical characteristics, such as light, temperature, salinity, pressure, spatial orientation and current regimes, as well as the interactions between biotic and abiotic factors (Terlizzi and Faimali, 2010).

As the vast majority of oil and gas platforms worldwide are constructed in soft substrate, the fauna on the structure tends to be inherently different from the surrounding benthic fauna. However, even if platforms are erected in the vicinity of natural hard substrates, the fouling fauna is generally distinctive (Page et al., 2010). This may be a result, in part, of the structure reaching from the seafloor to the surface allowing for increased primary producer activity and bioaccumulation in a location where it would not otherwise be possible (Daigle et al., 2013). Regardless, artificial structures expand the habitat of distinct fouling communities into areas of both soft and hard substrates on the continental shelf of the GoM.

On oil and gas platforms, shallow fouling communities are generally dominated by a few taxa with hardened shells. In the GoM barnacles tend to dominate the nearshore structures, whereas bivalves are more prevalent on offshore structures, in addition to extensive growth of hydroids (**Figures 2B**, **3**) (Lewbel et al., 1987; Bull and Kendall, 1994; Page et al., 2010).

These structures can become colonized and integrated into fouling metacommunities fairly rapidly. Nearly 1 year after the installation of HI-389A, surveys were conducted from the surface to the 37 m horizontal supports and describe the establishment of fouling mats with hydroids and macroalgae (Boland, 2000). Bearded fireworms (*Hermodice carunculata*) and two species of sea urchin (*Diadema antillarum* and *Arbacia punctulata*) were present in noticeable amounts at this time (Boland, 2000). Hermatypic corals were also recorded on HI-389A in 1990, 9 years after installation, supporting the idea that these rigs provide settling surface for reef-builders (Boland, 2000).

Documented Invasions

There is an ongoing debate whether artificial reefs in the nGoM act as 'stepping stones' for non-indigenous or invasive species. In most cases, there is no definitive answer as to whether a non-indigenous species would be present in the area if there were no artificial reefs. Knowledge of a species' life history and its behavior in other regions can provide some insight about the invasion history and may guide future management decisions. Here we review the evidence for a few non-indigenous taxa and their presence on natural and artificial structures in the nGoM.

Lionfish

Two species of Indo-Pacific lionfish, the red lionfish (*Pterois volitans*) and the devil firefish (*Pterois miles*) are established throughout the Caribbean, and their detrimental effects on native fauna are well documented (reviewed in Albins and Hixon, 2013; Côté et al., 2013). *P. volitans* and *P. miles* are morphologically similar and can only be distinguished by different numbers of dorsal and caudal spines, but their distinct genetic signatures confirm them as separate species, with *P. volitans* representing 93% of the sequenced specimens (Hamner et al., 2007). Genetic diversity within each species is low, indicating single, rapid invasions (Hamner et al., 2007).

Lionfish were first sighted in the nGoM in 2010 (Nuttall et al., 2014). By 2013, their numbers had increased exponentially on both natural and artificial reefs, but their densities on artificial reefs were two orders of magnitude higher and they exhibited a more varied diet than on natural reefs (Dahl and Patterson, 2014). Their rapid growth rates suggest that biomass is increasing even more rapidly than the numbers of individuals (Dahl and Patterson, 2014).

Some contributing factors to the success of *Pterois* spp. in the GoM include: buoyant egg masses and long-lived larvae [28 days (Ahrenholz and Morris, 2010; Morris et al., 2011)], limited number of natural predators (Mumby et al., 2011; Diller et al., 2014), rapid growth rate (Green et al., 2011), and high reproductive success (Albins and Hixon, 2013). Fogg et al. (2017) examined the reproductive biology of *P. volitans* in the nGoM. Comparative reproductive data from the native range of the species are surprisingly sparse, but it appears that reproductive output is higher in the nGoM than in the native range.

NOAA, partnering with several other organizations, has been conducting annual 'Lionfish Invitationals' since 2015 to document and capture lionfish in the FGBNMS. While this effort will greatly contribute to the scientific study of lionfish in the nGoM, it likely does not significantly reduce their populations. Nuttall et al. (2014) detected nearly 400 lionfish, including both species, in mesophotic environments down to 112 m on 14 banks surveyed by ROV, with the highest counts between 80 and 90 m depth. At the time of the study, the eastern banks were more heavily invaded than the western banks. Three of the western banks (Horseshoe Bank, 29 Fathom Bank and Bright Bank) seemed to still be free of lionfish.

Paxton et al. (2019) provide indirect support that artificial reefs have contributed to the lionfish invasion in the nGoM. Their survey of fish abundance and diversity on 30 artificial and natural reefs off the coast of North Carolina show that tropical fish at their distribution edge, particularly planktivorious and piscivorous species, have higher abundances on artificial than on natural reefs. They conclude that artificial structures probably act as stepping stones for northward expansion of motile tropical fish species in the face of climate change.

The Regal Demoiselle, *Neopomacentrus cyanomos*

This small (<10 cm) species of damselfish is the latest documented newcomer in the nGoM, including the FGBNMS (Bennett et al., 2019; Nuttall et al., 2019). The Indo-Pacific/Indian Ocean species was first reported from natural reefs in the southern GoM off the coast of Veracruz in 2013 (González-Gándara and de la Cruz-Francisco, 2014). Johnston and Akins (2016) modeled the invasive potential of this species and concluded that currents in the southern GoM were not conducive to long-distance transport of *N. cyanomos* larvae. Nonetheless, around the same time, *N. cyanomos* was reported from Cayo Arcas on the southwestern corner of Campeche Bank, ca. 350 km distant from the original sighting (Robertson et al., 2016). In this area it was reported as 'superabundant' on the coral reef as well as on an oil platform which housed 'thousands' of individuals (Robertson et al., 2016). Subsequent reviews of video footage showed that the species was already present in 2013, but remained unrecognized at the time (Robertson et al., 2016).

In 2017, Bennett et al. (2019) surveyed 138 sites, including natural and artificial reefs, off the Alabama coast. While no *N. cyanomos* were sighted on natural reefs, several hundred of

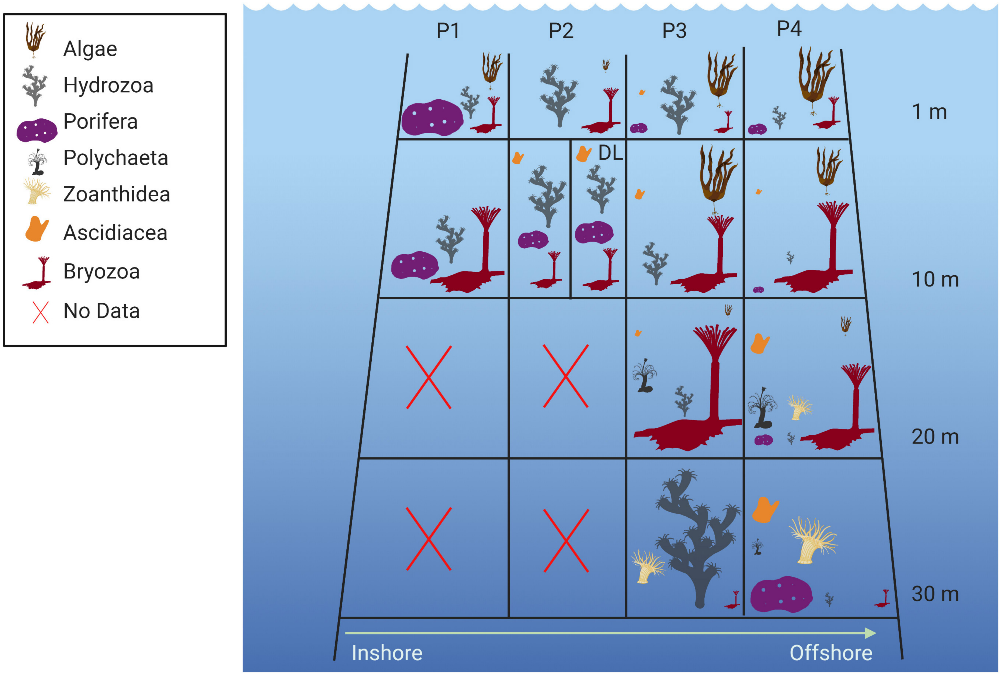

FIGURE 3 | Zonation of fouling communities on four platforms (P1–P4) off the Louisiana coast from Lewbel et al. (1987). The size of the respective symbols represents the relative contribution of the taxon to the percent cover. The platforms were located in 12 to 46 m of water and fouling communities were sampled at 1 and 10 m depth at all platforms and additionally at 20 and 30 m depth at P3 and P4. At P2, an additional sampling station (P2-DL) was established above a produced water outlet. Note that scleractinian corals were not sampled on P1–P4 but were reported (but not quantitatively sampled) from other platforms in the area.

the non- native damselfish were discovered in groups of 10–35, primarily juveniles, on five petroleum platforms and one concrete structure. It is unclear whether they reached these locations via ship ballast water (the Ports of Mobile, AL and Tampico, Veracruz are well-connected through shipping routes) or whether early life stages may have been transported there via the Loop Current. Although it was initially uncertain whether *N. cyanomos* would be able to survive the colder winter water temperatures in the nGoM, Bennett et al. (2019) confirmed their presence in 2018. In late June, 2018, NOAA reported the presence of *N. cyanomos* at Stetson Bank where schools of several 100 individuals were observed on multiple pinnacles and inside sponges (Nuttall et al., 2019). The ecological impact of this most recent invasion is difficult to predict, but the possible displacement of native damselfish species is a concern.

Cup Corals: *Tubastrea* spp.

Tubastrea coccinea, also known as the orange cup coral, is an Indo-Pacific non-zooxanthellate scleractinian stony coral (Sheehy and Vik, 2010) which was introduced to the Caribbean in 1943 and in the GoM in the 1960s. It now has a pantropical distribution and is considered the most abundant scleractinian species in both the tropical Pacific and Atlantic (Cairns, 1994). A second species, the green cup coral *Tubastrea micranthus*, was first detected in 2006 on a single platform (GI-93-B) off the coast of Louisiana (Sammarco et al., 2010), but had appeared on eight additional platforms within a 20 mile radius of GI-93-B by 2014 (Sammarco et al., 2014b). The two species show clear depth preferences: whereas *T. coccinea* is generally found above 78 m, *T. micranthus* occupies deeper portions of the platforms, down to 138 m (Sammarco et al., 2013). Recently, a third species, the Indo-Pacific *T. tagusensis,* has been reported for the first time on offshore plantforms in the GoM (Figueroa et al., 2019). Although sampling was limited, in some sites *T. tagusensis* seemed to outnumber *T. coccinea*. Morphologically, *T. tagusensis* is very similar to *T. coccinea,* and although it can be distinguished from its congener using molecular tools, misidentification of *T. tagusensis* as *T. coccinea* may have occurred in the past. This complicates attempts to understand the history and timing of *T. tagusensis* GoM invasion. If *T. tagusensis* has only recently invaded the GoM, Figueroa et al. (2019) argue it may be expanding rapidly and potentially outcompeting *T. coccinea*, thus posing a new threat to the GoM ecosystems.

Tubastrea coccinea exhibits a predominantly hermaphroditic reproduction, with typical non-feeding cnidarian larvae, planulae that settle on the appropriate substrate after 1 to 3 days. However, the planulae can survive and be competent for up to 100 days (Fenner, 2001), thus showing massive potential for dispersal. *T. coccinea* has multiple reproductive cycles per year, and can also reproduce asexually, all traits that generally favor invasive species success. Assemblages of *T. coccinea* have been reported fouling hulls of boats (Cairns, 2000) and the species is believed to have been introduced by shipping. In the GoM, after being reported on oil and gas platforms, it was reported on a range of human-made structures, such as sunken vessels and other artificial reefs (Shearer, 2009). Although there is evidence that *T. coccinea* takes advantage of newly formed habitat, it can sometimes be found on established reef communities, including in the FGBNMS. Removal experiments in the FGBNMS have shown that *T. coccinea* has a very rapid recolonization rate (Precht et al., 2014). Off the coasts of Mexico, Texas, and Louisiana, it has been shown to colonize artificial reefs and oil rigs within a few years of their installation (Fenner, 2001) and it has been rapidly expanding its invasive range (Creed et al., 2017). On oil and gas platforms in the nGoM, *T. coccinea* is most abundant in relatively shallow waters, peaking at about 17 m (Sammarco et al., 2004), although it can be found at deeper sites (Sammarco et al., 2013). Its depth distribution may be limited by environmental factors such as sedimentation and turbidity associated with river discharge (Sammarco et al., 2013).

Tubastrea coccinea is an excellent competitor for space and, in parts of its invasive range, it has been shown to outcompete local coral species (Creed, 2006; Lages et al., 2011; Riul et al., 2013) and cause tissue necrosis to colonies that come in contact with its polyps (dos Santos et al., 2013). It can also impact mussel beds (Mantelatto and Creed, 2015), and alter local community structure and biodiversity (Lages et al., 2011).

