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FEATURE ARTICLE

A multi-tiered assessment of fish community responses to habitat restoration in a coastal lagoon

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ABSTRACT: Essential fish habitat is critical for foraging, breeding, or as refugia. As such, restoration of these habitats has the potential to increase the diversity and abundance of fishes. Here, we explored how fish communities responded in the first 12–24 mo following oyster reef restoration. Study sites included 8 restored reefs plus 4 live and 4 dead reefs as controls. Oyster reef metrics (e.g. density, height, thickness) and fish abundance and diversity metrics were quantified, including species richness, Shannon diversity, Simpson's diversity, and Pielou's evenness. Species composition was explored further to identify indicator species and assess habitat preferences. Patterns of fish community diversity and species composition were compared to oyster reef metrics to discern what oyster reef characteristics best predict fish diversity. Results showed that intertidal oyster reefs were structurally restored and shifted from resembling negative control reefs to positive control reefs within 12–24 mo. Across all treatment types, oyster shell height and reef thickness were the best predictors of fish diversity. However, at the fish community level, assemblages at restored reefs were similar to those at positive and negative controls. Species-level analyses suggest treatment types have unique indicator species, including *Chilomycterus schoepfi* (striped burrfish) for dead reefs, *Lutjanus synagris* (lane snapper) for restored reefs, and *Gobiosoma robustum* (code goby) for live reefs. This work suggests fishes can be used as higher trophic level indicators of restoration success, and ecosystem-based approaches, such as habitat restoration, can restore essential fish habitat, thus benefiting fish communities while moving coastal ecosystems toward sustainability.

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Dead oyster reef pre-restoration, during restoration after raking reef down to mean water level and placing oyster mats, and 3 yr post-restoration.

Image: Linda Walters

KEY WORDS: Diversity · Ecosystem-based management · Indicator species · Oyster reef · Indian River Lagoon

1. INTRODUCTION

Essential fish habitat (EFH) is defined as 'those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity' (United States Congress 1976, Section 3) and is used, in combination with other ecosystem-based management (EBM) strategies, as a mechanism to protect and improve habitats critical to fish survival. Oyster reefs

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are one EFH-type and comprise a critical component of many estuarine seascapes (Luckenbach et al. 1995, Lehnert & Allen 2002, Kingsley-Smith et al. 2012). Oyster reefs support resident species, positively influence abundance and size of transient fish, and are known for their production of ecosystem services including shoreline protection, wave attenuation, improved water clarity, linking trophic levels (TLs), and creation of physical structure (Peterson et al. 2003, Coen et al. 2007, Gregalis et al. 2009, Lewis et al. 2020, Loch et al. 2020). However, oyster reefs are vulnerable to anthropogenic stressors due to their proximity to human development, and their areal extent has decreased greatly over time (Zu Ermgassen et al. 2012, Teichert et al. 2016). As oyster reefs are of critical importance to mitigate threats facing coastal ecosystems, their restoration has the potential to increase fish diversity and abundance and the production of associated ecosystem services (Peterson et al. 2003, Coen et al. 2007, Gittman et al. 2016). Understanding how oyster reef restoration impacts fish assemblages and community diversity will improve our ability to mitigate negative impacts on fish communities through coastal habitat restoration (Peterson et al. 2003).

The degradation of coastal habitats leads to a shift in the proportional composition of a broader habitat mosaic by decreasing the amount of relatively degraded and healthy habitat (Grabowski et al. 2005, Gregalis et al. 2009, Gittman et al. 2016). Oyster reef restoration often aims to restore the proportion of live reef following degradation (Luckenbach et al. 1995, Harding & Mann 1999, Loch et al. 2020). However, relatively few studies have been able to determine if higher TLs such as fish communities utilize degraded, restored, and live reefs in similar manners (Rezek et al. 2017, Loch et al. 2020). A knowledge gap exists when assessing fish responses to restoration in a shifting habitat mosaic, from the community level to the individual species level (Loch et al. 2020). To generate a novel understanding of how restoration of coastal ecosystems — including essential habitats such as oyster reefs — impacts (positively or negatively) fish community diversity will require targeted studies to assess the response of the fish community following restoration and knowledge regarding whether or not certain fish species use different components of the broader habitat mosaic.

Community diversity can refer to various characteristics in an ecosystem, ranging from species richness (number of species) to more complex indices incorporating both the number and proportion of species (Gray 1997). These community diversity metrics share the goal of quantitatively describing the assortment of species found within a region. Much debate has surrounded the link between species diversity and ecosystem structure, function, stability, and resilience (Grime 1997, Schwartz et al. 2000, Loreau et al. 2001, Tilman et al. 2014). Despite these competing views, ecologists broadly agree there are benefits to increased diversity, but the degree of benefits conferred varies among ecosystems. These diversity-related linkages are being explored; experimental studies support a positive relationship between diversity and ecosystem function, but generalities about the role of diversity in ecological communities, particularly in restored habitats, are few (Purvis & Hector 2000, Balvanera et al. 2006, Tilman et al. 2014). Understanding if and how species within the fish community differentially use degraded, restored, and natural habitats in coastal waters could provide a means by which natural resource managers and restoration practitioners could assess restoration success at higher TLs by monitoring representative fish species. For instance, if clear associations exist between individual fish species and reef characteristics, identifying indicator species for treatment types could act as a diagnostic tool by identifying species indicative of the stage of restoration as it proceeds along its developmental trajectory following restoration and informing how reefs are being utilized (Bergquist et al. 2006).

To address these needs, we collected fish community data from natural and restored oyster reefs to explore fish community dynamics in response to restoration of EFH. Aims of this study were to (1) quantify how physical oyster reef characteristics change 1–2 yr post-restoration; (2) explore how the fish community responds post-restoration and identify indicator species of natural and restored reefs; and (3) investigate what physical oyster reef characteristics best explain changes in the fish community. Previous studies suggest increased habitat complexity, through restoration of degraded reefs, will result in greater fish abundance and diversity than at dead reefs with decreased habitat complexity. Additionally, species assemblages of restored reefs are predicted to resemble dead reefs at the beginning of the sampling period and transition to resemble live reefs over time. Combined, the knowledge generated in this study will help explain how the fish community responds to oyster reef restoration, identify indicator species of degraded, restored, and natural oyster reefs, and provide insight that can be used to better inform the development of more effective EBM strategies.

2. MATERIALS AND METHODS

2.1. Study region

Data were collected in Mosquito Lagoon, located in the northernmost portion of the Indian River Lagoon (IRL), Florida, USA (Fig. 1). The IRL is one of the largest estuaries in the USA, spanning more than 250 km. It is tidally restricted (~0.33 m), relatively shallow (average water depth: ~1 m), and composed of a mosaic of EFH including oyster reefs, seagrass beds, mangrove forests, and coastal wetlands (Gilmore 1977, Garvis et al. 2015). The relatively rich fish community found in the lagoon comprises more than 270 taxa (Gilmore 1977, 1995, Snelson 1983, Troast et al. 2020). The IRL is composed of 3 distinct but connected bodies of water that form the broader lagoon system: Mosquito Lagoon, Banana River, and the Indian River proper.

