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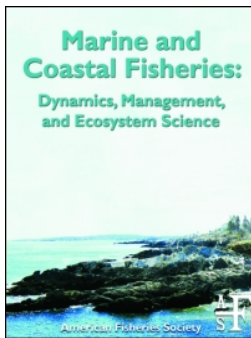
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To cite this article: Rachel N. Arney, Catheline Y. M. Froehlich & Richard J. Kline (2017) Recruitment Patterns of Juvenile Fish at an Artificial Reef Area in the Gulf of Mexico, Marine and Coastal Fisheries, 9:1, 79-92, DOI: [10.1080/19425120.2016.1265031](https://doi.org/10.1080/19425120.2016.1265031)

To link to this article: <https://doi.org/10.1080/19425120.2016.1265031>



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Published online: 01 Mar 2017.



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ARTICLE

Recruitment Patterns of Juvenile Fish at an Artificial Reef Area in the Gulf of Mexico

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Abstract

In 2011 the Texas Parks and Wildlife Department and the Coastal Conservation Association of Texas deployed over 4,000 concrete culverts in a designated artificial reef area off Port Mansfield, Texas, to enhance habitat for sport fish species in the Gulf of Mexico. A study was conducted to assess juvenile fish recruitment at varying culvert densities within the artificial reef area. Standard monitoring units for the recruitment of reef fish (SMURFs) were used to sample juvenile fish, and these collections were compared with visual scuba surveys. The 0.027-m³ SMURFs were placed at four different culvert densities (0, 1–50, 51–100, and 101+ culverts in a 30-m radius) and sampled during 2013 to 2014. Measurements of rugosity, vertical relief, and percent cover were collected to elucidate factors that drive juvenile recruitment. Average species richness was highest at sites with no culverts and lowest at dense culvert sites. Species compositions were significantly different between sampling locations with no culverts and all locations with culverts; average similarity was 33.8%. Belted Sandfish *Serranus subligarius* was the most ubiquitous species among all sampling locations. Visual scuba surveys at the same locations showed lower diversity indices of the juvenile fish community than observed by SMURFs and were only 14% similar to the community sampled by the SMURFs. These findings suggest SMURFs are a more effective tool for examining juvenile fish at an artificial reef due to the cryptic nature of juveniles and the low visibility around shallow reefs. Additionally, commercially important Yellowedge Grouper *Hyporhamphus flavolimbatus*, Warsaw Grouper *H. nigritus*, and Red Snapper *Lutjanus campechanus* juveniles were only found at SMURFs at sampling locations with no culverts. The presence of juveniles of these key species suggest that fisheries management may benefit from creating low-relief reef patches away from the main reef where juvenile fish can recruit and grow.

Artificial reefs are used throughout the world's oceans as marine habitat enhancement and mitigation tools to augment exploited fish populations subjected to anthropogenic effects (Bohnsack and Sutherland 1985; Alevizon and Gorham 1989; Carr and Hixon 1997; Pickering and Whitmarsh 1997). When optimally designed, an artificial reef can provide important habitat for postsettlement fish and other benthic reef macrofauna (Bohnsack 1989). Thus, an increase in available shelter can potentially increase juvenile fish populations and overall fish

abundances (Alevizon and Gorham 1989; Ambrose and Swarbrick 1989; Rilov and Benayahu 2000).

Postsettlement survival is known to dictate species abundance and richness of various adult populations of reef fish (Kaufman et al. 1992; Vigliola and Harmelin-Vivien 2001; Gratwicke and Speight 2005a; Johnson 2007). Studies conducted on Threespot Damselfish *Stegastes planifrons* (Williams and Sale 1981) and Bluehead *Thalassoma bifasciatum* (Victor 1986) show that population dynamics are not controlled by reef characteristics alone

Subject editor: Debra J. Murie, University of Florida, Gainesville

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Received November 3, 2016; accepted November 13, 2016

but by predation rates, as well as stochastic processes (Shulman and Ogden 1987). Differences in postsettlement survival among species can be due to geographic location, variable water masses carrying eggs and larvae, and physiological and morphological characteristics of the cohorts (Shulman and Ogden 1987; Tupper and Boutilier 1995; Johnson 2007). Newly settled fish are restricted to small home ranges and may settle over sand or reef substrate (Sale and Douglas 1981; Barnes 2003). After settlement, reef fish mortality is very high (Rooker et al. 1998; Barnes 2003; Almany 2004), primarily due to predation (Carr and Hixon 1997; Almany 2003). Thus, there is a trade-off between optimal habitat availability and predation risks affecting recruit survival rates (Werner et al. 1983; Grabowski et al. 2005).

Habitat requirements for some fish groups, such as family Lutjanidae (Gallaway et al. 2009) and subfamily Epinephelinae (Coleman et al. 2000), change rapidly with development and growth. Postsettlement, individuals follow directed movements to new habitats at several life stages (Szedlmayer and Shipp 1994; Ross and Moser 1995; Gallaway et al. 1999, 2009). Therefore, varied substrates are needed in their early life history, and such habitat may be an essential component of recruitment to natural and artificial reef systems. Some explanations for the postsettlement movements are habitat partitioning of young and adults to avoid aggression or predation and ontogenic shifts in food requirements (Lecchini et al. 2007). Due to changing habitat and life history requirements, the amount of reef complexity required for the development of a diverse fish community needs to be considered during planning and construction of artificial reefs.

Habitat complexity is known to increase fish abundances on reefs (Charbonnel 2002; Almany 2004; Grabowski et al. 2005; Gratwicke and Speight 2005b). An artificial reef that provides more shelter, complex spaces, and offers room for primary producers shows increased species metrics (Gratwicke and Speight 2005b). Substrate rugosity (Chandler et al. 1985), vertical relief (Luckhurst and Luckhurst 1978), and percent substrate cover (Gratwicke and Speight 2005b) at an artificial reef are important factors to be considered as predictors of reef fish populations.

The majority of juvenile fish studies rely solely on visual scuba surveys; however, issues arise in this singular approach (Sale et al. 1980; Victor 1986). Although diver visual censuses are nondestructive, this method has difficulty in quantifying very small fish or nocturnal fish (Brock and Norris 1989). Visually identifying species composition also allows for human error when assessing small cryptic reef fish or juveniles in low visibility or turbid waters and in areas of high surface complexity (Brock 1982). In a recent study, Ammann (2004) designed standard monitoring units for the recruitment of reef fish (SMURFs), where portable artificial substrate units allowed easy removal and quantification of fish recruits (Ammann 2004). Because juveniles are often difficult to visually census due to their cryptic nature (Valles et al. 2006), the use of SMURFs can allow for an easier means of characterizing the juvenile community.

The overall goal of our research was to determine if juvenile fish use habitat differently depending on the structural density and topographic complexity at sampling locations within a culvert reef and whether the juvenile populations observed were representative of the resident adult populations. To do this, SMURFs were deployed along varying densities of concrete culvert reefs as well as bare areas. Juvenile populations were sampled with SMURFs, and juvenile and adult populations were also observed using scuba surveys. The specific objectives of the study were to determine (1) if juvenile fish abundance, richness, diversity, and evenness, based on SMURF collections, differed among culvert densities, (2) whether increases in substrate rugosity, vertical relief, and percent cover of culvert sampling locations resulted in differences in juvenile species composition, and (3) to compare any differences in the juvenile species composition from SMURFs with that of the adult and juvenile populations observed in scuba surveys.

METHODS

Study area.—The study was conducted at the South Padre Island Reef (PS-1047), located 11.3 km east of Port Mansfield, Texas (26°31'31.68"N and 97°8'43.15"W, Figure 1). In 2011, the Texas Parks and Wildlife Department and the Coastal Conservation Association of Texas sank about 4,000 concrete culverts within a 1-km² grid, at 20-m depth, which added to the approximate 700 culverts and a sunken tugboat deployed in the southeast corner of the reef in 2008. The culverts were roughly 1 m in diameter by 3-m long, with a volume of 2.4 m³ (include inside space), and were indiscriminately deployed in various densities across the reefing area. Bare areas of open sand and silt were present around the perimeter and within the reefing area.

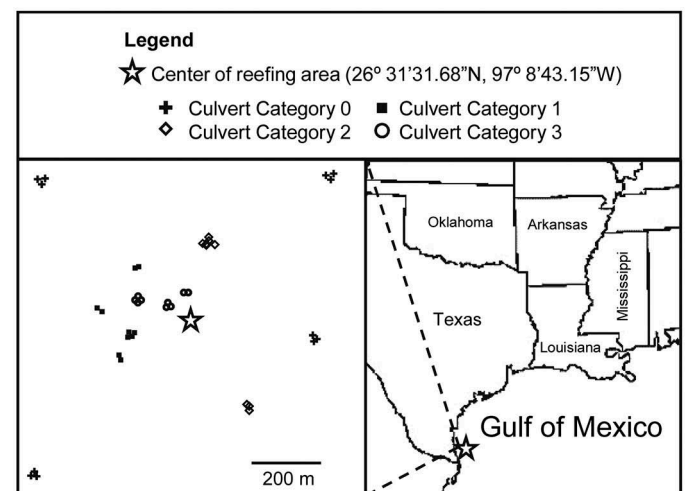


FIGURE 1. Location of the South Padre Island Artificial Reef (PS-1047), 11.3-km east of Port Mansfield, Texas, showing the 13 sampling locations for standard monitoring units for the recruitment of juvenile reef fish (SMURFs) and scuba surveys. Samples were collected from locations within four culvert-density categories (see Table 1).