Acorn Barnacles

Anthropogenic transport of acorn barnacles (Cirripedia) probably dates back many centuries, as they are some of the most common fouling organisms on ship hulls. Additionally, their nauplius larvae are long-lived and able to survive long passages in ballast water (Cohen et al., 2014). As such, the native distributions of most species are hard to determine and species are often characterized as 'cryptogenic' (of unknown geographic origin). Like many other fouling organisms, most barnacle species are difficult to identify, especially because many characteristics of their shell and appendages can be plastic depending on environmental conditions (Cohen et al., 2014). Carlton et al. (2011) list four non-native species of barnacles in the GoM and reconstruct their invasion history. In chronological order, the four species are *Balanus trigonus*, *Amphibalanus amphitrite*, *Amphibalanus reticulatus,* and *Megabalanus coccopoma*. *B. trigonus* has been established the longest, probably introduced in the mid- to late 1800s on ship hulls and is now abundant throughout the nGoM (Gittings, 1985; Carlton et al., 2011). The two *Amphibalanus* species first appeared in the 1950s (Carlton et al., 2011). *M. coccopoma* is native to the eastern Pacific and was first reported in the GoM by Perrault (2004) from jetties in Louisiana. *M. coccopoma* is a large barnacle with a characteristically pink shell. Cohen et al. (2014) examined mitochondrial sequence divergence in this species throughout its native and invasive range. Their study revealed that there were likely multiple invasions in the Southeastern US and Brazil. The species is now common on oil and gas structures (Gittings, 2009). Other *Megabalanus* species may be established in the GoM as well.

The environmental implications of introduced barnacles are not well-understood because there are often no baseline data from before the invasion. Large barnacles like *M. coccopoma* may be particularly successful in competing with smaller species, as they are able to occupy space faster and possibly filter feed more efficiently. Fouling by large barnacles on artificial structures can also add substantial weight and volume to a structure and affect its hydrodynamic properties. The survival and northern expansion of the tropical *M. coccopoma* may be limited by water temperature (Crickenberger et al., 2017), but warming temperatures may facilitate its northward spread in the future.

Tunicates: *Didemnum perlucidum*

The invasion history of the colonial tunicate, *Didemnum perlucidum,* in the GoM remains poorly documented. Culbertson and Harper (2002) report that between 1998 and 2000, divers observed a thin white layer of this encrusting species that almost completely covered structure High Island A-532 from 27 m to least 42 m depth (the depth limit of the SCUBA surveys). High Island A-532 is located 12 nautical miles from Stetson Bank (part of the FGBNMS) in 58 m of water and was installed as an artificial reef in 1997. *D. perlucidum* was also observed on several nearby structures within 12 nautical miles (Culbertson and Harper, 2002). The species can be characterized as cryptogenic. It was originally described from the island of Guadeloupe (Monniot, 1983), but it is uncertain whether its native range included the Caribbean. *D. perlucidum* is distributed worldwide in tropical and subtropical waters and is most prevalent on artificial structures (Dias et al., 2016). Its most recent appearance has been in Western Australia where it was first detected in 2010 and has since spread to the Northern Territories (Smale and Childs, 2012; Bridgwood et al., 2014; Dias et al., 2016). Ascidians have very short-lived larval stages, and introductions are therefore likely a result of the propagation of adults from fouling communities on boat hulls or rafting debris. Dias et al. (2016) studied genetic diversity of *D. perlucidum* worldwide, including a population from the GoM (Veracruz, Mexico), using cytochrome *c* oxidase subunit I (COI) sequence data. They found that genetic diversity is low, with a single haplotype (Haplotype 1) present in most locations. This likely indicates that most of the populations are relatively recent introductions. However, as *D. perlucidum* reproduces both sexually and asexually through budding, the genetic uniformity may be partially attributable to clonal organization. The GoM population actually included Haplotypes 1 and 3 but it is unclear whether the two haplotypes represent two separate introductions or local speciation. More sensitive molecular markers are needed to resolve finer scale population differentiation for this species.

EMERGING CONCERNS

Artificial reefs may not only provide habitat to newly arriving species, but may also promote habitat-limited native species which could lead to shifts in trophic structure and ecosystem function in the Gulf of Mexico. Furthermore, some of these species, notably jellyfish and *Gambierdiscus* species dinoflagellates, may raise public health concerns if their abundance increases, as is likely under predicted climate change scenarios.

Implications of Oil and Gas Structures for Jellyfish Blooms

Jellyfish (Scyphozoa, Cnidaria) go through seasonal pulses in response to environmental triggers, and rapidly produce enormous biomass that impacts the marine food chain. Three jellyfish species have formed massive blooms in the GoM: the moon jelly, *Aurelia* sp. 9; the Atlantic sea nettle, *Chrysaora quinquecirrha,* and the Australian spotted jellyfish, *Phyllorhiza punctata* (Graham, 2001; Robinson and Graham, 2013; Chiaverano et al., 2016; Frolova and Miglietta, 2020). Patches of *P. punctata* covering up to 150 km and composed of an estimated 5.6×10^6 medusae have been reported. These super swarms threaten large commercial fisheries and can cause millions of dollars in damage (Graham et al., 2003).

In contrast to the relatively large pelagic medusa stages, the benthic scyphozoan polyps are microscopic and have never been detected in the GoM. Because most of the naturally available benthic habitat in the GoM is soft sediment and unsuitable for polyp attachment, it has been hypothesized that the polyps have successfully colonized artificial substrates, such as oil and gas platforms (Graham et al., 2003; Duarte et al., 2013). A recent body of literature indicates that artificial substrates, including oil and gas platforms, are suitable substrate for scyphozoan polyps (van Walraven et al., 2016; Dong et al., 2018) and play an important role in the frequency and magnitude of jellyfish blooms (Duarte et al., 2013). Moreover, there is evidence that the removal of artificial structures may limit jellyfish bloom occurrence (Jin et al., 2017) and that artificial platform-originating planulae (cnidarian larval stage) play an important role in sustaining local jellyfish populations (Vodopivec et al., 2017).

Occurrence of Ciguatera Toxin-Producing Dinoflagellates

The complex fouling communities on artificial structures also represent potential habitat for benthic/epiphytic dinoflagellates of the genus *Gambierdiscus*, the causative agent of ciguatera fish poisoning (CFP). Ciguatera is the most common foodborne illness related to finfish consumption (Friedman et al., 2017), with estimates of up to 500,000 poisonings per year (Fleming et al., 1998) in tropical and subtropical regions. *Gambierdiscus* dinoflagellates are well-known from coral reef areas, where they are found primarily on the surface of macroalgae. They are consumed by herbivores and detritivores, and the toxins they produce persist through successive trophic levels, eventually contaminating large, mobile, predatory finfish species that are targeted in many recreational and commercial fisheries. Economic impacts associated with ciguatera, ranging from loss of fishing revenue to morbidity from illness, can be considerable; the annual impact of ciguatera in the U.S. was estimated to be in excess of $20 million (Anderson et al., 2000).

While several island regions of the U.S. and its territories (Puerto Rico, the U.S. Virgin Islands, Hawaii) are considered to be hyperendemic for ciguatera, the only ciguatera-endemic mainland region is the Florida coast (Lehane and Lewis, 2000). In contrast, the nGoM has been considered to be at low or unknown risk for ciguatera (Lewis, 2001) because it comprises mainly soft sediment benthos that is not hospitable for *Gambierdiscus* spp. and water temperatures that are thought to be too low for vigorous growth (Kibler et al., 2017). In addition to the ongoing proliferation of artificial hard substrate, there has also been a steady increase in sea surface temperatures over the past decades (Muller-Karger et al., 2015). Villareal et al. (2007) reported the first findings of *Gambierdiscus* spp. in the northern GoM, from six oil platforms and also on floating *Sargassum* seaweed. The authors also hypothesized that the increase in artificial structure in the GoM would facilitate colonization of the area by *Gambierdiscus* spp., thereby aiding range expansion as sea surface temperatures warmed.

Since that first record in the nGoM, diverse *Gambierdiscus* communities have been reported within the FGBNMS in the nGoM (Tester et al., 2013). Five of the seven species known from the Caribbean were found at the east and west Banks, at depths > 45 m, and the authors estimate that conditions at the FGBNMS would provide 200 days of optimal growth conditions annually. The diversity and widespread distribution across the Banks suggests that these communities are able to persist throughout the year. Sea surface temperatures are predicted to continue increasing in the region (Moore et al., 2008), which would increase the number of optimal growing days for *Gambierdiscus* spp. in the nGoM (Tester et al., 2013), and therefore the risk for ciguatera (Tester et al., 2010; Gingold et al., 2014). Another risk factor is range expansion due to warmer waters. As sea surface temperatures increase, *Gambierdiscus* species distributions may shift northward (Hallegraeff, 2010; Parsons et al., 2012), facilitated by the presence of artificial structures in the GoM, which can act as 'stepping stones' for expansion.

Ciguatera cases are routinely reported from the nGOM region. A review of case reports and surveys in Florida estimated the annual incidence at 5.6 cases per 100,000 population, although the incidence rates are higher for the counties in which it is most common (Radke et al., 2015). Export of fish means that ciguatera cases are not always restricted to the source area (CDC, 2009). In the northern GoM, ciguatera cases were reported in 1998 from fish caught off of an oil platform in the region (CDC, 2006) and in 2007 from a gag grouper caught at the FGBNMS (FGBNMS, 2019). The 2007 event was one cause for the FDA to issue a 2008 ciguatera toxin alert for fish caught in the nGoM near the FGBNMS. This later resulted in an industry guidance document for seafood processors, cautioning them about purchasing reef fish caught in areas that were considered to be at risk for ciguatera, including the GoM and the FGBNMS specifically (U.S FDA, 2013). This guidance remains in effect today.

It is clear that the causative agents of ciguatera, *Gambierdiscus* spp., are present throughout the GoM, and that they become sufficiently abundant, at least periodically, to result in toxic fish and human poisonings. Predictions of future risk are difficult because we have so little information on *Gambierdiscus* spp. in the nGoM, which harbors the greatest density of artificial structures. *Gambierdiscus* dinoflagellates occur in multispecies assemblages, and the level of toxicity varies between species (Pisapia et al., 2017), thus both community composition and relative abundance affect ciguatera risk. However, there have been no quantitative measures of *Gambierdiscus* species diversity and abundance from the GoM. We also do not know whether nGoM populations are long-term residents or recent immigrants, and if they are locally sustaining or depend on dispersal from hydrographically connected regions. Populations of *Gambierdiscus* spp. in the US Virgin Islands and the Florida Keys show significant genetic differentiation (Sassenhagen et al., 2018), which suggests that *Gambierdiscus* spp. populations may be fairly isolated. To understand the likelihood and consequences of range expansion in the region, we need to understand the current community composition and distribution within the GoM, the occurrence and routes of dispersal, and the connectivity of nGoM populations to other 'pockets' of *Gambierdiscus* spp. in the Gulf and Caribbean.

FISHERIES ENHANCEMENT

The primary argument in favor of artificial reefs is the enhancement of fisheries, including the recovery of overfished populations (Pickering and Whitmarsh, 1997; Shipp and Bortone, 2009; Bull and Love, 2019). There are two competing hypotheses about the role of artificial reefs for fish stocks (Bohnsack and Sutherland, 1985; Bohnsack, 1989; Pickering and Whitmarsh, 1997): the production hypothesis states that artificial structures increase fish stocks in an ecosystem by providing additional shelter and food, while the attraction hypothesis posits that artificial structures attract fish from nearby areas by providing shelter and food, thus only leading to a redistribution of the existing fish stock.

The red snapper (*Lutjanus campechanus*) fishery, dating back to the mid 1800s, is one of the most important in the GoM, and its history has been reviewed in several recent publications (Shipp and Bortone, 2009; Cowan et al., 2011; Bull and Love, 2019). Other commonly fished species associated with artificial reefs in the nGoM are gray snapper (a.k.a. mangrove snapper, *Lutjanus griseus*, Fischer et al., 2005); vermillion snapper (*Rhomboplites aurorubens*; Allman, 2007), red grouper (*Epinephelus morio,* Bull and Kendall, 1994), greater amberjack (*Seriola dumerilii,* Stanley and Wilson, 1989) and gray triggerfish (Herbig and Szedlmayer, 2016). Artificial reefs are often cited as the primary reason for the recovery of red snapper stocks after the collapse of the commercial fishery in the 1980s (e.g., Shipp and Bortone, 2009), but this notion has repeatedly been called into question. Stanley and Wilson (2000) estimated that artificial reefs have increased the available snapper habitat in the nGoM by only 4.1%, and (Cowan et al., 2011) argued that the recovery only commenced recently, although artificial reefs have existed for decades prior.

When evaluating the impact of artificial reefs on fish populations in the nGoM, the type of reef, location, density, depth and vicinity to other natural and artificial reefs are important factors to consider. There is evidence (Ajemian et al., 2015) that standing platforms support the highest species richness. In this context, a platform depth of around 50 m has been reported to be the most conducive to enhancing fish stocks (Ajemian et al., 2015), likely because this depth represents a transition between coastal and offshore zones. However, there is also evidence of a negative correlation between fish biomass and reef density (Strelcheck et al., 2005). Fish population surveys conducted at HI-389A, a recently reefed platform near the east FGB, found significant overlap in fish community composition between the natural and artificial reefs, but species richness on the artificial structure remained lower than on the natural reef, despite their geographic vicinity (Rooker et al., 1997). Similarly, new artificial reefs deployed near existing natural habitats housed fewer juvenile red snapper than those deployed at larger distances (Mudrak and Szedlmayer, 2012).

These findings show that there is evidence for both production and attraction of fish to artificial structures. Which process dominates can greatly vary temporally and spatially. Broughton (2012) argues that rather than focusing on the dichotomy between production and attraction, a broader evaluation of the ecosystem function of artificial structures and their wide-ranging effects on fisheries is necessary (see Research Priority 3); but there is little doubt that artificial structures have become important components of fisheries species demographies in the GoM.

FUTURE RESEARCH PRIORITIES AND CONCLUSION

We have reviewed the current literature on the roles of artificial reefs in the nGoM in facilitating the establishment of non-native species, promoting population increases of previously habitat-limited species, and their impact on fisheries. There are still large gaps in our understanding of the organismal communities inhabiting the artificial structures that are a prominent part of the nGoM ecosystem, and their interactions with established natural communities like those at the FGBNMS. Based on our review, we have identified three research priorities aimed at improving our understanding of the community ecology of artificial reefs in the nGoM (**Table 1**). For each, we outline potential research approaches, with an emphasis on novel techniques that can be used to provide insight to long-standing questions.

