An analysis of the early life history in gray triggerfish (*Balistes capriscus*) based on small artificial patch-reefs.

Stephen T. Szedlmayer

Peter A Mudrak

Contact author: Stephen Szedlmayer, szedlst@auburn.edu, 251-767-8565

School of Fisheries, Aquaculture and Aquatic Sciences, Auburn University

8300 Hwy. 104 Fairhope, AL 36532

Abstract—Densities of juvenile (age-0 and age-1) gray triggerfish (*Balistes capriscus*) were compared over a nine-year period (2007 to 2015), based on SCUBA visual estimates on small (1.42 m^3) artificial patch-reefs in the northern Gulf of Mexico. This time period included years both before and after the Deepwater Horizon oil spill in 2010 that provided for an evaluation of the effect of the oil spill on densities of juvenile gray triggerfish on patch-reefs. Densities of juvenile gray triggerfish on patch-reefs were also compared to catch-per-unit-effort (CPUE = number caught/H) of juvenile gray triggerfish from trawl surveys by the Southeast Area Monitoring and Assessment Program (SEAMAP) that has been used as an index of juvenile gray triggerfish density in the Gulf of Mexico. High densities of age-0 gray triggerfish in 2013, 2014, and 2015 on patch-reefs indicated years of higher potential year-classes of gray triggerfish. These densities had a significant inverse correlation with sea surface temperature during the spawning season in June and July. The density of age-0 gray triggerfish in October 2010 was similar in 2007 before the oil spill and in 2011 after the oil spill, but was lower than the high densities observed in 2013, 2014, and 2015. Also, the density of age-1 gray triggerfish in June 2011 was similar to other years. Thus, the present study did not detect an effect of the 2010 Deepwater Horizon oil spill on the density of juvenile gray triggerfish on patch-reefs. Changes in densities of juvenile gray triggerfish suggested a density dependent relation, and yielded a mean estimated instantaneous natural mortality rate (*M*) of 1.44. Densities of age-0 gray triggerfish were significantly higher on patch-reefs located 500 m from larger reef structure than on patch-reefs located 15 m from larger reef structure. In 2011, juvenile gray triggerfish densities were higher on patch-reefs on the east side compared to patch-reefs on the west side of the study area. Removals of red snapper and other reef fishes in 2013 did not affect juvenile gray triggerfish densities. There was a positive relation between the densities of age-0 and age-1

gray triggerfish and indicated that age-0 gray triggerfish may select initial recruitment reefs with older conspecifics. There was also a significant positive correlation between age-0 gray triggerfish and red snapper, *Lutjanus campechanus*, and other reef fish densities in October, and between age-1 gray triggerfish and red snapper densities in June. There was a significant correlation between age-0 gray triggerfish densities on patch-reefs in October and CPUE of gray triggerfish from the SEAMAP fall trawl surveys. However, in June there was no significant correlation between the density of age-1 gray triggerfish on patch-reefs and CPUE from SEAMAP trawl surveys. The SCUBA diver visual survey method used in the present study was validated with comparisons to drop-net-rotenone samples that indicated similar estimates of densities and lengths of juvenile gray triggerfish on patch-reefs. Thus, the patch-reefs visual survey methods used here can provide indexes of juvenile gray triggerfish abundance.

Introduction

Gray triggerfish (*Balistes capriscus*) are common on reefs in the northern Gulf of Mexico, with most of the gray triggerfish landings in the Gulf of Mexico coming from the areas east of the Mississippi River (SEDAR 43, 2015). While gray triggerfish landings are small relative to other reef fish species in the Gulf of Mexico, they are gaining importance as fishers turn to gray triggerfish as an alternative target species as management restrictions limit other fisheries (Harper and McClellan, 1997; Valle et al., 2001). This in turn has led to increased restrictions on the gray triggerfish fishery, a need for more accurate data, and an improvement in understanding gray triggerfish life history.

Accurate stock assessment and management of marine reef fish benefits from an understanding of juvenile settlement. Management efforts are more effective if year-class strength can be estimated before juveniles enter the fishery, rather than back-calculating year-class strength after a year-class moves into the exploited fishery. The open nature and large size of marine habitats makes accurate measurement of juvenile fish density difficult. Accurately predicting year-class strength could allow quotas to be increased when it can be anticipated that large year-classes will enter the fishery, and stocks could be protected from overfishing by decreasing quotas as less abundant year-classes enter the fishery. Presently, density estimates of juvenile gray triggerfish in stock assessments are based on trawl surveys (SEDAR 43, 2015). However, such estimates may be unsuitable for gray triggerfish, as juveniles spend an extended period in pelagic habitats associated with floating sargassum and debris before settling and quickly moving to structured habitat in the fall (Dooley, 1972; Bortone et al., 1977; Wells and Rooker, 2004; Simmons and Szedlmayer, 2011). Therefore, other survey methods may be more appropriate for determining the density of juvenile gray triggerfish, especially after they settle to benthic habitats and move to reef structure.

Small isolated reefs (patch-reefs) have long been used to experimentally manipulate reef fish communities (Sale, 1980; Doherty, 1982; Steele, 1998). Patch-reefs can be easily manipulated and can facilitate experimental designs that address specific questions. Recently, several studies have used artificial patch-reefs to evaluate different aspects of juvenile red snapper, *Lutjanus campechanus*, and gray triggerfish biology (Simmons and Szedlmayer, 2011; Mudrak and Szedlmayer, 2012, 2020; Szedlmayer and Mudrak, 2014). These studies deployed patch-reefs with identical designs in the same areas and at similar times each year from 2007 to 2015. Mudrak and Szedlmayer (2020) used these data to compare juvenile red snapper densities over time.

The objective of the present study is to re-examine these patch-reef surveys to evaluate interannual differences in juvenile gray triggerfish density. This analysis will provide annual density estimates that can be used in gray triggerfish stock assessment efforts. These data will also provide estimates of natural mortality that are also important for gray triggerfish stock assessments. Annual densities on patch-reefs will be compared with catch-per-unit-effort (CPUE = catch/H) from SEAMAP trawl surveys presently used as an index of juvenile gray triggerfish abundance. These annual densities will also be compared to environmental conditions such as temperature. Comparisons will also be made to the densities of older conspecifics and other reef fishes that may affect juvenile gray triggerfish densities. These insights may be useful in future efforts to predict juvenile gray triggerfish densities. These visual surveys of patch-reefs will also provide an evaluation of the effect of the 2010 Deepwater Horizon oil spill on juvenile gray triggerfish because surveys were taken both before and after the spill. Importantly, juvenile gray triggerfish densities on patch-reefs were compared over patch-reef distance from larger reef structure, patch-reef location, and the density of resident red snapper and other reef fishes on patch-reefs. The potential influence of these factors on juvenile gray triggerfish densities will enhance our understanding of early life history and ecology of this important species.

Methods

Reef design and surveys

Each patch-reef had a total volume of 1.42 m^3 and consisted of a plastic pallet (1.22 × 1.02 × 0.14 m), 10 concrete blocks (41 × 20 × 10 cm), and a plastic crate (65 × 35 × 28 cm; Figure 1). Patch-reefs were assembled with 122 cm plastic cable ties with a breaking strength of 79 kg. A small plastic float (5.1 × 12.7 cm) was attached to each of the reef corners and floated 1 m above the reef. A larger float (15.2 cm diameter) was attached to the center of the patch-reef and floated 1 m above the patch-reef. The floats added vertical structure to the patch-reef and facilitated patch-reef relocations with sonar. The patch-reefs were anchored to the seafloor by attachment to a 1.2 m ground anchor with a 3 m length of 1.3 cm diameter nylon rope. All patch-reefs were placed at least 500 m apart and 15 or 500 m away from any known reefs in the area (Mudrak and Szedlmayer, 2012).

Patch-reefs were visually surveyed by SCUBA divers. Divers identified fish to species, counted all fish present on the patch-reef, and estimated their size in 25-mm total length (TL) intervals. Gray triggerfish sizes were based on fork length (FL) due to the extended rays on their long caudal fins. Divers took up stationary positions 2 m from the patch-reef and counted all fish within visible range of the patch-reef over an approximate 15-min survey period. Fish distances from patch-reefs varied and were not measured, thus all densities were calculated as number of fish/m^3 patch-reef size. However, diver visibility typically exceeded maximum fish distances from the reef due to the small size of the patch-reefs. If diver visibility was determined to be less than the 3 m distance to the far side of the reef (i.e., divers could not count all fish on the far side of the reef) the reef survey was not included. Some of the patch-reefs became partially buried after storms. If more than 50 % of a patch-reef was buried, the estimate of fish density from that patch-reef was not included. The age of gray triggerfish observed was estimated based on FL as determined from previous studies. All gray triggerfish greater than 305 mm FL were considered age-2 or older. Gray triggerfish were considered age-0 in May, June and July when less than 76 mm FL, in August when less than 102 mm FL, in September when less than 127 mm FL, in October when less than 152 mm FL, in November when less than 178 mm FL, and in December when less than 203 mm FL (Simmons and Szedlmayer, 2011). No surveys were conducted from January through April. At the time of the diver surveys, temperature, salinity and dissolved oxygen were measured within 1 m of the seafloor with a remote YSI 6920 meter. If more than one water condition reading was taken at a reef site during a survey, we used the mean of temperature, salinity, and dissolved oxygen for that survey in all analyses (Table 1).

Interannual comparisons

The densities of age-0 and age-1 gray triggerfish were compared among deployment dates, locations, and survey dates (Table 2). Patch-reefs deployed at the same time and location were referred to as a reef set (Table 2; Figure 2). The patch-reefs (described above) were deployed with 10 to 30 patch-reefs per set. One set of patch-reefs was deployed each year, with the exception of 2010 when three patch-reef sets (N = 10 patch-reefs for each set, N = 30 total patch-reefs) were deployed to evaluate the effect of the Deepwater Horizon oil spill on reef-associated fish assemblages (Table 2). The offshore location was 19 – 23 km from shore and ranged in depth from 17 – 24 m (Figure 2). The inshore location was 12 – 16 km from shore and ranged in depth from 14 – 18 m (Figure 2). If there was more than one survey in the same month, the highest mean density of age-0 gray triggerfish per survey was used for interannual comparisons of density. In 2008, no patch-reefs could be located after Hurricane Gustav (1 September 2008). In 2009, patch-reefs could not be located or were damaged after Hurricane Ida (10 November 2009). In 2011, one patch-reef could not be located after tropical storm Lee (4 September 2011), and in 2012 four patch-reefs could not be located after Hurricane Isaac (28 August 2012).

Patch-reefs were deployed with experimental designs to examine the effects of proximity to larger reefs, spatial distribution, and the addition or removal of potential predators and competitors (Simmons and Szedlmayer, 2011; Mudrak and Szedlmayer, 2012; Szedlmayer and Mudrak, 2014). However, for comparing densities among years we only used fish densities on patch-reefs that were deployed in July or August, placed at least 500 m from other known reefs, and without fish artificially added or removed from a patch-reef.

Diver visual surveys allowed comparisons of gray triggerfish densities for four months among years (Table 2). The density of gray triggerfish observed in August included surveys from eight years (2008 to 2015), in September from five years (2007, 2009, 2010, 2012, and 2014), in October from six years (2007, 2010, 2011, 2013, 2014, and 2015) and in June from six years from patch-reefs that were deployed the previous year (2007, 2010, 2011, 2013, 2014, and 2015).

The Deepwater Horizon oil spill occurred from 20 April to 15 July 2010 (NOAA, 2010; Allan et al., 2012), and was predicted to affect local fish populations (Rooker et al., 2013). In 2010, 10 patch-reefs were deployed in July at an offshore location (Off-Jul2010) that was the same location as the 2008 and 2009 patch-reefs (Mudrak and Szedlmayer 2012; Figure 2). Two additional patch-reef sets (each with $N = 10$) were deployed in August 2010. The Off-Aug2010 reef set was deployed at the same offshore location as the Off-Jul2010 reef set, and the In-Aug2010 reef set was placed closer to shore (Figure 2). Gray triggerfish densities from the three reef sets deployed in 2010 were analyzed separately when comparing the effect of interannual differences in density, due to differences in location and deployment date that may affect gray triggerfish densities (Szedlmayer and Mudrak, 2014). All reef sets after 2010 were deployed at the inshore study location (Figure 2).

Age-0 and age-1 gray triggerfish interactions

We compared the densities of age-0 and age-1 gray triggerfish on patch-reefs with Pearson correlation analysis, but only used densities from patch-reefs that were not manipulated (i.e. deployed in July or August at the offshore or inshore locations at least 500 m from other reefs, with no fish added or removed). Surveys from August, September, and October were analyzed separately, and June surveys were not compared because few age-0 gray triggerfish were present on patch-reefs in June.

Interactions with other species

Densities of gray triggerfish were compared to the density of other reef fish species residing on unmanipulated patch-reefs. For August, September, and October, we used partial correlations to compare the density of juvenile (age-0 and age-1) gray triggerfish with the density juvenile red snapper (age-0 and age-1) with the effects of other reef fish removed. In June, partial correlations were used to compare the density of juvenile gray triggerfish with the density juvenile red snapper with the effects of other reef fish removed, and to the total fish density with red snapper removed. Other reef fish was defined here as all fish counted in visual surveys except for red snapper and open habitat or pelagic species. Open habitat or pelagic species removed from visual estimates included Atlantic bumper, *Chloroscombrus chrysurus*, blue runner, *Caranx crysos*, flounder, *Paralichthys sp.*, grass porgy, *Calamus arctifrons*, king mackerel, *Scomberomorus cavella*, lizardfish, Synodontidae, longspine porgy, *Stenotomus caprinus*, lookdown, *Selene vomer*, round scad, *Decapterus punctatus*, searobin, *Prionotus sp.*, Spanish mackerel, *Scomberomorus maculatus*, and spot, *Leiostomus xanthurus*.