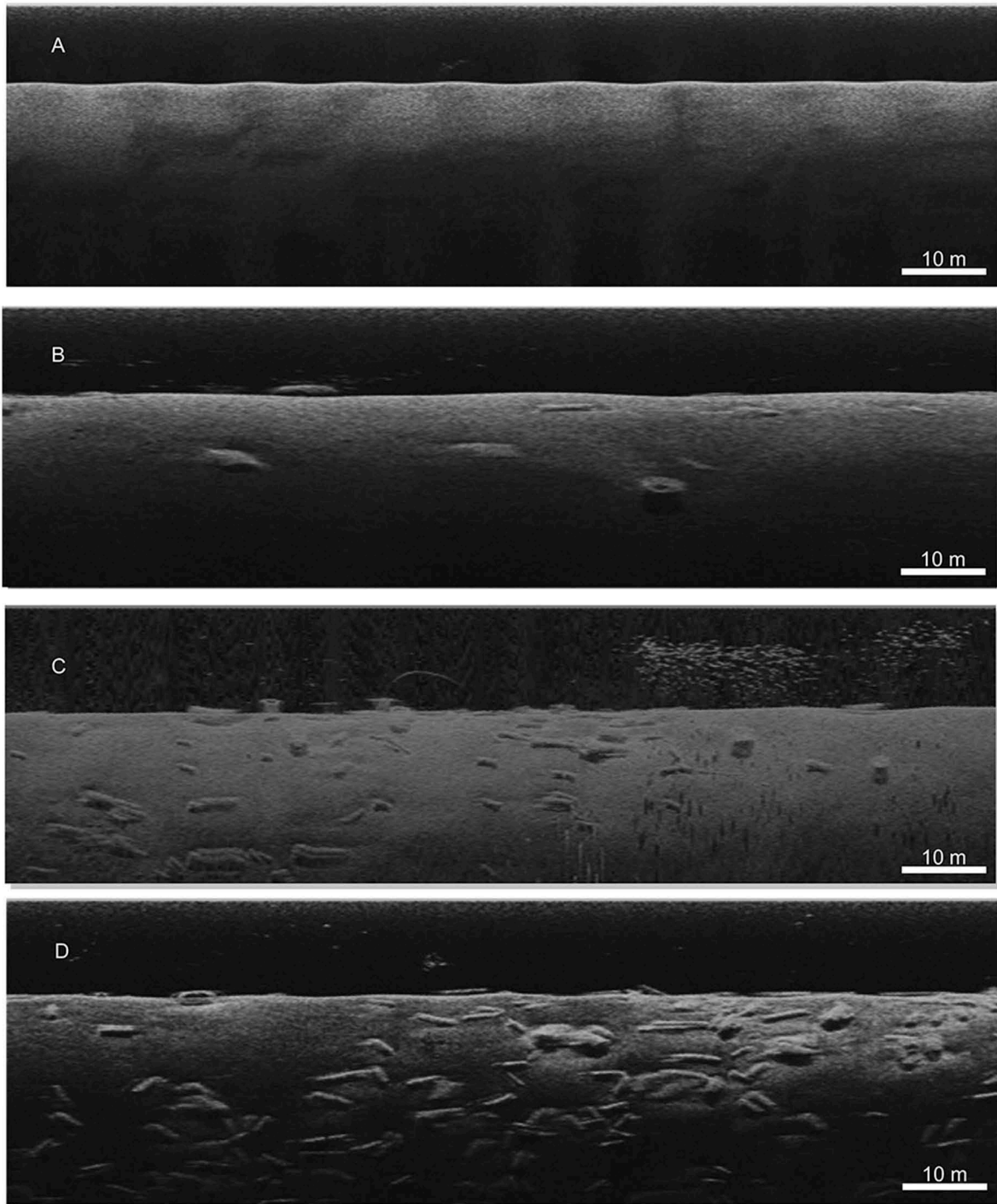


FIGURE 2. Side-scan sonar images of the four culvert density categories within a 30-m radius: (A) category 0 = zero culverts, (B) category 1 = 1–50 culverts, (C) category 2 = 51–100 culverts, and (D) category 3 \geq 101 culverts.

Small, naturally occurring reef patches, ranging from 21 to 625 m², were within the reefing area but were further than 100 m away from any sampling location in this study.

Sampling locations and characterization.—Thirteen sampling locations were selected within the reefing area using

side-scan sonar (Hummingbird 1198 C SI unit, Johnson Outdoors Marine Electronics, Eufaula, Alabama; Figure 1). Locations were placed into four categories based on culvert density within a 30-m radius: category 0 = zero culverts; category 1 = 1–50 culverts; category 2 = 51–100 culverts;

category 3 = 101+ culverts (Figure 2). Side-scan recordings were processed with the programs HumViewer v.86 (<http://humviewer.cm-johansen.dk/>) and SonarTRX v. 13.1 (Leraand Engineering Inc., Honolulu, Hawaii), then transferred into ImageJ (<https://imagej.nih.gov/ij/>; ImageJ 1.48p, Wayne Rasband, National Institutes of Health) for analysis. Reef characteristics of average rugosity, vertical relief, and percent substrate cover were calculated for each of the four culvert categories. Rugosity measurements for each sampling location were made by tracing a transect over all culverts (or bare ground) within a 60-m diameter and then dividing the transect by the straight line distance of 60 m. Vertical relief at each sampling site was quantified by measuring the height of every object (or bare space) every 1 m across a 60-m transect using ImageJ. Percent substrate cover was estimated in 30-m radius circles for each side-scan image in ImageJ.

Design of SMURFs.—To characterize juvenile fish arrival at the artificial reef, SMURFs were deployed at PS-1047. Each SMURF contained two replica coral pieces constructed of polyurethane and mounted on a 900-cm² cement block. Each SMURF was enclosed with plastic netting (Figure 3) and had a total volume of 0.027 m³. The plastic net had a grid size of 2.54 cm² that was chosen to reduce surface area for biofouling and to allow only newly-settled juveniles access into and out of the structures while excluding larger predators (Ammann 2004).

Sampling regime.—Forty five collection attempts were made over the 13 sampling locations between June 2013 and July 2014. Six of the SMURF samples (one sample = pooled data from two SMURFs placed 6 m apart) were not collected due to sediment burial or movement from the placement location following storms. This yielded 39 SMURF samples successfully collected from 13 sampling locations within the four culvert categories (Table 1).

The SMURFs were retrieved via scuba by first enclosing the structure and fish within the structure in a 900- μ m mesh capture bag. The bagged SMURF was then brought to the surface with a lift bag. As divers approached the SMURF with a capture bag, all visible species were noted. Most species of fish surrounding the SMURF would dart into the structure when approached. Fish surrounding the SMURFs that were not typically captured in the bag, such as Red Snapper *Lutjanus campechanus*, were visually identified and quantified on scuba surveys done immediately prior to SMURF retrievals (see below). Once the diver placed the bag over a SMURF, the small mesh and structure of the bag did not allow any escapees. Paired SMURF collections from each sampling location collected on the same day were pooled, and fish were identified to species and measured for total length (mm). All SMURFs retrieved were scrubbed clean with a brush and freshwater and redeployed the same day. Temperature data

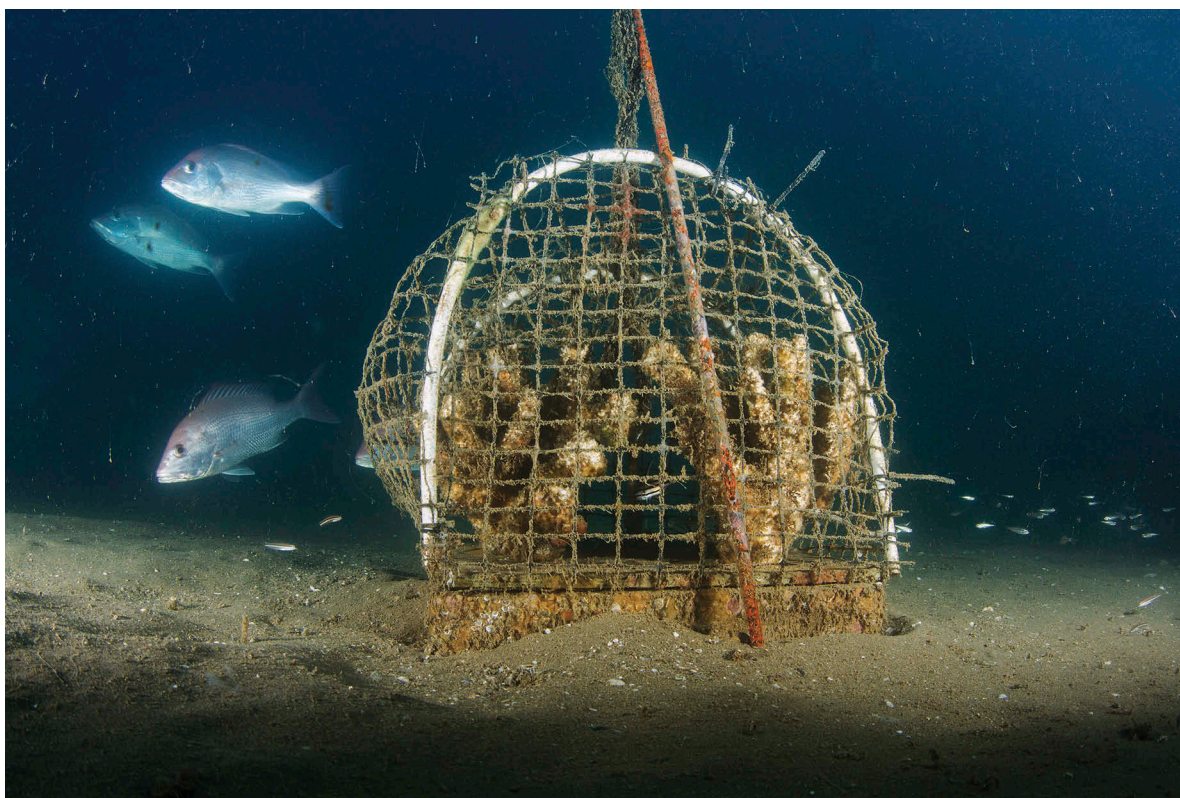


FIGURE 3. Standard monitoring unit for the recruitment of juvenile reef fish (SMURF), including two replica coral pieces mounted to a 30.5-cm² cement block and covered with plastic netting with grid sizes 2.54 cm². Photo courtesy of Seth Patterson.