Priority 1

Understand the taxonomic composition of communities on both artificial and natural reefs and how it varies in space and time.

Rationale

We have summarized the evidence for the invasion of some species, but other invasives may have gone unnoticed, as thorough taxonomic surveys have been and continue to be rare. Repeated and continual sampling is critical for detecting new invasions and expansions of existing ones, as well as the appearance of native taxa at new sites. This is especially important for taxa of public health and economic concern, such as jellyfish (see section "Implications of Oil and Gas Structures for Jellyfish Blooms") and *Gambierdiscus* spp. dinoflagellates (see section "Occurrence of Ciguatera Toxin-Producing Dinoflagellates"). Systematic spatial sampling will help us to understand how structure density and proximity to different habitat types may influence community composition, population density, and

TABLE 1 | Proposed research priorities for artificial reefs in the nGoM, methods to address the priorities and their prospective outcomes.

Research priority	Methods	Outcomes
Priority 1: Understand the taxonomic composition of communities on both artificial and natural reefs and how it varies in space and time	Traditional taxonomy	Improve diversity estimates of fouling communities; establish identification guides
	DNA barcoding	Improve taxonomic resolution; establish reference databases for native, non-native species and potentially harmful species (e.g., jellyfish polyps; *Gambierdiscus* spp. dinoflagellates)
	Metabarcoding/metagenomics	Improve efficiency of diversity estimates without the need for labor-intensive traditional taxonomy
	eDNA	Detect presence of species from seawater samples without the need to sample the organism itself.
	Settlement plates (e.g., ARMS)	Improve diversity estimates of fouling communities; observe community succession
	Regular, high resolution sampling of organismal communities on artificial and natural reefs	Improve diversity estimates of fouling communities; detect population increases in potentially harmful species (e.g., jellyfish polyps; *Gambierdiscus* spp. dinoflagellates)
Priority 2: Understand the connectivity of and interactions between natural and artificial reefs	Biophysical modeling combined with high resolution physical oceanography	Describe resilience of reef metapopulations of the nGoM; Identify potential for habitat expansions; Identify high-risk areas for species invasions
	Frequent monitoring of artificial and natural reefs via SCUBA, ROV or other visual surveys, with emphasis on high-risk areas	Early detection of non-native species
	Population genetics/genomics	Model population connectivity, Tracking of origins and invasion pathways of non-native species
	Otolith microchemistry (see also Priority 3)	Assessment of site fidelity to nursery grounds
Priority 3: Multi-year monitoring of fish populations on artificial and natural reefs, including survival and recruitment rates and movement patterns	Reef fish visual censuses (RVC)	Estimates of diversity and abundance of fish on natural and artificial reefs
	Hydroacoustic and video surveys	Fast and non-destructive estimates of habitat use
	Multibeam sonars	Detection and delimitation of large fish aggregations
	Stereo video surveys	Improved accuracy of size estimates; classification of ontogenetic stages
	Otolith microchemistry	Assessment of site fidelity to nursery grounds
	Otolith structural analysis	Aging of fish
	Population genetics/genomics (see also Priority 2)	Model population connectivity

ecosystem function, as well as their potential as stepping stones for habitat expansion.

Research Approaches

Although time and labor-intensive, traditional taxonomy remains an important tool for the characterization of organismal communities. Standardized identification guides are a prerequisite to accurately detect changes in community composition and assess their downstream effects. In addition to traditional taxonomy, genetic and genomic methods are becoming more cost and time efficient as technology advances, and they are particularly useful for the detection of microscopic or cryptic taxa and life stages. They allow the taxonomic identification of individual organisms (DNA barcoding) (Hebert et al., 2003; Miller, 2007) as well as the analysis of community composition (metabarcoding or metagenomics). Environmental DNA (eDNA) from seawater can provide broad coverage of community membership that circumvents the limits of discrete sampling of organisms from substrate (Thomsen et al., 2012). Sampling can also be standardized by deployment of settlement plates. An excellent example of this is the Autonomous Reef Monitoring Systems (ARMS), simple stacks of PVC plates built using a standardized design. Settling organisms are processed using standardized procedures, allowing for direct comparisons between different habitat types or geographic regions (Leray and Knowlton, 2015). If multiple ARMS are deployed on the same structure for different lengths of time, they can also be used to study community succession. In addition, the ARMS provide information on the potential for invasions. Taxa that have dispersed to the area but would otherwise be unable to settle in the adjacent occupied habitat could colonize the ARMS, thus providing information on migration and dispersal. These same samples could be utilized as described in Priority 2 to examine connectivity across the region. Regular monitoring of natural reefs, with emphasis on predicted high risk areas and with increased vigilance after disturbance events such as the sudden mortality event in the East Flower Garden Banks in 2016 (Johnston et al., 2019) may help mitigate any negative effects, e.g., by active removal of invasive species.

Priority 2

Understand the connectivity of and interactions between natural and artificial reefs.

Rationale

Although the debate is still ongoing, there is increasing evidence that artificial reefs can act as stepping stones to facilitate species invasions and range expansions into the nGoM. Non-native and invasive species may negatively affect the health and resiliency of the natural reef communities. Further, the linkages between natural and artificial habitats are not clear – do they act as source or sink? Do artificial habitats promote or reduce genetic diversity within metapopulations? Do they provide trophic subsidies? This is important knowledge for not just introduced or non-native species, but also for indigenous taxa.

Research Approaches

The composition of natural and artificial reef communities is a crucial determinant of their ecosystem function. Understanding the connections between and within these two habitat types is essential for understanding how the current ecosystem state developed, and how it may change in response to disturbance. Biophysical modeling can be used to assess the likelihood of non-native species colonizing natural reefs from nearby artificial structures and to identify high risk focus areas for increased monitoring. In conjunction with high-resolution physical oceanography, biophysical modeling has become an important tool in the estimation of larval dispersal and connectivity in the ocean (Kool et al., 2012), and is especially useful when assessing the metapopulation effects of habitat expansion or removal (Henry et al., 2018), or for designing protected areas (White et al., 2014; Chollett et al., 2017). Biophysical dispersal models can be especially powerful when coupled with population genetics/genomics studies (e.g., Lee et al., 2013; Baltazar-Soares et al., 2018). Population genetic methods can reveal the extent of connectivity or isolation between habitats, provide insight into the source and history of a population, and even assess the extent and direction of migration between sites. Coupled biophysical-genetic models have been applied to habitats on the continental shelf of the nGoM (Garavelli et al., 2018; Studivan and Voss, 2018) but need to be extended to include more taxa with varied life histories.

Priority 3

Examine the broader role of artificial habitats in fisheries, past attraction and production, including more accurate estimates of survival and recruitment rates and movement patterns.

Rationale

The processes of attraction and production of fish to artificial reefs can vary greatly temporally and spatially. Rather than focusing on the attraction/production dichotomy, multi-year monitoring of fish populations on artificial and natural reefs can generate a more nuanced view of the role of artificial reefs for overall ecosystem health and fisheries.

Research Approaches

Continuation of the Reef Fish Visual Censuses (RVC) (Bohnsack and Bannerot, 1986) conducted in the nGoM (e.g., Rooker et al., 1997; Hickerson et al., 2012) would be beneficial to continue monitoring the fish populations, but these methods are expensive (both in time and cost). Otolith microchemistry can be used to determine nursery areas of fish and thus track site fidelity (Patterson et al., 1998; Zapp Sluis et al., 2012). Otolith structural analysis is well-established to age fish, including red snapper (Bortone and Hollingsworth, 1980; Patterson et al., 2001; Wilson and Nieland, 2001). Combining hydroacoustic and video technologies hold great promise for fast and non-destructive surveys of fish populations to identify and monitor habitat use at these sites (Reynolds et al., 2018). Novel stereo video techniques enable more accurate length estimates and allow for improved classification of ontogenetic stages (Davis et al., 2015; Elliott et al., 2017). In addition, the modification and utilization of multibeam sonars provides a new avenue for monitoring and characterizing larger fish populations (Melvin, 2016) although the methods may be limited by depth and adverse weather conditions.

In summary, the nGoM hosts a remarkable diversity of distinct habitats with their associated biological communities, ranging from thriving coral reefs to chemosynthesis-driven cold seep assemblages. Among these diverse habitats, artificial reefs are the newest additions and have led to ongoing 'ocean sprawl' (Duarte et al., 2013; Bishop et al., 2017). While some artificial structures have been in place for about three centuries (Horrell and Borgens, 2014), the majority are active or reefed oil and gas extraction platforms that were deployed over the past 50 years. Other anthropogenic activities, such as shrimp trawling, have long fundamentally altered the GoM ecosystem. It could be argued that the GoM ecosystem has reached a point of no return (Sommer et al., 2019) and the best solution may be to support the services provided by the 'novel ecosystems' of artificial structures (Hobbs et al., 2014) rather than trying to restore the GoM its original condition. Whether we choose to protect the current ecosystem or attempt restoration, it is critical to understand the function of artificial structures.

AUTHOR CONTRIBUTIONS

AS, DE, and MM conceived the idea for this review article. AS wrote the sections "Introduction," "Fouling Communities," "Documented Invasions," "Lionfish," "The Regal Demoiselle, *Neopomacentrus cyanomos,*" "Acorn Barnacles," "Tunicates: *Didemnum perlucidum,*" and "Fisheries Enhancement." MM contributed to the sections "Cup Corals: *Tubastrea* spp.," and "Implications of Oil and Gas Structures for Jellyfish Blooms." DE contributed to the section "Occurrence of Ciguatera Toxin-Producing Dinoflagellates." DH contributed to the section "Connectivity: Stepping Stones, Metapopulations, Resilience, and Replacement." CG provided the figures and contributed the additional text for several sections. All authors contributed to the section "Future Research Priorities and Conclusion," **Table 1**, the final editing, and revisions of the manuscript.

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On a Reef Far, Far Away: Anthropogenic Impacts Following Extreme Storms Affect Sponge Health and Bacterial Communities

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Terrestrial runoff can negatively impact marine ecosystems through stressors including excess nutrients, freshwater, sediments, and contaminants. Severe storms, which are increasing with global climate change, generate massive inputs of runoff over short timescales (hours to days); such runoff impacted offshore reefs in the northwest Gulf of Mexico (NW GoM) following severe storms in 2016 and 2017. Several weeks after coastal flooding from these events, NW GoM reef corals, sponges, and other benthic invertebrates ∼185 km offshore experienced mortality (2016 only) and/or sub-lethal stress (both years). To assess the impact of storm-derived runoff on reef filter feeders, we characterized the bacterial communities of two sponges, *Agelas clathrodes* and *Xestospongia muta*, from offshore reefs during periods of sub-lethal stress and no stress over a three-year period (2016—2018). Sponge-associated and seawater-associated bacterial communities were altered during both flood years. Additionally, we found evidence of wastewater contamination (based on 16S rRNA gene libraries and quantitative PCR) in offshore sponge samples, but not in seawater samples, following these flood years. Signs of wastewater contamination were absent during the no-flood year. We show that flood events from severe storms have the capacity to reach offshore reef ecosystems and impact resident benthic organisms. Such impacts are most readily detected if baseline data on organismal physiology and associated microbiome composition are available. This highlights the need for molecular and microbial time series of benthic organisms in near- and offshore reef ecosystems, and the continued mitigation of stormwater runoff and climate change impacts.

Keywords: *Agelas clathrodes*, coral reef, flood, Flower Garden Banks National Marine Sanctuary, Gulf of Mexico, Hurricane Harvey, bacterial community, *Xestospongia muta*

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INTRODUCTION

Tropical coral reef ecosystems have evolved in the context of nutrient-poor (oligotrophic) waters. Thus, when nutrient-laden (eutrophic) terrestrial runoff mixes with reef-associated waters, this can directly or indirectly stress or kill reef organisms (Knight and Fell, 1987; Kerswell and Jones, 2003; Fabricius, 2005; Humphrey et al., 2008). Terrestrial runoff exposes reef organisms to decreased salinity, and increased levels of turbidity and contaminants (e.g., microbial pathogens, chemical pollutants) (Fabricius, 2005). Terrestrial runoff can also reduce dissolved oxygen levels in reef-associated waters through several mechanisms (Nelson and Altieri, 2019). Terrestrial runoff can constitute a chronic stress in areas with developed coastlines or at river outflows, or an acute stress when floodwaters generated by extreme storms move offshore. Floodwaters originating in urban areas may constitute a greater threat, if they contain high nutrient and contaminant loads due to overflows of wastewater management systems (Chen et al., 2019; Humphrey et al., 2019). Storm-associated runoff is increasingly recognized as a threat to reefs since the intensity and precipitation associated with tropical storms is increasing with climate change (Knutson et al., 2010; Emanuel, 2017).

Although various studies document the impacts of terrestrial runoff on coral reefs, few works specifically address runoff derived from floodwaters; all of these latter works focus on nearshore, shallow water reefs (Ostrander et al., 2008; Lapointe et al., 2010). It has been assumed that offshore or deep (e.g., mesophotic) reefs are unlikely to interact with terrestrial runoff (Szmant, 2002). For example, reefs within the Flower Garden Banks (FGB) National Marine Sanctuary (northwest Gulf of Mexico, **Figure 1A**) occur ∼185 km offshore in relatively deep water (20–30 m), boast some of the highest coral cover (∼55%) in the wider Caribbean and have been generally presumed to be protected from land-based stressors (Johnston et al., 2016). Low salinity 33 parts per thousand) water from terrestrial runoff has been detected within surface waters of the FGB for the past several decades (Dodge and Lang, 1983; Deslarzes and Lugo-Fernandez, 2007; Kealoha, 2019); however, the impact of these waters on reef ecosystem health has not been directly studied.