Environmental correlations

Bottom temperatures were measured with temperature loggers (U22-001, Onset Incorporated) deployed at one of three stations over the time period of the present study. These stations were located 31 – 32 km southeast of Dauphin Island Alabama U.S., at depths of 26 – 30 m. Sea surface temperatures were obtained from the 42012 data buoy located 81 km southeast of Mobile Alabama U.S. (NOAA, 2020). For comparisons with age-0 gray triggerfish densities each month, and age-1 gray triggerfish densities in June, we used the mean of all bottom or sea surface temperatures for each month. In addition, the densities of age-0 gray triggerfish in

October and age-1 gray triggerfish in June were compared to the mean sea surface and bottom temperatures in June and July, which corresponds to the gray triggerfish spawning season (Simmons and Szedlmayer, 2012; Lang and Fitzhugh, 2015).

Mortality Estimates

For mortality estimates we used density estimates of gray triggerfish from patch-reefs deployed in July or August that were at least 500 m from larger reef structures and without fish experimentally added or removed. In addition to the offshore and inshore locations, this included reefs located at the West and East sites in 2011 and the East site in 2015 (Figure 2). To be used in mortality estimates, the patch-reef needed a fall visual survey on or after 29 September, and a visual survey the next summer. Surveys prior to 29 September were not included because age-0 gray triggerfish were still recruiting the patch-reefs and densities were increasing. A total of 104 patch-reefs fit these criteria. The highest densities of age-0 gray triggerfish observed on each patch-reefs in the fall were used to calculate the mean densities of age-0 gray triggerfish each year. The first surveys of those same patch-reefs the next summer were used to calculate the mean density of age-1 gray triggerfish. Survival (S) was calculated as the mean density of age-1 gray triggerfish on patch-reefs in the summer divided by the mean density of age-0 gray triggerfish observed the previous fall each year. Total instantaneous mortality (Z), was calculated with the equation $Z = -\ln(S^{(365/t)})$ were t = the mean number of days between the fall and summer surveys that year. The mean Z was calculated from the mean of the annual mortality estimates from each year. However, in 2011 mean densities of gray triggerfish increased over winter and Z was undefined and not included.

Comparison to SEAMAP trawl surveys

The densities of gray triggerfish from diver visual surveys of unmanipulated patch-reefs were compared to the catch-per-unit-effort (CPUE = catch/H) of gray triggerfish estimated from trawl surveys (Southeast Area Monitoring and Assessment Program – SEAMAP; Gulf States Marine Fisheries Commission 2018). For comparisons, we only used SEAMAP trawl surveys that were taken during the same time periods as the patch-reef visual surveys. These included SEAMAP trawl surveys in June and October of each year. Also, we only used SEAMAP CPUE trawl surveys between longitudes -89° and -85° W, corresponding to the mouth of the Mississippi River to Cape San Blas, Florida. Most gray triggerfish collected by trawl were measured to FL. For all gray triggerfish measured by TL, their lengths were converted to FL with the equation FL = 0.811 × TL + 16.942. This equation was derived from a linear regression of gray triggerfish FL to TL, for fish collected with drop-net-rotenone sampling of patch-reefs ($N = 33$). The same length (FL) to age relation used to estimate age from length estimates by diver surveys of patch-reefs was applied to gray triggerfish length (FL) from SEAMAP trawl surveys. The CPUE of age-0 gray triggerfish from SEAMAP October surveys was compared to the density estimates of age-0 gray triggerfish on patch-reefs in October. The CPUE of age-1 gray triggerfish from SEAMAP June surveys was compared to the density estimates of age-1 gray triggerfish on patch-reefs in June. For the comparison of SEAMAP trawl CPUE to diver visual density estimates, the densities of juvenile gray triggerfish from Off-Aug2010 and In-Aug2010 patch-reefs were combined to obtain an estimate of the density of juvenile gray triggerfish on patch-reefs for 2010.

Effects of distance from larger reef structure

In 2008, 2009, and 2010, we examined the effect of patch-reef proximity to larger artificial reefs on the density of juvenile fish on patch-reefs (Mudrak and Szedlmayer, 2012). Each year we deployed 10 patch-reefs 15 m (Near) from the larger steel cage artificial reefs (2.5 x 1.3 x 2.4 m) and 10 patch-reefs 500 m (Far) from the large steel cage artificial reefs for the Off-Jul2008, Off-Jul2009, and Off-Jul2010 deployments. Both the Near and Far patch-reefs were deployed and surveyed at the same time each year, and allowed for comparisons of juvenile gray triggerfish densities on patch-reefs in areas used by predators and competitors to densities on patch-reefs away from known predators and competitors.

2011 Spatial experiment

In 2011, there were three patch-reef sets deployed at a Center site, a West site and an East site. The Center site (In-Jul2011, $N = 10$) was 13 km south of the coastline (30.107ºN, 87.958ºW), the West site ($N = 10$) was 30 km west of the center site, and the East site ($N = 10$) was 30 km east of the center site (Figure 2). All three patch-reef sets were deployed and surveyed at similar times and allowed for comparisons of juvenile gray triggerfish densities at larger spatial scales. Over the winter, eight patch-reefs were lost at the West site, possibly due to shrimp trawling. Therefore, the gray triggerfish density estimates on the remaining two patch-reefs were not used for analysis in June due to low sample size. This experiment was repeated in 2012, but

Hurricane Isaac buried many of the patch-reefs at the East and West sites on 28 August 2012, and sample sizes were too low for spatial comparisons in 2012.

2015 spatial experiment

In 2015, it was possible that the 100 patch-reefs that were previously deployed at the inshore location over the years since 2010 were providing a source of age-1 red snapper, gray triggerfish, and other reef fish that could quickly colonize any new reefs built in the immediate area. These age-1 individuals may affect the density of age-0 individuals (Mudrak and Szedlmayer 2012; Szedlmayer and Mudrak 2014; Mudrak and Szedlmayer 2020). To examine this possibility two patch-reef sets were deployed in 2015. One patch-reef set was deployed at the Center site (In-Jul2015, $N = 15$) 500 m from previous patch-reef deployments, and one patch-reef set (2015 East site, $N = 15$) was deployed 11 km east of the Center site (Figure 2). These two patch-reef sets were deployed and surveyed at similar times in 2015. The 2015 East site was selected so that all patch-reefs were at least 1 km from other known reefs in the area. Placing patch-reefs 11 km to the east allowed for comparisons of gray triggerfish densities both with (center) and without (east) a near-by source of immigrants.

Removal experiment

In 2013, we applied a removal experiment to examine the effects of age-1 red snapper and other reef associated fish species on age-0 gray triggerfish densities. In June, 30 patch-reefs were deployed at the center site (June patch-reefs). Fish were able to colonize these June patch-reefs for one month prior to the start of the removal treatments. In July, 10 of these June patch-reefs had all fish removed (All Removal). Scuba divers placed a 3-m radius cast net (drop-net) over the reef and buried the lead line in the sand. Scuba divers then dispensed rotenone onto the patch-reef and collected all fish in the net. For a red snapper only removal (RS Removal), 10 of the June patch-reefs had only red snapper removed with fish traps on 6 and 8 August 2013. The traps (1.2 × 1.5 × 0.6 m; Collins 1990) were baited with squid *Loligo* sp., and gulf menhaden *Brevoortia patronus*. The trap was set next to (< 5 m) each patch-reef for 15 minutes before retrieval. All captured red snapper were removed from the patch-reef, while all other captured fish were immediately released at the patch-reef site. The other 10 patch-reefs deployed in June 2015 served as a control with no removals (Control Reefs).

In July, we also deployed 10 new patch-reefs and defined these as a "New Reef" treatment (In-Jul2013). These New Reefs served as empty patch-reefs with few if any resident fish, because there was little time for fish recruitment before they were surveyed. These manipulations of patch-reefs with removals and non-removal allowed for determinations of the effects of resident reef fish on the recruitment of age-0 gray triggerfish.

Comparisons of visual surveys to drop-net-rotenone sampling

Patch-reefs ($N = 14$) were first visually surveyed prior to drop-net-rotenone collections. Immediately after visual surveys, drop-net-rotenone collections were carried out. These visual and drop-net-rotenone surveys were completed on four patch-reefs in November 2012 and 10 patch-reefs in July 2013. All fish collected with drop-nets were placed on ice and returned to the laboratory. In the laboratory all fish were identified to species, weighed (nearest 0.1 g) and lengths measured (standard length, FL, TL mm). These visual surveys followed by drop-net-rotenone collections allowed for validation of visual surveys methods used to estimate the number and length of gray triggerfish on patch-reefs.

Statistical analysis

Annual densities of juvenile gray triggerfish were examined for possible effects of the various treatments with generalized linear models (GLIMMIX; SAS 9.4) with negative binomial distributions and logarithm-link functions (Huelsenbeck and Crandall, 1997; Seavy et al., 2005; Bolker et al., 2009). In the August comparisons, 1 was added to all age-0 gray triggerfish densities on patch-reefs for statistical analysis due to the large number of reefs (72 %) with densities = 0. If significant differences were detected among densities, specific differences were identified with a Tukey multiple comparison test (Zar, 2010). In our statistical analyses, interannual comparisons of mean densities in August, September, October, and June were analyzed with separate tests (i.e., not all reef sets were surveyed all months analyzed). However, when comparing the effects of differences in distance from larger reef structure, patch-reef locations, and fish removals we used a repeated measures (RM) analysis.

A Pearson's product-moment correlation coefficient was calculated to determine the association between the CPUE from trawls to densities on patch-reefs from visual surveys, to compare densities of age-0 and age-1 gray triggerfish, and to compare gray triggerfish densities with temperature. In addition, to determine if density dependent mechanisms were occurring, we compared mean age-0 gray triggerfish densities in the fall to total mortality (Z) each year. Partial correlation was used to compare densities of gray triggerfish, red snapper, and other reef fishes.

Drop-net-rotenone samples were compared to visual estimates with a Fisher's exact test. All statistical differences were considered significant at P d 0.05.

Results

Annual variation of juvenile gray triggerfish density on patch-reefs

The density of age-0 gray triggerfish observed on small artificial patch-reefs varied widely in the fall among years. In comparison, the age-1 densities the following summer showed less variation among years (Figure 3). The density of age-0 gray triggerfish was significantly different among years in August ($F_{7,81} = 3.80$, $P = 0.001$; Figure 4), September ($F_{6,63} = 29.3$, $P < 0.001$; Figure 5), and October ($F_{6,70} = 37.81$, $P < 0.001$; Figure 6). Similarly, the density of age-1 gray triggerfish was significantly different among years in August ($F_{7,81} = 21.8$, $P < 0.001$; Figure 4), September ($F_{6,63} = 9.03$, $P < 0.001$; Figure 5), October ($F_{6,70} = 2.79$, $P = 0.017$; Figure 6), and in June ($F_{6,84} = 8.27$, $P < 0.001$; Figure 7).

Age-0 and age-1 gray triggerfish

There was a significant positive relation between age-0 and age-1 gray triggerfish density in August ($r = 0.24$, $P = 0.026$, $N = 89$ patch-reefs), September ($r = 0.43$, $P < 0.001$, $N = 70$ patch-reefs), and October ($r = 0.24$, $P = 0.037$, $N = 77$ patch-reefs).

Correlations with other species

A total of 57 species of reef fish were counted in the present study. Species that comprised more than 1% of the total fish counted include red snapper (34.4%), tomtate, *Haemulon aurolineatum*, (17.9%), pigfish, *Orthopristis chrysoptera*, (12.1%), gray triggerfish (11.5%), vermilion snapper, *Rhomboplites aurorubens*, (6.3%), rock sea bass, *Centropristis philadelphica*, (4.5%), Atlantic spadefish, *Chaetodipterus faber*, (3.1%), sand perch, *Diplectrum formosum*, (2.5%), lane snapper, *Lutjanus synagris*, (2.4%), and pygmy filefish, *Stephanolepis setifer*, (1.6%).

In October, gray triggerfish densities were positively correlated with total reef fish densities ($r = 0.24$, $P = 0.037$) with the effect of red snapper density removed, and red snapper density ($r = 0.42$, $P < 0.001$, $N = 77$ patch-reefs) with the effect of total reef fish density removed. In June, there was no correlation between gray triggerfish densities and total reef fish densities ($r < 0.001$, $P = 0.994$) with the effects of red snapper density removed, but there was a significant correlation with red snapper densities ($r = 0.40$, $P < 0.001$, $N = 91$ patch-reefs) with the effect of total reef fish density removed.

Environmental conditions

Bottom temperature data were available for most of the present study except November 2008 – September 2010. There was no significant correlation between bottom temperature and age-0 gray triggerfish density in August ($r = 0.32$, $P = 0.526$, $N = 6$), September ($r = -0.86$, $P = 0.339$, $N = 3$), or October ($r = 0.70$, $P = 0.120$, $N = 6$). There was no significant correlation between bottom temperature and age-1 density in June ($r = 0.11$, $P = 0.829$, $N = 6$). There was also no significant correlation between mean bottom temperatures in the June and July spawning season each year and age-0 gray triggerfish density in October (r = -0.50, P = 0.386, N = 5), or with age-1 gray triggerfish density the following June (r = -0.63, P = 0.259, N = 5).

