An analysis of early life history in vermilion snapper, *Rhomboplites aurorubens*, based on diver visual surveys of artificial patch-reefs.

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Abstract

Densities of age-0 and age-1 vermilion snapper, *Rhomboplites aurorubens*, were compared over a nine-year period (2007 to 2015), based on SCUBA visual estimates of densities on small (1.42 m^3) artificial reefs (patch-reefs) in the northern Gulf of Mexico. This time period included years both before and after the Deepwater Horizon oil spill in 2010 and provided an evaluation of the effect of the oil spill on this species. Densities of juvenile vermilion snapper on patch-reefs were also compared to catch (number caught/H) of juvenile vermilion snapper from trawl surveys by the Southeast Area Monitoring and Assessment Program (SEAMAP) that has been used as an index of juvenile density in the Gulf of Mexico. High densities of age-0 vermilion snapper in 2009, 2014, and 2015 on patch-reefs indicated years of higher potential year-classes of vermilion snapper. Vermilion snapper densities on patch-reefs were not significantly correlated with bottom temperature or sea surface temperature. The density of age-0 vermilion snapper at an offshore location in 2010 was similar to 2007 before the oil spill and for years after the oil spill. Vermilion snapper were less abundant at an inshore location based on their absence from patch-reefs in 2010, 2011, and 2012. We could not determine if these absences were the result of the 2010 oil spill or some other factor. Declines in densities of juvenile vermilion snapper over winter suggested high natural mortality rates ($M = 3.87$) and there were no indications of density dependence for this species. We did not detect a predation or competitive effect by resident fishes as there were no significant differences in juvenile vermilion sapper densities on reefs that were near (15 m) or far (500 m) from larger reef structure. In 2011, vermilion snapper were present on patch-reefs deployed at an east site and absent on patch-reefs deployed at a center site and a west site. Experimental removals of red snapper and other reef fishes in 2013, did not affect juvenile vermilion snapper densities. No

significant relation was detected between age-0 and age-1 densities of vermilion snapper. This indicated that age-0 vermilion snapper were not affected by the presence of older conspecifics, or that age-1 vermilion snapper densities in the present study were too low to influence age-0 densities. There was a significant positive correlation between the densities of juvenile (age-0 and age-1) vermilion snapper and red snapper, *Lutjanus campechanus*, in September, and between age-0 vermilion snapper density and the densities of age-0 tomtate, *Haemulon aurolineatum*, and other reef fishes in October. In 2015, there were higher densities of age-0 vermilion snapper on patch-reefs located farther to the east, but it was not determined if this difference was caused by lower initial densities of other resident reef fishes at the east site, or by the location of the patch-reefs. There was a significant correlation between the density of age-0 vermilion snapper on patch-reefs in October and catch-per-unit-effort (CPUE = catch/H) of vermilion snapper from SEAMAP fall trawl surveys east of the Mississippi River. However, in June there was no significant correlation between the density of age-1 vermilion snapper on patch-reefs and CPUE from SEAMAP summer trawl surveys. The visual survey methods of patch-reefs yielded significantly different estimates of densities and size of juvenile vermilion snapper when compared to samples taken with drop-net and rotenone. However, the error in size estimation was small and individuals were still assigned to the correct age class from visual surveys. The patch-reef surveys used in this study have potential for use in developing indexes of juvenile vermilion snapper abundance. However, further validations are needed of diver visual estimates of juvenile vermilion snapper on patch-reefs by comparisons with other methods before this method is widely applied.

Introduction

Vermilion snapper support both commercial and recreational fisheries in the Gulf of Mexico. Presently, vermilion snapper are not considered overfished and are not undergoing overfishing (SEDAR-67 2020). However, vermilion snapper stocks may experience higher fishing mortality as restrictions on other reef fish species cause fishers to target vermilion snapper as an alternative (Schirripa 2000; Moncrief et al. 2018). Vermilion snapper are also preyed upon by reef fish such as red snapper and greater amberjack, *Seriola dumerili* (Manooch and Haimovici 1983; Szedlmayer and Brewton 2020). It is possible that vermilion snapper stocks could decline as stocks of their predators recover. Therefore, it is important to monitor vermilion snapper stocks to ensure they remain healthy as these potential sources of mortality increase.

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 portion of the fishery. The open nature and large size of marine nursery habitats make accurate measurement of juvenile fish density difficult. Accurately predicting year-class strength could allow quotas to be increased when it can be anticipated that larger 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 vermilion snapper in stock assessments are based on trawl surveys (SEDAR-67 2020). However, if juvenile vermilion snapper reside on structured habitat, trawl sampling may be an ineffective sampling technique for this species. Therefore, other survey methods may be more appropriate for determining the density of juvenile vermilion snapper 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 ecological questions. Recently, several studies have used artificial patch-reefs to evaluate different aspects of juvenile red snapper and gray triggerfish biology (Simmons and Szedlmayer 2011; Mudrak and Szedlmayer 2012, 2020a; Szedlmayer and Mudrak 2014). These studies deployed patch-reefs with identical designs, in the same general area, and at similar time periods each year from 2007 to 2015.

The objective of the present study was to re-examine these patch-reef visual surveys to evaluate interannual differences in juvenile vermilion snapper density. This re-examination will produce a measure of density each year that can be used as an index of abundance, for inclusion in vermilion snapper stock assessment efforts. Based on these visual surveys we can estimate natural mortality rates, which are important for modeling vermilion snapper population dynamics. Annual densities will be compared with catch-per-unit-effort (CPUE) from SEAMAP trawl surveys presently used as an index of juvenile vermilion snapper abundance. These annual densities from patch-reefs will also be compared to both sea surface and bottom temperature. We will also compare juvenile vermilion snapper densities to the densities of older conspecifics and other reef fishes. In addition, because data are available for years both before and after the 2010 Deepwater Horizon oil spill, we will assess possible effects of this oil spill on juvenile vermilion snapper densities. Finally, we will examine the effects of patch-reef location, distance from larger reef structure, and the densities of red snapper and other reef fishes on vermilion snapper densities that could potentially yield further insights into the early life history of vermilion snapper.