Mosquito Lagoon is recognized for its recreational fishing opportunities and is regarded as the 'redfish capital of the world' (*Sciaenops ocellatus*; Kahn 2012). Within the boundaries of the Mosquito Lagoon are the state-designated Mosquito Lagoon Aquatic Preserve, Merritt Island National Wildlife Refuge, and Canaveral National Seashore. The predominant benthic habitats of Mosquito Lagoon are characterized by intertidal oyster reefs to the north and seagrass beds and salt marshes to the south (Walters et al. 2017). Since 1943, these habitats have declined by 24% within Mosquito Lagoon and 40% within Canaveral National Seashore (Beck et al. 2011, Zu Ermgassen et al. 2012, Garvis et al. 2015). To mitigate these losses in Mosquito Lagoon, oyster reef and living shoreline restoration has been ongoing for the past decade (Birch & Walters 2012).

2.2. Experimental design

In total, 8 restored oyster reefs were compared against 4 'dead' reefs and 4 'live' reefs (16 original focal study sites). Sites were sampled once before restoration and for 1–2 yr after restoration to examine how fish communities responded temporally to the restoration. Area of the reefs ranged from 16 to 25 m^2, and they were naturally occurring (i.e. not man-made) prior to restoration. Of the 8 restored oyster reefs, 4 were restored in June 2017 (1–4 are referred to as '2017 Reefs'), and 4 were restored in June 2018 (5–8, referred to as '2018 Reefs'). Site Restore 3, restored in June 2017, was removed from analyses due to extensive storm damage and loss of the restored area from Hurricane Irma.

Dead reefs were common in the study site and consisted of mounds of dead oyster shells with very few, if any, areas containing live oysters. These reefs were identified by relatively high vertical profiles (~1 m above bare bottom) where the reef was never fully submerged at any water level and were composed of dead loose oyster shell lying on the substrate (Boudreaux et al. 2006, Stiner & Walters 2008). Dead reefs were once live reefs until high-energy boat wakes eroded the relatively soft sediment around live reefs, resulting in live oyster clusters breaking off and washing up

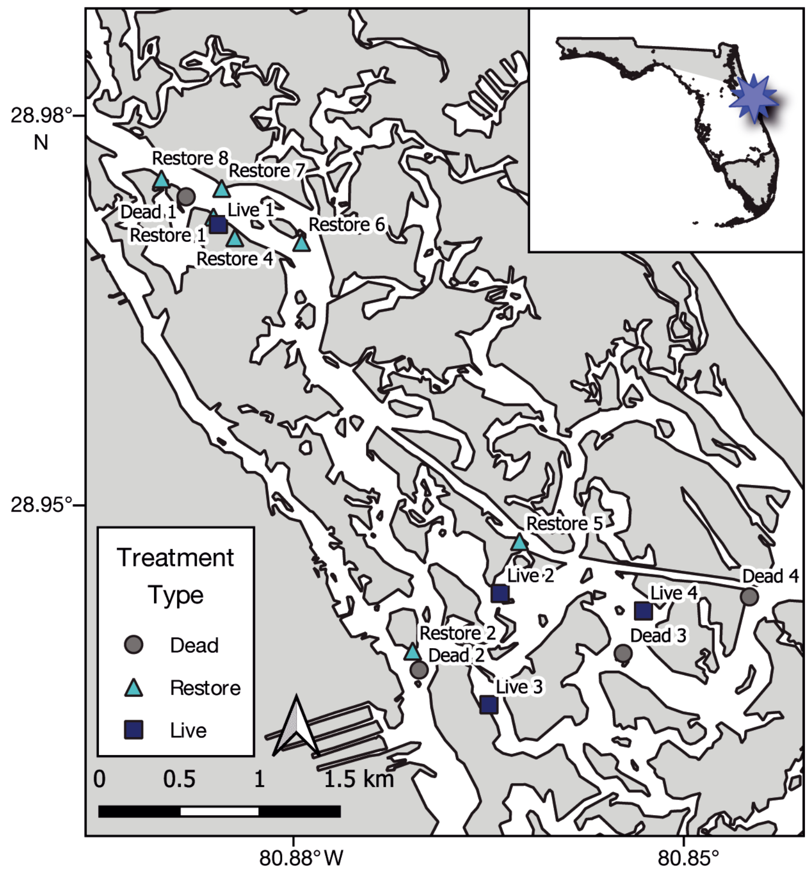

Fig. 1. Mosquito Lagoon, Florida, USA. Points: experimental design sites for oyster reef restoration. Gray circles: dead sites; light blue triangles: restore sites; navy squares: live sites. Inset map with blue star: relative location of sampling area along Florida's east coast

on top of the reef where they desiccated, over time creating a dead reef consisting of mounds of oyster shell well above mean water level (Wall et al. 2005). Restore sites were restored by raking down 'dead' oyster reef shell mounds to mean water level, as oyster reefs need to be submerged periodically to avoid desiccation. Next, 'clean' oyster shell halves (shells were sundried for several months), were affixed by the bottom of the shell to 0.25 m^2 Vexar mesh mats so they stood vertical on the mat; these are referred to as oyster mats. The mats were placed on the raked area, secured together, and weighted with concrete weights to the sediment (Garvis et al. 2015). Restored reefs were converted from large oyster shell mounds well above mean water level pre-restoration to low-lying areas just below water level, using vertical oyster shells for structure post-restoration. This method produces a restored oyster reef by providing structure at mean water level where local oyster recruits (spat) settle and mature into a live reef over time. Live reefs are characterized by residing at mean water level, so the reef is submerged at high tide and uncovered at low tide, has a relatively low vertical profile, and contains dense live oysters of many size classes.

2.3. Sampling methods

Oyster reefs were monitored following methods outlined in Baggett et al. (2015) and Chambers et al. (2018). In brief, five 0.25 m^2 quadrats for each reef were haphazardly thrown for sampling, and on restored reefs, centered over the closest oyster mat to most accurately quantify oyster metrics. Live oyster density was determined by counting the number of live oysters per quadrat and averaging all quadrats per reef. Live oysters were present at some dead reefs but were few in number. Oyster shell height was derived from the mean of 50 live oyster lengths counted per quadrat per reef (Baggett et al. 2015). Reef thickness is a metric used on low-relief intertidal oyster reefs in Mosquito Lagoon to track fine-scale changes in vertical reef height above the sediment over time, with the expectation that reefs will continue to increase in height via oyster growth and recruitment until they reach the maximum for growth enabled by the local tidal range (Chambers et al. 2018). On each of 10 haphazardly selected quadrats per reef, the greatest reef height in each quadrat (high point) and the mean of 5 haphazardly selected thicknesses (thickness) per quadrat per reef were recorded with a metal rod placed into the reef; its depth was recorded and then mean values were calculated per reef.