Since 2015, the Texas coast has experienced several flooding events related to extreme storms: Memorial Day Flood of 2015; Tax Day Flood of 2016, Hurricane Harvey in 2017, and Hurricane Imelda in 2019. Each of these floods impacted Central Texas nearshore ecosystems, including salt marshes (Congdon et al., 2019; Oakley and Guillen, 2019) and oyster beds (Kiaghadi and Rifai, 2019). It has been assumed that floodwaters would not impact the benthic reef ecosystem at 20–30 m depth; however, three months after Tax Day flooding in 2016, a localized mortality event occurred on a portion of the East Bank (EB) of the FGB. During the mortality event, approximately 82% of corals in a 0.06 km^2 area experienced partial or full mortality (Johnston et al., 2019), and mortality in many other benthic invertebrates, such as sponges, was also observed. Although data on abiotic conditions on the reef at EB during the 2016 mortality event are not available, measurements from nearby sites suggest that poor water quality from floodwaters moving offshore and low dissolved oxygen levels played a role in the mortality event (Le Hénaff et al., 2019; Kealoha et al., 2020). Then, in late August of 2017, Hurricane Harvey released more than one meter of rainfall over the course of six days in some areas of southeastern Texas (Blake and Zelinsky, 2018). Although surface salinity was slightly depressed near the FGB following Hurricane Harvey, much of the water mass diverted southwest along the coast (Roffer et al., 2018), and no mass mortality was observed on the reef (Wright et al., 2019).

Benthic reef invertebrates, such as sponges, harbor a diversity of microbial symbionts (e.g., bacteria, archaea, protists, fungi and viruses) that contribute to their health and nutrition. Yet, these microbial communities can be disrupted (change in richness, alpha- or beta-diversity, or community composition) by environmental stress, including terrestrial runoff, leading to microbial dysbiosis (Zaneveld et al., 2016; Ziegler et al., 2016; Slaby et al., 2019). For example, the ‘Anna Karenina Principle’ or AKP (Zaneveld et al., 2017) predicts that dysbiotic host individuals are more dissimilar in microbial community composition than healthy host individuals. The AKP has previously been detected in corals (Zaneveld et al., 2016; Claar et al., 2020; Howe-Kerr et al., 2020) as well as reef sponges (Lesser et al., 2016). Previous work has shown the utility of using filter-feeding sponges as monitoring tools for fecal-coliform contamination in near-shore environments (Longo et al., 2010; Maldonado et al., 2010). Therefore, we tested whether changes to microbial symbioses in offshore reef sponges were detectable following storm-derived coastal flood events. We leverage the Tax Day Flood (2016) and Hurricane Harvey (2017) as natural ‘experimental treatments’ applied to two high-microbial-abundance sponge species (*Xestospongia muta* and *Agelas clathrodes*; **Figures 1B,C**) at the EB and West Bank (WB) of the FGB. Bacterial communities were sampled from sponges and seawater at four time points: August 2016 (two weeks after the localized mortality event at EB), September 2017 (immediately after Hurricane Harvey), October 2017 (one month after Hurricane Harvey), and October 2018 (approximately one year following Hurricane Harvey) (**Figure 1D**). No flood events occurred in southeast central Texas during 2018, and thus samples from this time point function as an ‘experimental baseline.’ We hypothesized that: (1) sponge-associated bacterial communities shift during flood years (relative to the no-flood year) and (2) flood year bacterial communities contain genetic signatures of terrestrial-derived bacteria. Understanding how and when environmental stressors influence sponge-microbe associations, and the subsequent implications for sponge health and function, is important as sponges increase in abundance and in ecological importance on Caribbean reefs (Bell et al., 2013; Pawlik and McMurray, 2020).

RESULTS

Reduced Surface Salinity at the FGB Following Floods

In the vicinity of the FGB, mean surface salinity is generally variable, ranging between 28.5 ppt and 36 ppt, from early June

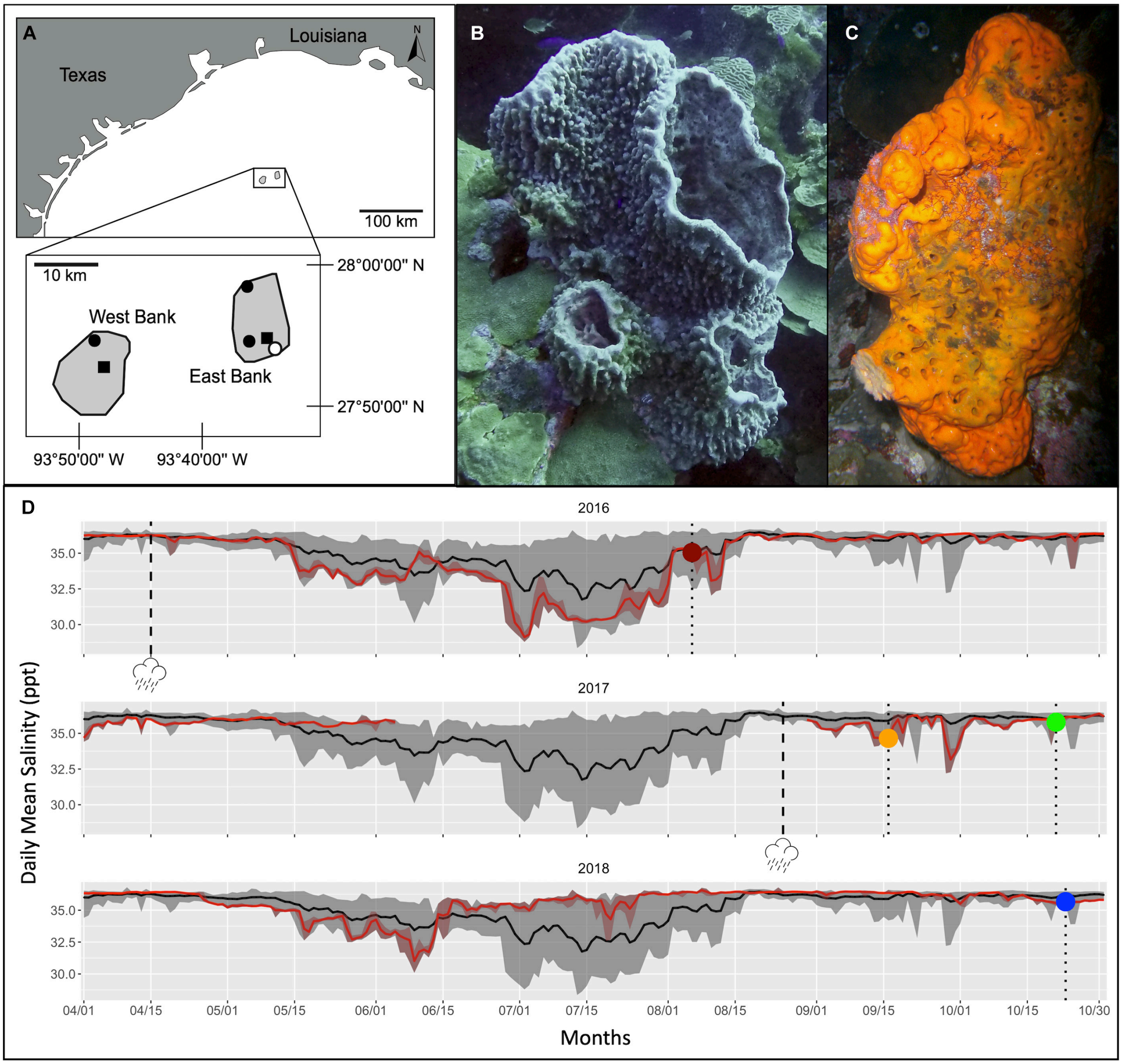

FIGURE 1 | Summary of study site, host taxa, and local abiotic conditions associated with this study. **(A)** map of Flower Garden Banks National Marine Sanctuary (northwest Gulf of Mexico) with sites of sponge and seawater collection indicated. Filled circles represent seawater column sample collection sites; filled squares represent Buoy 2 and Buoy 4 (sponge, seawater column, and near reef seawater collection) and open circle represents location of TABS Buoy V (surface salinity data collection); **(B)** representative *Xestospongia muta* sponge; **(C)** representative *Agelas clathrodes* sponge; **(D)** surface Salinity (ppt) at buoy V spanning the months April through October in which sampling occurred for this study. Black lines represent daily means from 2006 to 2018 and gray shaded areas encompass minimum and maximum values from 2006 to 2018. Red lines represent daily means for 2016–2018, individually. Dashed lines with storm icon represent dates of terrestrial flooding. Dotted lines with symbols represent mean daily values on each sample collection date: dark red circle = 6 August 2016, orange circle = 16 September 2017, green circle = 21 October 2017, and blue circle = 23 October 2018.

through late-August (shaded gray areas in **Figure 1D**). In early spring and in fall, however, surface salinity is more consistent (∼33–36 ppt). Approximately 30 days after the 2016 Tax Day Flood impacted Texas, a period of depressed mean surface salinity (relative to the mean surface salinity for a thirteen-year period: 2006–2018) was recorded from 16 May 2016 to 12 August 2016 at Texas Automated Buoy System (TABS) Real Time Ocean Observations, Buoy V (located within the sanctuary boundaries of EB, open circle **Figure 1A**). Average surface salinity was 1.2 ppt lower than the thirteen-year mean during this period; the most significant deviation occurred around 2 July 2016 when mean surface salinity reached a minimum of 29.1 ppt (3.8 ppt below the thirteen-year mean). In 2017, surface salinity remained >35 ppt until early June. TABS Buoy V data are unavailable for much of June to August 2017, so it is unclear how surface salinity changed in the months preceding Hurricane Harvey. Two abrupt reductions in surface salinity (to 32.6 ppt and 32.7 ppt) were recorded near the FGB during mid-to-late September 2017 following Hurricane Harvey, before surface salinity returned to >35 ppt in October. In contrast, no significant influence of freshwater was recorded in 2018 and surface salinity remained above 35 ppt after mid-June.

When the 2016 mortality event was discovered on 25 July 2016, recreational divers reported 'low visibility and green coloration in the water column' at EB (Johnston et al., 2019); on this date, mean surface salinity had been lower than the thirteen-year mean for 44 days. Collections of live but visually impacted sponges as well as healthy sponges were collected on 6 August 2016, approximately four days after surface salinity had returned to 35 ppt (**Figure 1D**). Sampling immediately post-Hurricane Harvey on 16 September 2017 occurred when mean surface salinity was 34.6 ppt, or 1.3 ppt lower than the thirteen-year mean (**Figure 1D**). During sampling that occurred approximately one-month post-hurricane Harvey (on 21 October 2017), mean surface salinity had been >35 ppt for 19 days prior to sampling (**Figure 1D**). Samples during the no-flood year were collected on 23 October 2018, which had a mean surface salinity of 35.7 ppt; surface salinity had been >35 ppt for 94 days (**Figure 1D**).

Acute Shifts in Sponge- and Seawater-Associated Bacterial Communities Following Flood Events

Paired-end Illumina MiSeq sequencing of the V4 region of the bacterial 16S rRNA gene yielded 5,350,216 high quality sequences from a total of 139 samples that included healthy and impacted sponges (*A. clathrodes*, $n = 54$; *X. muta*, $n = 45$) as well as seawater ($n = 40$) (**Table 1**, **Supplementary Table 1**). After removal of Mitochondrial, Chloroplast, and Unassigned reads, the total pool of bacterial sequences were assigned to 11,828 Amplicon Sequence Variants (ASVs). Samples clustered into 4 distinct groups (**Figure 2**), which were all significantly different from each other (Analysis of Similarities (ANOSIM): $p < 0.001$; **Supplementary Table 2**). These groups were: (1) seawater samples; (2) diseased sponges of both species; (3) visually healthy *A. clathrodes*; and (4) visually healthy *X. muta*. Because each sponge species and the seawater samples had distinct bacterial communities, subsequent analyses were conducted on each group individually. Additionally, within each sponge species and within seawater samples, there were no differences between EB and WB sites (ANOSIM: $p > 0.05$; **Supplementary Table 3**); therefore, sites were grouped for subsequent beta-diversity analyses.

Bacterial communities of *X. muta*, *A. clathrodes*, and seawater samples were all significantly disrupted during both flood years, relative to the no-flood year. Within *X. muta* samples, bacterial communities in Aug. 2016 and Sept. 2017 shifted in a similar way and Oct. 2017 shifted in another; all three flood-associated dates were significantly different than the no-flood year (**Figure 3A**; ANOSIM: $p < 0.05$, **Supplementary Table 4**). In *A. clathrodes*, bacterial communities associated with flood years shifted in different ways (**Figure 3B**; ANOSIM: $p < 0.05$, **Supplementary Table 4**). In seawater samples, bacterial communities were also distinct in both flood years, and, interestingly, samples taken directly above the reef bottom ('Reef Water') differed from samples taken from higher in the water column on the same date (Oct. 2017) (**Figure 3C**; ANOSIM: R = 0.516, $p = 0.002$; **Supplementary Table 4**).