TABLE 1. Days deployment by year and month of standardized monitoring units for the recruitment of reef fish (SMURFs) by location and culvert density category within a 30-m radius: 0 = zero culverts, 1 = 1–50 culverts, 2 = 51–100 culverts, and 3 ≥ 101 culverts. Asterisks indicate sample was retrieved after more than 150 d of deployment and only used in species presence–absence comparisons.

Culvert category	Location	2013					2014					
		Jun	Jul	Aug	Sep	Oct	Feb	Mar	Apr	May	Jun	Jul
0	1	24			87				97			
0	2			36			189*				40	
0	3			66		59						30
0	4								219*	30	40	
1	1		37			95					238*	30
1	2										40	43
1	3			52							310*	
1	4										53	30
2	1	28			87		151*			97		40
2	2						151*			42	41	
3	1			79		53						
3	2			36			189*					40
3	3		43		63					221*	28	

were recorded hourly using Onset HOBO temperature data loggers placed 0.5 m above each SMURF.

Because some SMURFs could not be recovered for long periods (151–301 deployment days; Table 1) and in some cases became partially buried or fouled, the entire data set was only used to create a species occurrence list to describe the population. A reduced data set containing 31 SMURF samples with maximum deployment duration of 97 d was used to compare the juvenile SMURF populations among culvert categories. The latter data set contained samples from June, July, August, and September of 2013 and May, June, and July of 2014. At least two replicates of each category from 2013 were used (average = 55 d deployed, SD = 6), and at least four replicates of each category were used in 2014 (average = 45 d, SD = 5; Table 1). Data collected from each SMURF sample were treated as independent within each category for analyses because SMURFs were completely removed and cleaned before redeployment. Any fish determined to be subadult or adult according to body size and coloration pattern of the species were excluded from further analyses. Juvenile Red Snapper were only observed at SMURFs in bare areas (Category 0), but never captured in samples. Therefore, Red Snapper were only used in presence–absence comparisons. Tomate *Haemulon aurolineatum* arrived in heavy pulses solely in June and July of both 2013 and 2014. To analyze the juvenile population without Tomate, a “minus *H. aurolineatum*” data set was used.

As permitted by visibility (i.e., >2 m), 21 concurrent visual scuba surveys (Froehlich and Kline 2015) of adult and juvenile fish populations were conducted at the exact same sampling locations and on the same days as the retrieval of SMURFs. Juveniles and large fish were distinguished based on coloration and body size. All observers conducting visual scuba surveys were trained to identify all known reef fishes in the area. Reef-

associated fish were surveyed following an established stationary cylinder census (Bannerot and Bohnsack 1986), and smaller, more cryptic fish were visually sampled while the diver roved around the reef (Froehlich and Kline 2015).

Statistical analyses.—A one-way ANOVA was used to test for significant differences between juvenile species richness among the four different culvert categories. One analysis was run for total fish captured in SMURFs up to 97 d, and an additional ANOVA analysis was run on the “minus *H. aurolineatum*” data set. When necessary, data were $\log(x + 1)$ -transformed to meet assumptions of normality and homogeneity of variance. Statistical significance was set at $\alpha = 0.05$. Univariate analyses were completed using the SPSS statistical package (version 22.0).

The “minus *H. aurolineatum*” data set was $\log(x + 1)$ -transformed due to the large number of rare species and samples where a few species had high abundances. Transformed data were then compared against the four culvert categories and the month sampled, using a permutational analysis of variance (PERMANOVA) with 9,999 permutations and a Bray–Curtis similarity matrix (Verdiell-Cubedo et al. 2012). Average monthly temperatures and sampling months were assessed as covariates. A Principal Components Analysis (PCA) was applied to further analyze the effects of reef characteristics and average monthly temperatures on the “minus *H. aurolineatum*” PERMANOVA analysis (Verdiell-Cubedo et al. 2012). A separate PERMANOVA using presence–absence data was run to compare the 21 paired SMURF samples and scuba surveys. The similarity percentages test (SIMPER) was applied to determine which species were driving dissimilarities in all PERMANOVA analyses (Rilov and Benayahu 2000). Nonmetric multidimensional scaling (NMDS) plots were prepared to visualize any differences in all PERMANOVA analyses (Rilov and Benayahu 2000). Multivariate

analyses were completed using PRIMER-E software (version 6.1.16) with PERMANOVA+ (version 1.0.6).

RESULTS

A total of 746 individual juvenile fish were collected with SMURFs from 30 different species, comprising 17 families (Table 2). Four individuals sampled from SMURFs were determined to be subadults, according to body size and coloration pattern, and were excluded from further analyses. Haemulidae was the dominant family (41.1%), followed by Serranidae (19.7%) and Lutjanidae (18.4%). The dominant species in each

of these three families was Tomtate (41.1%), Belted Sandfish (10.7%), and Lane Snapper (10.1%), respectively.

We collected 31 SMURF samples after a maximum of 97 deployment days, yielding 681 individual juvenile fish (Table 2). There were no significant differences in any species indices by culvert category when Tomtates were included ($P > 0.05$, Figure 4). Once Tomtates were removed from analysis (“minus *H. aurolineatum*” dataset), due to their heavy pulses in summer months, average juvenile species richness significantly increased as culvert density decreased (ANOVA: $F_{3, 12.6} = 5.2$, $P = 0.02$; Figure 5). Upon further analysis of the “minus *H. aurolineatum*” data set, average juvenile species richness was significantly higher

TABLE 2. Fish collections data from standard monitoring units for the recruitment of reef fish (SMURFs) from June 2013 to July 2014 from 13 different sampling locations at the artificial reef (PS-1047) off Port Mansfield, Texas. Whether the species was also observed as a juvenile or an adult during the concurrent visual scuba surveys is noted, but species only observed in scuba surveys are not listed.

Family	Common and scientific name	Total number	Percent of total	Mean (SE) total length (mm)	Observed in scuba surveys
Antennariidae	Sargassumfish <i>Histrion histrio</i>	1	0.1	23	
Balistidae	Gray Triggerfish <i>Balistes capriscus</i>	1	0.1	54	Adult
Batrachoididae	Gulf Toadfish <i>Opsanus beta</i>	7	0.9	47 (7)	
Blenniidae	Crested Blenny <i>Hypleurochilus geminatus</i>	2	0.3	39 (1)	
Blenniidae	Seaweed Blenny <i>Parablennius marmoratus</i>	65	8.7	37 (1)	Adult
Chaetodontidae	Spotfin Butterflyfish <i>Chaetodon ocellatus</i>	1	0.1	20	Juvenile, adult
Chaetodontidae	Reef Butterflyfish <i>Chaetodon sedentarius</i>	2	0.3	26 (5)	Juvenile, adult
Haemulidae	Tomtate <i>Haemulon aurolineatum</i>	307	41.1	37 (<1)	Juvenile, adult
Holocentridae	Squirrelfish <i>Holocentrus adscensionis</i>	1	0.1	51	
Labridae	Slippery Dick <i>Halichoeres bivittatus</i>	34	4.5	48 (5)	Juvenile, adult
Lutjanidae	Red Snapper <i>Lutjanus campechanus</i>	60	8.0	^a	Juvenile, adult
Lutjanidae	Lane Snapper <i>Lutjanus synagris</i>	75	10.1	45 (8)	Adult
Lutjanidae	Vermilion Snapper <i>Rhomboplites aurorubens</i>	2	0.3	44 (6)	Adult
Monacanthidae	Scrawled Filefish <i>Aluterus scriptus</i>	2	0.3	^a	Adult
Monacanthidae	Planehead Filefish <i>Stephanolepis hispidus</i>	2	0.3	100 (54)	Adult
Ophidiidae	Atlantic Bearded Brotula <i>Brotula barbata</i>	1	0.1	133	
Phycidae	Southern Hake <i>Urophycis floridana</i>	1	0.1	69	
Pomacanthidae	French Angelfish <i>Pomacanthus paru</i>	1	0.1	18	Juvenile, adult
Pomacanthidae	Cocoa Damselfish <i>Stegastes variabilis</i>	13	1.7	28 (8)	Juvenile, adult
Sciaenidae	Cubby <i>Pareques umbrosus</i>	14	1.9	63 (9)	Juvenile, adult
Scorpaenidae	Spotted Scorpionfish <i>Scorpaena plumieri</i>	4	0.5	31 (8)	Adult
Serranidae	Rock Sea Bass <i>Centropristis philadelphica</i>	40	5.4	72 (6)	Adult
Serranidae	Dwarf Sand Perch <i>Diplectrum bivittatum</i>	2	0.3	54	Adult
Serranidae	Rock Hind <i>Epinephelus adscensionis</i>	4	0.5	56 (9)	Juvenile, adult
Serranidae	Yellowedge Grouper <i>Hyporthodus flavolimbatus</i>	1	0.1	53	Adult
Serranidae	Warsaw Grouper <i>Hyporthodus nigritus</i>	3	0.4	81 (40)	Adult
Serranidae	Scamp <i>Mycteroperca phenax</i>	10	1.3	60 (8)	Adult
Serranidae	Whitespotted Soapfish <i>Rypticus maculatus</i>	7	0.9	62 (6)	Adult
Serranidae	Belted Sandfish <i>Serranus subligarius</i>	80	10.7	43 (2)	Adult
Tetraodontidae	Bandtail Puffer <i>Sphoeroides spengleri</i>	3	0.4	17 (5)	Adult

^aObserved but never measured.