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. Small plastic floats (5.1 × 12.7 cm) were attached to each of the four corners, and a larger float (15.2-cm diameter) was attached to the center of each patch-reef. All floats were attached 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 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 and estimated sizes in 25-mm total length (TL) intervals. Divers held a stationary position 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 varied and were not measured, and all densities were calculated as density per m^3 reef size. However, diver visibility typically exceeded the 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 surveys were discontinued. 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 in the analysis. The age of vermilion snapper observed was estimated based on TL as determined by a two factor Von Bertalanffy growth equation reported by Moncrief et al. (2018). All vermilion snapper greater than 279 mm TL were considered age-2 or older. Vermilion snapper were considered age-0 in May, June, and July when less than 76 mm TL, in August when less than 102 mm TL, in September when less than 127 mm TL, and in October, November, and December when less than 152 mm TL. No surveys were conducted in January, February, March, or 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 environmental measurement was taken at a reef site during a survey, we used the mean values temperature, salinity, and dissolved oxygen for analyses. Temperature ranged from 22.9 to 30.0 °C, salinity from 29.0 to 36.2 ppt and dissolved oxygen (DO) from 2.0 to 6.5 ppm (Table 1).

Annual comparisons

The densities (number of fish/m^3 of patch-reef size) of age-0 and age-1 vermilion snapper 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 vermilion snapper per survey was used for annual comparisons of juvenile fish densities. In 2008, all patch-reefs were lost after Hurricane Gustav (1 September 2008). In 2009, patch-reefs were lost or damaged after Hurricane Ida (10 November 2009). In 2011, one patch-reef was lost after tropical storm Lee (4 September 2011), and in 2012 four patch-reefs were lost 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 data allowed comparisons of vermilion snapper densities among years in four months (Table 2). The density of vermilion snapper observed in August included data 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 for 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). Vermilion snapper densities from these three reef sets in 2010 were analyzed separately when comparing the effect of interannual differences in density, because differences in location and deployment date could be associated with differences in the density of vermilion snapper (Szedlmayer and Mudrak 2014). All reef sets after 2010 were deployed at the inshore study location (Figure 2).

Age-0 and age-1 vermilion snapper interactions

We compared the densities of age-0 and age-1 vermilion snapper 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 no age-0 vermilion snapper were observed.

Interactions with other species

Densities of vermilion snapper were compared to the density of other reef fish species residing on unmanipulated patch-reef. For August, September, and October, we used partial correlations to compare the density of juvenile (age-0 and age-1) vermilion snapper 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 all vermilion snapper with the density all red snapper with the effects of other reef fish 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 that were observed but not included in patch-reef density 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*.

In August, September, and October, we used partial correlations to compare the density of juvenile vermilion snapper to the density of juvenile tomtate, *Haemulon aurolineatum*, with the effect of other reef fish removed. Other reef fish was defined here as all fish counted in visual surveys except for tomtate and open habitat or pelagic species. In June, the density of all age classes of vermilion snapper and tomtate were compared with the effect of all other reef fish removed. The June survey was before recruitment of age-0 individuals of either species to the patch-reefs. Age-0 tomtate were defined as individuals less than 102 mm in August, September, and October based on a Von Bertalanffy growth curve relation (Norberg 2015).

In August, September, October, and June we used correlation analysis to compare the density of juvenile vermilion snapper to the total density of all other reef fish. Other reef fish was defined here as all fish counted in visual surveys except red snapper, vermilion snapper and open habitat or pelagic species.

Environmental correlations

Bottom temperature was 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 vermilion snapper densities each month, and age-1 vermilion snapper densities in June, we used the mean of all bottom or sea surface temperatures for each month.

Mortality estimates

We used density estimates of vermilion snapper 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 for mortality estimates. In addition to the offshore and inshore locations, this included reefs located at the West, East and 2015 East sites (Figure 2). To be used in mortality estimates, the patch-reef needed a fall visual survey and a visual survey the next summer. A total of 127 patch-reefs fit these criteria. The highest density of age-0 vermilion snapper observed on individual patch-reefs in the fall were used to calculate a mean density of age-0 vermilion snapper each year. The first survey of these same patch-reefs the next summer was used to calculate a mean density of age-1 vermilion snapper. Survival (S) was calculated as the mean density of age-1 vermilion snapper on patch-reefs in the summer divided by the mean density of age-0 vermilion snapper observed the previous fall for each year. Total instantaneous mortality (Z), was calculated as $Z = -\ln(S^{(365/t)})$, were t = the mean number of days between the fall and summer surveys for each particular year. Mean Z was calculated as the mean of the annual mortalities observed each year. However, in 2011 and 2013 mean densities of vermilion snapper increased over winter causing annual survival rates greater than one. Therefore, Z estimates from 2011 and 2013 were undefined and not included in further analyses.

Comparison to SEAMAP trawl surveys

The densities of vermilion snapper from diver visual surveys of patch-reefs were compared to the catch-per-unit-effort (CPUE = catch/H) of vermilion snapper 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 trawl surveys that were taken east of the Mississippi River (> - 89° W). Most vermilion snapper collected by trawl were measured by fork length (mm FL), and these were converted to TL with the equation TL = 1.128 × FL – 2.112 (Moncrief et al. 2018). We applied the same TL to age relation that was used to estimate age for fish from patch-reefs, to estimate age from length for vermilion snapper collected by trawl. The mean CPUE of age-0 vermilion snapper from October trawls was compared to the mean density estimates of age-0 vermilion snapper on patch-reefs in October. The mean CPUE of age-1 vermilion snapper from June trawls was compared to the mean density estimates of age-1 vermilion snapper on patch-reefs in June. For the comparison of trawl CPUE to patch-reef surveys in 2010, we used a mean density of juvenile vermilion snapper derived from both the Off-Aug2010 and In-Aug2010 reef sets.