Sea surface temperature data was available for all years beginning in 2009. There was no significant correlation between monthly mean sea surface temperature and age-0 gray triggerfish density in August (r = 0.06, P = 0.891, N = 7), September (r = 0.74, P = 0.261, N = 4), or October (r = 0.66, P = 0.228, N = 5), or between monthly mean sea surface temperature and mean age-1 gray triggerfish density in June (r = 0.13, P = 0.837, N = 5). However, there was a significant negative correlation between the mean sea surface temperature during the spawning season in June and July and the density of age-0 gray triggerfish on patch-reefs in October each year (r = -0.94, P = 0.018, N = 5), and this pattern continued with a significant negative correlation between age-1 gray triggerfish densities on patch-reefs in June, and the mean sea surface temperature when those fish were spawned the previous June and July (r = -0.93, P = 0.023, N = 5). In the years examined, the mean sea surface temperature for the June and July spawning season ranged from a low of 28.4° C in 2013 to a high of 30.1° C in 2010.

Mortality

Among the patch-reefs deployed in July or August that did not have fish experimentally added or removed, there were 104 that were surveyed both in the fall and the following summer. The fall surveys of individual patch-reefs occurred between 29 September and 10 December each year, with most surveys in October. The first survey in the spring of these 104 patch-reefs varied from 2 to 30 June. The time between surveys ranged from 189 to 258 days with a mean of 234 days between surveys. Gray triggerfish densities increased over winter in 2011, and mortality rates were not estimated. Mortality (*Z*) in years with observed declines in density ranged from a low of $Z = 0.41$ in 2010 to a high of $Z = 2.18$ in 2018 (Table 3). There was a marginally significant positive relation between mean age-0 gray triggerfish density each fall and *Z* that year ($r = 0.81$, $P = 0.052$, $N = 6$). The mean *Z* based on all years was 1.44 after removing 2011 from the calculation.

Comparison to SEMAP trawl surveys

There was a significant positive correlation between mean age-0 gray triggerfish densities on patch-reefs and mean CPUE in SEMAP trawl surveys each October ($r = 0.85$, $P = 0.034$; Table 4; Figure 8). There was no significant correlation between age-1 gray triggerfish densities on patch-reefs and CPUE in SEMAP trawl surveys in June ($r = -0.34$, $P = 0.508$; Table 4; Figure 9).

Distance from larger reef structure

Densities of age-0 gray triggerfish in the fall, and age-1 gray triggerfish the following summer were significantly higher on patch-reefs that were far from larger reef structure compared to patch-reefs that were near to larger reef structure (RM $F_{1,58} = 19.16$, $P < 0.001$). In August, few age-0 gray triggerfish were present on patch-reefs that were near (mean ± SE 0.0 ± 0.0, $N = 30$) or far from larger reef structure (0.07 ± 0.05, $N = 30$). In September, age-0 densities had increased, and densities were lower on patch-reefs that were near (0.28 ± 0.11, N = 20) compared to patch-reefs that were far from larger reef structure (1.41 ± 0.34, N= 20). This pattern persisted with age-1 densities in the following July (Near = 0.99 ± 0.53, N = 5; Far = 3.94 ± 2.14, N = 5). There was no significant difference in age-1 gray triggerfish densities on patch-reefs that were near or far from larger reef structure in August (Near = 0.21 ± 0.08, N = 30; Far = 0.23 ± 0.11, N = 30), or in September (Near = 0.35 ± 0.14, N = 20; Far = 0.39 ± 0.15, N = 20, RM $F_{1,58}$ = 0.07, P = 0.791).

Spatial distribution of reefs

Densities of the 2011 year-class (age-0 in 2011, age-1 in 2012) of gray triggerfish on patch-reefs were significantly different among locations, with the highest densities at the East site, intermediate densities at the Center site, and lowest densities at the West site (RM $F_{2,27}$ = 20.81, P < 0.001; Figure10). Densities of the 2010 year class (age-1 in 2011) of gray triggerfish on the 2011 patch-reef were also significantly different among locations, again with the highest densities at the East site, intermediate densities at the Center site, and lowest densities at the West site (RM $F_{2,27}$ = 23.37, P < 0.001; Figure 11).

2015 spatial distribution

Densities of the 2015 year-class (age-0 in 2015, age-1 in 2016) of gray triggerfish on patch-reefs deployed in 2015 were significantly different among locations ($F_{1,28}$ = 11.22, P = 0.002), time ($F_{2,55}$ = 56.37.49, P < 0.001), and location x time interaction ($F_{2,55}$ = 14.77, P < 0.001; Figure 12). The densities of 2015 year class gray triggerfish were significantly higher on the Center site compared to the East site in October, but no significant differences between sites were observed in August or the following June (Figure 12). Densities of the 2014 year-class (age-1 in 2015) of gray triggerfish on the 2015 patch-reefs were not significantly different among locations ($F_{1,28}$ = 3.13, P = 0.088), or time ($F_{1,28}$ = 1.66, P = 0.208), but there was a significant location x time interaction ($F_{1,28}$ = 14.91, P < 0.001, Figure 13). The densities of 2014 year-class gray triggerfish were significantly higher at the Center site compared to the 2015 East site in August, but no significant differences between sites was observed in October (Figure 13).

Removal experiment

Densities of the 2013 year-class (age-0 in 2013, age-1 in 2014) of gray triggerfish on patch-reefs deployed in 2013 were not significantly affected by removal treatments (RM $F_{3,36}$ = 1.24, P = 0.309; Figure 14). There was also no significant difference in densities of the 2012 year-class (age-1 in 2013) of gray triggerfish on the 2013 patch-reefs due to removal treatments (RM $F_{3,36}$ = 0.19, P = 0.899; Figure 15).

Drop-net-rotenone sampling

Among the 14 patch-reefs that were surveyed visually and with drop-net-rotenone collections, 12 had at least one gray triggerfish detected by one or both survey methods, and all patch-reefs had less than 10 individuals detected by either method. Among the 12 patch-reefs with detected gray triggerfish, three had the same number of individuals for both methods, and nine had counts that differed by one individual between the two methods. Overall, 32 gray triggerfish were counted by visual surveys, and 33 gray triggerfish were captured by drop-nets. Visual examination of the

28 individuals detected by both methods, indicated that 46 % (N = 13) had measured fork lengths that matched the 25 mm size interval visually estimated by divers, 21 % (N = 6) had estimated size intervals one interval smaller than their measured length, 21 % (N = 6) had visual estimates one interval larger than their measured length, and 11 % (N = 3) were two intervals larger than their measured length. Incorrect visual size estimation caused five individuals (18%) to be assigned a different age compared to the measured length, with all five assigned an older age. However, a Fisher's exact test comparing the number of gray triggerfish observed in each of the 25 mm size interval by each survey method was not significantly different (P = 0.155).

Discussion

Annual variation

In August and September, densities of age-0 gray triggerfish on patch-reefs were low in most years. Therefore, the October survey was better for comparing age-0 gray triggerfish densities among years. One of the objectives of the present study was to determine if the Deepwater Horizon oil spill affected the density of age-0 gray triggerfish. First, the present October surveys indicated that there were similar age-0 gray triggerfish densities before the spill in 2007, during the spill in 2010 and after the spill in 2011. Second, these densities of age-0 gray triggerfish at both the inshore and offshore locations for 2007, 2010 and 2011 were much lower than densities in 2013, 2014, and 2015. Third, the density of age-1 gray triggerfish in June 2011 was similar to other years, suggesting that there was not a year-class failure in 2010. Thus, gray triggerfish densities on patch-reefs in the present study indicated that the Deepwater Horizon oil spill had little effect on age-0 gray triggerfish.

Interestingly, in 2010, similar densities of age-0 gray triggerfish were observed on patch-reefs deployed at the offshore and inshore locations. This is in contrast to red snapper, which showed lower densities at the offshore location (Szedlmayer and Mudrak 2014; Mudrak and Szedlmayer, 2020). This may represent a difference in habitat preference between these two species, with red snapper densities indicating a preference for inshore habitats, while gray triggerfish densities indicating no preference for inshore and offshore reef locations.

The present study clearly indicated higher densities of age-0 gray triggerfish in the later years examined. There were two events that may explain the substantial increases in density. First, was an increase in the abundance of sargassum in the Atlantic. Wang et al. (2019) document a large increase in the amount of sargassum present in the Atlantic Ocean beginning in 2011. The amount of sargassum has continued to increase since that time. This represents an increase in the amount of habitat potentially available to pre-settlement age-0 gray triggerfish, which may account for higher densities of post-settlement individuals. The abundance of sargassum is likely to remain high for the foreseeable future and may lead to continued high densities of age-0 gray triggerfish.

A second important possible explanation is likely driven by restrictions placed on the directed fishery to improve the stock. In 2012 the gray triggerfish quota was reduced in order to rebuild the stock (SEDAR 43, 2015). This led to the commercial and recreational fisheries being closed in June and represents the first time that gray triggerfish season was not open for the entire year. In 2013, both the commercial and recreational bag limits were reduced, a permanent closed season was established for June and July, and the recreational season was closed earlier than anticipated. Since 2013, recreational gray triggerfish seasons have closed early each year. The reduced harvest and expected increase in spawning biomass could have led to the increased age-0 densities. However, these two factors (sargassum increase and increased harvest limits) both occurred at similar time periods that corresponded with the increases in age-0 densities, making it difficult separate their influence.

Age-0 and age-1 gray triggerfish correlations

The present study indicated a positive correlation between the densities of age-0 and age-1 gray triggerfish. While this relation did not fully explain the variation seen in age-0 densities (i.e. low r^2 values), it is in contrast to the negative correlation observed between age-0 and age-1 red snapper on these same patch-reefs (Mudrak and Szedlmayer, 2012, 2020; Szedlmayer and Mudrak, 2014). A possible explanation for this difference may be related to a major difference in early life histories of red snapper and gray triggerfish. Gray triggerfish spend an extended time period associated with floating sargassum before settling to benthic structure. The larger sizes of gray triggerfish at settlement likely makes them less susceptible to gape limited predators, and better able to compete with conspecifics and other fishes present on the patch-reef. Other reef fishes are also known to preferentially settle on reefs with conspecifics present (Sweatman, 1983, 1988; Lecchini et al., 2005). Other possible explanations for the positive relation between age-0 and age-1 gray triggerfish include: 1) juvenile triggerfish prefer patch-reefs with greater numbers of conspecifics, 2) patch-reefs were located in areas that provided better habitat and food resources, or 3) patch-reefs were easier to locate and attracted more fish of both age classes.

Other species correlation

The diverse fish assemblages on these patch-reefs could allow for many correlation tests, especially if those species are then further divided into age classes. To avoid running many tests with increased probability of a type-I error, we analyzed only the months of October when gray triggerfish densities were highest, and June after the occurrence of overwinter mortality. The positive partial correlation to total reef fish densities (excluding red snapper) in October, along with the significant partial correlation with red snapper density in October suggests that patch-reefs with more fish supported higher densities of gray triggerfish. These patch-reefs may have had better food resources, or perhaps more resident fish makes a patch-reef easier to locate for juveniles in search of reef habitat.

The positive correlation observed between gray triggerfish and red snapper in October and June is in contrast to the negative interactions between these two species observed by Simmons and Szedlmayer (2018). However, the present study did not experimentally remove gray triggerfish from reefs as carried out in this previous study (Simmons and Szedlmayer, 2018). Therefore, in the present study we can conclude that patch-reefs with more gray triggerfish tended to have more red snapper, but cannot determine if there would have been more red snapper if the gray triggerfish had been removed.

Environmental correlations

There was a negative correlation between mean sea-surface temperatures in June and July and the mean density of age-0 gray triggerfish in October each year. Cooler surface temperatures may be conducive for egg and larval survival, sargassum import or growth, or could be linked to currents or water masses that encourage the importation or retention of larvae and pelagic pre-settlement juveniles (Antoni and Saillant, 2017; Wang et al., 2019). This correlation continued, with a significant relation between age-1 gray triggerfish densities in June, and the mean sea-surface temperature when those fish were spawned the previous June and July. However, this result should be viewed with caution because there were only five years with an October patch-reef survey and June – July sea surface temperature data. The differences in density between years may have occurred due to other factors such as increased spawning stock, increased sargassum, or other favorable conditions not directly linked to temperature. In future studies, as longer term data sets become available, sea-surface temperature in June and July should be considered as a possible factor for year to year variability in age-0 and age-1 year-class strength.

Mortality

In the present study we assumed that after patch-reefs reached maximum densities, declines in abundance were attributed to mortality rather than emigration. For the most part the mean density of gray triggerfish declined each year between the fall and the following summer. One exception occurred in 2011, where the mean density of gray triggerfish increased from fall to spring and mortality was undefined. While the density of age-0 gray triggerfish in 2011 was similar to other years of the present study, they were relatively low. Therefore in 2011, the immigration of only a small number of individuals over the winter and spring caused higher counts in the summer than were observed the previous fall.

The observed mortality rates indicated density dependent regulation of gray triggerfish survival on patch-reefs, with higher survival in years of lower densities and lower survival in years of high densities. Density dependent mortality is further supported by the significant correlation between mean age-0 gray triggerfish densities in the fall and Z. However, despite indications of density dependent mortality rates, years with higher age-0 densities still had the potential to result in higher age-1 densities the following year.

The observed mortality rate is reported as Z because it represents all sources of mortality. However, this Z is likely the same as M because these fish are below the minimum size limits for the directed fishery, they are residing on small patch-reefs that are difficult to find and target by fishers, and if a trawl passed over the patch-reef the patch-reef would be damaged or lost entirely.

Due to the open nature of these patch-reefs mortality estimates should be treated with caution, i.e., emigration may cause mortality to be overestimated. However, at the time of writing, these estimates represent the only mortality estimates of juvenile gray triggerfish. Based on these estimates a mean M of 1.44 is recommended for October to June over the first winter period, with density dependence altering this rate in years of low or high gray triggerfish densities. This M estimate is higher than the age-0 and age-1 natural mortality rates recommended in SEDAR 43 of $M = 0.790$ and $M = 0.571$ (SEDAR 43, 2015). However, 2013, 2014, and 2015 were years of high gray triggerfish densities, and accounted for 60 % (3 of 5) of the years used to calculate mean M in the present study. With observed evidence of density dependence, mean M may be lower if age-0 gray triggerfish densities do not remain high in future years.