Two gear types were used to sample fishes utilizing benthic habitat on all reef types. Lift nets sampled the reef to target relatively sedentary reef residents (Lewis et al. 2021), and center bag-seines sampled the water column directly adjacent to the target habitat. Taxa caught in seines are relatively transient species that utilize the reef for foraging, refugia, and other behaviors — but not exclusively, as is the case for the relatively sedentary reef residents collected from lift nets.

Lift nets consisted of 0.6 × 0.6 m PVC quadrats fitted with 1.5 mm, 16 kg delta mesh. Six lift nets were deployed along the reef: three 0.5 m above and three 0.5 m below approximate mean tidal level. One oyster mat, similar to those used in restoration, was placed in the lift net. Nets were deployed during the day, soaked for 7 d, and retrieved at approximately mean tidal level. Lift nets were near water level on live and restored reefs (post-restoration) and above water level at dead reefs due to the vertical profile of the reef types. Lift nets were picked up swiftly by hand, the mat was shaken down inside the net to catch concealed organisms, and fish were identified and enumerated. Seines were approximately 21 m long and 2 m high with a 2 × 2 m center bag. Seine netting was 3.2 mm square, 16 kg delta knotless nylon with floats along the top and leads along the bottom. Nets were dragged approximately 30 m by hand parallel to the reef, and catches were identified and enumerated. For both gear types, all fish collected were identified to the lowest taxonomic level. Samples were processed in the field or laboratory, depending on time and weather. Species that were difficult to identify were brought to the lab for identification. Temperature, salinity, dissolved oxygen, and Secchi depth were recorded at time of sampling.

Sampling frequency varied with gear type. In summer 2017, lift nets were deployed at reefs once pre-restoration and following restoration at 1 and 2 wk, 1, 2, and 3 mo, and then every 3 mo through to the end of the study period. Due to logistical constraints, the 2 wk post-restoration sampling was dropped in summer 2018. Seines for the 2017 reefs were conducted once pre-restoration, 1 d post-restoration, and at 1 wk, 2 wk, 1 mo, 6 wk, 2 mo, 3 mo, and then every 3 mo thereafter. The 2 wk and 6 wk sampling periods were dropped in summer 2018 for logistical reasons. In total, 24 mo of post-restoration data were used in these analyses for sites restored in summer 2017, and 12 mo of post-restoration data were used for summer

2018 restoration sites. All sampling occurred between the daylight hours of 08:00 and 17:00 h; samples within time periods were collected within days of each other (<3 d). Order of sampling was chosen in an effort to best sample during mean water level combined with general field day logistics.

2.4. Data management

Abundance data were fourth-root transformed to allow rare species to influence the statistical tests and down-weight the effect of more abundant schooling fish. Species including *Anchoa mitchilli*, *A. lyolepis*, and *A. hepsetus* were grouped into *Anchoa* spp. These species were grouped due to their similarity in ecological function as forage fish and difficulty in identification to species.

2.5. Statistical methods

All analyses were completed using R statistical software v.3.6.0 (R Core Team 2019) in R Studio (RStudio Team 2018). Principal component analysis (PCA) was performed on oyster reef metrics (oyster density and height, and reef thickness and high point) to determine changes in physical reef characteristics over the study period among treatment types. Treatment types were grouped to better identify treatment change over time. Additionally, abiotic water metrics (temperature, salinity, dissolved oxygen, and Secchi depth) were compared among treatment types. Abundance and diversity metrics including species richness, Shannon's diversity, Simpson's diversity, and Pielou's evenness were quantified for each site across sampling periods using the R package 'vegan' (Oksanen et al. 2013). Differences in abundance and diversity metrics among treatment types were tested using 1-way ANOVAs. Following significant omnibus tests, post hoc Tukey's HSD tests were conducted to identify statistical differences.

Non-metric multidimensional scaling (NMDS) was conducted using the R package 'vegan' to compare species assemblages. Species abundance data were averaged by time period per treatment type and then normalized, and dissimilarities were calculated with Bray-Curtis dissimilarity. Cluster analyses were performed within the NMDS to determine the *k*-means 'best clusters' from hierarchical clustering. Indicator species were determined using the R package 'Indicspecies', which calculates an indicator value (IndVal) for species based on *a priori* grouping (i.e. treatment type). IndVal is a combination of additional metrics: (*A*) the exclusivity to the group of sites analyzed and (*B*) the number of sites within a group where the species is present (De Cáceres & Legendre 2009). The higher the IndVal metric, the greater the value of a particular species as an indicator of that particular habitat type. Here, indicator species were considered representative species of the treatment types, and provide insight into the species utilizing dead, live, and restored oyster reefs. TLs of indicator species were retrieved from FishBase (Froese & Pauly 2019).

Akaike's information criterion (AIC) model selection was used to determine which oyster metrics best described trends in diversity. Oyster metrics examined were oyster density, reef thickness, reef height, and oyster shell height. Reef high point was excluded from predictive models due to its collinearity with reef thickness. Thickness was selected over reef high point as it was a better overall predictor of fish diversity indices. Environmental Fit (EnvFit) tests were conducted using 'vegan' to determine which reef metrics were most highly correlated with fish community assemblages (Oksanen et al. 2013).

3. RESULTS

3.1. Habitat restoration and water quality

PCA explained approximately 93% of the variability among oyster reefs. The first principal component accounted for 74.9% of variability among oyster reefs, driven by oyster density, oyster reef high point, and thickness. The second principal component accounted for 17.83% of variability and was driven by oyster shell height (Fig. 2). Grouping samples by treatment (ellipses of Fig. 2) revealed restored oyster reefs have physical properties intermediate between dead and live reefs pre- and immediately post-restoration (smaller symbols in Fig. 2), and over time they become more similar to live oyster reefs (larger symbols in Fig. 2).

Sites were spread latitudinally, and small changes in abiotic variables were recorded. Temperatures ranged from a low of 14.1°C to a high of 37.7°C across all sites, with mean annual temperatures per treatment type ranging from 27.1 to 27.7°C. Salinities range from 25.0 to 43.0 ppt, with mean annual salinities per treatment type ranging from 33.7 to 33.9 ppt. Dissolved oxygen ranged from 3.1 to 9.8 mg l^{-1}, and mean annual dissolved oxygen among treatment types ranged from 6.1 to 6.5 mg l^{-1}. Secchi depth ranged from 0.2 to 1.9 m, and mean annual Secchi