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 larger steel cage artificial reefs (2.5 x 1.3 x 2.4 m) and 10 patch-reefs at a distance of 500 m (Far) from 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, which allowed for comparisons of juvenile vermilion snapper densities on patch-reefs in areas used by predators and competitors to densities on patch-reefs away from known sources of predators and competitors. One Near patch-reef in August 2009 had densities of age-0 vermilion snapper too large for divers to count. For this patch-reef, photographs were used to estimate densities of age-0 vermilion snapper. All age-0 fish were counted in a subsampled portion of the photo and extrapolated to estimate the total number of fish in the photo. A second close-up photo of the patch-reef was used to estimate the proportion of vermilion snapper among the identifiable fish.

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 2011 patch-reef sets were deployed and surveyed at similar times and allowed for comparisons of juvenile vermilion snapper densities at larger spatial scales. Over the winter, eight patch-reefs were lost at the West site, possibly due to shrimp trawling. Therefore, the density estimates of vermilion snapper on the remaining two patch-reefs at the West site were not used for analysis in June due to low sample size. This deployment of East, Center, and West patch-reefs 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). 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 of the center site patch-reefs allowed for comparisons of vermilion snapper 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 vermilion snapper 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 Removed). 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 vermilion snapper.

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 for analysis. 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 density and size of vermilion snapper on patch-reefs.

Statistical analysis

Annual densities of juvenile vermilion snapper 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). Due to the many zero density counts on patch-reefs, one was added to the vermilion snapper density on all patch-reefs being compared. If significant differences were detected among densities, specific differences were identified with a Tukey multiple comparison test (Zar 2010). In our statistical analyses, annual comparisons of mean densities were analyzed with separate tests for August, September, October, and June (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 design (RM).

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 vermilion snapper, and to compare vermilion snapper densities with temperature. In addition, to determine if density dependent mechanisms were occurring, we compared mean age-0 vermilion snapper densities in the fall to total mortality (Z) each year. Partial correlation was used to compare densities of vermilion snapper, 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 vermilion snapper density on patch-reefs

The density of age-0 vermilion snapper observed on small artificial patch-reefs in the fall varied among years, and few age-1 vermilion snapper remained on patch-reefs the following summer (Figure 3). The density of age-0 vermilion snapper was significantly different among years in August ($F_{9,99} = 8.29$, $P < 0.001$; Figure 4), September ($F_{6,63} = 13.7$, $P < 0.001$; Figure 5), and October ($F_{6,70} = 17.2$, $P < 0.001$; Figure 6). The density of age-1 vermilion snapper was not significantly different among years in August ($F_{79,99} = 0.22$, $P = 0.991$; Figure 4) or September ($F_{6,63} = 1.26$, $P = 0.287$; Figure 5). There were significant differences in age-1 vermilion snapper densities among years in October ($F_{6,70}$ = 2.94, P = 0.013; Figure 6), and in June ($F_{6,84}$ = 5.92, P < 0.001; Figure 7).

Age-0 and age-1 vermilion snapper

There were no significant correlations between age-0 and age-1 vermilion snapper densities in August (r = -0.01, P = 0.935, N = 89 patch-reefs), September (r = -0.04, P = 0.749, N = 70 patch-reefs) or October (r = -0.03, P = 0.766, 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 (17.9%), pigfish, *Orthopristis chrysoptera*, (12.1%), gray triggerfish (11.5%), vermilion snapper (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%).

Juvenile (age-0 and age-1) vermilion snapper density was not significantly correlated with juvenile red snapper density in August (r = -0.087, P = 0.369, N = 109 patch-reefs), or October (r = -0.08, P = 0.517, N = 77 patch-reefs). There was a significant correlation between juvenile vermilion snapper densities and juvenile red snapper densities in September (r = 0.28, P = 0.020, N = 70 patch-reefs). The density of all vermilion snapper was not significantly correlated with the density of all red snapper in June (r = 0.04, P = 0.703, N = 91 patch-reefs).

Juvenile vermilion snapper density was not significantly correlated with juvenile tomtate density in August (r = -0.01, P = 0.907, N = 109 patch-reefs), or September (r = 0.02, P = 0.862, N = 70 patch-reefs). There was a significant correlation between juvenile vermilion snapper and juvenile tomtate densities in October (r = 0.38, P < 0.001, N = 77 patch-reefs). The density of all vermilion snapper was not significantly correlated with the density of all tomtate in June (r = -0.02, P = 0.832, N = 91 patch-reefs).

The density of juvenile vermilion snapper was not significantly correlated with total reef fish density in August (r = -0.08, P = 0.434, N = 109 patch-reefs), or September (r = -0.06, P = 0.649, N = 70 patch-reefs). There was a significant correlation between juvenile vermilion snapper density and total reef fish density in October (r = 0.42, P < 0.001, N = 77 patch-reefs). The density of all vermilion snapper density was not significantly correlated with total reef fish density in June (r = 0.016, P = 0.879, N = 91 patch-reefs).

Environmental conditions

Bottom temperature data were available for most of the present study except November 2008 – September 2010. There were no significant correlations between bottom temperature and age-0 vermilion snapper density in August (r = 0.25, P = 0.631, N = 6), September (r = -0.40, P = 0.735, N = 3), or October (r = 0.05, P = 0.922, N = 6). There was no significant correlation between bottom temperature and age-1 vermilion snapper density in June (r = 0.50, P = 0.314, N = 6).

Sea surface temperature data were available for all years beginning in 2009. There was no significant correlation between monthly mean sea surface temperature and age-0 vermilion snapper density in August (r = -0.47, P = 0.291, N = 7), September (r = -0.25, P = 0.754, N = 4), or October (r = -0.10, P = 0.867, N = 5), or between monthly mean sea surface temperature and mean age-1 vermilion snapper density in June (r = -0.75, P = 0.146, N = 5).