SEAMAP trawl surveys

In October there was a significant correlation between the density of age-0 gray triggerfish on patch-reefs and the CPUE of age-0 gray triggerfish from SEAMAP trawl surveys. However, CPUE for gray triggerfish in the SEAMAP trawl surveys was always less than one, meaning that many hours of trawling were necessary to obtain a representative sample. Also, in two years of lower abundance, trawls failed to catch any age-0 gray triggerfish, meaning trawl surveys were not able to distinguish among years of lower densities and complete year-class failures. This indicates that even with a significant correlation between trawls and patch-reef estimates, patch-reefs provided a more accurate method for measuring age-0 gray triggerfish densities.

There was no significant correlation between age-1 gray triggerfish densities on patch-reefs and trawl CPUE in June. This was not surprising because there was less variation in gray triggerfish densities on patch-reefs in June than in October, and trawls caught very few age-1 gray triggerfish because it is likely that most were residing on structured habitat.

Distance from larger reef structure

Age-0 gray triggerfish densities were lower on patch-reef that were near larger reef structures, and age-0 gray triggerfish were not observed on these larger reef structures. This is the same pattern as observed for age-0 red snapper (Mudrak and Szedlmayer, 2012). Similar to age-0 red snapper, age-0 gray triggerfish likely use small low relief structures at settlement because such habitats lack larger predators, and later move to larger reef structure when they are larger and less vulnerable to predation. For example, the minimum size of gray triggerfish observed in camera surveys of larger reefs was 145 mm FL (DeVries et al., 2015), while smaller individuals were routinely observed on patch-reefs in the present study. This is an important life history trait and future surveys attempting to measure age-0 gray triggerfish density need to include some type of low relief nursery habitats.

Spatial distributions

In 2011, juvenile gray triggerfish of age-0 and age-1 were most abundant on the patch-reefs deployed farthest to the east. Densities were intermediate at the Center site and lowest on the West site patch-reefs. This may indicate better habitat conditions for gray triggerfish as one moves from west to east within the present study area. Szedlmayer and Mudrak (2014) measured substrates with higher silt-mud content to the west, and higher sand content to the east. These coarser sediments may be preferred by gray triggerfish. The East site was also farther from the Mississippi and Mobile River discharges, and the reduced sedimentation and other freshwater influences may be preferred by gray triggerfish. The pattern observed in gray triggerfish is opposite of the pattern observed on the same patch-reefs with red snapper (Szedlmayer and Mudrak, 2014). This suggests that either the supply of settlers or the habitat preferences of these two species differs, with red snapper being more abundant to the west, and gray triggerfish more abundant to the east.

Periodic hypoxic events at the West site also influenced the habitat suitability for gray triggerfish at the West site. For example, in 2011 hypoxic conditions occurred at the West site in late August and hypoxic conditions may have affected the Center site as well (Szedlmayer and

Mudrak, 2014). The measured hypoxic events occurred in late August and were no longer present when the patch-reefs were surveyed again in October. While the exact timing of the end of hypoxic conditions is unknown, it probably occurred before the peak of age-0 gray triggerfish settlement in October. However, the hypoxia effects on benthic invertebrates and reef epifauna on patch-reefs at the West site may have made them less preferred habitat for age-0 gray triggerfish.

2015 spatial experiment

In 2015 patch-reefs at the Center site were quickly colonized by age-1 gray triggerfish, at much higher densities than the East site. This was most likely due to the remaining patch-reefs and resident fish assemblages from previous deployments ($N = 100$) at the Center site since 2010. These remaining fish assemblages would then serve as a nearby source of new immigrants. However, the higher densities of age-1 gray triggerfish at the Center site did not persist into the later fall, and densities of age-1 gray triggerfish on the Center and East sites were similar in the later October survey in 2015.

The initial densities of the 2015 year-class (age-0 in 2015, age-1 in 2016) of gray triggerfish were significantly higher on the Center site in the October survey, but densities were similar at the Center and East sites the following June 2016. A positive correlation between age-0 and age-1 gray triggerfish densities was observed in the present study and indicates that a higher initial colonization of age-1 fish on the Center site may have resulted in greater densities of age-0 fish. Other reef fish are known to select settlement sites occupied by conspecifics, and the mechanism of this could be age-0 fish following chemical cues released by conspecifics (Sweatman, 1983, 1988; Lecchini et al., 2005). These higher initial densities of gray triggerfish on the Center site did not persist as density dependent mechanisms began to affect gray triggerfish densities at both sites.

Removal experiment

The removal experiments did not detect any significant effects on either age-0 or age-1 gray triggerfish densities. Rather than concluding that the density of red snapper and other reef associated fishes had no effect on juvenile gray triggerfish densities, it is more likely that the removal treatments were not successful in effectively lowering fish densities. For example, age-1 gray triggerfish densities should have been lower on the All Removed and New Reef treatments in the fall, but no significant density reductions were observed. More frequent removal treatments may be required to detect potential effects of reef fish density on gray triggerfish.

Drop-net-rotenone vs visual estimates

Drop-net sampling occurred in years and months when gray triggerfish abundance was less than 10 individuals per patch-reef. At these densities, both methods produced similar estimates, i.e., the difference between the two methods was within one individual on each patch-reef and for the overall total abundance. Drop-net sampling allowed for the validation of visual length estimates, and most individuals counted in visual surveys were within one 25 mm size interval of their measured length. Thus, as long as the size of most age-0 and most age-1 individuals differ by at least 50 mm, then few individuals will be assigned to the incorrect age class and conclusions based on visual size estimates will be valid.

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Table 1. Environmental conditions associated with visual surveys for juvenile gray triggerfish: Temperature = Temp, salinity = Sal and dissolved oxygen = DO measured within 1 m of the seafloor during each survey. If more than one measurement was recorded, the mean value is displayed.

	August			September			October			June		
Reef Set	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L	Temp °C	Sal ‰	DO mg/L
Off-Aug2007	–	–	–	–	–	–	–	–	–	22.9	34.3	4.5
Off-Jul2008	–	–	–	–	–	–	–	–	–	–	–	–
Off-Jul2009	23.6	29.0	5.7	28.2	29.3	6.8	–	–	–	–	–	–
Off-Jul2010	23.7	32.2	2.4	26.4	33.1	3.8	–	–	–	–	–	–
Off-Aug2010	–	–	–	26.3	33.0	2.4	24.8	33.7	6.5	–	–	–
In-Aug2010	–	–	–	28.2	30.6	2.0	24.0	36.2	5.8	–	–	–
In-Jul2011	25.3	35.5	2.4	–	–	–	24.2	33.3	5.5	–	–	–
In-Jul2012	–	–	–	–	–	–	–	–	–	–	–	–
In-Jul2013	–	–	–	–	–	–	27.9	31.6	–	–	–	–
In-Jul2014	–	–	–	30.0	32.3	–	–	–	–	27.1	33.6	–
In-Jul2015	28.9	34.3	5.6	–	–	–	25.6	32.5	4.5	23.9	34.8	–

Table 2. Location and deployment date for patch-reef sets surveyed off Alabama, in the northern Gulf of Mexico. Reef sets located inshore (12 – 16 km) are prefixed with "In", and reef sets located offshore (19 – 23 km) are prefixed with "Off". Reef *N* = the number of reefs deployed in each reef set (Reef set name). Survey *N* = number of reefs surveyed for each month (not all reefs deployed were surveyed each month). Dates of surveys are listed within each month.

			Surveys							
Reef Set name	Reef *N*	Deployed	August	*N*	September	*N*	October	*N*	June	*N*
Off-Aug2007	30	1-9Aug07	-	-	27Sep07	10	26Oct07	10	10-19Jun08	24
Off-Jul2008	10	24-28Jul08	6-15Aug08	10	-	-	-	-	-	-
Off-Jul2009	10	9-10Jul09	4-6Aug09	10	9-10Sep09	10	-	-	-	-
Off-Jul2010	10	14-15Jul10	2-3Aug10	10	9-20Sep10	10	-	-	-	-
Off-Aug2010	10	25Aug10	-	-	9Sep10	10	21Oct10	10	30Jun11	10
In-Aug2010	10	24Aug10	-	-	8Sep10	10	18Oct10	10	9Jun11	10
In-Jul2011	10	19-20Jul11	29-30Aug11	10	-	-	26Oct11	9	14Jun12	9
In-Jul2012	10	19Jul12	8Aug12	10	25Sep12	6	-	-	-	-
In-Jul2013	10	18Jul-1Aug13	27-29Aug13	10	-	-	30Sep-16Oct13	9	5-17Jun14	10
In-Jul2014	14	22-24Jul14	21-22Aug14	14	8-10Sep14	14	30Sep-2Oct14	14	2-4Jun15	14
In-Jul2015	15	28Jul15	21-28Aug15	15	-	-	30Sep-7Oct15	15	13-22Jun16	14

Table 3. Juvenile gray triggerfish total instantaneous mortality (*Z*) observed each year, and mean Z based on all years except 2011. Mortality is based on the decline between the maximum density of age-0 gray triggerfish observed on patch-reefs in the fall surveys and the density of age-1 gray triggerfish observed on the first summer survey the following year. In 2011 there was an increase in density, and mortality was not calculated. The number of patch-reefs with available data each year = *N*.

Year	*N*	*Z*
2007	18	1.10
2010	20	0.41
2011	21	-
2013	9	1.92
2014	14	2.18
2015	22	1.62
Mean	–	1.44

Table 4. Mean CPUE ± SE (catch/H) of age-0 and age-1 gray triggerfish and the total number of trawl tows conducted by the SEAMAP trawl surveys by year. Only years with corresponding visual estimates of juvenile gray triggerfish on patch-reefs were compared.

Year	Season	Age	Mean CPUE	Trawl *N*
2007	Fall	0	0 ± 0	34
2010	Fall	0	0.27 ± 0.17	51
2011	Fall	0	0 ± 0	17
2013	Fall	0	0.73 ± 0.56	11
2014	Fall	0	0.49 ± 0.21	45
2015	Fall	0	0.49 ± 0.20	26
2008	Summer	1	0.12 ± 0.09	49
2011	Summer	1	0.22 ± 0.16	40
2012	Summer	1	0.32 ± 0.32	31
2014	Summer	1	0.11 ± 0.11	36
2015	Summer	1	0.15 ± 0.09	51
2016	Summer	1	0.03 ± 0.03	28

List of Figures

Figure 1. Small patch-reef design that was deployed in the present study, off coastal Alabama, U.S., in the northern Gulf of Mexico.

Figure 2. Locations of artificial patch-reefs deployed and visually surveyed on the Alabama continental shelf in the northern Gulf of Mexico from 2007 to 2015. All symbols represent sets of patch-reefs containing 10 to 30 individual patch-reefs placed at least 500 m apart. Reef set captions indicate location and month-year of deployment, e.g., Off-Aug2007 were patch-reefs (N = 30) deployed at the offshore location in August 2007.

Figure 3. Mean density (number/m^3) of gray triggerfish on patch-reefs deployed each year. Densities observed prior to 1 January represent age-0 gray triggerfish, while densities observed after 1 January represent age-1 gray triggerfish.

Figure 4. Mean densities (number/m^3) of (A) age-0 and (B) age-1 gray triggerfish on patch-reefs in August by year. Different letters indicate significant differences (P d 0.05), and age-0 and age-1 densities were analyzed separately. Error bars = SE.

Figure 5. Mean densities (number/m^3) of (A) age-0 and (B) age-1 gray triggerfish on patch-reefs in September by year. Different letters indicate significant differences (P d 0.05), and age-0 and age-1 densities were analyzed separately. Error bars = SE.

Figure 6. Mean densities (number/m^3) of (A) age-0 and (B) age-1 gray triggerfish on patch-reefs in October by year. Different letters indicate significant differences (*P* d 0.05), and age-0 and age-1 densities were analyzed separately. Error bars = SE.

Figure 7. Mean densities (number/m^3) of age-1 gray triggerfish on patch-reefs in June the year after the patch-reefs were deployed. Different letters indicate significant differences (*P* d 0.05). Error bars = SE.

Figure 8. Comparison of mean density (number/m^3) of age-0 gray triggerfish on patch-reefs in October to mean CPUE (catch/H) of age-0 gray triggerfish from October SEAMAP trawl surveys conducted between the Mississippi River and Cape San Blas in the northern Gulf of Mexico each year.

Figure 9. Comparison of mean density (number/m^3) of age-1 gray triggerfish on patch-reefs in June to mean CPUE (catch/H) of age-1 gray triggerfish from June SEAMAP trawl surveys conducted between the Mississippi River and Cape San Blas in the northern Gulf of Mexico each year.

Figure 10. Mean density ± SE of the 2011 year-class (age-0 in 2011, age-1 in 2012) of gray triggerfish on patch-reefs at the West, Center, and East sites for patch-reefs built in July 2011. Different letters indicate significant differences (*p* d 0.05). The June survey of the West was not included in the analysis due to small sample size.