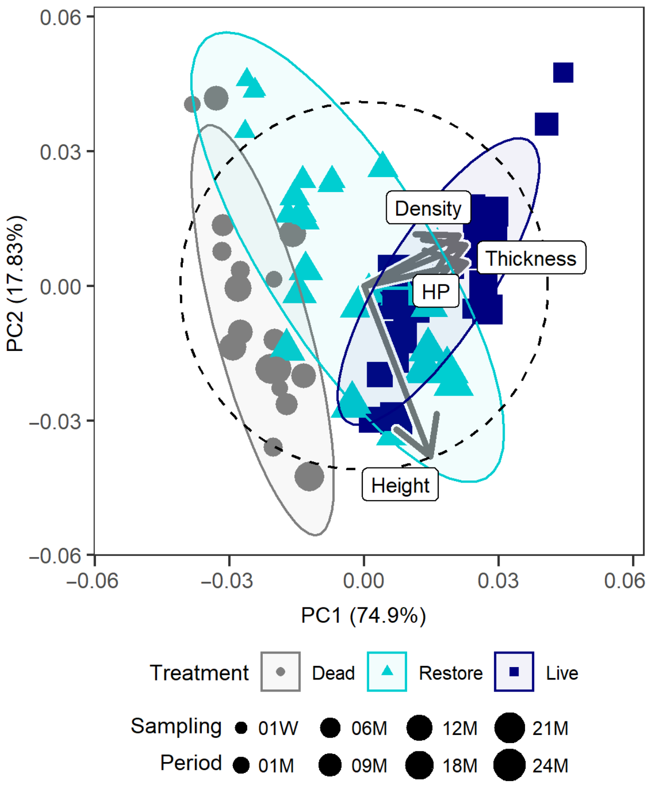

Fig. 2. Principal component analysis of oyster reef metrics from 2017 and 2018 reefs. Treatment type is categorized by color and shape: gray circles: dead reefs (negative controls); light blue triangles: restore reefs; navy squares: live reefs (positive controls). Smaller points are sampling events soon after restoration and increase in size with time since restoration. Dead and live reefs cluster separately, with restore reefs originally clustering nearer to dead reefs but clustering nearer to live reefs as time progresses

depth among treatment types ranged from 0.6 to 0.7 m. Small ranges and similar mean values in abiotic conditions suggest water quality parameters were comparable among all sampling sites.

3.2. Fish community

A total of 97 027 individuals were captured from May 2017 to June 2019, representing 67 taxa (Table S1 in the Supplement at www.int-res.com/articles/suppl/m698p001_supp.pdf). Seining collected 95 907 individuals representing 61 taxa, and lift nets collected 1120 individuals representing 32 taxa. *Anchoa* spp. were most abundant in seine catches (n = 60 219), representing 62.79 % of the catch. Completing the top 10 most abundant taxa were *Eucinostomus* spp. (mojarras; n = 12 116; 12.63 %), *Leiostomus xanthurus* (spot; n = 6425; 6.7 %), *Lagodon rhomboides* (pinfish; n = 2737; 2.85 %), *Harengula jaguana* (scaled sardine; n = 2415; 2.52 %), *E. harengulus* (tidewater mojarra; n = 2280; 2.38 %), *Clupeidae* spp. (herrings/sardines; n = 1993; 2.08 %), *Diapterus auratus* (Irish mojarra; n = 1610; 1.68 %), *E. gula* (Jenny mojarra; n = 1559; 1.63 %), and *Menidia* spp. (silversides; n = 1176; 1.23 %). The top 10 species accounted for 96.49 % of total seine net catch.

The most abundant taxa found in lift nets were *Gobiosoma* spp. (gobies, small or unidentified), with 252 individuals representing 22.50 % of the overall lift net catch. The remaining top 10 lift net taxa were *G. robustum* (code goby; n = 162; 14.46 %), *Ctenogobius boleosoma* (darter goby; n = 139, 12.41 %), *G. bosc* (naked goby; n = 124; 11.07 %), *Lutjanus griseus* (mangrove snapper; n = 109; 9.73 %), *Eucinostomus* spp. (mojarras; n = 71, 6.34 %), *Bairdiella chrysoura* (silver perch; n = 52, 4.64 %), *Archosargus probatocephalus* (sheepshead; n = 44; 3.93 %), *L. rhomboides* (pinfish; n = 40; 3.57 %), and *Opsanus tau* (oyster toadfish; n = 28; 2.50 %). The top 10 species accounted for 91.15 % of the total lift net catch.

3.3. Temporal analysis of restoration effects on abundance and diversity

Of reefs restored in 2017, live reefs generally had the highest values of abundance and diversity among gear types and time from restoration, except for Pielou's evenness where the trend was equivocal (Fig. 3). In lift net catches, restored and dead reefs had similar abundance, species richness, and Shannon diversity, but differed in Simpson diversity and evenness; however, these metrics had larger variation. In lift nets, significant differences among treatments ($p < 0.1$) occurred pre-restoration in all metrics except Simpson diversity; restored and live reefs were significantly different while dead reefs were intermediate. Significant differences occurred again at 2 and 48 wk post-restoration. Live reefs were significantly different from dead and restored reefs (Fig. 3). In seine catches, reef types were not significantly different until Week 20. Significant differences ($p < 0.1$) occurred directly after restoration for Shannon and Simpson's diversity, with restored and live reefs differing (Fig. 3). Restored reefs and live reefs had higher abundances than dead reefs at 2 wk post-restoration. Differences in species richness and evenness occurred in Week 8, with dead reefs having higher species richness and lower evenness than other treatment types. In