Disruption of bacterial communities during both flood years included significant increases in community dispersion (or variation) as well as significant increases in community (or ASV) richness. Within *X. muta* samples, bacterial communities in Aug. 2016 and Sept. 2017 had significantly higher dispersion compared to the no-flood year, but the variability of bacterial communities in Oct. 2017 was lower than other flood-associated dates as well as the no-flood year (ANOVA with Tukey's comparisons: $p < 0.01$, **Figure 3D**). In *X. muta,* there was a significant difference in ASV richness across Date (GLM: F = 6.00, $p = 0.002$) and Health State (GLM: F = 11.19, $p = 0.002$), but not by Site (GLM: F = 2.29 $p = 0.139$). Communities from Aug. 2016 and Sept. 2017 had higher ASV richness than communities from the no-flood year, and diseased *X. muta* communities had higher ASV richness than visually healthy *X. muta* communities. Bacterial communities in *A. clathrodes* also displayed higher dispersion during both flood years compared to the no-flood year (ANOVA: $p < 0.05$; **Figure 3E**). There was also a significant difference in ASV richness across Date (GLM: F = 9.49, $p = 0.0001$) and Health State (GLM: F = 43.14, $p = 0.0001$), but not by Site (GLM: F = 0.13 $p = 0.724$). Communities from both flood years had higher ASV richness than communities from the no-flood year, and affected *A. clathrodes* communities had higher ASV richness than visually healthy *A. clathrodes* communities. Seawater bacterial communities also displayed higher dispersion during both flood years compared to the no-flood year (ANOVA: $p < 0.05$; **Figure 3F**). However, in the 2017 flood year, Reef Water, but not Seawater Column samples had higher dispersion compared to the no-flood year. There was a significant difference in ASV richness across Date (GLM: F = 48.03, $p = 0.0001$) and Sample Type (GLM: F = 72.95, $p = 0.0001$), but not by Site (GLM: F = 1.32 $p = 0.258$). Communities from both flood years had higher ASV richness than the no-flood year. In *X. muta*, *A. clathrodes*, and seawater samples, Shannon Diversity was not impacted by Date, Health Status/Sample Type, or Site (GLM: $p > 0.05$).

Disruptions to bacterial communities of *X. muta*, *A. clathrodes*, and seawater samples during flood years are also reflected in significant changes in the relative abundance of several bacterial taxa (as assessed by DESeq2 analysis). *X. muta* bacterial communities during the no-flood year were dominated by Chloroflexi (21.4 ± 1.2%), Gammaproteobacteria (14.3 ± 1.0%), Acidobacteria (13.1 ± 1.6%), and Actinobacteria (10.1 ± 1.3%) (**Supplementary Figure 1a**). In *X. muta*, Flavobacteriaceae, Poribacteria, SAR86 clade, and Cyanobiaceae were enriched in both Aug. 2016 and Sept. 2017, but no bacterial Family was enriched or depleted across all three flood-associated dates (**Supplementary Table 5**). In *A. clathrodes,* bacterial communities during the no-flood year were also dominated by Chloroflexi (22.7 ± 1.2%), Gammaproteobacteria (15.3 ± 1.0%), Actinobacteria (15.1 ± 1.6%), and Acidobacteria (13.6 ± 0.6%) (**Supplementary Figure 1b**). Numerous (35) bacterial Families were enriched in Aug. 2016 as compared to

TABLE 1 | Summary of sample collections from two reef sponge species and seawater at the East Bank (EB) and West Bank (WB) of the Flower Garden Banks National Marine Sanctuary (northwest Gulf of Mexico) and amplicon sequencing results of the V4 region of the 16S rRNA gene from sponge-associated bacterial communities.

					Sequence Analysis Summary		
Species	**Date**	**Site**	**Health Status/ Sample Type**	**N**	**High Quality Sequences$^{\#}$**	**Observed ASVs^**	**Shannon H'**
Agelas clathrodes	Aug. 2016	EB	Diseased	4	82301 (6770)	566 (155)	5.63 (1.05)
		EB	Healthy	8	87281 (5447)	256 (18)	5.35 (0.10)
		WB	Healthy	5	61383 (8044)	228 (27)	4.78 (0.34)
	Oct. 2017	EB	Healthy	9	24524 (2381)	108 (9)	4.92 (0.29)
		WB	Healthy	8	23624 (1176)	117 (7)	4.69 (0.35)
	Oct. 2018	EB	Healthy	10	27019 (1076)	161 (6)	5.71 (0.07)
		WB	Healthy	10	27064 (940)	150 (4)	5.47 (0.11)
Xestospongia muta	Aug. 2016	EB	Diseased	5	61714 (13840)	472 (42)	6.37 (0.23)
		EB	Healthy	2	99128 (851)	383 (59)	6.39 (0.68)
		WB	Healthy	3	96607 (9213)	270 (52)	5.19 (0.95)
	Sept. 2017	EB	Healthy	10	30765 (5108)	295 (25)	6.35 (0.15)
	Oct. 2017	EB	Healthy	2	26604 (576)	260 (12)	6.92 (0.06)
		WB	Healthy	3	26935 (589)	194 (32)	5.63 (0.67)
	Oct. 2018	EB	Healthy	10	28151 (2510)	209 (9)	6.27 (0.12)
		WB	Healthy	10	27609 (1686)	201 (11)	6.08 (0.16)
Seawater	Aug. 2016	EB	Water Column	2	100423 (27637)	334 (35)	6.47 (0.05)
		WB	Water Column	2	101348 (12277)	355 (25)	5.57 (0.59)
	Oct. 2017	EB	Reef Bottom	5	11449 (1518)	253 (41)	6.75 (0.25)
		WB	Reef Bottom	8	15487 (1572)	228 (10)	6.26 (0.07)
		EB	Water Column	7	39965 (5434)	409 (18)	6.66 (0.05)
		WB	Water Column	5	43300 (6047)	401 (10)	6.53 (0.15)
	Oct. 2018	EB	Water Column	7	19396 (816)	224 (13)	6.08 (0.14)
		WB	Water Column	4	13174 (4077)	184 (26)	5.66 (0.20)

Richness (Observed ASVs^) and diversity (Shannon H') were calculated from rarefied ASV tables. Data are presented as mean ± (sem). $^{\#}$*quality filtering included removal of low quality, short, Mitochondrial, Chloroplast, and Unassigned reads. ^Amplicon Sequence Variants (ASVs) after rarefying to equal depth (9,000 reads).*

the no-flood year; in contrast, only 5 Families were enriched in Oct. 2017 (**Supplementary Table 5**). In *A. clathrodes*, bacterial Families with potential human and marine pathogens (Enterobacteriaceae and Vibrionaceae) were enriched in Aug. 2016, and one Family (Stappiaceae) was enriched in both flooding years (**Supplementary Table 5**). For both sponge species, seven Families (Cyanobiaceae, Clostridiaceae, Desulfovibrionaceae, Halieaceae, Poribacteria, Vibrionaceae, and Vicinamibacteraceae) were enriched during flood-associated dates. For Aug. 2016, Desulfovibrionaceae was the most enriched bacterial Family in both sponge species. Seawater bacterial communities during the no-flood year were dominated by Alphaproteobacteria (36.9 ± 0.9%), Cyanobacteria (31.2 ± 2.4%), and Gammaproteobacteria (14.1 ± 0.9%) (**Supplementary Figure 1c**). Many (95) diverse seawater-associated bacterial Families were enriched in each flood year, but only Burkholderiaceae, Pseudomonadaceae, SAR86 clade were enriched in both flood years (**Supplementary Table 5**). One bacterial Family (Halieaceae) was enriched during flood-associated dates in all three sample types.

Over 322 ASVs (198, 123, and 212 ASVs in *X. muta*, *A. clathrodes,* and seawater communities, respectively) were significantly associated with flooding events as detected by Indicator Species Analysis (Indicator Value > 0.3, $p < 0.05$; **Supplementary Table 6**). Eleven Indicator ASVs were detected in both sponge species in Aug. 2016, and one Indicator ASV was detected in both Aug. 2016 and Sept. 2017 (**Table 2**). No ASVs were significantly associated with Oct. 2017 in both sponge species. ASVs classified as *Halodesulfovibrio* or *Desulfovibrio* (sulfate-reducing taxa) were associated with the Aug. 2016 flooding event in both sponge species. Additionally, 5 ASVs classified as *Prochlorococcus* and *Synechococcus* (photosynthetic marine Cyanobacteria) were associated with flood years in both sponge species. An increase in one Indicator ASV, classified as *Synechococcus spongarium*, was the largest driver of differences in healthy *X. muta*-associated communities in Aug. 2016 and Sept. 2017 compared to the no-flood year (as assessed by Similarity Percentages (SIMPER) analysis). This *Synechococcus spongarium* ASV was not present in any *A. clathrodes* or seawater samples. Eight ASVs classified as *Prochlorococcus* and *Synechococcus* were also Indicator ASVs associated with flood years in seawater samples (**Supplementary Table 6**); however, none of these seawater-associated Cyanobacterial Indicator ASVs were present in any sponge samples. No Indicator ASV identified for seawater was also identified for a sponge species.

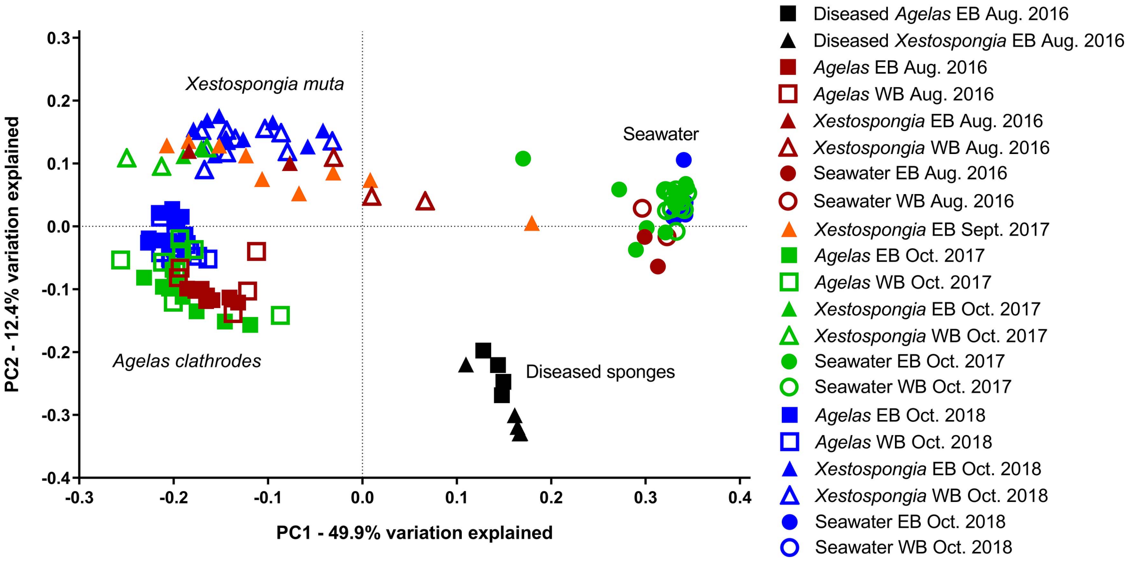

FIGURE 2 | Principle Coordinate Analysis of the weighted UniFrac distance matrix for bacterial communities analyzed in this study. Squares = *Agelas clathrodes* samples; Triangles = *Xestospongia muta* samples; Circles = Seawater samples. Black symbols = samples from diseased sponges (August 2016); Red symbols = visually healthy sponge samples (August 2016). Orange symbols = samples collected immediately following Hurricane Harvey (Sept. 2017) from visually healthy sponges; Green symbols = samples collected 1 month following Hurricane Harvey (Oct. 2017) from visually healthy sponges. Blue symbols = samples collected in a no-flood (baseline) year from visually healthy sponges (Oct. 2018). Empty symbols = samples collected from East Bank (EB); filled symbols = samples collected from West Bank (WB) of the Flower Garden Banks National Marine Sanctuary (northern Gulf of Mexico).

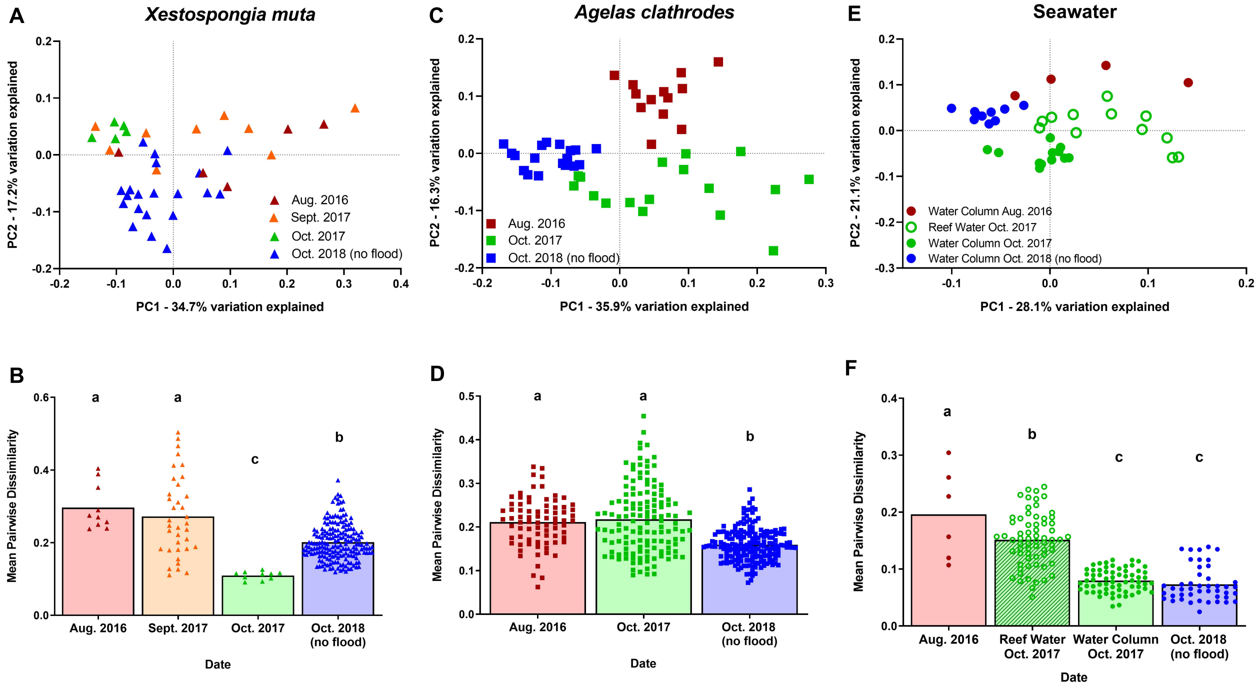

FIGURE 3 | Sponge-associated bacterial communities differed in composition and variability following extreme storm-derived floods. Principle Coordinate Analysis of the weighted UniFrac distance matrices for **(A)** visually healthy *Xestospongia muta*, **(C)** visually healthy *Agelas clathrodes*, and **(E)** seawater bacterial communities. Mean (with individual value dots) pairwise dissimilarity values for **(B)** *X. muta*, **(D)** *A. clathrodes*, and **(F)** seawater bacterial communities. Red = August 2016; Orange = September 2017; Green = October 2017; Blue = October 2018 associated with no flooding stress. Bars represent mean with individual value dots. Within a species, bars that do not share a letter are significantly different based on ANOVA with Tukey's multiple comparisons ($p < 0.05$).