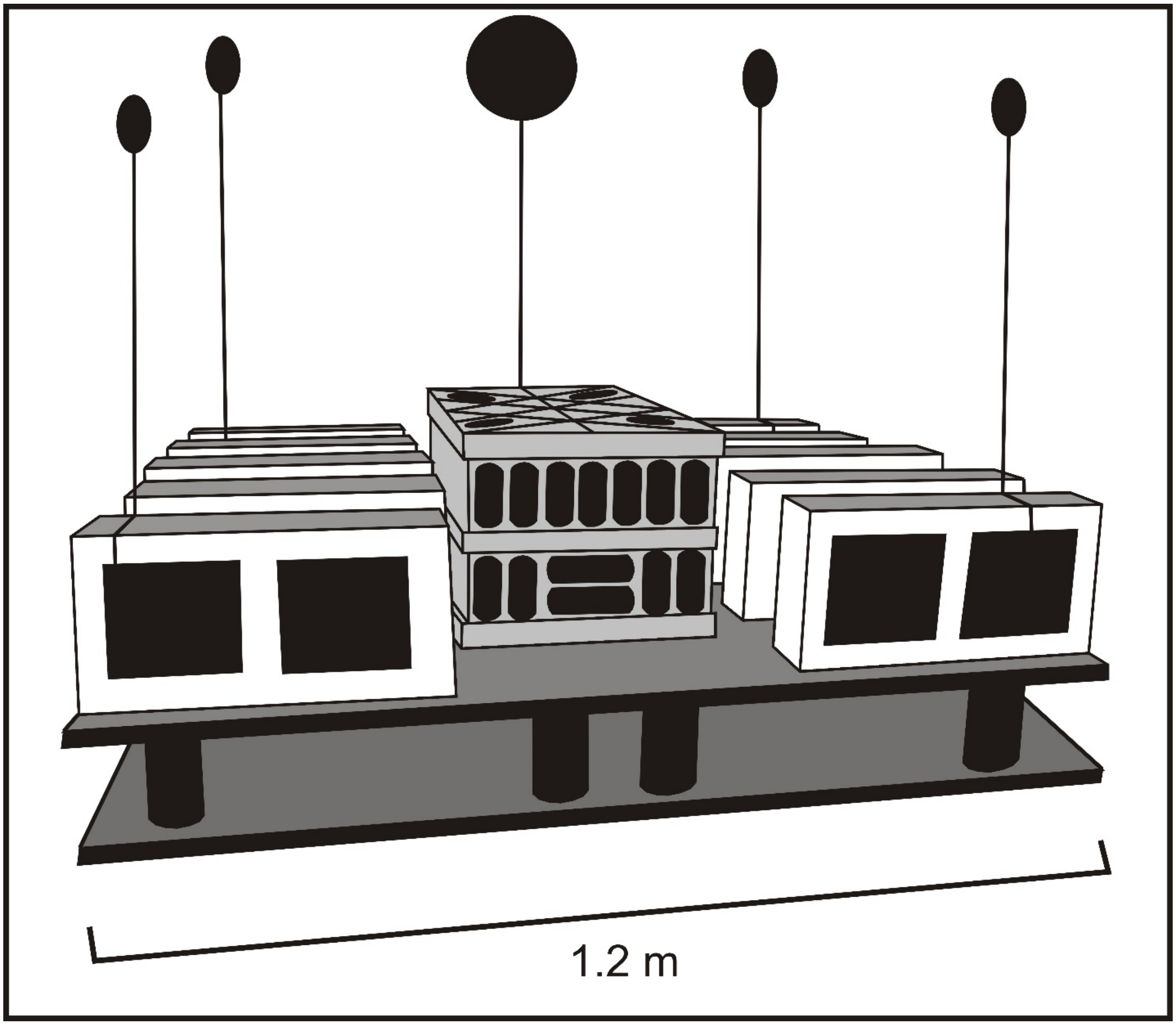
Figure 11. Mean density ± SE of the 2010 year-class (age-1 in 2011) of gray triggerfish on patch-reefs at the West, Center, and East sites for patch-reefs built in July 2011. Different letters indicate significant differences (*p* d 0.05).

Figure 12. Mean density ± SE of the 2015 year-class (age-0 in 2015, age-1 in 2016) of gray triggerfish on patch-reefs at the Center and 2015 East sites for patch-reefs built in July 2015. Different letters indicate significant differences (*p* d 0.05).

Figure 13. Mean density ± SE of the 2014 year-class (age-1 in 2015) of gray triggerfish on patch-reefs at the Center and 2015 East sites for patch-reefs built in July 2015. Different letters indicate significant differences (*p* d 0.05).

Figure 14. Mean density ± SE of the 2013 year-class (age-0 in 2013, age-1 in 2014) of gray triggerfish on patch-reefs deployed in June 2013 with no manipulation (Control Reefs), with all resident fish removed in July (All Removal), with only red snapper removed in July (RS Removal), and deployed in July with no manipulation (New Reefs). No significant differences were observed (*p* d 0.05).

Figure 15. Mean density ± SE of the 2012 year-class (age-1 in 2013) of gray triggerfish on patch-reefs deployed in June 2013 with no manipulation (Control Reefs), with all resident fish removed in July (All Removal), with only red snapper removed in July (RS Removal), and deployed in July with no manipulation (New Reefs). No significant differences were observed (*p* d 0.05).



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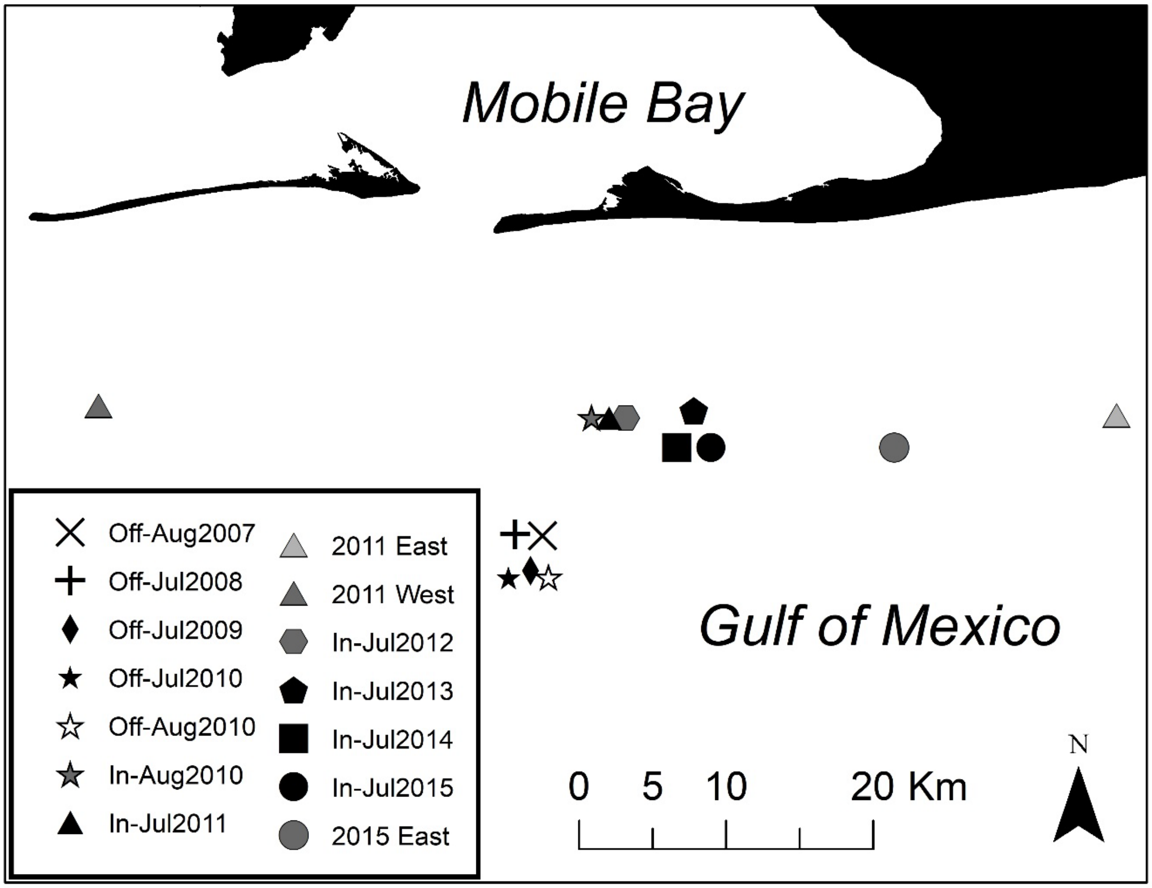

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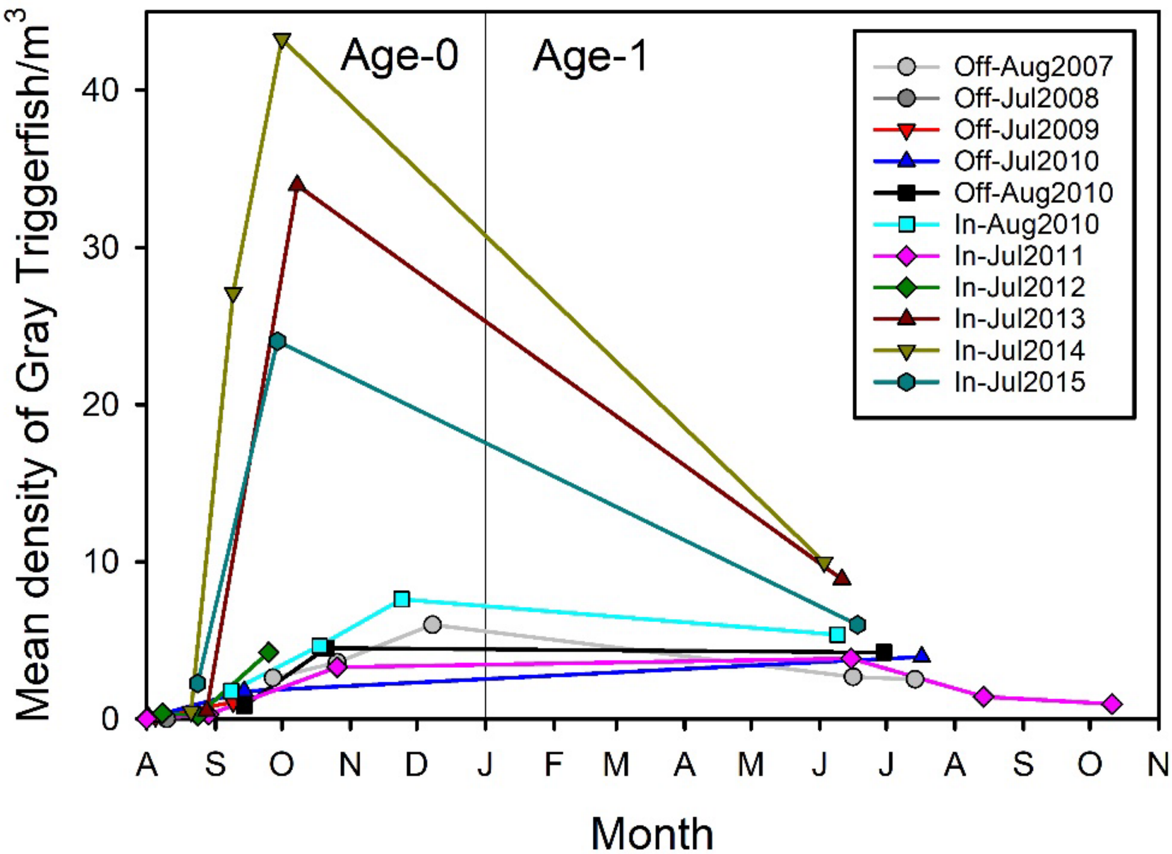

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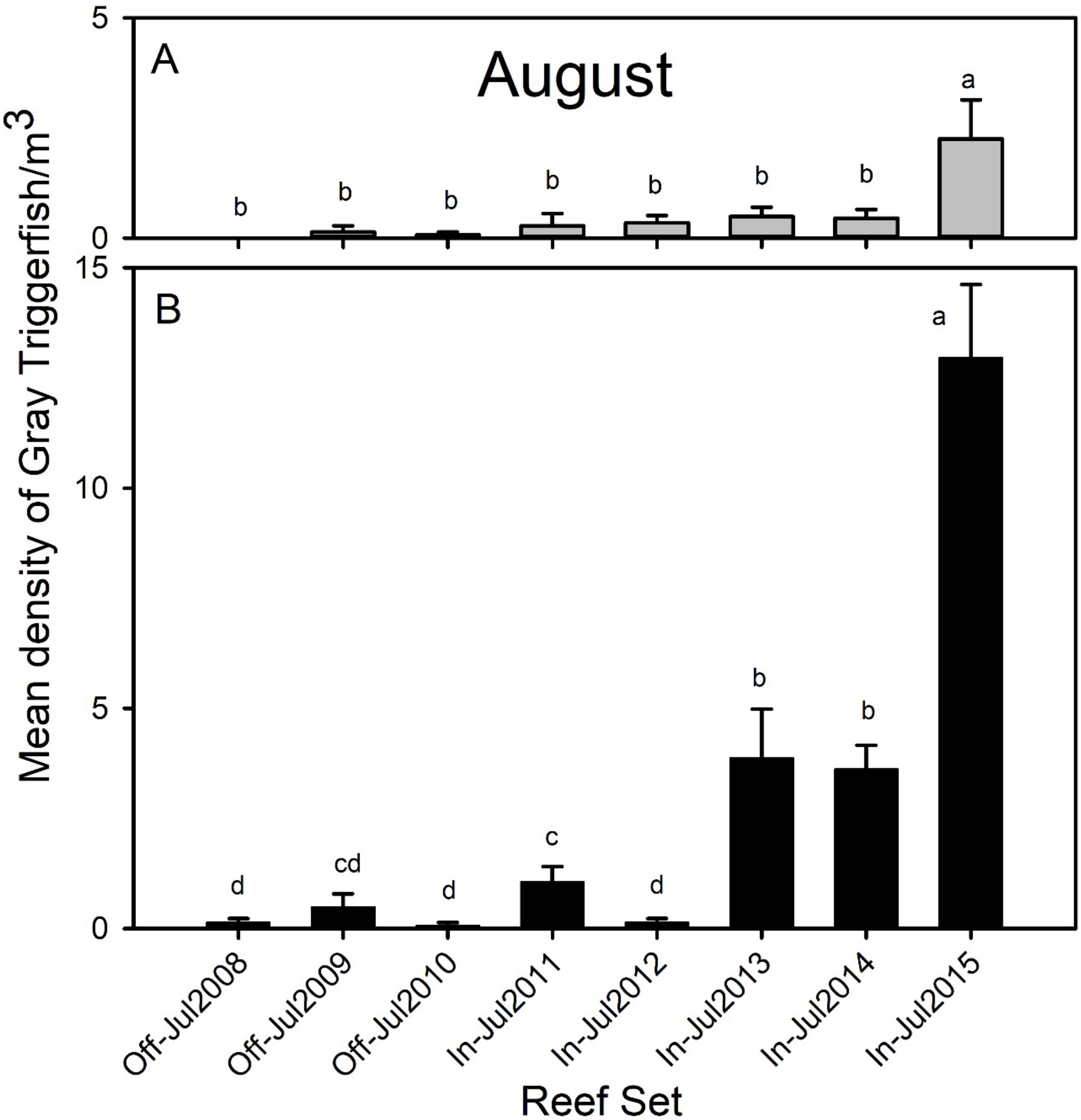