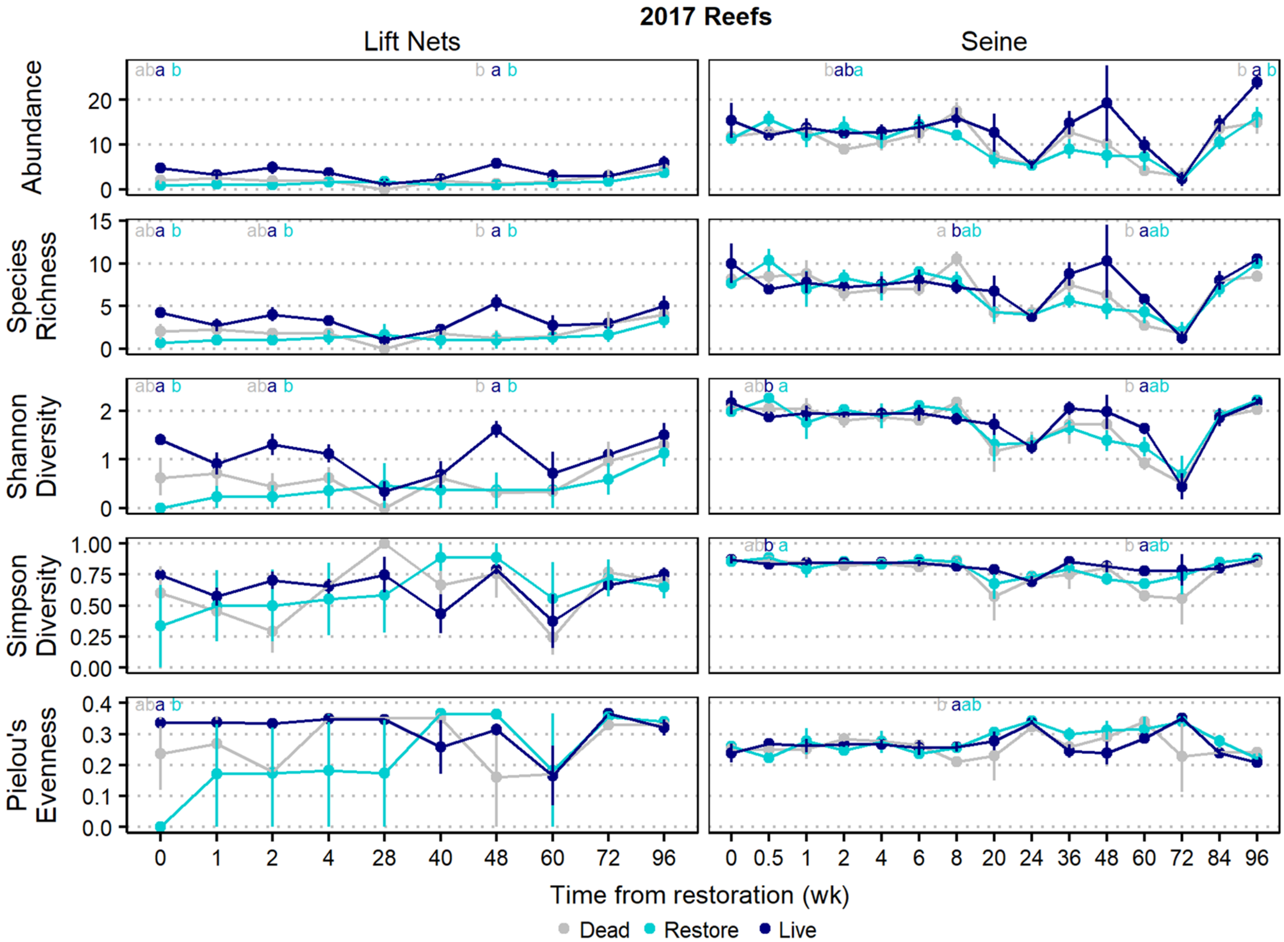

Fig. 3. Mean abundance and diversity values of each treatment type over time (in weeks) for lift net and seine catches of 2017 reefs. Treatment type is categorized by color: light gray: dead reefs (negative controls); light blue: restore reefs; navy: live reefs (positive controls). Error bars: ±SE. Live reefs often have greatest values of abundance and diversity. Restored reefs had greater Simpson diversity in lift nets over time. In general, restored reefs were similar or greater than dead reefs. Letters represent significant differences ($p < 0.1$) among treatment types at a given sampling period, as determined by post hoc Tukey HSD tests

Week 60, live reefs had the highest values of species richness, Shannon and Simpson diversity, and were significantly different than dead reefs; restored reefs grouped between them. At Week 96, live reefs had higher abundance than both dead and restore reefs (Fig. 3).

Of reefs restored in 2018, live reefs generally had higher values of diversity throughout the sampling period (Fig. 4). In lift net catches, significant differences only occurred pre-restoration, with live reefs differing from both dead and restored reefs. All reef types became more similar over time. In seine catches, significant differences ($p < 0.1$) occurred at 12 wk for species richness, Shannon diversity, and Simpson diversity, where dead and live were different and restore reefs grouped between those treatment types (Fig. 4). Restored reefs had the lowest evenness at this time period, differing from dead reefs, with live reefs grouping between. Restored reefs' abundance and species richness more closely grouped with dead than live reefs in the last 2 sampling periods.

Two groups were determined from *k*-means clustering of species assemblage groups based on seine catch by treatment type over the sampling period. However, these groups contained all treatment types, and trends appeared to be dominated more by sampling time post-restoration rather than treatment type (i.e. fish assemblages at the end of the study were distinct from those at the beginning of the study, but fish catches at all 3 treatment types were more similar during each sampling period than when compared among treatment types). Similarly, lift net cluster analyses had inconclusive results.