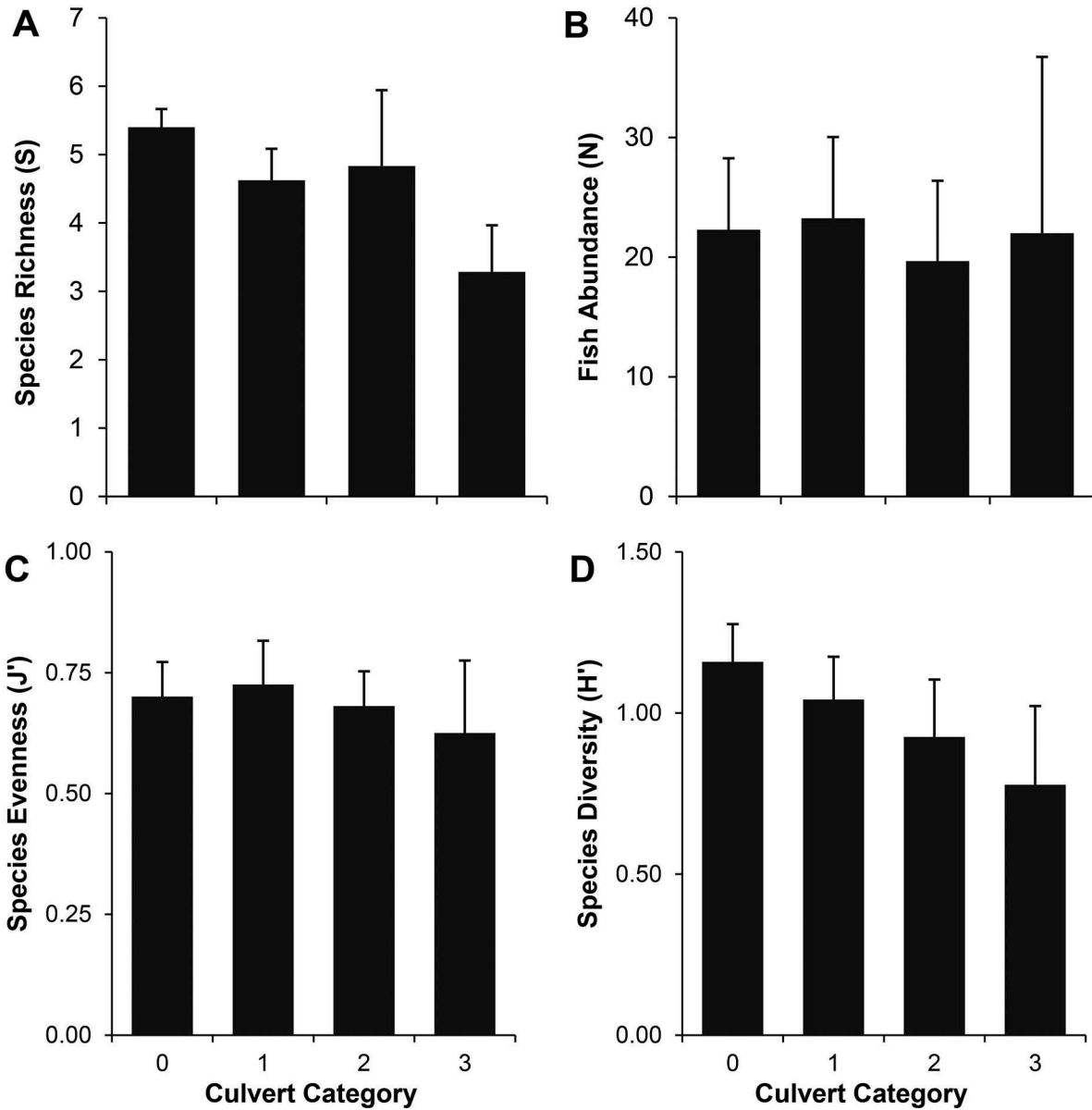


FIGURE 4. Average (+1 SE) (A) species richness (S), (B) abundance (N , number of fish per culvert category), (C) species evenness (J'), and (D) species diversity (H') of all juvenile fish collected (including Tomtate) by SMURFs (standard monitoring units for the recruitment of juvenile reef fish) at the four culvert categories (see Figure 2). No significant differences were observed.

at category 0 (5.13 species, SD = 0.35) than at category 3 (2.71 species, SD = 0.47 species; Games–Howell: $P = 0.01$).

Fish species composition of juvenile recruits sampled with SMURFs, excluding Tomtates, was significantly different between culvert categories (PERMANOVA: pseudo- $F = 2.2$, $P = 0.03$) and average monthly temperature (pseudo- $F = 2.7$, $P = 0.04$) but was not significantly different within months sampled (pseudo- $F = 1.7$, $P = 0.06$). There was no significant interaction between temperature and culvert category (pseudo- $F = 0.5$, $P = 0.9$) or month and culvert category (pseudo- $F = 0.8$, $P = 0.7$). Fish composition of all juvenile recruits at culvert category 0 was significantly different

from the other three culvert categories; however, there was no significant difference between the three categories containing culverts (Table 3, Figure 6).

Lane Snapper was the predominant species at culvert category 0, and Belted Sandfish contributed the most to the species similarities among category 0 sampling locations at 36.1% (Table 4). Seaweed Blenny was the predominant species at categories 1 and 2, Belted Sandfish contributing the most similarity 34.0% and 61.7%, respectively. Belted Sandfish was both the predominant species and the species with the highest composition similarity at category 4 with 87.7% similarity among the sampling locations.