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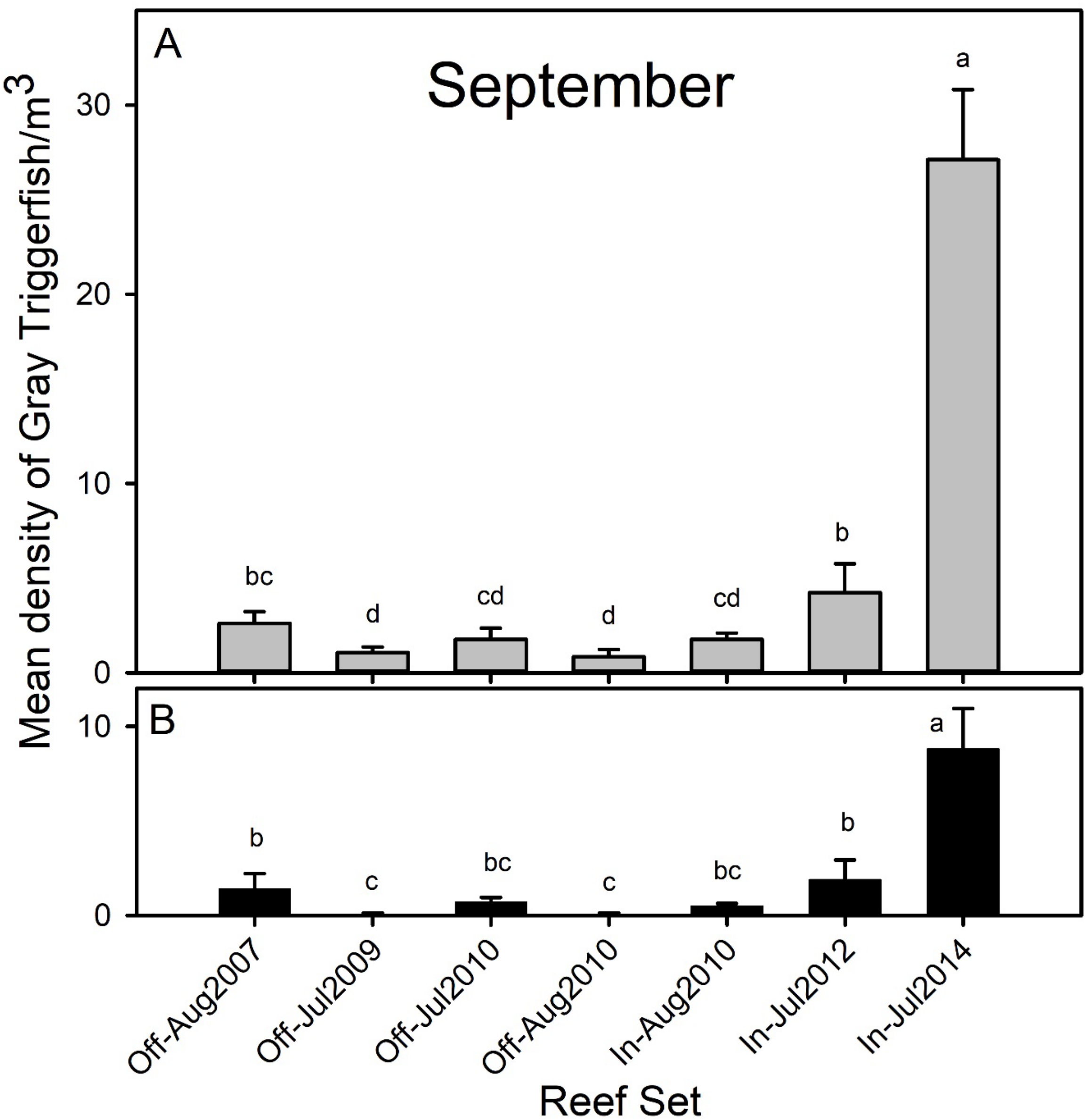

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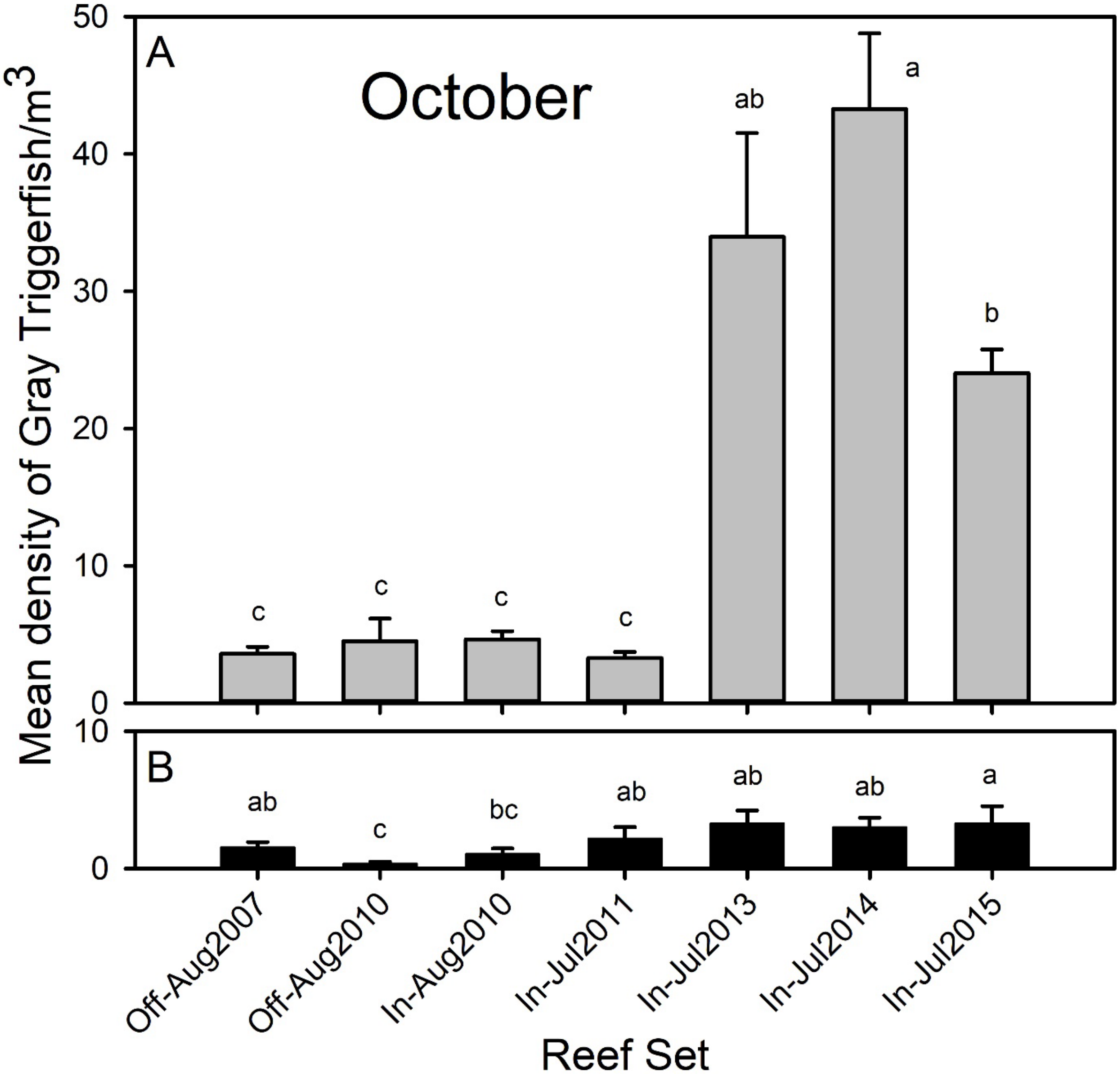

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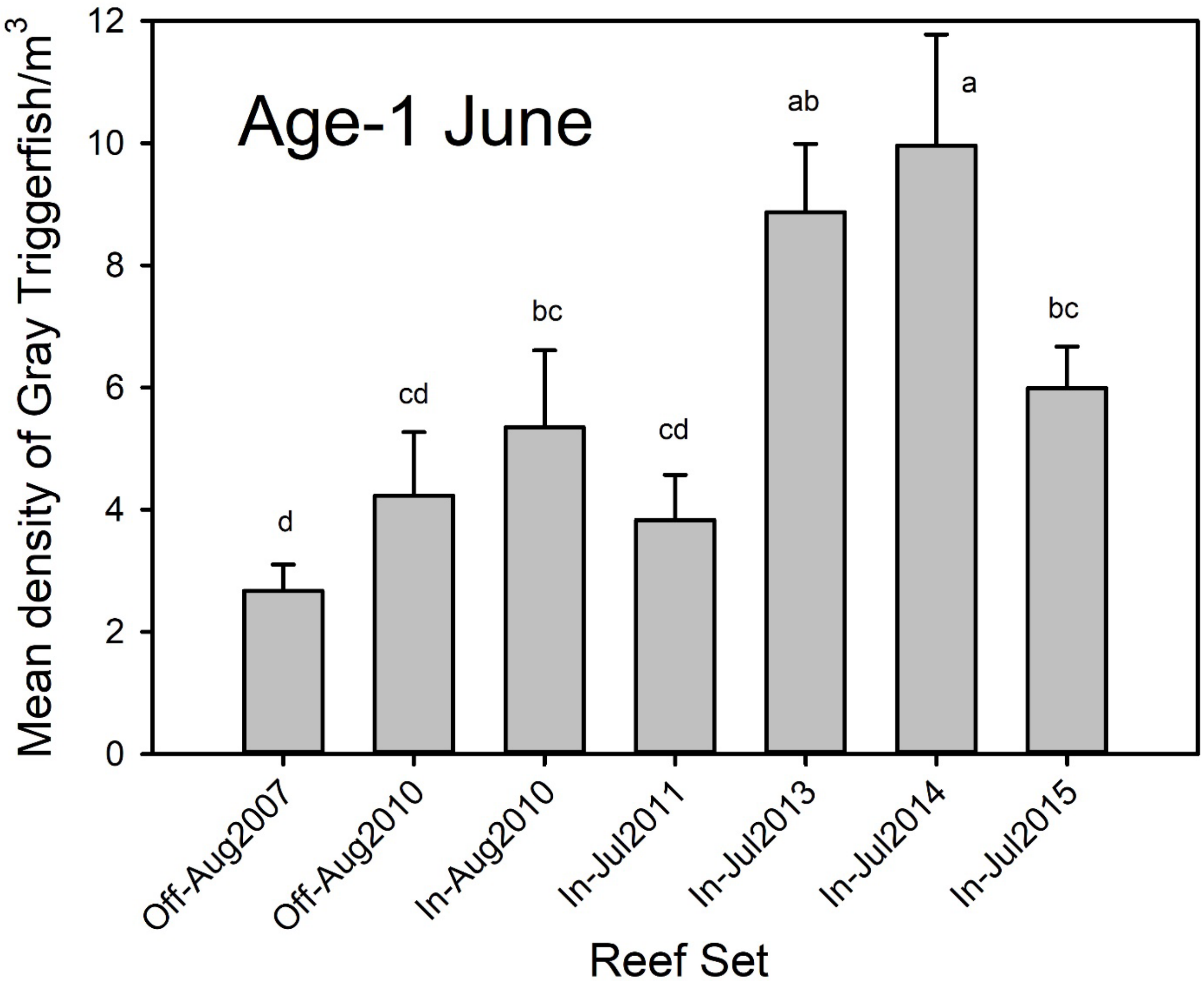