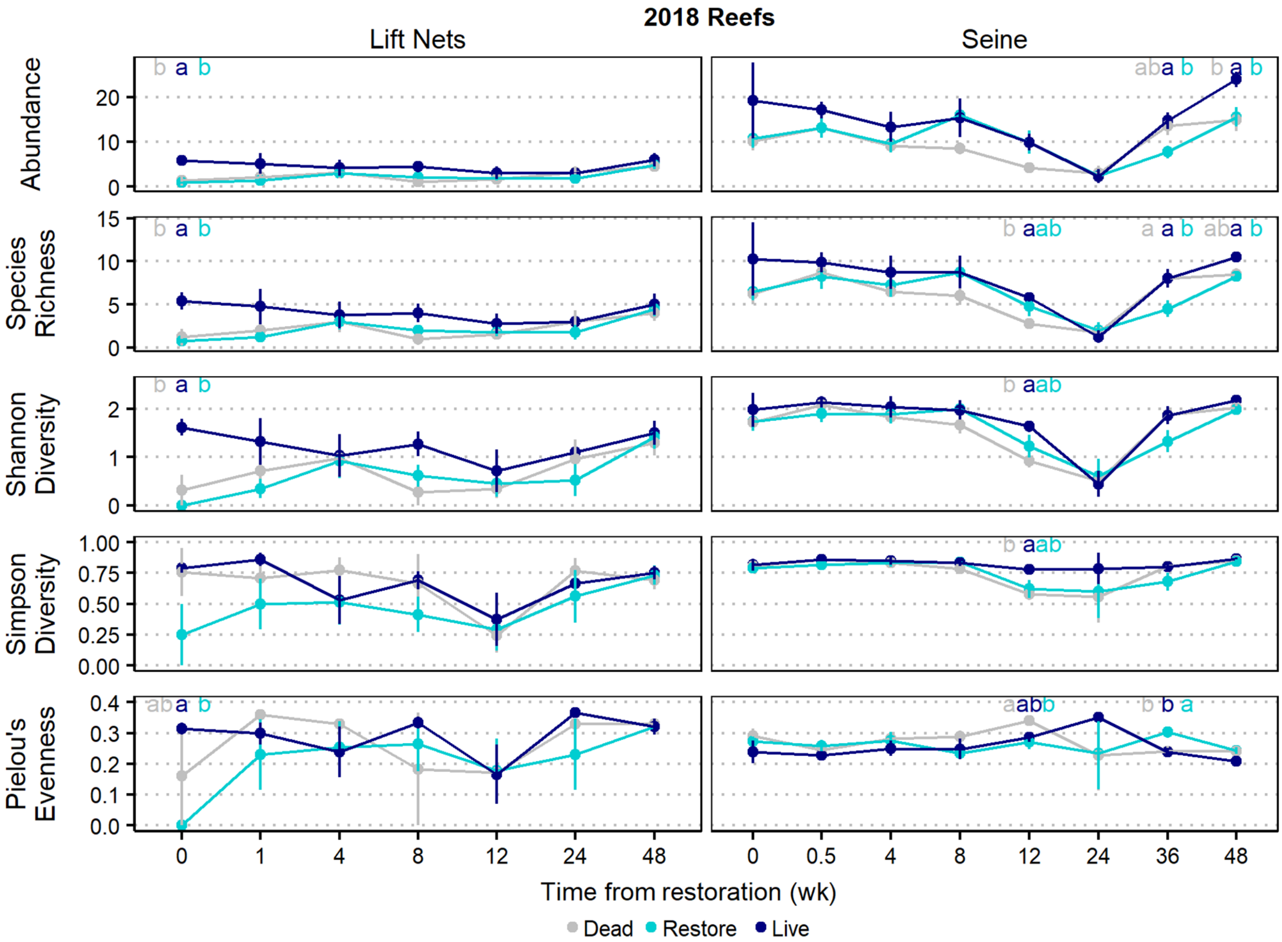

Fig. 4. Mean abundance and diversity values of each treatment type over time (in weeks) for lift net and seine catches of 2018 reefs. See Fig. 3 for details

3.4. Community composition and indicator species

Indicator species identified representative species of the 3 reef types. For seine catches, *Chilomycterus schoepfi* (striped burrfish; IndVal = 0.25) and *Sphoeroides nephalus* (southern puffer; IndVal = 0.21) represented dead reefs; restored reefs were represented by *Lutjanus synagris* (lane snapper; IndVal = 0.38) and *G. robustum* (code goby; IndVal = 0.32), *Stephanolepis hispidus* (planehead filefish; IndVal = 0.25); and *Symphurus plagiusa* (blackcheek tonguefish; IndVal = 0.25) were representative of live reefs (Table 1).

Lift net catches had representative species only for live reefs and con-

Table 1. Indicator species per reef treatment type for seine and lift net gear types. 'IndVal': indicator value of the species based on *'A'* and *'B'* statistics, where *'A'* represents relative exclusivity to a single treatment type and *'B'* represents the proportion of sites where the species is found within a treatment type. All species listed are significant (p < 0.05). For common names, see Table S1

Species	Trophic level	Seine			Lift nets		
		IndVal	*A*	*B*	IndVal	*A*	*B*
Dead							
Chilomycterus schoepfi	3.5	0.25	1.00	0.06			
Sphoeroides nephalus	3.5	0.21	0.75	0.06			
Restore							
Lutjanus synagris	4.2	0.38	0.71	0.20			
Live							
Gobiosoma robustum	3.2	0.32	0.77	0.13	0.54	0.57	0.51
Stephanolepis hispidus	2.6	0.25	1.00	0.06			
Symphurus plagiusa	3.2	0.25	0.85	0.07			
Gobiosoma bosc	3.2				0.53	0.58	0.49
Eucinostomus spp.	3.0				0.48	0.94	0.24

sisted of *G. robustum* (IndVal = 0.54), *G. bosc* (naked goby; IndVal = 0.53), and *Eucinostomus* spp. (mojarras; IndVal = 0.48). Restored reefs had the highest-TL representative species, *L. synagris* (TL = 4.2), and live reefs had the lowest-TL representative species, *S. hispidus* (TL = 2.6). For both gear type catches, 'IndVal' values were dominated by the '*A*' component, representing exclusivity to the treatment type.

3.5. Fish community response to habitat metrics

Fish diversity was best predicted by oyster shell height for 3 of the diversity metrics: abundance, Shannon diversity, and Pielou's evenness (Table 2). However, differences in AIC values were relatively small, indicating there were not strong differences among metrics. Species richness was best described by oyster density, reef thickness, and oyster height combined, while Simpson's diversity was best predicted by oyster reef thickness (Table 2).

EnvFit tests showed oyster shell height to be the primary driver of species assemblages for both gear type catches (Fig. 5). Lift net catches were also impacted by high point of the reef, thickness, and oyster density. Similarly, oyster density and reef thickness and high point were secondary drivers of seine catches. These loadings may be influ-

Table 2. Akaike's information criterion (AIC) table of fish abundance and diversity response to physical oyster reef metrics. Fish response metrics include abundance, species richness, Shannon diversity, Simpson diversity, and Pielou's evenness. Oyster reef metrics include oyster density, reef thickness, and shell height. AIC_C: AIC adjusted for small sample sizes. Models that explain each diversity metric best are presented in **bold**

Variables	Abundance			Species richness			Shannon diversity			Simpson diversity			Pielou's evenness		
	AIC_C	ΔAIC_C	df	AIC_C	ΔAIC_C	df	AIC_C	ΔAIC_C	df	AIC_C	ΔAIC_C	df	AIC_C	ΔAIC_C	df
Density	838.7	4.4	3	622.6	6.6	3	193.2	2.8	3	−134.1	0.8	3	−341.2	3.6	3
Thickness	835.4	1.0	3	618.6	2.6	3	191.7	1.3	3	**−134.9**	**0.0**	**3**	−342.6	2.1	3
Height	**834.4**	**0.0**	**3**	617.3	1.3	3	**190.4**	**0.0**	**3**	−134.6	0.3	3	**−344.8**	**0.0**	**3**
Density + thickness	836.1	1.7	4	617.6	1.6	4	191.7	1.3	4	−133.3	1.6	4	−341.6	3.2	4
Density + height	836.5	2.1	4	619.3	3.3	4	192.2	1.9	4	−132.5	2.4	4	−342.8	2.0	4
Thickness + height	835.0	0.6	4	617.8	1.8	4	192.1	1.8	4	−133.0	1.9	4	−342.9	1.9	4
Density + thickness + height	835.4	1.0	5	**616.0**	**0.0**	**5**	191.9	1.5	5	−131.4	3.5	5	−342.1	2.7	5