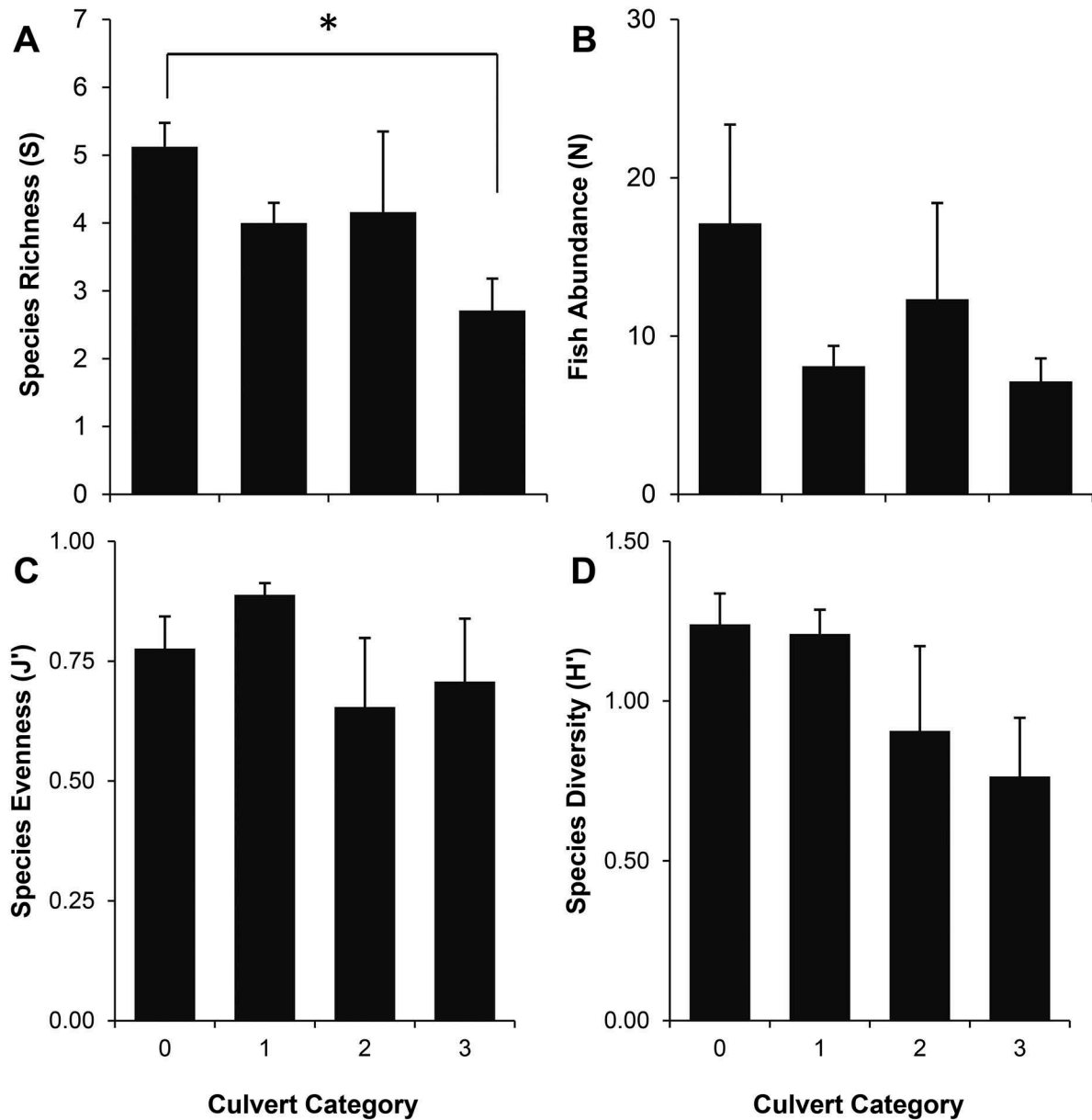


FIGURE 5. Average (+1 SE) (A) species richness (S), (B) abundance (N , number of fish per culvert category), (C) species evenness (J'), and (D) species diversity (H') for all juvenile fish collected (excluding Tomtate) by SMURFs (standard monitoring units for the recruitment of juvenile reef fish) at the four culvert categories (see Figure 2). Asterisks denote significance at $P < 0.05$.

The species contributing most to dissimilarities between category 0 and the three categories with culverts was Lane Snapper. Conversely, Slippery Dick, Belted Sandfish, and Seaweed Blenny contributed to dissimilarities between categories 1–3, respectively.

Habitat–Species Associations from SMURF Collections

Two axes of the PCA of the environmental variables explained 82.6% of their variance (Figure 7A). Rugosity, vertical relief, and percent cover were highly associated with PC1, and average monthly temperature was highly associated with PC2. A habitat

gradient was observed along PC1, sites moving from lower values of rugosity, vertical relief, and percent cover to higher values of each. For PC2, warm water temperatures and high rugosity ranged down to cooler temperatures and lower rugosity (Figure 7A).

The main juvenile species in SMURFs associated with higher measures of rugosity, vertical relief, and percent substrate cover were Tomtate, Slippery Dick, Belted Sandfish, and Seaweed Blenny (Figure 7B). Warsaw Grouper and Red Snapper juveniles showed positive correlations with increased water temperature and PC2. Lane Snapper and Warsaw Grouper juveniles showed negative correlations with PC1 and PC2,

TABLE 3. PERMANOVA pairwise comparisons of culvert categories and juvenile fish compositions (excluding Tomtate, i.e., “minus *H. aurolineatum*” data set) from standard monitoring units for the recruitment of reef fish (SMURFs; see Table 1 for culvert categories). Asterisks denote significance at $P < 0.05$.

Groups (culvert categories)	Pseudo- <i>F</i>	<i>P</i> -value	df
0 versus 1	1.83	0.01*	9
0 versus 2	1.84	0.01*	7
0 versus 3	1.91	0.01*	7
1 versus 2	1.02	0.42	7
1 versus 3	1.30	0.14	10
2 versus 3	0.56	0.87	5

indicating a strong preference for cooler water temperatures and bare environments lacking structure.

Comparison of SMURF Collections and Scuba Surveys

The juvenile fish communities sampled by the SMURFs were significantly different from the adult communities sampled via concurrent visual scuba surveys (PERMANOVA, pseudo- $F = 8.7$, $P = 0.001$). Nearly double the number of species were observed in the adult scuba population than the juvenile SMURF samples (Table 5). Higher total abundance was also observed in the adult scuba-sampled population than the juvenile SMURF samples

(Table 5). Comparing the pooled data from each method, there was a clear segregation of species collected as juveniles in SMURFs to those observed via scuba as adults, more juvenile species recruiting to bare sampling locations (category 0; Figure 8). Although no reef-associated adults were observed via scuba surveys at category 0 (bare areas), a few benthic species were observed during scuba surveys but were never observed in SMURFs. Scuba observations of adult fish and sampling of the juvenile population with SMURFs showed an 85.1% dissimilarity in the total species sampled (Table 6). Three significant groupings of species composition were observed at the 40% level, showing a majority of SMURF juveniles grouping together separately from adults observed via scuba (Figure 8). The species contributing the most similarity to the juvenile population was Belted Sandfish (54.7%) and to the adult population was Red Snapper (21.0%). A SIMPER analysis showed 85.1% average dissimilarity between the two populations, Belted Sandfish, Seaweed Blenny, Red Snapper, Lane Snapper, and Atlantic Spadefish being the top five contributing species.

The juvenile population observed via scuba was significantly different from the juvenile population sampled with SMURFs (PERMANOVA: pseudo- $F = 15.3$, $P = 0.001$). Although more juvenile individuals were observed in scuba surveys, there were more than double the number of species observed in the juvenile SMURF samples than juveniles observed via scuba (Table 5). Species diversity (H') values were also higher in the SMURF samples than scuba surveys (Table 5). Juvenile Belted Sandfish contributed the most

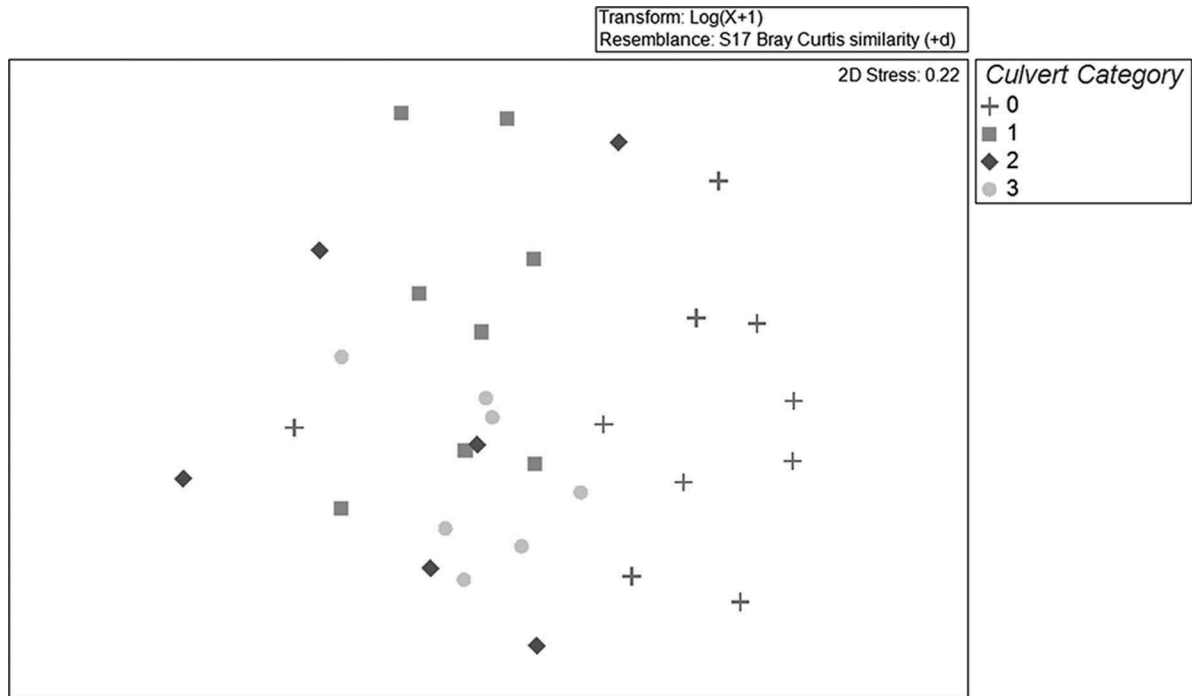


FIGURE 6. Nonmetric multidimensional scaling (NMDS) ordination plot of juvenile species compositions, sampled by SMURFs (standard monitoring units for the recruitment of juvenile reef fish), based on culvert densities (see Figure 2). The two-dimensional stress value presented in the upper right hand corner represents the accuracy of the NMDS plot. The closer two points are to each other the more similar their species compositions.

TABLE 4. Top four dominant juvenile fish species collected from standard monitoring units for the recruitment of reef fish (SMURFs) at each culvert category (see Table 1). Similarity Percentages Test (SIMPER) of the highest contributing species to community composition similarity among all sites in each category is given by percentage values in parentheses. The analysis did not include Tomtate (i.e., “minus *H. aurolineatum*” data set) because this species arrived in heavy pulses only in June and July of 2013 and 2014.