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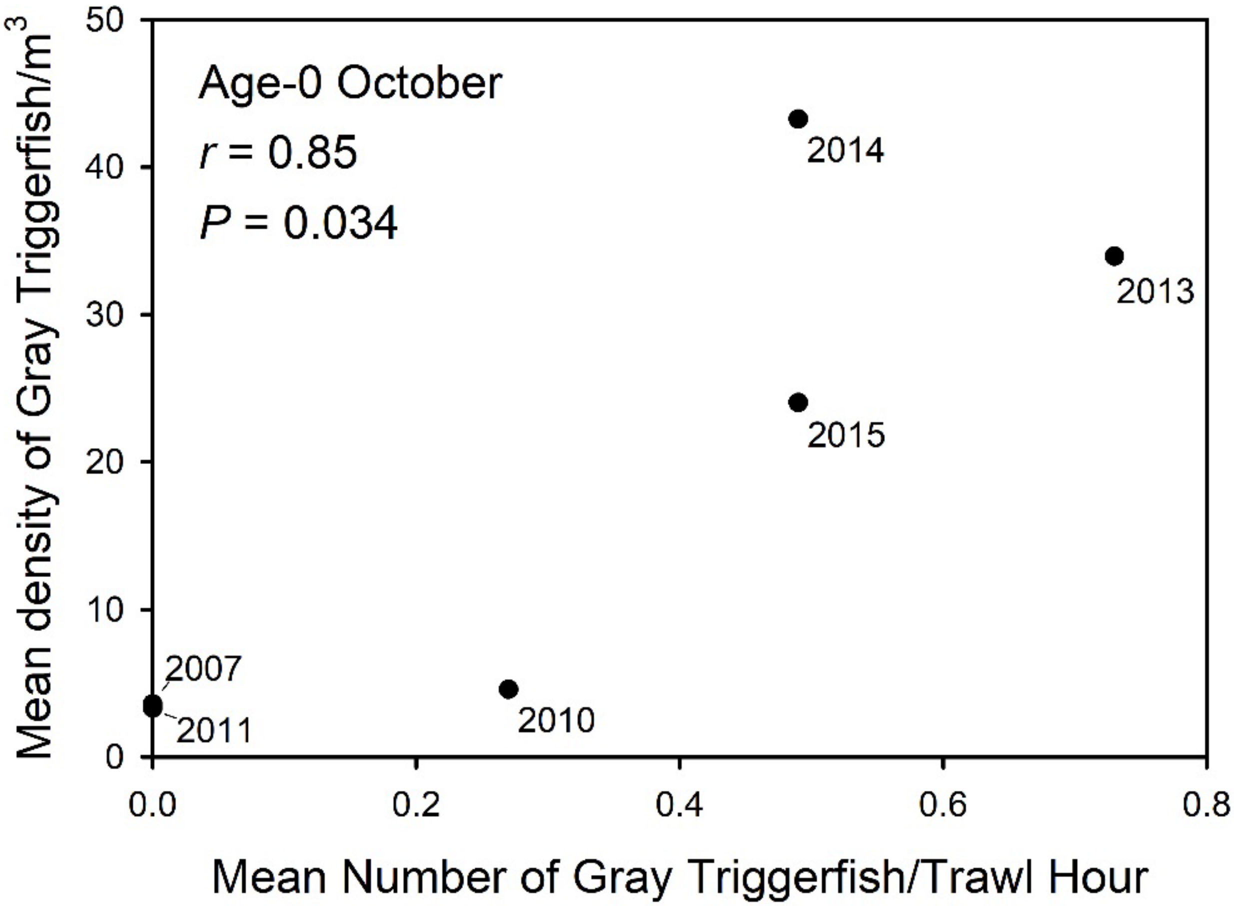

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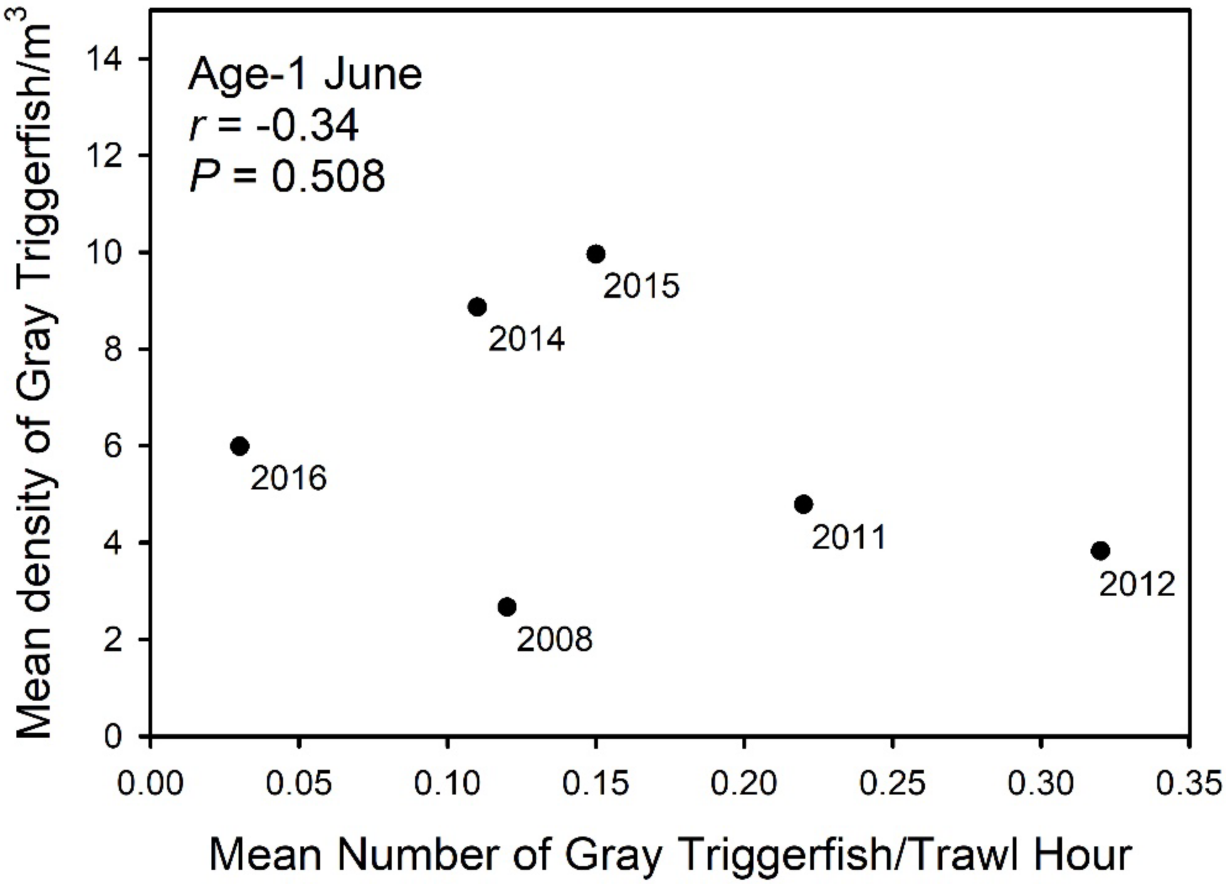

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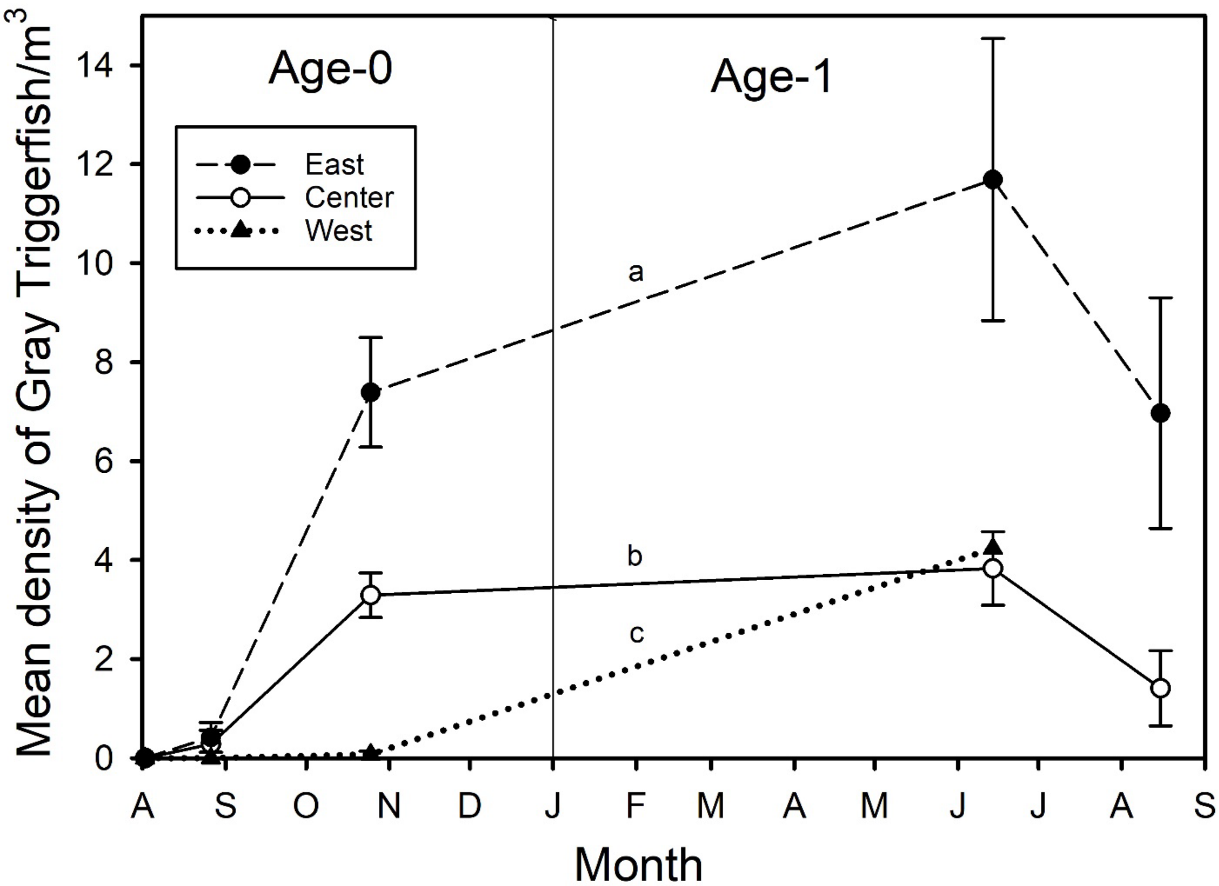

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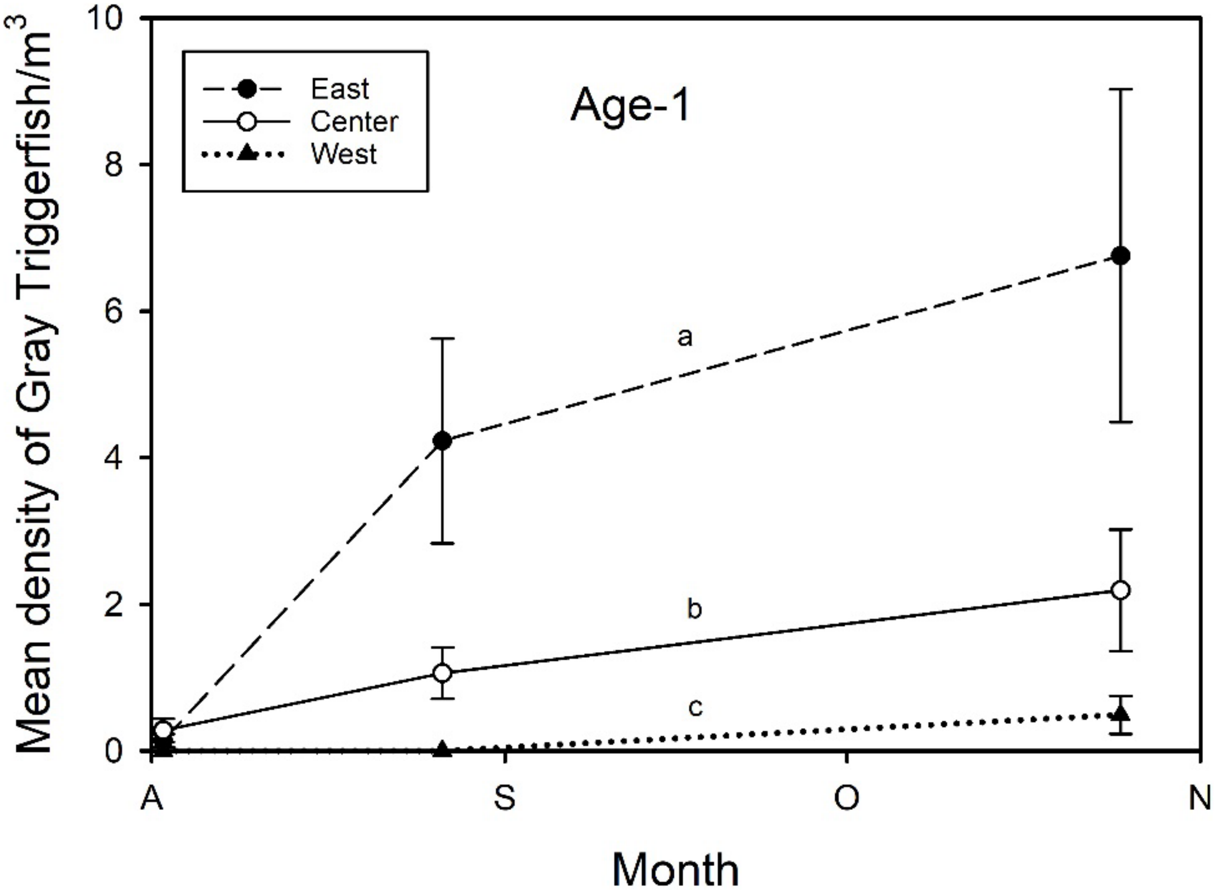