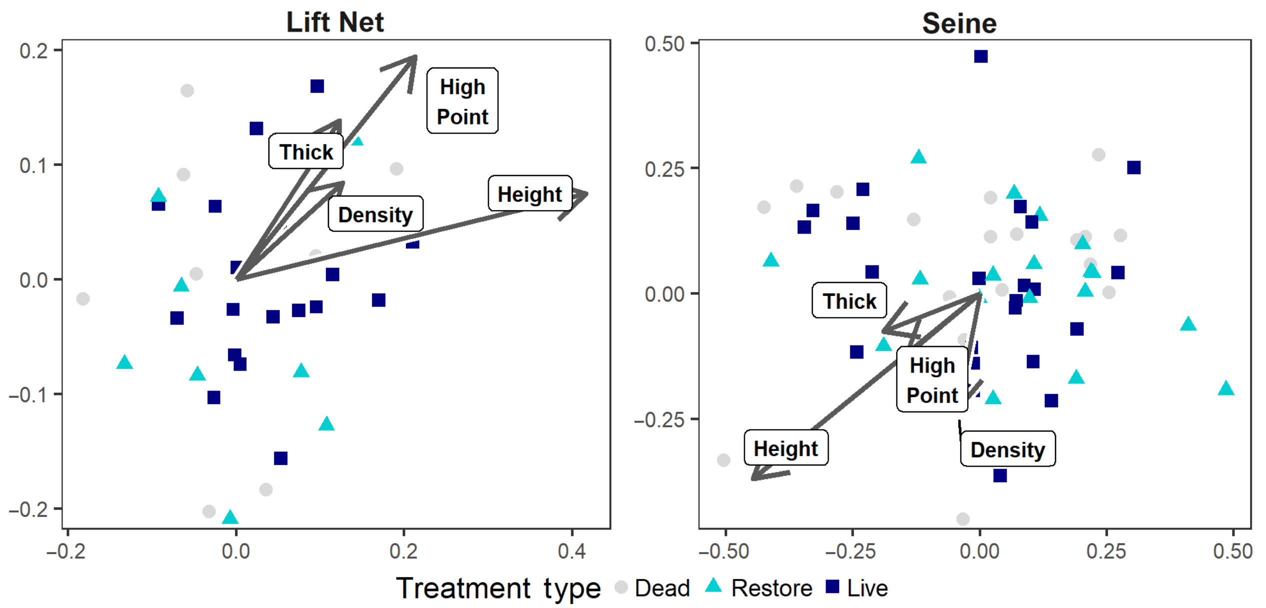

Fig. 5. Environmental fit tests for lift net and seine catch species assemblages compared to oyster reef metrics, including oyster shell height, reef high point, reef thickness, and oyster density. Axes represent the first (*x*-axis) and second (*y*-axis) non-metric multidimensional scaling axis which maximizes rank-order correlation between distance measures and distance in ordination space. Height is a dominant driver for both gear catches; remaining metrics are of comparable magnitude and drive species assemblages in similar ways

enced by season as well as changes in species assemblages, as no clear clustering of treatment types occurred.

4. DISCUSSION

Restoration is ongoing in many coastal systems to mitigate habitat losses and help maintain ecosystem function and services. Here, oyster-based metrics of restoration success suggest restoration of the benthic habitat was successful. At restored reefs, oyster density, shell height, oyster reef thickness and high point, which all formerly resembled dead reefs, resembled live reefs within 12 mo post-restoration. Defining restoration success, however, depends on the desired outcome and the metric(s) of success (Coen & Luckenbach 2000, Baggett et al. 2015). Evaluating how the fish community responds to habitat restoration, from diversity to species composition, and understanding what factors may influence these responses, can provide insight into developing more effective restoration strategies.

Examining temporal shifts in abundance and diversity of fish assemblages provides a greater understanding of the effect of habitat restoration on the broader ecosystem. In most cases, live reefs had the highest mean values of diversity. Oyster metrics on restored reefs shifted from those of dead reefs to live reefs (Fig. 2), but temporal trends in fish abundance and diversity at dead and live reefs were similar at times, suggesting that variability in catches and temporal changes obscured potential differences in treatment types. Furthermore, seasonality had a strong influence across all treatment types: fewer individuals and species were captured during winter months, which subsequently affected diversity indices calculated during winter, with smaller differences among treatment types. In restoration, benefits may impact areas beyond the immediate reef, causing similar trends in other reef types, including dead reefs. In both years of restoration, there was an increase in seine catch diversity immediately following restoration, which could be explained by the 'disturbance' of the restoration process. The water column was churned during restoration, which had the potential to attract fish (captured in seines) to the restoration area (Davis et al. 2006). After the initial peak, there was a decrease in diversity indices followed by gradual increases over a period of 12–18 mo. During this time oyster reefs are maturing, and results are likely due to growth of oysters on restored reefs.

A priori hypotheses of oyster restoration success, regarding fish community composition, predicted dead and live reef species assemblages would cluster separately prior to restoration, with restored reefs initially clustering with dead reefs. Following restoration, recruitment and maturation of the oyster reef would result in the species assemblage at restoration sites shifting from the dead reef assemblage toward the live reef assemblage, as demonstrated by oyster reef metrics (Fig. 2). Due to variability in the catch data and overlap in the fish community among sites and treatments, this trend was not detected when assessing overall fish community composition. As there was no clear separation in fish species assemblages at dead and live reefs at the onset of the study, it lessened the statistical ability to quantify community-wide shifts following restoration. The species assemblages and ensuing community clusters were based primarily on sampling period, which suggests shifts in community assemblage may be obscured by seasonal changes in the fish community.

Reefs restored in 2018 appear to have responded more rapidly and strongly to restoration than reefs restored in 2017. Comparing oyster reef metrics from 2017 to 2018 for all reefs, overall oyster density decreased, while oyster shell height and reef high point and thickness increased. However, these differences were minimal and thus were likely not drivers of differences in success. Other factors to consider are inherent annual variability in fish recruitment or the natural variability in the existing fish assemblage among sites. For example, in 2017, grey snapper *Lutjanus griseus* was relatively abundant and lane snapper *L. synagris* was relatively uncommon, but in 2018, relative abundances were reversed. This inherent variability in recruitment between years could have contributed to different abundances and assemblages of species colonizing sites following restoration. If annual variability in the species assemblage varied with respect to treatment types due to temporal variability in colonization and recruitment, this could explain the differences observed comparing 2017 and 2018 reefs and the ultimate assessment of how habitat restoration influences the fish community.

Understanding indicator species at oyster reefs informs how specific fish are utilizing reefs. Dead reefs in Mosquito Lagoon are composed of dead shell and have high vertical profiles and low habitat complexity (Wall et al. 2005). Striped burrfish *Chilomycterus schoepfi* and southern puffers *Sphoeroides nephalus* were identified as indicator species for dead reefs, as the high vertical profile of this habitat provides substrate inhabited by gastropods and crabs on which these species prey (Motta et al. 1995). Lane snapper *L. synagris*, an indicator species for restored reefs, is a transient reef-associated sportfish. Restored reefs may represent an ideal foraging habitat for juvenile, higher-level sportfish. Less mature oyster reefs may provide relatively good habitat and structural complexity prey fish use for refugia, while are not too complex for the snapper to have difficulty foraging (Flynn & Ritz 1999, Coen et al. 2007). Thus, reefs of intermediate structural complexity appear to provide greater foraging opportunities than more structurally complex live reefs. Indicator species in seines were selected due to their high exclusivity to each treatment type. Several taxa of relatively sedentary lower-TL species (e.g. gobies) were identified as indicator species for live reefs, many of which are known oyster reef residents (Tolley & Volety 2005, Lewis et al. 2021). These species represent different guilds within the broader fish community in terms of how they uniquely utilize each reef type. As resource managers assess various EBM strategies to benefit ecological communities and multiple species of fish simultaneously, these findings can help guide the decision-making process by informing if and where habitat restoration should be considered.