Rank	Category 0	Category 1	Category 2	Category 3
1	Lane Snapper	Seaweed Blenny	Seaweed Blenny	Belted Sandfish (87%)
2	Belted Sandfish (36%)	Slippery Dick	Belted Sandfish (61%)	Slippery Dick
3	Rock Sea Bass	Belted Sandfish (34%)	Rock Sea Bass	Cocoa Damselfish
4	Red Snapper	Lane Snapper	Gulf Toadfish	Seaweed Blenny

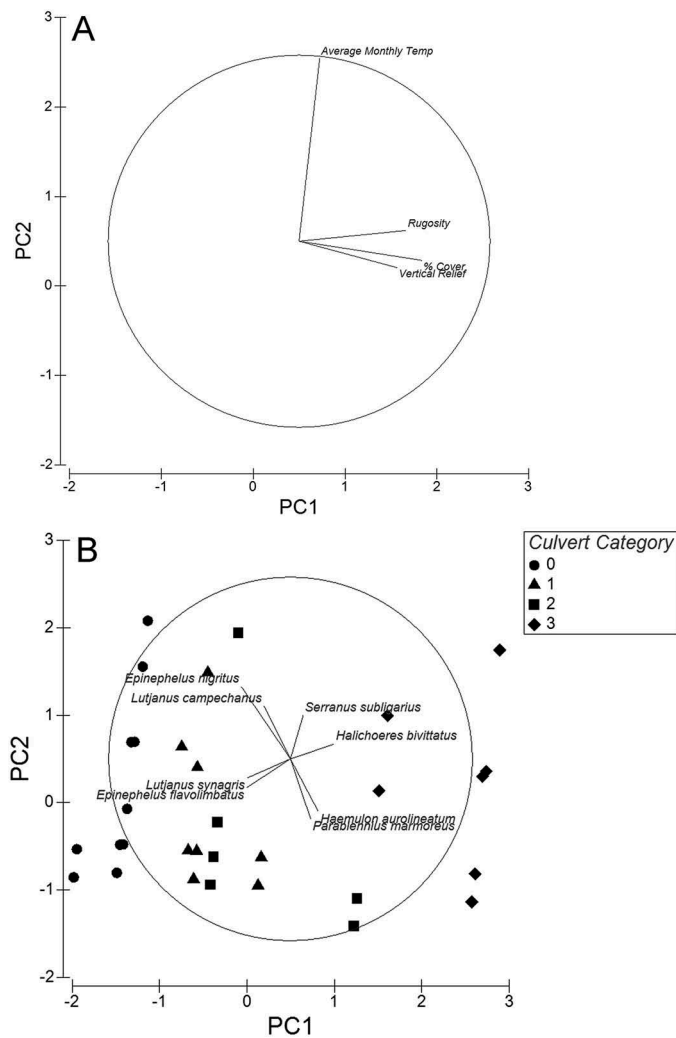


FIGURE 7. Principal components analysis (PCA), showing four environmental variables as ordination vectors. (A) PC1 accounts for 57.7% of variation among rugosity, vertical relief, and percent cover. PC2 accounts for 24.9% of variation in average monthly temperature. (B) PCA showing the location of 31 sampling efforts from June 2013 to July 2014, based on culvert category (see Figure 2) and different fish species sampled by SMURFs (standard monitoring units for the recruitment of juvenile reef fish), in relation to the environmental variables. PC values and variables are the same for both panels A and B. Juvenile fish species shown include dominant and commercially important species among the categories.

similarity to the SMURF samples, whereas Cubbyu was the most ubiquitous juvenile species in scuba surveys.

Juvenile and adult populations from the scuba surveys were significantly different from one another (PERMANOVA: pseudo- $F = 14.6$, $P = 0.0001$). Adult populations had higher species richness, total abundance, species evenness, and species diversity than juvenile populations surveyed with scuba (Table 5). Adult and juvenile populations surveyed with scuba were 97.4% dissimilar, and the top four species attributing to the dissimilarities were Red Snapper, Cubbyu, Cocoa Damselfish, and Slippery Dick. Cubbyu and Cocoa Damselfish were only observed as juveniles with scuba, while juvenile Red Snapper were only observed once, but adults were abundant.

Unique reef-associated fish recruited to the SMURFs as juveniles, and although their densities were low, few were observed as adults in the visual scuba surveys on the reef. Six species of unique or commercially important species that recruited to the SMURFs as juveniles but were not observed in the adult community included Bearded Brotula, Warsaw Grouper, Sargassum Fish, Gulf Toadfish, Crested Blenny, and Southern Hake.

DISCUSSION

The largest differences in species community composition occurred between sampling locations with culverts and those without culverts. Moreover, the juvenile fish assemblages captured in SMURFs were very different from the adult communities observed via scuba surveys. These differences suggest that low structural complexity is driving juvenile survival in the study area. Almany (2004) discovered juvenile recruit abundance increased in the absence of predators, and Shulman (1985) found both predator and reef structure to influence the abundance of reef fish. Our results show that when structural density increases, juvenile fish species indices sampled with SMURFs tended to decrease. On a microcosm scale important to juvenile fish (cm), culvert reef material (as seen at our study location) is not structurally complex; thus, some of this difference may be due to higher predator abundance in the denser culvert sampling locations (Froehlich and Kline 2015). Some species observed in this study, such as those from families Lutjanidae (Snappers) and subfamily Epinephelinae (Groupers), have complex ontogenic changes in habitat preference as they grow, while other species, such as wrasse (Cheney et al.

TABLE 5. Average (\pm SE) diversity indices (S , N , J , H') of the juvenile population sampled by standard monitoring units for the recruitment of reef fish (SMURFs) from June 2013 to July 2014 and the adult and juvenile populations sampled concurrently via visual scuba surveys.

Diversity indices	SMURF juveniles	Scuba adults	Scuba juveniles
Richness (S)	4.33 \pm 0.42	7.29 \pm 1.27	1.71 \pm 0.39
Abundance (N)	15.71 \pm 3.14	62.62 \pm 10.11	25.86 \pm 10.60
Evenness (J')	0.73 \pm 0.05	0.51 \pm 0.08	0.26 \pm 0.08
Diversity (H')	1.03 \pm 0.10	1.15 \pm 0.18	0.31 \pm 0.09

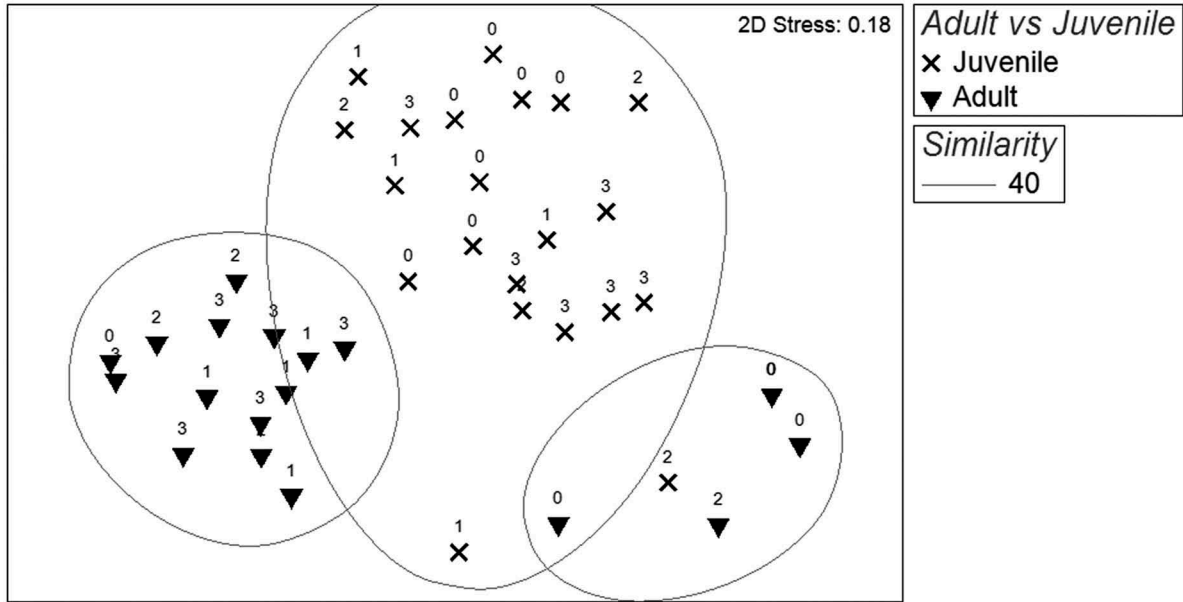


FIGURE 8. Nonmetric multidimensional scaling (NMDS) ordination plot of the adult and juvenile fish communities from all sample locations in the study period. Adult fish communities were sampled via visual scuba surveys while juvenile fish communities were sampled with SMURFs (standard monitoring units for the recruitment of juvenile reef fish). Comparisons were made at the same sampling locations in the reef. Numbers 0–3 represent the four culvert-density categories (see Figure 2). Three significant groupings of species composition are seen at the 40% species similarity level. The two-dimensional stress value presented in the upper right hand corner represents the accuracy of the NMDS plot. The closer two points are to each other, the more similar their species compositions.

TABLE 6. Similarity percentages test (SIMPER) showing top 10 species dissimilarity between the juvenile SMURF (standard monitoring units for the recruitment of reef fish) and the concurrent adult scuba sampling of fish communities. Total dissimilarity between the two populations was 85.1%. The contribution percentage indicates each species’ contribution to the overall 85.1% dissimilarity between the two communities.

Species	Juvenile SMURF rank	Adult scuba rank	Contribution (%)
Belted Sandfish	1	2	9.9
Seaweed Blenny	2	5	6.7
Red Snapper	7	1	6.6
Lane Snapper	3	8	5.6
Atlantic Spadefish <i>Chaetodipterus faber</i>	8	3	5.1
Slippery Dick	5	9	4.9
Gray Triggerfish	9	4	4.6
Tomtate	6	7	4.1
Sheepshead <i>Archosargus probatocephalus</i>	10	6	3.8
Rock Sea Bass	4	10	3.7

2009) and angelfish (Brockmann and Hailman 1976), persist and do well in dense reef areas as juveniles by serving as mutualistic cleaners to larger predators. These differences in juvenile life history could also explain some of the differences between culvert structural categories seen in the present study.