TABLE 2 | Bacterial taxa unique to both *X. muta* and *A. clathrodes*-associated bacterial communities following recent flooding events* according to Indicator Species Analysis.

Date	Amplicon Sequence Variant ID	Taxonomy (Phylum_Class_Family_Genus)	Host	Indicator Value	*P*-value
Aug. 2016	64805be33440e427c18e31e0d5e6094b	Bacteroidota_ Bacteroidia_ Saprospiraceae_ *Phaeodactylibacter*	*X. muta*	0.577	0.028
			A. clathrodes	0.379	0.004
	ccd8d5e31ad9bfa58066251ea1138225	Bacteroidota_ Bacteroidia_ Flavobacteriaceae_NA	*X. muta*	0.577	0.028
			A. clathrodes	0.343	0.002
	e09f2d58d292332880fe9e37607469e1	Desulfobacterota_ Desulfovibrionia_ Desulfovibrionaceae_ Halodesulfovibrio	*X. muta*	0.573	0.028
			A. clathrodes	0.385	0.000
	e4a5985be454d1e8a3d50a2ab6ea7a8b	Desulfobacterota_ Desulfovibrionia_ Desulfovibrionaceae_ Halodesulfovibrio	*X. muta*	0.525	0.003
			A. clathrodes	0.386	0.000
	e51947121c608cf15031596f9d0c09eb	Desulfobacterota_ Desulfovibrionia_ Desulfovibrionaceae_NA	*X. muta*	0.461	0.028
			A. clathrodes	0.397	0.000
	0261a50c7edb68abf5e65bb5094ce011	Desulfobacterota_ Desulfovibrionia_ Desulfovibrionaceae_NA	*X. muta*	0.426	0.028
			A. clathrodes	0.524	0.000
	5546361caf3e42e50fb56d85a11571f2	Proteobacteria_ Alphaproteobacteria_Clade I_Clade Ia	*X. muta*	0.533	0.025
			A. clathrodes	0.511	0.001
	2ef8937fcfef105310d9aae9f65c08ab	Proteobacteria_ Gammaproteobacteria_ Kangiellaceae_ Aliikangiella	*X. muta*	0.577	0.028
			A. clathrodes	0.341	0.004
	b47b6e5813cfd4b7690b522531f10aa4	Proteobacteria_ Gammaproteobacteria_ Thioglobaceae_ SUP05 cluster	*X. muta*	0.826	0.000
			A. clathrodes	0.393	0.015
	efa28eb526ec0c3caa54fd35809774e1	SAR324 clade_Marine group B_ NA_NA	*X. muta*	0.577	0.027
			A. clathrodes	0.393	0.015
	9442980515ce7f911bb4cc9c372db4e8$^{\#}$	Proteobacteria_ Gammaproteobacteria_ SAR86_clade_NA	*X. muta*	0.805	0.000
			A. clathrodes	0.669	0.001
Aug. 2016 and Sept. 2017	4bf34e939f3102402abec9deab0319b3	Proteobacteria_ Gammaproteobacteria_ Nitrosococcaceae_ AqS1	*X. muta* (Sept. 2017)	0.489	0.036
			A. clathrodes (Aug. 2016)	0.382	0.016

*Analysis was conducted on each sponge species individually. *No ASVs associated with Oct. 2017 (1 month post-Hurrricane Harvey) flooding were present in both X. muta and A. clathrodes-associated bacterial communities.*

Sponge Bacterial Communities Show Signs of Wastewater Contamination After Flooding

Thirty bacterial ASVs were classified as Family Enterobacteriaceae and were recovered from most samples of both sponge species. Of these 30 Enterobacteriaceae ASVs, 23 were further classified as *Escherichia coli*. In *X. muta,* bacterial communities had low abundances (<0.1%) of Enterobacteriaceae (**Figure 4A**), displaying no significant differences across Date (GLM: $H = 0.52$, $p = 0.674$), Site (GLM: $F = 1.01$, $p = 0.321$), or Health Status (GLM: $F = 0.59$, $p = 0.445$). In contrast, *A. clathrodes* bacterial communities had a significantly higher abundance of Enterobacteriaceae in diseased samples compared to visually healthy samples (GLM: $F = 66.11$, $p = 0.0001$) and in Aug. 2016 samples compared to other dates (GLM: $F = 5.24$, $p = 0.009$). For example, diseased and visually healthy *A. clathrodes* samples in Aug. 2016 contained 7.91 (±1.83)% and 1.44 (±0.64)% Enterobacteriaceae, respectively, whereas in Oct. 2017 and the no-flood year, Enterobacteriaceae abundance was <0.1% (**Figure 4B**, **Supplementary Figure 1d**). No Enterobacteriaceae ASVs were detected in any seawater samples, and no Enterobacteriaceae ASVs were identified in Indicator Species Analysis as being significantly associated with either flood year (**Supplementary Table 6**).

To test the hypothesis that FGB sponges were exposed to wastewater-derived bacteria from storm generated floodwaters, seawater and sponge samples were screened for seven human pathogens using quantitative PCR. Diseased and visually healthy sponge samples collected in both flood years yielded positive detection for 2 out of 7 human pathogens screened: *Escherichia coli* and *Klebsiella pneumoniae* (**Figures 4C,D**). No human pathogens were detected in sponges sampled during the no-flood year (**Figures 4C,D**). In *X. muta*, *E. coli* abundance was highest in visually healthy samples from Aug. 2016, with a mean of 1.96×10^3 ($\pm$ 1.40×10^3) gene copies per g tissue, compared to a mean of 8.96×10^1 ($\pm$ 8.54×10^1) and 6.90×10^1 ($\pm$ 2.18×10^1) gene copies per g tissue for diseased samples

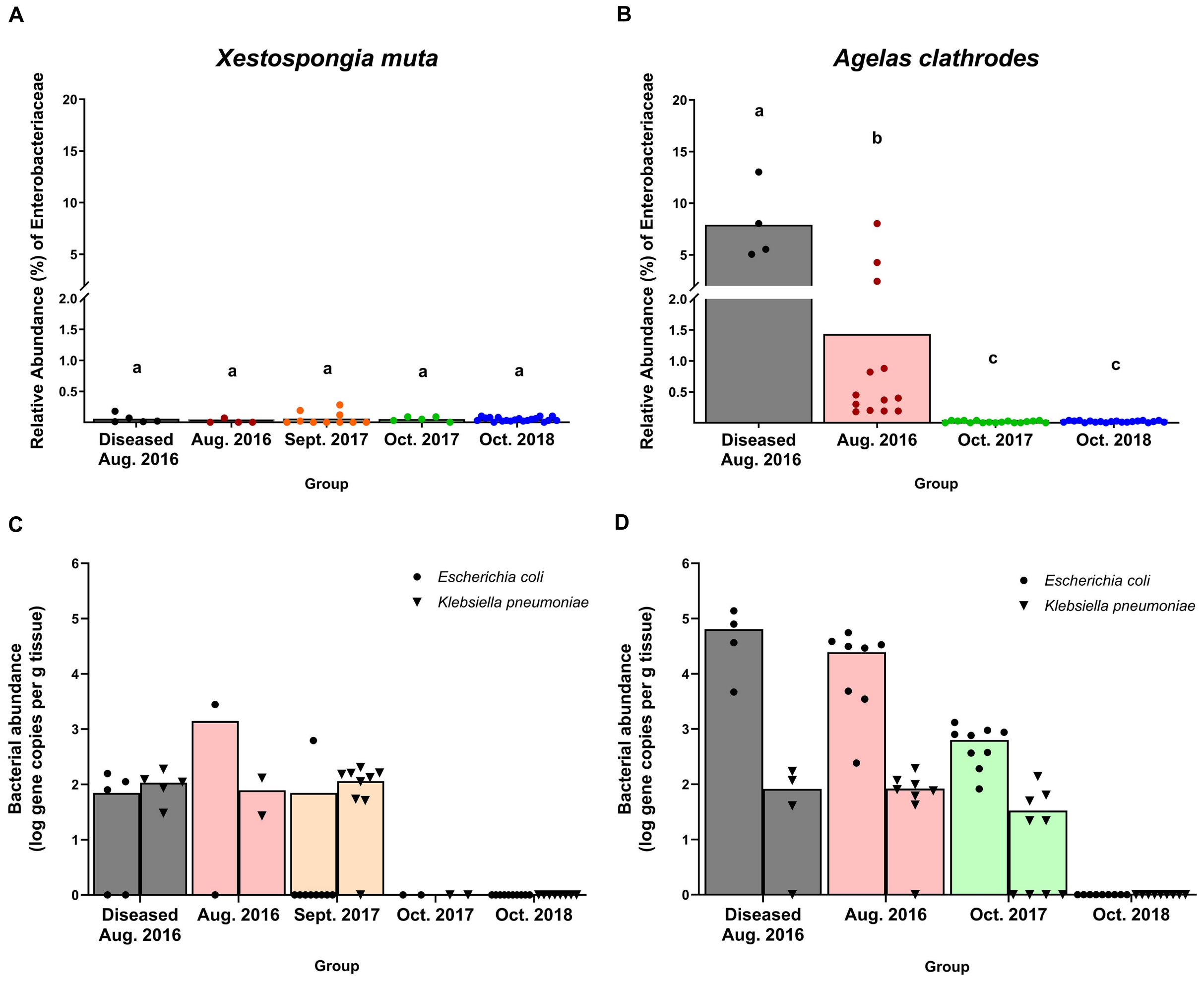

FIGURE 4 | Relative abundance of sequences in the Family Enterobacteriaceae **(A,B)** and to specific human pathogens (*Escherichia coli* and *Klebsiella pneumoniae*) **(C,D)** across sites and years. Data in **(A,B)** are based on Illumina MiSeq amplicon sequencing of the V4 region of the bacterial 16S rRNA gene. Data in **(C,D)** are quantitative PCR amplification of the bacterial *ybbW* and *phoE* genes for *E. coli* and *K. pneumoniae*, respectively. All data are presented as mean with individual value dots. Black bars = affected sponges in 2016; red bars = visually healthy sponges in August 2016; orange bars = visually healthy sponges in September 2017; green bars = visually healthy sponges in October 2017; blue bars = visually healthy sponges in October 2018 (no flood, baseline year). Groups that share a letter in **(A,B)** are not significantly different based on a Generalized Linear Model with Tukey's multiple comparisons across groups within a species. ND, not detected.

from Aug. 2016 and visually healthy sponges from Sept. 2017, respectively (**Figure 4C**). However, *E. coli* was detected in only one *X. muta* sample in Sept. 2017. In *X. muta*, *K. pneumoniae* abundance was similar across groups, averaging 1.08 × 10^2 (±5.78 × 10^1), 7.84 × 10^1 (±7.27 × 10^1), and 1.06 × 10^2 (± 6.74 × 10^1) gene copies per g tissue for diseased samples from Aug. 2016, visually healthy sponges from Aug. 2016, and visually healthy sponges from Sept. 2017, respectively (**Figure 4C**). In *A. clathrodes*, *E. coli* was more abundant in samples from Aug. 2016, with means of 6.47 × 10^4 (±5.76 × 10^4) and 2.85 × 10^4 (±1.79 × 10^4) gene copies per g tissue for diseased and visually health sponges, respectively, compared to Oct. 2017, with a mean of 6.26 × 10^2 (±4.17 × 10^2) gene copies per g tissue (**Figure 4D**). In *A. clathrodes*, *K. pneumoniae* was less abundant (>2 orders of magnitude difference) compared to *E. coli*, displaying similar abundance across groups where it was detected, averaging 8.22 × 10^1 (± 7.65 × 10^1), 8.36 × 10^1 (± 5.68 × 10^1), and 4.61 × 10^1 (± 3.29 × 10^1) gene copies per g tissue for diseased samples from Aug. 2016, visually healthy sponges from Aug. 2016, and visually healthy sponges from Oct. 2017, respectively (**Figure 4D**). No seawater samples tested positive for *E. coli* or *K. pneumoniae*. No sponge samples tested positive for *Enterococcus* spp., *Pseudomonas aeruginosa*, *Salmonella enterica*, *Serratia marcescens*, and *Staphylococcus aureus* (data not shown).

DISCUSSION

Bacterial Communities of Offshore Reef Sponges Are Disrupted Following Major Flooding Events

It has been assumed that remote benthic marine ecosystems (>100 km from land) are not significantly affected by terrestrial runoff. Our findings, however, suggest that floodwaters can reach and impact offshore benthic reef organisms. Bacterial communities of both *X. muta* and *A. clathrodes* showed disruptions to their community structure following two flood events in 2016 and 2017, relative to sponges collected during the same season in a no-flood year in 2018. Furthermore, we quantified an increased relative abundance of Enterobacteriaceae and two known human pathogens (*E. coli* and *K. pneumoniae*) in post-flood sponge samples, indicating that bacteria of terrestrial origin may interact with offshore reefs following extreme storm events.