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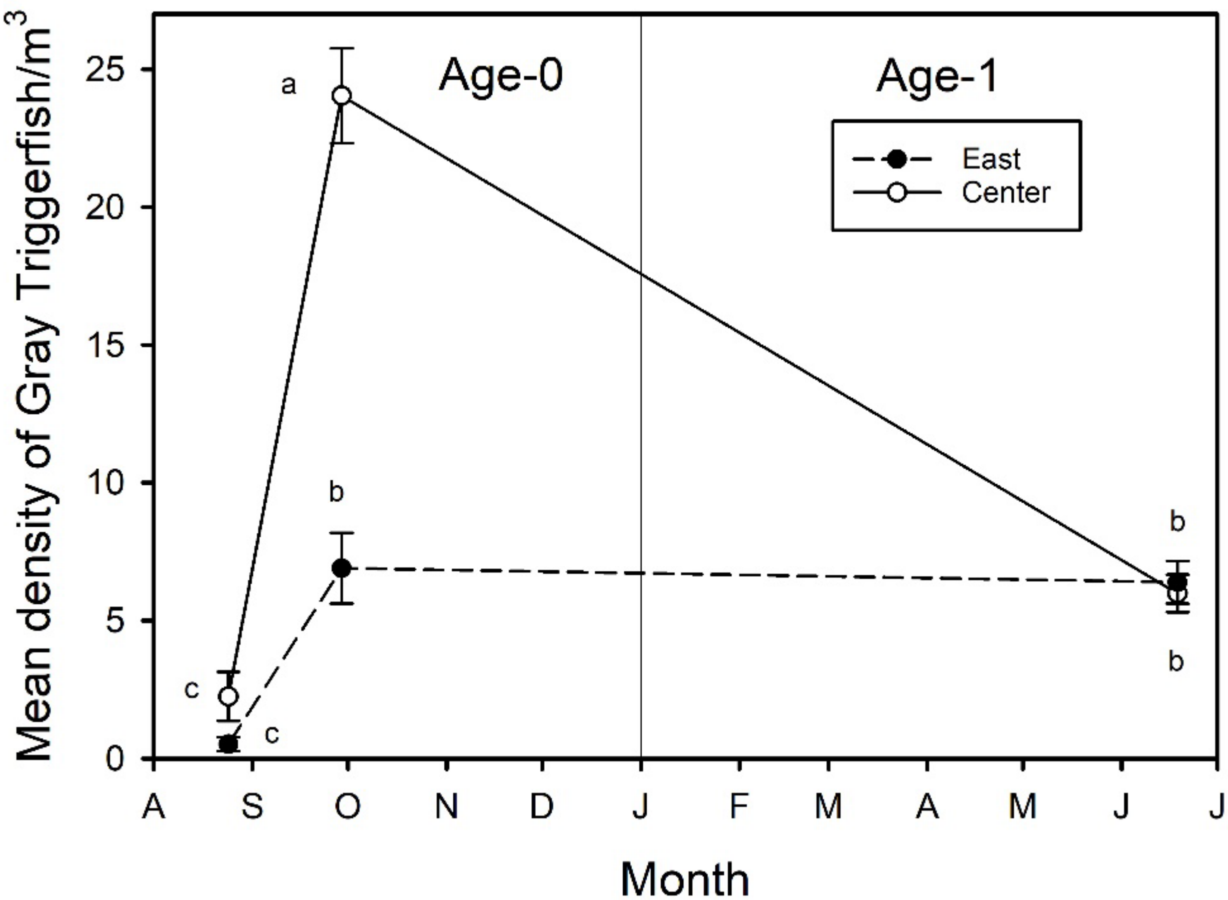
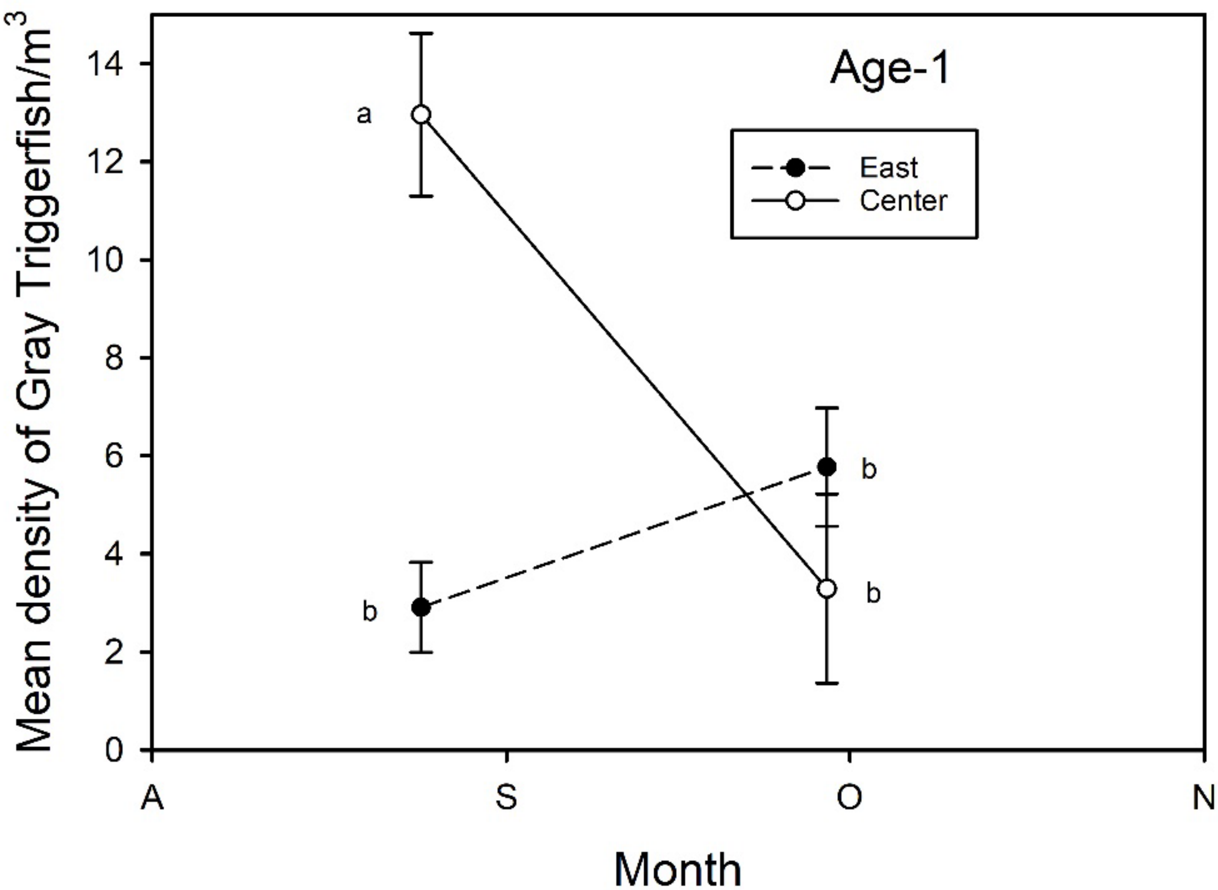


Figure 12. Mean density ± SE of the 2015 year-class (age-0 in 2015, age-1 in 2016) of gray triggerfish on patch-reefs at the Center and 2015 East sites for patch-reefs built in July 2015. Different letters indicate significant differences (p d 0.05).



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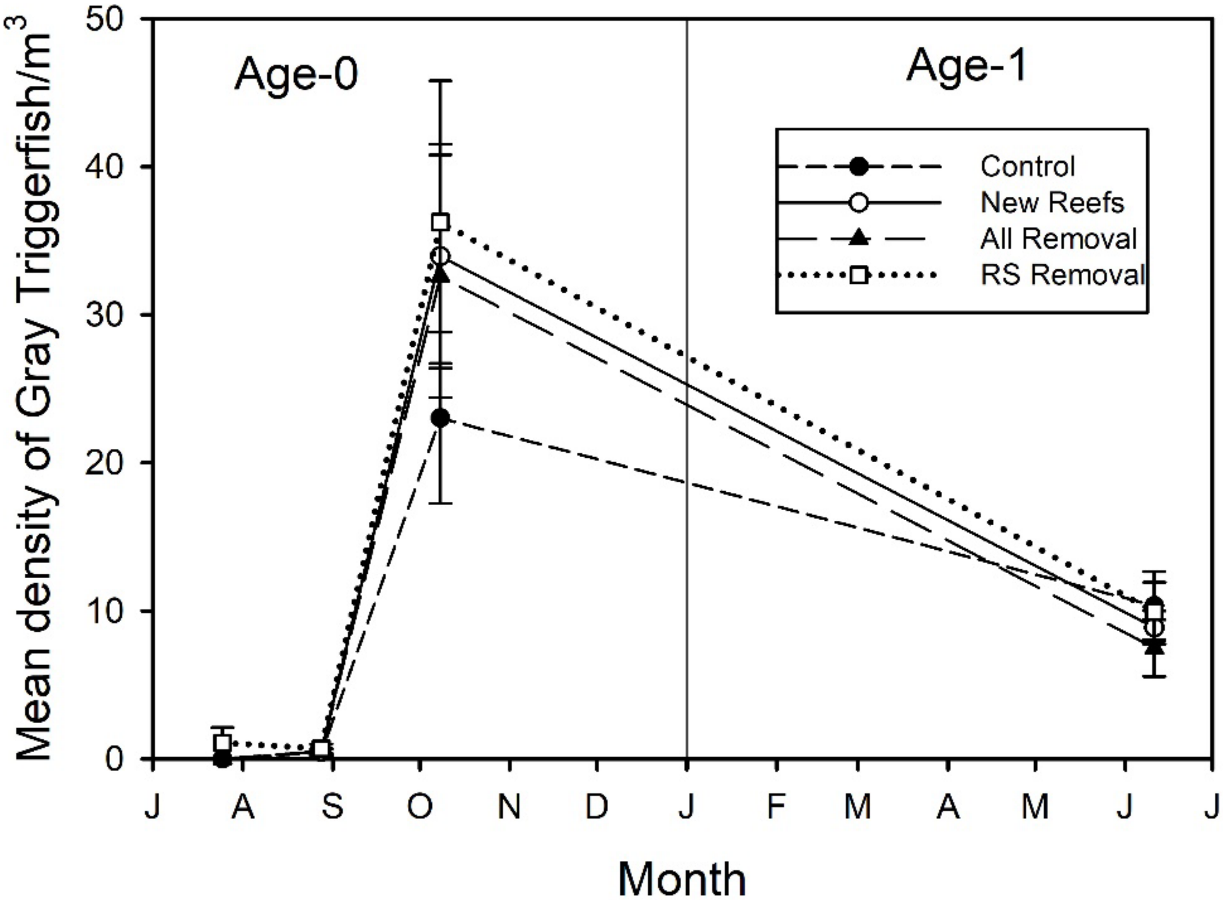

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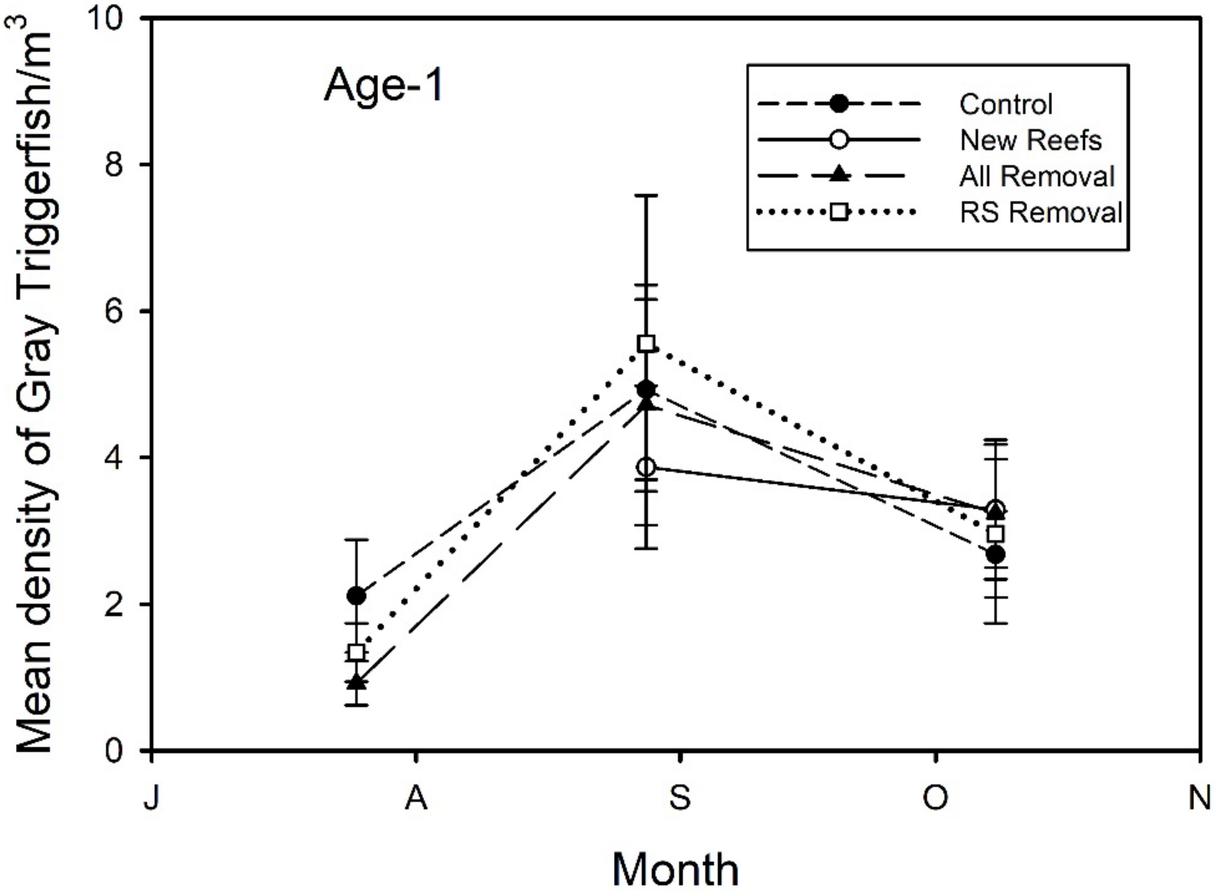

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