Mortality

Among the patch-reefs deployed in July or August that did not have fish experimentally added or removed, there were 127 patch-reefs that were surveyed both in the fall and the following summer. The time between the fall survey with the highest mean age-0 vermilion snapper density and the first survey the next summer ranged from 189 to 353 days with a mean of 263 days between surveys. Vermilion snapper densities increased over winter in 2011 and 2013, and mortality rates were not estimated. Mortality (Z) in years with observed declines in density ranged from a low of Z = 2.69 in 2014 to a high of Z = 4.76 in 2010 (Table 3). There was no significant relation between mean age-0 vermilion snapper density each fall and Z for that year (r = 0.464, P = 0.3537, N = 6).

Comparison to SEMAP trawl surveys

There was a significant positive correlation between mean age-0 vermilion snapper densities on patch-reefs and mean CPUE in SEMAP trawl surveys each October (r = 0.93, P = 0.008; Table 4; Figure 8). There was no significant correlation between age-1 vermilion snapper densities on patch-reefs and CPUE in SEMAP trawl surveys in June (r = -0.17, P = 0.748; Table 4; Figure 9).

Distance from Larger Reef Structure

There was no significant difference in age-0 vermilion snapper densities on patch-reefs that were Near or Far from larger reef structure in August (mean ± SE; Near = 39.72 ± 38.90, *N* = 30; Far = 3.62 ± 3.52, *N* = 30) or September (Near = 51.37 ± 35.69, N = 20; Far = 51.37 ± 35.24, *N*= 20), and this pattern persisted with age-1 densities the following July (Near = 0, *N* = 5; Far = 0.14 ± 0.14, *N* = 5; RM $F_{1,58}$ = 0.44, $P < 0.512$). There was no significant difference in age-1 vermilion snapper densities on patch-reefs that were Near or Far from larger reef structure in August (Near = 0.02 ± 0.02, *N* = 30; Far = 0.16 ± 0.12, *N* = 30), or in September (Near = 0.14 ± 0.08, *N* = 20; Far = 0.11 ± 0.08, *N* = 20, RM $F_{1,58}$ = 1.04, $P = 0.312$).

Spatial distribution of reefs

Densities of the 2011 year class (age-0 in 2011, age-1 in 2012) of vermilion snapper on patch-reefs deployed in 2011were significantly different among locations, with the highest densities at the East site, and no vermilion snapper present at the Center or West sites (RM $F_{2,27}$ = 50.9, $P < 0.001$; Figure10). Densities of the 2010 year class (age-1 in 2011) of vermilion snapper on patch-reefs deployed in 2011were were not significantly different among locations (RM $F_{2,27}$ = 3.1, $P = 0.061$; Figure 11).

2015 spatial distribution

Densities of the 2015 year class (age-0 in 2015, age-1 in 2016) of vermilion snapper on patch-reefs deployed in 2015 were significantly different among locations ($F_{1,28}$ = 62.6, $P <$ 0.001), time ($F_{2,55}$ = 10.7, $P <$ 0.001), and location x time interaction ($F_{2,55}$ = 6.28, P = 0.004; Figure 12). Age-0 vermilion snapper densities were significantly higher on the 2015 East site compared to the center site and remained higher the following year in June (Figure 12). Densities of the 2014 year class (age-1 in 2015) of vermilion snapper on patch-reefs deployed in 2015 were significantly affected by location ($F_{1,28}$ = 53.8, $P <$ 0.001), and time ($F_{1,28}$ = 9.26, P = 0.005), but not by a location x time interaction ($F_{1,28}$ = 3.7, P = 0.066, Figure 13).

Removal experiment

Densities of the 2013 year class (age-0 in 2013, age-1 in 2014) of vermilion snapper on patch-reefs deployed in 2013 were not significantly affected by removal treatments (RM $F_{3,36}$ = 0.27, P = 0.843; Figure 14). There was also no significant difference in densities of the 2012 year-class (age-1 in 2013) of vermilion snapper on the 2013 patch-reefs (RM $F_{3,36}$ = 0.14, P = 0.938; Figure 15).

Drop-net-rotenone sampling

Among the 14 patch-reefs that were surveyed visually and with drop-net-rotenone collections, 10 had at least one vermilion snapper detected by one or both survey methods, and all patch-reefs had less than 35 individuals detected by either method. Among the 10 patch-reefs with detected vermilion snapper, three had the same number of individuals for both methods (these three patch-reefs only had one individual present), four had counts that differed by one individual between the two methods, two differed by two individuals, and one differed by 10 individuals. A total of 59 vermilion snapper were counted in the visual survey, and 63 vermilion snapper were captured by drop-nets. Comparison of the 52 individuals detected by both methods indicated that 46 % ($N = 24$) had measured TL that matched the 25 mm size interval visually estimated by divers, 0 % had estimated size interval smaller than their measured length, and 54 % ($N = 28$) had visual estimates one interval larger than their measured length. A Fisher's exact test comparing the number of vermilion snapper observed in each of the 25 mm size intervals by each survey method was significantly different ($P < 0.001$). However, all visual size estimates assigned the same age as the measured length.

Discussion

Annual variation

There were significant differences detected among years for densities of age-0 vermilion snapper. Densities in August and September 2009 were higher than other years. Similarly, age-0 red snapper also showed high densities on patch-reefs in 2009 (Mudrak and Szedlmayer 2020). This indicates that in 2009 conditions were favorable for recruitment and survival for these two species. Also, densities in October 2014 and 2015 were significantly higher than most other years (except 2010). However, the factors that caused these high densities cannot be determined from the present study.