Bacterial communities associated with the two sponge species in this study exhibited some differences in the strength and duration of their response to flood water stress, likely because they harbored distinctive bacterial communities during the no-flood year. Bacterial communities associated with other sponge species have similarly exhibited variation in their resistance to some flood-associated stressors, such as elevated nutrients (Simister et al., 2012; Luter et al., 2014; Baquiran and Conaco, 2018) and/or reduced salinity (Glasl et al., 2018b). Larger shifts in *X. muta* bacterial communities were associated with the 2016 flood year. In contrast, *X. muta* bacterial communities were relatively resilient following the sub-lethal stress associated with the 2017 flood year, with Oct. 2017 communities being more similar to the no-flood year. Interestingly, *A. clathrodes* sponges exhibited larger shifts in its microbiota in 2017 compared to 2016. Wright et al. (2019) similarly found that interspecific differences were the strongest driver of host gene expression changes in two coral species at these same sites, in response to the same 2017 flood event (Hurricane Harvey, Oct. 2017). Host-specific differences of sponge microbiomes have also been demonstrated for other environmental disturbances, such as sedimentation and ocean acidification (Ribes et al., 2016; Pineda et al., 2017). Differences in host resistance/resilience to environmental changes or differences in a hosts' ability to regulate its bacterial community may explain why *X. muta* showed more ephemeral changes (and more dispersion) in response to the 2017 flood, whereas shifts in *A. clathrodes* bacterial communities lingered. This finding of increased dispersion in *X. muta* bacterial communities exposed to human disturbance is consistent with the AKP; however, direct tests of the AKP in would require sampling of the same individual through time to test for increases in bacterial dispersion with declines in host health.

Bacterial community shifts documented in both sponge species after these floods could be driven by a combination of several mechanisms including: (a) invasion of floodwater-derived bacteria into host tissues, (b) invasion of seawater-derived bacteria into host tissues, and/or (c) shifts in the abundance of sponge-associated bacteria already present in hosts. It is plausible that all three mechanisms contributed, albeit to different degrees, following each flood event. Invasion of floodwater-derived bacteria into host tissues is supported by the presence of human pathogens in sponge-tissue in Aug. 2016. Invasion of seawater-derived bacteria into sponge tissue is supported by the enrichment of *Synechococcus* and *Prochlorococcus*, generally free-living marine Cyanobacteria, in both sponge species. However, sponge-associated and seawater associated bacterial communities were distinct across all dates, with few shared ASVs across all dates. Furthermore, relevant changes to *X. muta* bacterial communities in Aug. 2016 and Sept. 2017 were driven primarily by the relative increase of a resident sponge-associated Cyanobacterium (*Synechococcus spongarium*), which was not present in any seawater samples. This suggests that shifts in the abundance of bacterial taxa already present in sponges drove much of the bacterial community shift documented after these floods. To confirm the mechanism(s) underlying such microbial shifts on reefs, robust manipulative experiments or 'before flood' environmental samples of seawater and benthic host tissues would be required.

Changes in environmental parameters during and after flood events potentially drive shifts in the structure and composition of sponge- and seawater-associated bacterial communities by promoting or inhibiting growth of particular bacterial taxa and/or reducing the capacity of the animal host to regulate its microbiome (Zaneveld et al., 2017; Pita et al., 2018). For example, floodwaters over the FGB in 2016 contained higher ammonium concentrations (Kealoha et al., 2020), which may be contributing to enrichment of *Synechococcus* which generally occurs in higher abundance in the more mesotrophic environments near coasts (Partensky et al., 1999). Surface salinity decreased at the FGB following both flood events, but salinity at depth (24 m), reported from instruments at the WB, was unchanged preceding and during the flood event in 2016 (Johnston et al., 2019), suggesting that changes in salinity did not directly impact sponge-associated communities. Measurements for other environmental parameters associated with terrestrial runoff, such as turbidity, nutrient content, and pH, are not available for waters at the collection sites within FGB following these flood events.

Wastewater Contamination of Sponges After Severe Flooding Reaches Offshore Marine Ecosystems

The increased abundance of Enterobacteriaceae in reef sponges 185 km offshore in the 2016 flood year, and, particularly, the detection of two fecal coliforms (*E. coli* and *K. pneumoniae*) in both flood years strongly suggest that FGB reefs were exposed to wastewater contamination after severe storms. Although the Family Enterobacteriaceae is ubiquitous in nature, occupying terrestrial, aquatic, and marine habitats, especially the intestine of homeothermic animals (Whitman, 2015), members of this group are not common or abundant members of the bacterial communities of sponges (Moitinho-Silva et al., 2017; Cleary et al., 2019). Other sources of Enterobacteriaceae, such as excreted waste from reef fish and marine mammals (Wallace et al., 2013) could explain the presence of this bacterial family across flood year sponge samples. Although the GoM has high ship traffic, it is unlikely that ship wastewater discharge represents a significant source of fecal coliforms to these reef organisms because it is prohibited for ships to discharge untreated human waste within the boundaries of the FGB National Marine Monument[1]. If any of these other potential sources drove

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[1] https://flowergarden.noaa.gov/about/regulations.html

the Enterobacteriaceae patterns in this study, then similar detections would be expected in all years. Other members of the Enterobacteriaceae, besides those screened for via qPCR, do not explain the presence of Enterobacteriaceae reads in samples across all sampling years because most Enterobacteriaceae ASVs were classified as *E. coli*. Given that no human pathogens were detectable from samples during the no-flood, the most parsimonious explanation for the Enterobacteriaceae detections in this study is that FGB reefs were exposed to land-based human wastewater via terrestrial runoff following the 2016 and 2017 floods.

We expected to find Enterobacteriaceae in seawater samples during one or both flood years; however, no members of this Family were observed in sequencing data or detected via qPCR. The dynamic, transient nature of seawater masses and the ability of sponges to filter feed, and thus, concentrate bacterial cells, may explain why Enterobacteriaceae was observed in sponge samples but not seawater samples. Fine-scale time series sampling of the seawater above FGB in the weeks following each flood event could have further resolved potential interactions among bacterial communities in near-reef seawater and benthic reef organisms. Unfortunately, logistical challenges stemming from the offshore location of the FGB precluded the collection of these samples. Although *X. muta* is larger and thus likely has a higher filtration rate (McMurray et al., 2008; Parra-velandia et al., 2014; Morganti et al., 2019), *A. clathrodes* had a higher frequency of detection of *E. coli* and contained this bacterial taxa at higher abundances. Interspecific differences in the digestion of filtered material (Lynch and Phlips, 2000) may have contributed to differences in the abundance of human pathogens between these two sponges. Regardless, this work demonstrates that sponge species can be effective tools for monitoring wastewater contamination in offshore, as well as nearshore, marine ecosystems, and that the species selected for monitoring requires consideration.

It is unclear whether wastewater-derived bacteria contributed to mortality at EB in July of 2016, but detection of wastewater contamination at FGB (especially in diseased *A. clathrodes* samples) raises the question: do fecal coliforms pose health risks to offshore reefs? Human or animal wastewater contamination is linked to negative impacts on coral communities, particularly based on the input of excess nutrients, but chemical, bacterial, and pharmaceutical contamination are also potential issues (Wear and Thurber, 2015). The wastewater-derived bacteria, *Serratia marcescens*, is a coral pathogen (Sutherland et al., 2010, 2011), and in Hawaii, fecal coliforms colonized coral tissues after exposure, potentially contributing to a major disease outbreak (Beurmann et al., 2018). There is little information on the effect of fecal coliform exposure on marine sponge health, but some sponges may be relatively tolerant, using bacterial cells as a source of nutrition (Chaves-Fonnegra et al., 2007). The surprisingly far reach of contaminated floodwaters observed here underscores the urgent need to understand how floodwaters impact the health and function of offshore reef environments. A key question to address is whether detection of *E. coli* and *K. pneumoniae* represent detection of DNA from dead wastewater-derived bacterial cells or whether living wastewater-derived bacteria are potentially interacting with sponges (and other marine life) following extreme storms. If wastewater-derived bacteria contaminating sponges are metabolically active, then we must determine how long they persist within the sponge microbiome and the extent to which these microbes impact sponge physiology and function. A better understanding of the interactions between benthic reef hosts and terrestrial-derived bacteria will support effective management and protection of offshore reef ecosystems, such as the FGB.

Comparisons of FGB Sponge Bacterial Communities to Those in the Wider Caribbean

This study is the first to characterize sponge-associated microbial communities from the northwest Gulf of Mexico (and the FGB), offering the opportunity for comparisons of sponge microbial communities across regions of the GoM and the Caribbean. *X. muta*-associated bacterial communities at the FGB in 2018 (no storm condition) were similar between EB and WB and were dominated by Phyla also commonly reported from *X. muta* in the Florida Keys, Bahamas, and greater Caribbean (i.e., Proteobacteria, Chloroflexi, Cyanobacteria, Poribacteria, and to a lesser extent, Acidobacteria, Actinobacteria, and Crenarchaeota (Schmitt et al., 2012; Olson and Gao, 2013; Montalvo et al., 2014; Fiore et al., 2015; Morrow et al., 2016; Villegas-Plazas et al., 2019). These previous studies report regional differences due to changes in relative abundance of these shared Phyla (Fiore et al., 2015; Morrow et al., 2016). *X. muta* bacterial communities from the FGB may also be regionally distinct, in particular containing a high abundance of Crenarchaeota archaea (∼10%) compared to what has been reported from other regions (<5%) (Fiore et al., 2013). Ammonia oxidizing Archaea, such as Nitrosomopumilaceae, play an important role in nitrogen cycling in *X. muta* (López-Legentil et al., 2010). Ammonia-oxidizing archaea are outcompeted in environments with higher levels of ammonium (Erguder et al., 2009), so the greater abundance of Nitrosomopumilaceae likely reflects the oligotrophic environment of the offshore FGB reefs during no storm conditions.

Bacterial communities of *A. clathrodes* at the FGB contained Phyla (i.e., Proteobacteria, Firmicutes, Actinobacteria, Chloroflexi, and Crenarchaeota) also present in other *Agelas spp.* from the Florida Keys, Belize, and Central Amazon Shelf (Olson and Gao, 2013; Deignan et al., 2018; Rua et al., 2018; Gantt et al., 2019). However, higher abundances of Archaea, especially Euryarchaeota and Crenarchaeota, and Firmicutes were found in other *Agelas* spp. (Deignan et al., 2018; Rua et al., 2018). Diseased sponges (both *A. clathrodes* and *X. muta*) sampled after the 2016 mortality event were dominated by Alphaproteobacteria, especially Rhodobacteraceae. Alphaproteobacteria were also enriched in sponges affected by *Agelas* Wasting Syndrome (Deignan et al., 2018), suggesting that this group of bacteria could play a role in pathogenesis and/or serve as a biomarker of disease risk for FGB sponge communities.

Mitigating the Impacts of Future Storms on Offshore Reefs

This study demonstrates that floodwaters following extreme storms can reach the vicinity of offshore reefs and may contribute to shifts and increased heterogeneity in the bacterial communities of sponges and other benthic reef organisms. Detection of bacteria typically associated with wastewater within these sponge samples illustrates that marine-terrestrial interactions, and thus, the potential impacts of human land and waste management practices, extend far beyond the shoreline. The GoM is regularly impacted by hurricanes, and thus marine communities in the region have evolved in a disturbance regime that includes bursts of storm-generated terrestrial runoff. However, the ongoing expansion of impermeable surfaces (e.g., concrete, pavement) that reduce water absorption by soil in Texas and other coastal areas, as well as changing extreme storm patterns (e.g., slower moving hurricanes with greater precipitation) are increasing the frequency and intensity of floodwater influx into marine environments.

This study of the potential impacts of the 2016 and 2017 floods was catalyzed because a mortality event affected the East Bank following the Tax Day Flood. We hypothesize that flood waters associated with other recent extreme storm events (e.g., 2015 Memorial Day Flood, flooding generated by Hurricane Imelda in September 2019) in the region likely also caused sub-lethal stress at the FGB. However, targeted sampling of FGB did not occur following these storms. Our findings clearly demonstrate the urgent need for: (1) continued mitigation of stormwater runoff and climate change impacts; and (2) establishment of surface and benthic microbial and water quality time series for near- and offshore reefs using standardized protocols. This latter program will ideally generate baseline data on the gene expression and microbiomes of key benthic reef taxa under normal conditions, providing critical context (Glasl et al., 2018a) in which to detect and mitigate floodwater-derived stress on reefs in order to understand their impact on benthic invertebrate physiology and reef ecosystem functions.