While some juvenile species exhibited no recruitment patterns in relation to reef structure type, we found that the deep-water reef species Warsaw Grouper and Yellowedge Grouper only recruited to SMURFs at the sites lacking any significant culvert reef structure in a 30-m radius. Both species are economically valuable in the Gulf of Mexico (Beets and Hixon 1994; Cook et al. 2009) and are especially vulnerable to over-fishing (Parker and Mays 1998). Additionally, another economically valuable and overfished species, Red Snapper, is known to inhabit muddy, sandy bottoms in the juvenile stage (Gallaway et al. 2009; Szedlmayer and Shipp 1994; Gallaway et al. 2009; Mudrak and Szedlmayer 2012). Juvenile Red Snapper were only observed once in the reefing area away from SMURFs, while they were often observed directly around SMURFs in bare sampling locations. Froehlich and Kline (2015) observed that larger adult Red Snapper exhibited a density-dependent effect, where significantly larger Red Snapper were found on the lowest density of culverts compared with areas of greater density (PS-1047). In captive experiments with young-of-the-year Red Snapper, Bailey et al. (2001) noted that while no cannibalism was observed, the presence of larger conspecifics prevented the use of structural habitat by young-of-the-year fish, potentially creating a habitat bottleneck.

We found that juveniles of three commercially important fish in the study region, Red Snapper, Warsaw Grouper, and Yellowedge Grouper, arrived at the bare areas and were likely attracted to the low relief structures (SMURFs). In a study conducted off St. Croix in the U.S. Virgin Islands, Adams and Ebersole (2002) found that 33 of 92 species used the back-reef as adults but settled at the rubble and patch reefs as juveniles; however, no juveniles larger than 3 cm were observed at the rubble and patch reefs. Observations of juveniles in areas lacking significant structure, as noted in several studies, suggests that reef design may benefit from small low-relief reef patches away from the main reef where juveniles can recruit and grow before moving to the higher relief areas.

Juvenile fish are likely to encounter more predators at dense reef areas (Shulman 1985; Doherty and Sale 1986; Steele 1996; Carr and Hixon 1997). Demersal fish predators such as Scamp *Mycteroperca phenax* (Matheson et al. 1986), Rock Hind *Epinephelus adscensionis* (Pereira 2014), and Spotted Scorpionfish *Scorpaena plumieri* (Heck and Weinstein 1989) were observed in scuba surveys at culvert sites (Froehlich and Kline 2015), and the juvenile Warsaw Grouper (Heemstra and Randall 1993) and Red Snapper (Gallaway et al. 2009) observed with SMURFs may have consumed other juvenile fish as they recruited to the reef area. Roving pelagic predators, such as Great Amberjack *Seriola dumerili*, Cobia *Rachycentron canadum*, and Crevalle Jack *Caranx hippos*, were observed at the reef via scuba visual surveys and are also known to consume juvenile fishes

(Pipitone and Andaloro 1995; Arendt et al. 2001; Smith-Vaniz and Carpenter 2007). An analysis of predation frequency was beyond the scope of our study; however, more work should be conducted to address this issue with tagging, stomach content analysis of predators, or sampling with caged and uncaged SMURFs to estimate predation.

We rarely observed adult individuals in areas without significant structure, which may allow juvenile recruitment to be more successful in these areas due to lower potential predation. Juveniles arriving at the reefing area were either recruiting more frequently to the areas with less structure or, due to density-dependent postsettlement losses like predation, were not surviving at the structurally denser areas (Shulman 1985). Low-relief shelter that is unattractive to larger individuals (i.e., potential predators), can aid in juvenile recruitment and growth (Carr and Hixon 1997). Furthermore, we found culvert density appeared to be negatively correlated with the presence of juveniles. Because reef fish mortality is highest immediately following postsettlement (Almany 2004), perhaps juveniles recruiting to the densest culvert patches suffered the highest mortality from itinerant predators. Doherty et al. (2004) found that 61% of nocturnally settling Bluespine Unicornfish *Naso unicornis* were lost due to predation over the reef. The species we observed may be settling evenly among the varying densities in the reef array; however, similar to the Bluespine Unicornfish, the species we observed may exhibit higher survival in the absence of predators.

Shifts in ontogeny and postsettlement movement also play a large role in determining where fish first arrive on a reef (Werner and Gilliam 1984; Ludwig and Rowe 1990; Dahlgren and Eggleston 2000; Rose et al. 2010). We found Belted Sandfish recruited to nearly every site in all four culvert categories regardless of culvert density; however, lower abundances and smaller recruits were seen at the bare sites, while higher abundances and larger individuals were observed at the densest culvert sites, suggesting a directed movement within the reef array based on ontogenic shifts. Similarly, a study conducted off the coast of Curaçao found nearly half the fish species studied changed habitat when metamorphosing from the juvenile to adult stage (Nagelkerken and van der Velde 2002), which suggests that these fishes made directed movements due to ontogenic changes in habitat preference from the surrounding mangroves, channels, and areas of low-relief to the coral reefs. Studies on French Grunt *Haemulon flavolineatum*, common to the Caribbean and western Gulf of Mexico, show shifts in habitat preference based on ontogeny. French Grunt settle in patch and low-lying rubble reefs and later moves to more complex coral reef habitat as adults (Grol et al. 2011). Similarly, Red Snapper also show ontogenic habitat movements with growth. Wells and Rooker (2009) found the gut contents of juvenile Red Snapper showed a diet composed of organisms from the open, sandy areas when inhabiting low-profile shell banks in the north-western Gulf of Mexico, indicating bare open spaces may be needed for foraging areas. Red Snapper also exhibit an ontogenic progression to higher vertical structure from age 0 to age 2, seeking

new habitats after quickly outgrowing their low-relief residences (Gallaway et al. 2009).

The SMURFs we used yielded different results than the scuba visual surveys for examining juvenile fish communities. Juvenile fish are cryptic and difficult to visually assess; thus, scuba surveys alone may not be capturing the entire community. Our SMURF samples exhibited nearly twice the juvenile species richness and triple the juvenile diversity of scuba surveys. While scuba visual surveys and SMURF-recruiting devices are complimentary methods for population analyses, our results, along with others (Ammann 2004; Valles et al. 2006), suggest that SMURFs are an effective method to examine juvenile fish communities.

The results of our study show that future artificial reef deployments can benefit from increased microhabitat heterogeneity in order to accommodate a variety of reef fish. While several juvenile species were not seen in scuba surveys and were only recorded in SMURF samples, they are likely settling in many areas around the reef and are either being predated upon or are moving to other areas. Thus, adding smaller habitat may benefit reefs by allowing increased juvenile survival. Numerous studies report an increase in diversity of benthic reef fish through an increase in habitat complexity (Luckhurst and Luckhurst 1978; Miller 1996; Depczynski and Bellwood 2004). Comparatively, smaller habitat can also provide compact, low-relief patches on the reef fringe where commercially valuable juveniles can recruit and grow. Gratwicke et al. (2006) demonstrated that juvenile reef fish use low-relief structures in lagoons as a nursery before shifting to the main coral reef as adults. Mudrak and Szedlmayer (2012) found higher recruitment of juvenile Red Snapper to smaller reefs far from the reef habitat intended for adults. Because reef-associated fish show shifts in habitat selection through ontogeny (Werner and Gilliam 1984; Dahlgren and Eggleston 2000; Vigliola and Harmelin-Vivien 2001; Gratwicke et al. 2006), the addition of microhabitat at the fringes and throughout an artificial reef constructed with culverts will probably increase the diversity of the adult population.

ACKNOWLEDGMENTS

The Texas Parks and Wildlife Department Artificial Reef Program and the Coastal Conservation Association of Texas provided partial funding of this project. Dale Shively contributed helpful information regarding the deployment of culverts at PS-1047. David W. Hicks assisted with statistical advice, and Heather D. Alexander provided comments that greatly improved this manuscript. The University of Texas Rio Grande Valley Scuba team contributed diving support. All applicable international and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