An important question in the present study was if juvenile vermilion snapper densities were affected by the 2010 Deepwater Horizon oil spill. Age-0 densities on the Off-Jul2010 and Off-Aug2010 patch-reefs were similar to densities on the Off-Aug2007 patch-reefs before the oil spill, and not statistically different from the In-Jul2013, In-Jul2014, and In-Jul2015 patch-reefs in some months. All surveys on the In-Aug2010, In-Jul2011, and In-Jul2012 patch-reefs observed a complete absence of juvenile vermilion snapper. However, mean densities of age-0 vermilion snapper on the Off-Jul2010 and Off-Aug2010 patch-reefs indicates that 2010 was not a year of complete year class failure. The absence of juvenile vermilion snapper on the In-Jul2010, In-Jul2011, and In-Jul2012 patch-reefs may be an indication of an oil spill effect, or it could be caused by patchy settlement of vermilion snapper in space and time. For example, it is possible that the offshore location offered better habitat or received more settlers than the inshore location. Similarly, in 2011 no age-0 vermilion snapper were observed at the Center site used in interannual comparisons, but low densities were observed on patch-reefs deployed farther to the east. These patterns make it difficult to determine if the low densities observed following the oil spill were caused by the spill, natural variability, or some other unknown variable.

Age-0 vermilion snapper appear to show different settlement patterns than the age-0 red snapper and gray triggerfish observed on these same patch-reefs. While red snapper and gray triggerfish densities did vary between years, they were consistently present each year of the study (Mudrak and Szedlmayer 2020; Szedlmayer and Mudrak 2022). Vermilion snapper had greater variability, with large schools present on some patch-reefs in some years, and complete absences in other years. Also, in contrast to red snapper and gray triggerfish, large schools of age-0 vermilion snapper were often observed on nearby larger reef structures. Age-0 red snapper and gray triggerfish typically seek out smaller structures where predation risk and competition are reduced, only moving to larger reef structure when larger sizes are obtained as age-1 or age-2 individuals (Gallaway et al. 2009; Mudrak and Szedlmayer 2012).

Conversely, there were no significant difference in juvenile vermilion snapper densities between patch reefs placed 15 m from larger reef structure, and the patch-reefs placed 500 m from larger reef structure (Mudrak and Szedlmayer 2012). In fact, there are some indications that vermilion snapper may prefer larger reef structures compared to the present study patch-reefs. For example, Szedlmayer and Brewton (2020) provided a photograph of a larger reef that contained such high densities of age-0 vermilion snapper that the actual reef structure was not visible. If vermilion snapper prefer to settle onto larger reefs such as those inhabited by adults, then patch-reefs may not be the best method to measure juvenile density as most recruits would reside on larger reefs, with patch-reefs only containing the spill over in years of exceptionally high densities. In addition, it is known that adult vermilion snapper prefer deeper water habitats compared to the patch-reef locations in the present study (Jaxion-Harm et al. 2018). If juvenile vermilion snapper have similar preferences future research should examine reefs at deeper depths for newly settled vermilion snapper.

Densities of age-1 vermilion snapper were low in the June surveys. This indicates that these fish either suffered high mortality rates, with few individuals surviving over the winter, or that vermilion snapper had emigrated from patch-reefs in search of larger reefs by June. Either way, this represents a difference in life history between juvenile vermilion snapper and juvenile red snapper and gray triggerfish. If vermilion snapper had emigrated rather than suffering mortality, this would be a difference in behavior compared to red snapper and gray triggerfish that had high densities of age-1 individuals on patch-reefs in June (Mudrak and Szedlmayer

2020; Szedlmayer and Mudrak 2022). If the decline is in fact caused by mortality, then the mortality rate for juvenile vermilion snapper is higher than other fish residing on the patch-reefs.

Divers often had difficulty in counting vermilion snapper, as small age-0 vermilion snapper can be difficult to identify. This is especially true when they are mixed with age-0 tomtate and round scad as was often observed. Vermilion snapper also appeared to show diver avoidance, and many vermilion snapper were observed at the edge of visibility away from the patch-reef. Therefore, visual estimates may have underestimated vermilion snapper densities simply due to visibility.

Age-0 and age-1 vermilion snapper relations

There were no significant correlations between the density of age-0 and age-1 vermilion snapper in any of the months examined. This is in contrast to red snapper, which showed a negative correlation between age-0 and age-1 densities and gray triggerfish which showed a positive correlation between age-0 and age-1 densities on the patch-reefs examined here (Mudrak and Szedlmayer 2012, 2020a, 2020b; Szedlmayer and Mudrak 2014). It may be that vermilion snapper show no preference for or against habitat inhabited by older conspecifics, but the densities of age-1 vermilion snapper on patch-reefs were low in all months examined and it is possible that age-1 densities were not high enough to affect age-0 densities.

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 a large number of tests, some of which would be expected to be significant based on probability alone (type-I error), only correlations with red snapper and age-0 tomtate were analyzed. Red snapper was selected because they were the most abundant species on the patch-reefs and represented a potential competitor or predator of juvenile vermilion snapper. Also, as red snapper stocks recover, it is important to measure their effect on other reef fishes. Juvenile (age-0 and age-1) tomtate were selected for analysis based on observations of juvenile tomtate and vermilion snapper schooling together on the patch-reefs.

There was a significant positive correlation between juvenile red snapper and vermilion snapper in September. This likely resulted from exceptionally high densities of both species in September 2009 (Mudrak and Szedlmayer 2020). No other significant relations were detected between the two species. The positive correlation observed in September does not support a competitive exclusion effect by red snapper on vermilion snapper for these early life history stages, as vermilion snapper were able to colonize patch-reefs despite high densities of red snapper.

There was also a significant positive correlation between juvenile vermilion snapper and tomtate in October. This positive correlation along with positive correlations between vermilion snapper and other reef fishes (after excluding tomtate and red snapper) suggests that patch reefs with favorable conditions led to higher densities of all reef fish species in October. These patch-reefs may have had better food resources, or perhaps higher densities of resident fishes increases the likelihood that new recruits will locate such a patch-reef.