MATERIALS AND METHODS

Pelagic Water Properties During Sample Collection Periods

The Flower Garden Banks National Marine Sanctuary (northwest Gulf of Mexico) is comprised of three banks: East Bank (EB), Stetson Bank and West Bank (WB) (**Figure 1A**). Surface salinity data, available from the Texas Automated Buoy System (TABS) Real Time Ocean Observations system archive[2] were used to assess the potential of flood waters to reach the vicinity of the FGB reef surface waters following recent severe storm events. To characterize local surface salinity (sensor depth of 2 m) in parts per thousand (ppt) representative for the FGB before, during, and after each sampling period, water property data collected each half hour for April - October for the years 2006 - 2018 were downloaded for TABS Buoy V (27°53.7960′N, 93°35.8380′W), which is located approximately 3 km from EB and 25 km from WB. Data were filtered to remove all timepoints containing no data and to exclude outlier data (i.e., measurements where salinity abruptly changed to <1 ppt or >70 ppt from 35 ppt). Data were not available (due to instrumentation failure) in 2007 and between the dates of 6 June 2017 through 30 August 2017. The remaining data were then plotted with ggplot2 package version 3.3.2 using code from https://github.com/rachelwright8/TagSeq_FGB_HurricaneHarvey. Data were summarized in **Figure 1D** as means (black line) and daily ranges (gray shading) for April to October over the thirteen-year period. To assess the lags between continental flooding (associated with an extreme storm) and changes in water quality at the FGB, daily salinity means and range data for April to October of individual years 2016–2018 (red lines and shading, respectively) were overlaid on surface salinity averages for the thirteen-year summary data. Daily means for each sponge sampling date were also calculated and plotted on top of the thirteen-year summary data with colored icons (**Figure 1D**). For sampling campaigns that spanned more than one day, only the first day of sampling was plotted (the maximum length of a sampling campaign was 5 days).

Sample Collections

Sponge samples were collected at four timepoints spanning 2016–2018 from two locations within the FGB; Buoy 4 at East Bank (27°52′54.84," 93°37′41.84") and Buoy 2 at West Bank (27°54′28.8," 93°36′0.72," **Figure 1A**, **Table 1**). At all sampling timepoints, fragments were collected from individual *A. clathrodes* and *X. muta* sponges. The same individual sponges were not repeatedly sampled across timepoints due to time constraints in available ship and dive time. In August 2016, samples were collected from 'diseased sponges' that were exhibiting progressive tissue loss, as well as from visually healthy sponges. Diseased sponges were sampled at the interface between lesion ad healthy tissue. Representative photos of diseased sponges are presented in Johnston et al. (2019). For all other timepoints, samples were collected from visually healthy sponges as diseased sponges were not observed. Samples were clipped from sponge individuals using health status and species-specific cutting shears that were wiped clean between samples. Each sample was placed in an individual sterile bag for transport to the surface. Once topside, each sample was immediately transferred to liquid nitrogen and stored at −20°C until further processing. In total, 109 sponge samples, collected from depths ranging 18–27 m, were analyzed in this study (individual sample metadata provided in **Supplementary Table 1**).

Seawater samples were collected at three locations over EB (Buoy 4, Grid site 43 and Grid Site 42) and 2 locations over WB (Buoy 2 and Grid Site 23) (**Figure 1A**, **Supplementary Table 1**). 'Grid' sites refer to sampling sites along a 10 × 10 km grid over the FGB which was established in response to the localized mortality event detected in July 2016 and is described further in Kealoha et al., 2020. In Aug. 2016, Oct. 2017, and Oct. 2018, seawater samples were collected from surface waters (<2 m depth) as well as within the water column (10–30 m depth) using a Niskin bottle rosette on a Seabird Electronic (SBE)

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[2] http://tabs.gerg.tamu.edu

25 CTD profiler. For August 2016, seawater collection preceded sponge collection by 4–6 days. For October 2017 and October 2018, seawater column samples were collected across the same dates as the sponges. Additionally, in Oct. 2017, seawater samples were collected by divers directly above the reef benthos at Buoys 4 and 2 (sites of sponge collection) over the same dates as the sponges. All CTD collected water samples were sieved with a 100-μm nylon net to exclude zooplankton. For each sample, 1000 mL of sieved seawater was then vacuum filtered (≤20 cm Hg) through a 47 mm, 0.22 μm Supor PES filter membrane (Pall) and immediately stored at −20°C. After returning to port, samples were transported on dry ice to Texas A&M University and stored at −80°C until DNA extraction.

Bacterial Community Analysis

DNA was extracted from 250 mg of sponge sample using the Nucleospin Soil DNA extraction kit (Takara Bio) and was submitted to the Baylor College of Medicine's Alkek Center for Metagenomics and Microbiome Research for high-throughput sequencing. High-throughput sequencing of the V4 hypervariable region of the 16S gene was conducted with 515f: 5′ GTGYCAGCMGCCGCGGTAA 3′ and 806rb: 5′ GGACTACNVGGGTWTCTAAT 3′ primers (Apprill et al., 2015) using the Illumina Mi-Seq (Paired-end 2 × 250 read) platform. DNA extraction blanks were not performed during extraction of the sponge samples; however, work on these samples was conducted in a lab in which no human wastewater, nor sponge (or reef) samples had ever been processed previously. Total DNA from seawater samples was extracted from filters using FastDNA Spin kits (MP Biomedical) with a BioSpec Mini-Beadbeater-24. Each sample was amplified in triplicate 25 μL reactions with the following cycling parameters: 95°C for 3 min, 30 cycles of 95°C for 45 s, 50°C for 60 s, and 72°C for 90 s, and a final elongation step at 72°C for 10 min. All amplifications were performed using the 515F-806R primer pair modified with barcodes and Illumina MiSeq adapters. DNA extraction blanks were performed on seawater samples and did not yield any amplification products. Following amplification, the triplicate products were combined together and run on a 1.5% agarose gel to assess amplification success and relative band intensity. Amplicons were then quantified with the QuantiFluor dsDNA System (Promega, Madison, WI, United States), pooled at equimolar concentrations, and purified with an E.Z.N.A. Cycle Pure PCR Clean-Up Kit (Omega Bio-Tek). The purified library was sequenced on the Illumina MiSeq platform (v2 chemistry, 2 × 250 bp) at the Georgia Genomics Facility (Athens, GA, United States).

Sequence analysis was conducted using QIIME2 v. 2019.10 pipeline (Bolyen et al., 2019). Pair-end, demultiplexed reads for all samples were combined, quality filtered, trimmed of poor-quality bases, de-replicated, chimera filtered, pair merged, and identified as amplicon sequence variants (ASVs) using the DADA2 plug-in (Callahan et al., 2016). Taxonomy was assigned by training a naïve-Bayes classifier on the V4 region of the 16S gene in the SILVA version 138 database (Quast et al., 2013) using the feature-classifier plugin (Bokulich et al., 2018). A 90% confidence threshold was used to retain classifications at each level of taxonomy. Low abundance ASVs (<2 occurrences over all samples) and non-prokaryotic ASVs (i.e., mitochondria, chloroplast, eukaryote, and unknown sequences) were removed. Rarefied ASV tables (rarefied to 9,000 reads per sample) were used to calculate alpha diversity metrics and to conduct beta diversity analyses using weighted UniFrac distance matrices.

Quantitative PCR for Human Pathogens Associated With Hurricane Harvey-Derived Floodwaters

Species-specific functional genes were chosen as biomarkers to detect and quantify fecal indicator bacteria (*Escherichia coli* and *Enterococcus spp.*), putative pathogenic bacteria in the Family Enterobacteriaceae (*Klebsiella pneumoniae*, *Serratia marcescens*, and *Salmonella enterica*), and other putative pathogenic bacteria (*Pseudomonas aeruginosa* and *Staphylococcus aureus*, **Supplementary Table 7**). These bacterial species were targeted because they were identified in qPCR screening and in high-throughput sequencing of terrestrial floodwater and sediment samples collected immediately following Hurricane Harvey (Yu et al., 2018). Sponge samples were screened for all seven bacterial species. Seawater samples were then screened for the bacterial species found in sponges (*E. coli* and *K. pneumoniae*).

Target gene amplicons were used to establish the standard curve between the threshold cycle (Ct) value and log10 (gene copies) for each pathogenic bacterium individually. To generate amplicons for target gene quantitation, genomic DNA of pure cultures of each bacterial strain was extracted using DNeasy PowerSoil Kit (Qiagen, Hilden, Germany) and target genes were amplified by conventional PCR (50 μL reactions) with EmeraldAmp GT PCR Master Mix (Takara Bio, thermocycler conditions listed in **Supplementary Table 7**). Five μL of each PCR product was visualized via gel electrophoresis to confirm amplification, and the remaining PCR product was cleaned using GeneJET PCR Purification Kit (Thermo Fisher Scientific, Waltham, MA, United States). Amplicon concentration was quantified using a Qubit 3 Fluorometer (Invitrogen) with dsDNA Broad Range Assay (Invitrogen), amplicon quality was assessed using a NanoDrop One (Thermo Scientific), and amplicon sequences were confirmed via Sanger sequencing. Verified amplicons were then serially diluted to create a set of standards of known concentrations, calculated by the Thermo Fisher DNA Copy Number Calculator[3]. Each standard curve was established by linear regression of the threshold cycle (C_T) values versus the log-normal (10 base) abundance of gene copies (10^8, 10^7, 10^6, 10^5, 10^4, 10^3, 10^2) from technical triplicates. R^2 values of least square fit ranged from 0.995–0.999 for all the standard curves. The qPCR amplification efficiency for all the biomarkers ranged from 92–105%, calculated by plotting average C_T vs. amplicon concentration (copies/μL) on a $\log_{10}$ scale. To assess gene copy number in a given sample, C_T values of samples were compared to a prepared standard

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[3] https://www.thermofisher.com/us/en/home/brands/thermo-scientific/molecular-biology/molecular-biology-learning-center/molecular-biology-resource-library/thermo-scientific-web-tools/dna-copy-number-calculator.html

curve that was included in triplicate with each qPCR run. Calculated copy number was normalized to g of wet sponge tissue and normalized to input DNA concentration of each sample as conducted previously (Radax et al., 2012; Moeller et al., 2019). The limit of quantification ranged from 20–100 gene copies.

Quantitative PCR reaction mix consisted of 5 μL 2x Power SYBR Green Master Mix (Applied Biosystems, Foster City, CA, United States), 1 μL DNA, 1.3 μL of each primer (10 μmol stock), and molecular-grade water, for a final volume of 10 μL. Primer specifications and thermocycler conditions for each pathogen are listed in **Supplementary Table 2**. All samples were run in triplicate on a QuantStudio 3 Real-Time PCR System (Thermo Fisher Scientific, Waltham, MA, United States) and were screened for all seven pathogens (**Supplementary Table 7**). Negative controls (no template) were run in triplicate for each qPCR experiment to monitor for potential contamination. The temperature profile for SYBR Green qPCR involved 95°C for 10 min, 45 cycles of 95°C for 15 sec and annealing/extension temperature of 54 – 65°C for 1 min. Melt curve analysis was conducted after PCR completion to ensure non-specific PCR products were not generated. Specificity of each qPCR assay was confirmed by testing for amplification in all pathogen strains used in this study as well as in four environmental isolates (*Vibrio* sp., *Alteromonas* sp., *Pseudoalteromonas* sp., and *Shewanella* sp.) previously cultured from FGB coral. No non-target strains amplified below a threshold cycle (C_T) of 30. Amplifications were considered positive if all three replicates amplified at a threshold cycle (C_T) less than 28 and melt curve analysis showed similar patterns to the standard.

Statistics

A weighted UniFrac distance matrix was used to calculate beta-diversity and to assess within group dispersion in bacterial communities and to construct Principle Coordinates Analysis (PCoA) plots to visualize differences in bacterial community structure between groups using QIIME2. PCoA was conducted for all samples (both sponge species), as well as for healthy samples of each species individually. Pairwise Analysis of Similarities (ANOSIM), conducted with 999 permutations, was used to test for significant differences in bacterial communities among categorical variables including species, health state, site, and collection date. To assess differences in bacterial abundance at the Family level, the unrarefied ASV table for each species was first summarized to Family level using tax_glom in phyloseq (v1.30.0). A negative binomial model was then fitted with the R package DESeq2 (v1.26.0) and Wald tests were used to test for differences in taxon abundance within each comparison of Date versus the 'baseline' Date (October 2018). Benjamini-Hochberg FDR tests were used to account for multiple comparisons, and Families with *p*-values less than 0.05 were identified as significantly differentially abundant. Indicator species analysis was performed to test the association between bacterial community and collection date, using indicspecies (v1.7.9) package in R. Significance was assessed with 9999 permutations, and ASVs with *p*-values less than 0.05 selected. PRIMER-E v6 (Primer-E Ltd) was used to conduct Similarity Percentages (SIMPER) analysis, which identified ASVs that contributed to differences between bacterial communities across Dates. Differences in ASV richness, Shannon Diversity, relative abundance of bacterial taxa, and quantified bacterial abundance data were analyzed within the three sample types (*X. muta*, *A. clathrodes*, and Seawater) individually using generalized linear models (GLM) with Site, Health State (healthy vs. affected sponge), Seawater sample type (water column vs. reef water), and Date as categorical predictors. If significant differences were detected, then a Tukey's HSD *post hoc* test was performed to examine the differences between the levels of the independent variables. Differences in mean community variability (mean pairwise dissimilarity) across Dates was assessed using ANOVA with Tukey's pairwise comparisons. All data are represented as mean (±SEM), unless otherwise stated.

DATA AVAILABILITY STATEMENT

The raw sequence data files are available in the NCBI Sequence Read Archive under accession numbers: SRP248232 for sponge samples, PRJNA509639 for Aug. 2016 seawater samples and PRJNA691373 for Oct. 2017 and Oct. 2018 seawater samples. Data files including Sample Metadata, ASV Table, ASV Taxonomy Assignment, and R script for DESeq and Indicator Species analysis are available on FigShare at https://figshare.com/account/home#/projects/82841.

AUTHOR CONTRIBUTIONS

AC, JBS, LS-V, LS, KS, and SWD obtained financial support and conceived experimental design, sampling strategy, site selection, and sampling methodologies for fieldwork. AS, CG, LH-K, and JAS contributed to data analysis. AS, LH-K, JAS, LS, and AC contributed to manuscript preparation including figures and tables. All authors contributed to dive support, sample collection, and/or sample processing, and reviewed manuscript drafts.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.608036/full#supplementary-material

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