- Adams, A. J., and J. P. Ebersole. 2002. Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series* 228:213–226.
- Alevizon, W. S., and J. C. Gorham. 1989. Effects of artificial reef deployment on nearby resident fishes. *Bulletin of Marine Science* 44:646–661.
- Almany, G. R. 2003. Priority effects in coral reef fish communities. *Ecology* 84:1920–1935.
- Almany, G. R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284.
- Ambrose, R. F., and S. L. Swarbrick. 1989. Comparison of fish assemblages on artificial and natural reefs off the coast of Southern California. *Bulletin of Marine Science* 44:718–733.
- Ammann, A. J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. *Journal of Experimental Marine Biology and Ecology* 299:135–154.
- Arendt, M. D., J. E. Olney, and J. A. Lucy. 2001. Stomach content analysis of Cobia, *Rachycentron canadum*, from lower Chesapeake Bay. U.S. National Marine Fisheries Service Fishery Bulletin 99:665–670.
- Bailey, H. K. IV, J. H. Cowan Jr., and R. L. Shipp. 2001. Experimental evaluation of potential effects of habitat size and presence of conspecifics on habitat association by young-of-the-year Red Snapper. *Gulf of Mexico Science* 2:119–131.
- Bannerot, S. P., and J. A. Bohnsack. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41.
- Barnes, H. 2003. Oceanography and marine biology, an annual review. CRC Press, Boca Raton, Florida.
- Beets, J., and M. A. Hixon. 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. *Bulletin of Marine Science* 55:470–483.
- Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* 44:631–645.
- Bohnsack, J. A., and D. L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science* 37:11–39.
- Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. *Bulletin of Marine Science* 32:269–276.
- Brock, R. E., and J. E. Norris. 1989. An analysis of the efficacy of four artificial reef designs in tropical waters. *Bulletin of Marine Science* 44:934–941.
- Brockmann, H. J., and J. P. Hailman. 1976. Fish cleaning symbiosis: notes on juvenile angelfishes (*Pomacanthus*, Chaetodontidae) and comparisons with other species. *Zeitschrift Für Tierpsychologie* 42:129–138.
- Carr, M. H., and M. A. Hixon. 1997. Artificial reefs: the importance of comparisons with natural reefs. *Fisheries* 22(4):28–33.
- Chandler, C. R., J. Sanders, and J. Landry. 1985. Effects of three substrate variables on two artificial reef fish communities. *Bulletin of Marine Science* 37:129–142.
- Charbonnel, E. 2002. Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). *ICES Journal of Marine Science* 59:S208–S213.
- Cheney, K. L., A. S. Grutter, S. P. Blomberg, and N. J. Marshall. 2009. Blue and yellow signal cleaning behavior in coral reef fishes. *Current Biology* 19:1283–1288.
- Coleman, F. C., C. C. Koenig, G. R. Huntsman, J. A. Musick, A. M. Eklund, J. C. McGovern, G. R. Sedberry, R. W. Chapman, and C. B. Grimes. 2000. Long-lived reef fishes: the grouper-snapper complex. *Fisheries* 25(3):14–21.
- Cook, M., G. R. Fitzhugh, and J. S. Franks. 2009. Validation of Yellowedge Grouper, *Epinephelus flavolimbatus*, age using nuclear bomb-produced radiocarbon. *Environmental Biology of Fishes* 86:461–472.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81:2227–2240.
- Depczynski, M., and D. R. Bellwood. 2004. Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Marine Biology* 145:455–463.
- Doherty, P. J., V. Dufour, R. Galzin, M. A. Hixon, M. G. Meekan, and S. Planes. 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology* 85:2422–2428.
- Doherty, P. J., and P. F. Sale. 1986. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* 4:225–234.
- Froehlich, C. Y. M., and R. J. Kline. 2015. Using fish population metrics to compare the effects of artificial reef density. PLOS (Public Library of Science) ONE [online serial] 10(9):e0139444.

- Gallaway, B. J., J. G. Cole, R. Meyer, and P. Roscigno. 1999. Delineation of essential habitat for juvenile Red Snapper in the northwestern Gulf of Mexico. *Transactions of the American Fisheries Society* 128:713–726.
- Gallaway, B. J., S. T. Szedlmayer, and W. J. Gazey. 2009. A life history review for Red Snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. *Reviews in Fisheries Science* 17:48–67.
- Grabowski, J. H., A. R. Hughes, D. L. Kimbro, and M. A. Dolan. 2005. How habitat setting influences restored oyster reef communities. *Ecology* 86:1926–1935.
- Gratwicke, B., C. Petrovic, and M. R. Speight. 2006. Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. *Environmental Biology of Fishes* 76:191–210.
- Gratwicke, B., and M. R. Speight. 2005a. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66:650–667.
- Gratwicke, B., and M. R. Speight. 2005b. Effects of habitat complexity on Caribbean marine fish assemblages. *Marine Ecology Progress Series* 292:301–310.
- Grol, M., I. Nagelkerken, N. Bosch, and E. Meesters. 2011. Preference of early juveniles of a coral reef fish for distinct lagoonal microhabitats is not related to common measures of structural complexity. *Marine Ecology Progress Series* 432:221–233.
- Heck, K. L. Jr., and M. P. Weinstein. 1989. Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. *Bulletin of Marine Science* 45:629–636.
- Heemstra, P. C., and J. E. Randall. 1993. *FAO species catalogue, vol. 16. Groupers of the world (family Serranidae, subfamily Epinephelinae): an annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper, and lyretail species known to date.* FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 125.
- Johnson, D. W. 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology* 88:1716–1725.
- Kaufman, L., J. Ebersole, J. Beets, and C. C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environmental Biology of Fishes* 34:109–118.
- Lecchini, D., S. Planes, and R. Galzin. 2007. The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. *Journal of Experimental Marine Biology and Ecology* 341:85–90.
- Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* 49:317–323.
- Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* 135:686–707.
- Matheson, R. H., G. R. Huntsman, and C. S. Manooch. 1986. Age, growth, mortality, food and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. *Bulletin of Marine Science* 38:300–312.
- Miller, P. J. 1996. The functional ecology of small fish: some opportunities and consequences. *Symposia of the Zoological Society of London*. 69:175–200.
- Mudrak, P. A., and S. T. Szedlmayer. 2012. Proximity effects of larger resident fishes on recruitment of age-0 Red Snapper in the northern Gulf of Mexico. *Transactions of the American Fisheries Society* 141:487–494.
- Nagelkerken, I., and G. van der Velde. 2002. Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? *Marine Ecology Progress Series* 245:191–204.
- Parker, R. O. Jr., and R. W. Mays. 1998. Southeastern U.S. deepwater reef fish assemblages, habitat characteristics, catches, and life history summaries. NOAA Technical Report NMFS 138.
- Pereira, P. H. C. 2014. “Swallowing it all” – extreme ingestion capability of juvenile reef fish. *Biota Neotropica* [online serial] 14(1).
- Pickering, H., and D. Whitmarsh. 1997. Artificial reefs and fisheries exploitation: a review of the “attraction versus production” debate, the influence of design and its significance for policy. *Fisheries Research* 31:39–59.
- Pipitone, C., and F. Andaloro. 1995. Food and feeding habits of juvenile Greater Amberjack, *Seriola dumerili* (Osteichthyes, Carangidae) in inshore waters of the central Mediterranean Sea. *Cybium* 19(3):305–310.
- Rilov, G., and Y. Benayahu. 2000. Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. *Marine Biology* 136:931–942.
- Rooker, J. R., S. A. Holt, M. A. Soto, and G. J. Holt. 1998. Postsettlement patterns of habitat use by sciaenid fishes in subtropical Seagrass Meadows. *Estuaries* 21:318–327.
- Rose, K. A., J. I. Allen, Y. Artioli, M. Barange, J. Blackford, F. Carlotti, and S. L. Hill. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 2:115–130.
- Ross, S. W., and M. L. Moser. 1995. Life history of juvenile Gag, *Mycteroperca microlepis*, in North Carolina estuaries. *Bulletin of Marine Science* 56:222–237.
- Sale, P. F., P. J. Doherty, and W. A. Douglas. 1980. Juvenile recruitment strategies and the coexistence of territorial pomacentrid fishes. *Bulletin of Marine Science* 30:147–158.
- Sale, P. F., and W. A. Douglas. 1981. Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. *Environmental Biology of Fishes* 6:333–339.
- Shulman, M. J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66:1056–1066.
- Shulman, M. J., and J. C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series* 39:233–242.
- Smith-Vaniz, W. F., and K. E. Carpenter. 2007. Review of the Crevalle Jacks, *Caranx hippos* complex (Teleostei: Carangidae), with a description of a new species from West Africa. *U.S. National Marine Fisheries Service Fishery Bulletin* 105:207–233.
- Steele, M. A. 1996. Effects of predators on reef fishes: separating cage artifacts from effects of predation. *Journal of Experimental Marine Biology and Ecology* 198:249–267.
- Szedlmayer, S. T., and R. L. Shipp. 1994. Movement and growth of Red Snapper, *Lutjanus campechanus*, from an artificial reef area in the north-eastern Gulf of Mexico. *Bulletin of Marine Science* 55:887–896.
- Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic Cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 52:1834–1841.
- Valles, H., D. L. Kramer, and W. Hunte. 2006. A standard unit for monitoring recruitment of fishes to coral reef rubble. *Journal of Experimental Marine Biology and Ecology* 336:171–183.
- Verdiell-Cubedo, D., M. Torralva, A. Andreu-Soler, and F. J. Oliva-Paterna. 2012. Effects of shoreline urban modification on habitat structure and fish community in littoral areas of a mediterranean coastal lagoon (Mar Menor, Spain). *Wetlands* 32:631–641.
- Victor, B. C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs* 56:145–160.
- Vigliola, L., and M. Harmelin-Vivien. 2001. Post-settlement ontogeny in three Mediterranean reef fish species of the genus *Diplodus*. *Bulletin of Marine Science* 68:271–286.
- Wells, R. J. D., and J. R. Rooker. 2009. Feeding ecology of pelagic fish larvae and juveniles in slope waters of the Gulf of Mexico. *Journal of Fish Biology* 75:1719–1732.
- Werner, E., G. G. Mittlebach, D. J. Hall, and J. F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64:1525–1539.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Williams, D. M., and P. F. Sale. 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within “One Tree Lagoon”, Great Barrier Reef. *Marine Biology* 65:245–253.