Mortality

In the present study we assumed that after patch-reefs reached maximum densities and declines in abundance were attributed to mortality rather than emigration. The mean density of vermilion snapper declined between the fall and the following summer for most years. However, in 2011 and 2013 densities increased from fall to summer and mortalities could not be estimated. This may possibly be explained by the overall low numbers of juvenile vermilion snapper in 2011 and 2013, where the immigration of 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 did not indicate density dependent mechanisms. Similar high mortality rates were observed in years of both higher and lower vermilion snapper densities. It is possible that density independent processes, such as recruitment drive vermilion snapper populations dynamics at the juvenile stage. It is also possible that densities of vermilion snapper observed on the present patch-reefs were too low to evaluate density dependent effects.

The observed mortality rate is reported as Z because it represents all sources of mortality. However, this could be assumed to represent M as these fish are below the minimum size limits for the directed fishery, and vermilion snapper are residing on small patch-reefs that are difficult to find and target with hook-and-line making release mortality unlikely. Also, if a trawl passed over the patch-reef the patch-reef would be damaged or lost entirely. Therefore, Z and M estimates were assumed the same.

While the open nature of these patch-reefs suggests that mortality estimates should be treated with caution, i.e., emigration may cause mortality to be overestimated, at the time of writing these estimates represent the only mortality estimates of juvenile vermilion snapper.

Based on these estimates, a mean *M* of 3.51 is recommended for the time period shortly after settlement to the following summer. This value is substantially higher than the age-0 and age-1 natural mortality rates recommended in SEDAR 67 of $M = 0.234$ and $M = 0.342$ (SEDAR-67 2020).

SEMAP trawl surveys

In October there were six years available for comparisons, and a significant correlation was detected between the density of age-0 vermilion snapper on patch-reefs and the CPUE of age-0 vermilion snapper in SEMAP trawl tows. Unfortunately, patch-reefs in 2009 that showed the highest age-0 vermilion snapper densities in September were not surveyed in October, and we were unable to make comparisons for that year. Also, an important caveat that needs consideration in the present density estimates is whether age-0 vermilion snapper prefer to settle directly onto larger reef habitats, if so both patch-reef and trawl surveys may be unsuitable for density estimations.

There were no significant correlations between age-1 densities on patch-reefs, and trawl CPUE in June. This is likely due to the low densities of age-1 vermilion snapper present on the patch-reefs in June. The density of age-1 vermilion sapper on patch-reefs was often lower than the CPUE in trawl samples. This is in contrast to red snapper and gray triggerfish, which had densities on patch-reefs many times higher than the CPUE in trawl sampling (Mudrak and Szedlmayer 2020; Szedlmayer and Mudrak 2022). There are several possible explanations: 1) patch-reefs were unsuitable habitat for age-1 vermilion snapper, 2) age-1 vermilion snapper avoided the divers and were not counted, or 3) trawl surveys occurred over habitat more suitable for vermilion snapper. This could be deeper water, areas father east, or perhaps the trawls ran close to or over larger reef habitats.

Spatial distributions

In 2011, age-0 and age-1 vermilion snapper were only present on the patch-reefs deployed farthest to the east. This may indicate better habitat conditions, or a better supply of settlers for vermilion snapper as one moves from west to east within the present study area. Szedlmayer and Mudrak (2014) indicated that substrates had higher silt content to the west and higher sand content to the east. These coarser sand substrates may be preferred by vermilion snapper. The East site was also a greater distance from the Mississippi River and Mobile River discharges that results in reduced sedimentation and other freshwater influences. In 2011 the West and possibly the Center site were affected by hypoxic conditions in August (Szedlmayer and Mudrak 2014). However, vermilion snapper were completely absent from the West and Center sites before the hypoxic event, indicating that hypoxia was not the cause of their absence.

2015 Spatial Experiment

In 2015, it was possible that the 100 patch-reefs deployed at the inshore location since 2010 were providing a source of early colonizers to new patch-reefs deployed in the area. Therefore, additional patch-reefs were deployed 11 km to the east to remove this potential source of immigrants. The patch-reefs at the Center site were initially colonized by higher densities of age-1 red snapper and gray triggerfish (Szedlmayer and Szedlmayer 2022). This in turn lead to lower initial densities of age-0 red snapper, which have a negative relation with age-1 conspecifics, and higher initial densities of age-0 gray triggerfish, which have a positive relation with age-0 conspecifics (Mudrak and Szedlmayer 2012; Szedlmayer and Mudrak 2014; Mudrak and Szedlmayer 2020; Szedlmayer and Mudrak 2022).

This experiment also observed a significant effect on vermilion snapper with higher densities of both age-0 and age-1 individuals on the 2015 East site, which was farther from known sources of immigrants. However, this study did not identify any relation between conspecifics and other reef fish that could easily explain the increased densities of vermilion snapper on the 2015 East site. It is possible that there was an unidentified negative relation between vermilion snapper and these early immigrants of age-1 red snapper or gray triggerfish at the center site. It is also possible that the 11 km distance between the two study sites was far enough to place the 2015 East site in an area with better habitat or a higher supply of settlers for vermilion snapper. For example, in the 2011 spatial experiment, vermilion snapper were only present on the East site. Therefore, while the effect of this 11 km distance to the east was significant, it is unclear what variable caused the effect.

Removal experiment

The removal experiment did not detect a significant effect on either age-0 or age-1 vermilion snapper densities. Rather than concluding that the density of red snapper and other reef associated fishes had no effect on juvenile vermilion snapper densities, it is more likely that the removal treatments were not successful in effectively lowering fish densities. Also, the removal experiment occurred in a year of low vermilion snapper densities. We suggest that future removal experiments be carried out during years with higher vermilion snapper densities.

Drop-net-rotenone vs visual estimates

Drop-net-rotenone samples can underestimate densities because not all individuals on a patch-reef are captured but cannot overestimate densities because it is not possible to capture more individuals than are present. Visual estimates are capable of either overestimating densities by counting individuals twice, or underestimating densities by missing individuals. The Fisher's exact test did find a significant difference between the visual counts and the drop-net catches. However, while drop-nets caught more individuals than were counted in the visual surveys, most of this difference came from a single patch-reef where 24 vermilion snapper were visually counted, and 34 vermilion snapper were caught in the drop-net.