Exploring what reef properties influence fish community diversity helps inform future restoration efforts with an emphasis on its role as EFH. Oyster height predicted 3 diversity measures best (abundance, Shannon diversity, and Pielou's evenness). Oyster height is associated with the maturity of the reef and growth over time, further indicating these indices of diversity increase as individual oysters grow larger. Reef thickness was another variable that was prominent throughout model selection. Reef thickness is a proxy for general oyster reef health and implies strong rates of recruitment and growth (Powell & Klinck 2007, Rodriguez et al. 2014, Baggett et al. 2015). Species richness was best described by all oyster metrics but primarily oyster height. The density of oysters and reef thickness contribute to reef habitat complexity, thereby regulating the types and numbers of species able to utilize the reef for foraging or as refugia.

These results support previous studies with increased fish diversity and abundance at undisturbed oyster reefs, both natural and restored (Harding & Mann 1999, Powers et al. 2003, Rodney & Paynter 2006, Loch et al. 2021, Mahoney et al. 2021, Searles et al. 2022). Responses in the fish community have been attributed to increased habitat complexity (vs. bare bottom habitat) but not necessarily increased complexity once complexity exists (Harding & Mann 1999, Peterson et al. 2003, Rezek et al. 2017). This indicates there is a binary state in which the reef either has enough complexity to support the fish community or does not. Fish density was double at restored oyster reefs compared to non-restored reefs in Chesapeake Bay (Rodney & Paynter 2006). Similar trends were seen here but at lower magnitudes. Diversity measures of live reefs were consistently higher than at other reefs but not twice as high as dead reefs, with restored reefs eventually reaching the levels measured at live reefs. Mature reefs in the Chesapeake study were 3–5 yr of age, while restored reefs in this study were at most 2 yr post-restoration. The response rate of restored oyster reefs in this study was more comparable to that in another subtropical estuary in Texas, where restored reefs were similar to natural oyster reefs at 15 mo post-restoration, with the community responding 1–2 yr following restoration (Rezek et al. 2017). Comparing these results to previous studies strengthens the linkages between habitat complexity and fish abundance and diversity. However, these results suggest response time may vary with latitude, and broader geographic factors may regulate the magnitude and rate of response of the fish community to habitat restoration and should be considered when assessing restoration success.

Although unique representative species were identified for the treatment types, quantifiable shifts in overall species assemblages were not evident. While many species are generalists and may use all treatment types, considering additional factors in restoration that may affect community-level responses could better inform how and when restoration is implemented. First, there was other EFH around the experimental sites. Studies show habitat types adjacent to reefs are vital in determining how and if fish use a given reef (Grabowski et al. 2005, Geraldi et al. 2009, Baggett et al. 2015). Fish communities respond to restoration of oyster reefs in areas of bare soft-bottom habitat more than restoration of reefs located next to marsh or seagrass habitat, as these are alternative forms of EFH (Grabowski et al. 2005). All restoration sites in this study were located near mangroves (within 10s of m) and other oyster reefs (within 10s–100s of m) which provide similar services to the fish community. The presence of neighboring habitats when combined with the results of the present study indicates the response of the fish community assemblage to restoration may not be as easily discernable in complex mosaics of EFH compared to restoration sites surrounded by predominately bare, soft-bottom habitat. This may be represented in pre-restoration metrics of abundance and diversity where dead reefs are sometimes intermediate between live and soon-to-be-restored reefs. Although the physical reef metrics of dead and restored reefs (pre-restoration) are the same, there are some differences in metrics of the fish community that could be attributed to other factors, like reef location and neighboring habitats. Furthermore, functional redundancy can occur when other EFH is readily available (Gittman et al. 2016). In Mosquito Lagoon, there are large expanses of oyster reef and mangroves the fish community can utilize. These habitats may be functionally redundant in terms of fish habitat use; however, they do not necessarily contribute similarly to the production of ecosystem services (Cook et al. 2014). Results of indicator species analyses suggest certain species have an affinity for particular habitat types, and a greater number of habitat types available leads to higher alpha diversity within a system (Alsterberg et al. 2017). More diverse mosaics of EFH types should lead to greater regional diversity by providing multiple areas inhabited by different assemblages of fish while simultaneously producing a greater suite of ecosystem services.

In addition to habitat mosaics, the spatial scale of restoration may also influence the response of the fish community (Grabowski et al. 2005). Live reefs in Mosquito Lagoon are often surrounded by other live reefs, compared to restored reefs which are chosen based on need for restoration; restored reefs are often patchy and located in areas of high boat traffic that resulted in the initial degradation and destruction of the reefs (Wall et al. 2005, Garvis et al. 2015). If large areas of reef or a network of smaller reefs were to be restored at once, a greater response in larger relatively transient fish may be detected (Grabowski et al. 2005). Benefits to the fish community may accrue more rapidly if many reefs in relatively close proximity are restored to generate a stronger localized footprint of available reef habitat (i.e. creating a 'meta-reef') as opposed to spreading reefs across a broader geographic region. In the present study, greater and more rapid positive effects occurred in the second set of restoration sites, when 3 of 4 restored reefs were relatively close in proximity, possibly surpassing an unknown spatial threshold. Testing how patchiness and spatial configuration of restoration sites impacts outcomes at the fish community level could increase the efficacy of future restoration designs and strategically guide the application of restoration resources.

Furthermore, distinct differences exist when viewing restoration outcomes over time. Annual variability in fish recruitment and its impact on the fish community is a well-known phenomenon, but considering these shifts in the fish community due to the spatial and temporal scale of restoration is an area in need of further investigation. The results of this study suggest after 2 yr of monitoring restored reefs are acting similarly to dead and live reefs, as all reefs are attracting fish due to their structure compared to sand bottom. While differences were found in the indicator species of the reef treatment types, differences among treatment types were less apparent in the broader fish assemblage. More time may be needed to fully understand the effects of oyster restoration on the fish community, related changes to oyster reef metrics, and the effects these may have on human communities, which in turn have reciprocal impacts on the environment (Kibler et al. 2018). Increasing the replicates of restored reefs within large-scale oyster restoration and exploring annual differences, combined with strategically selected control sites with greater differences, could allow for a better understanding of the most opportune times and locations to implement oyster restoration to achieve the greatest benefits for both the human and natural components of the ecosystem (Grabowski et al. 2005, Geraldi et al. 2009, Baggett et al. 2015).

Multiple benefits of oyster reef restoration projects are expected, and the success of these endeavors should not be determined by examining oyster metrics alone. Various biotic communities comprising an ecosystem may experience different responses and levels of improvement following restoration, but sustained production of ecosystem services should be an essential end goal. Gaining a better understanding of what characteristics of restoration result in improved ecosystem function and the production of associated ecosystem services will enable resource managers to tailor habitat restoration strategies within an ecosystem-based framework. This, in turn, will increase the capacity of resource managers to more effectively meet the needs of coastal communities and achieve their desired outcomes for a region (Gilby et al. 2018).

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