Drop-net sampling allowed for the validation of visual size estimates. All 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, few individuals will be assigned to an incorrect age and conclusions based on visual size estimates will be valid.

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Table 1. Environmental conditions associated with visual surveys for juvenile vermilion snapper: 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. 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	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 vermilion snapper total instantaneous mortality (*Z*) observed each year. Mortalities were based on the decline between the maximum density of age-0 vermilion snapper observed on patch-reefs in the fall surveys and the density of age-1 vermilion snapper observed on the first summer survey the following year. Mortality was not calculated for 2011 and 2013 because densities increased between fall and the following summer. The number of patch-reefs with available data each year = *N*. Mean *Z* was based on the mean for all years.

Year	*N*	*Z*
2007	28	3.40
2010	25	4.76
2011	21	
2013	10	
2014	14	2.69
2015	29	4.61
Mean	–	3.87

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

Year	Season	Age	Mean CPUE	Trawl *N*
2007	Fall	0	0 ± 0	34
2010	Fall	0	0.54 ± 0.36	93
2011	Fall	0	0 ± 0	17
2013	Fall	0	0.70 ± 0.49	76
2014	Fall	0	1.41 ± 0.44	193
2015	Fall	0	1.81 ± 0.51	142
2008	Summer	1	0.18 ± 0.13	49
2011	Summer	1	3.49 ± 0.69	156
2012	Summer	1	3.35 ± 0.76	140
2014	Summer	1	1.76 ± 0.49	204
2015	Summer	1	1.99 ± 0.43	215
2016	Summer	1	3.12 ± 0.59	141

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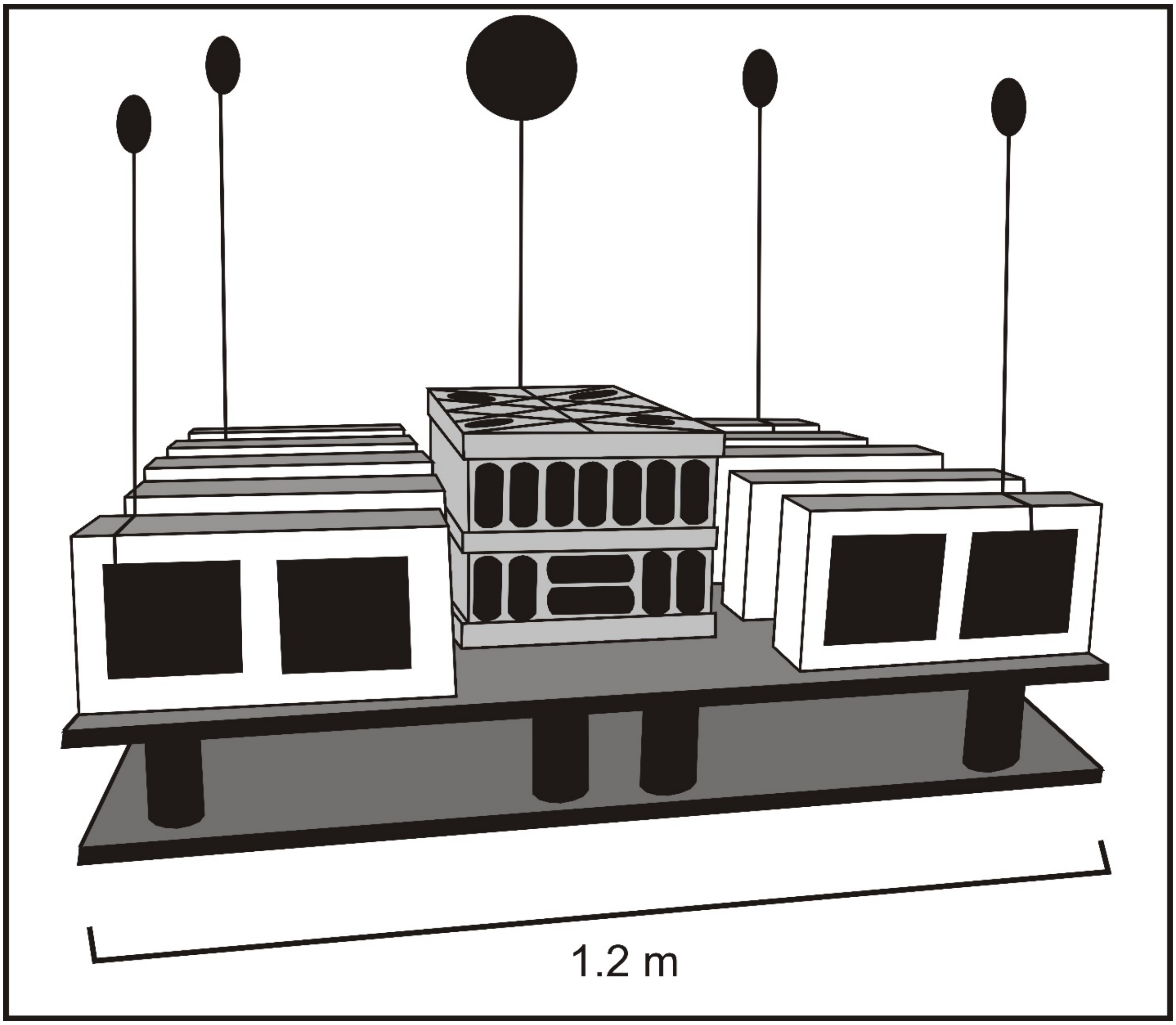

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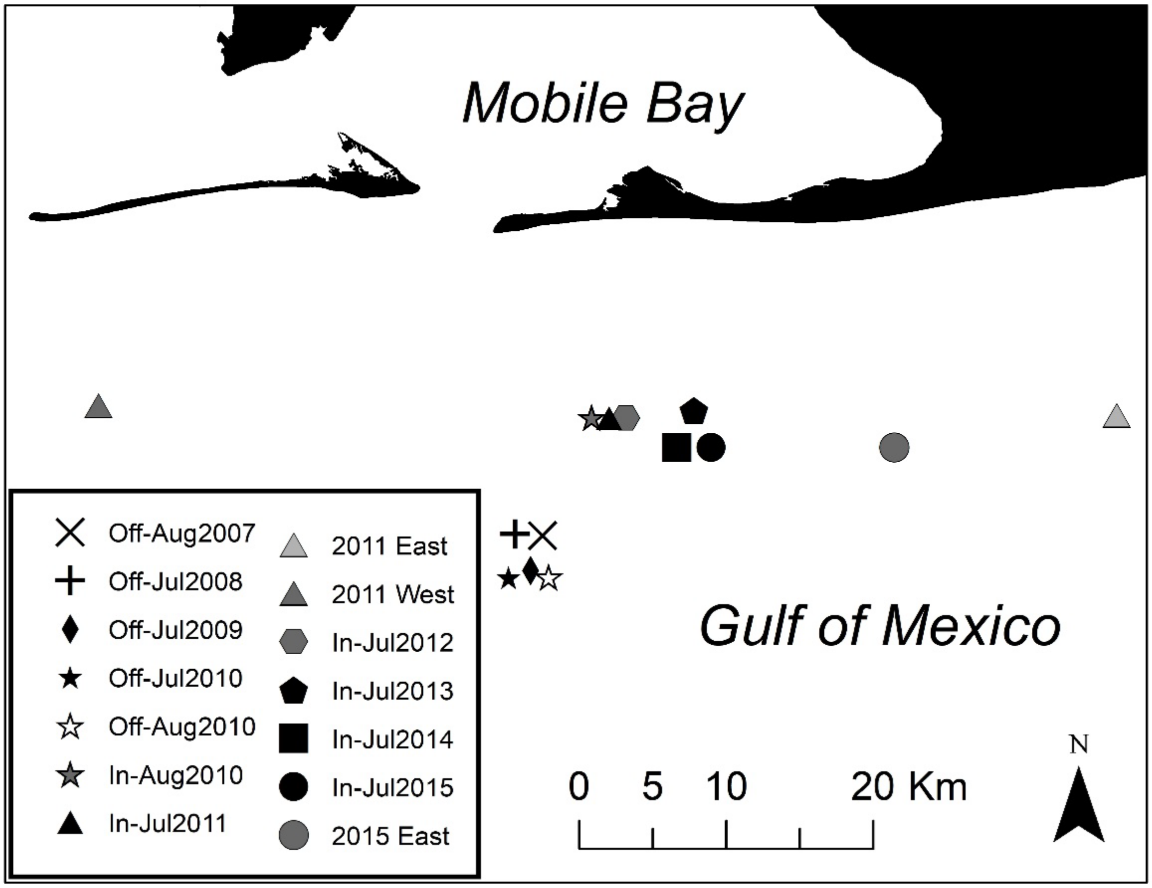

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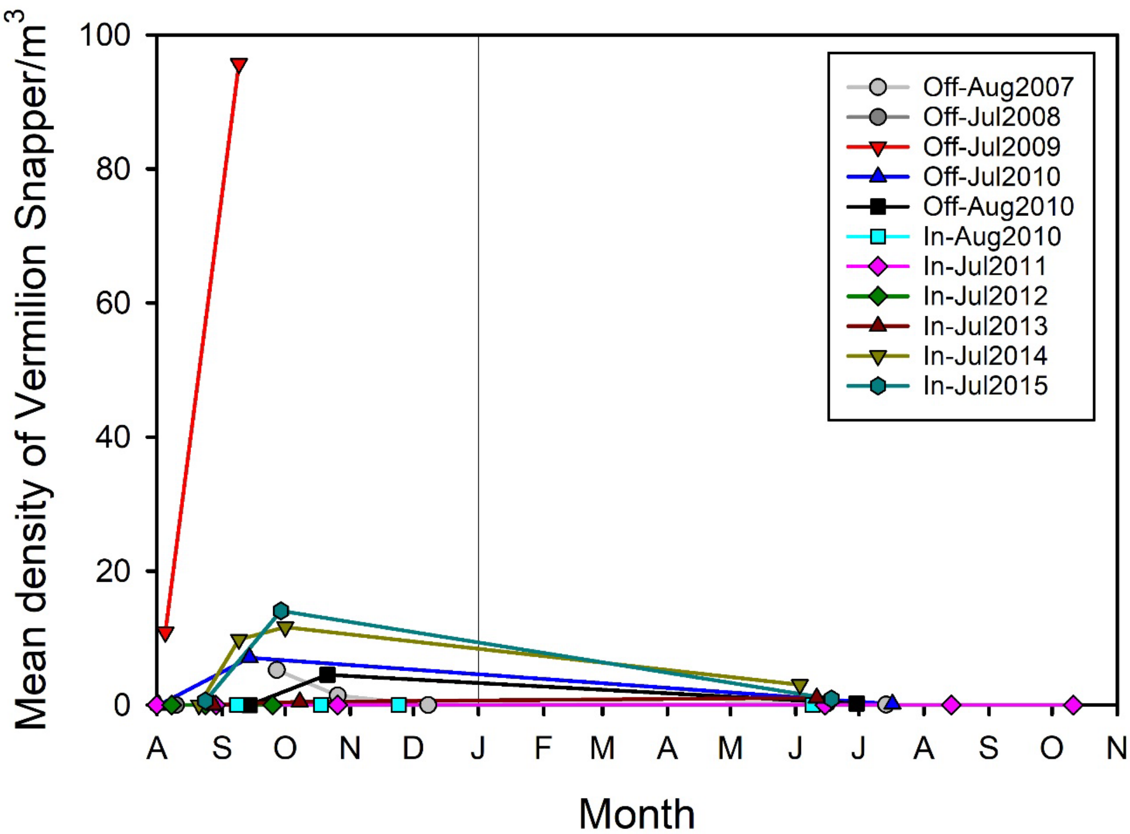

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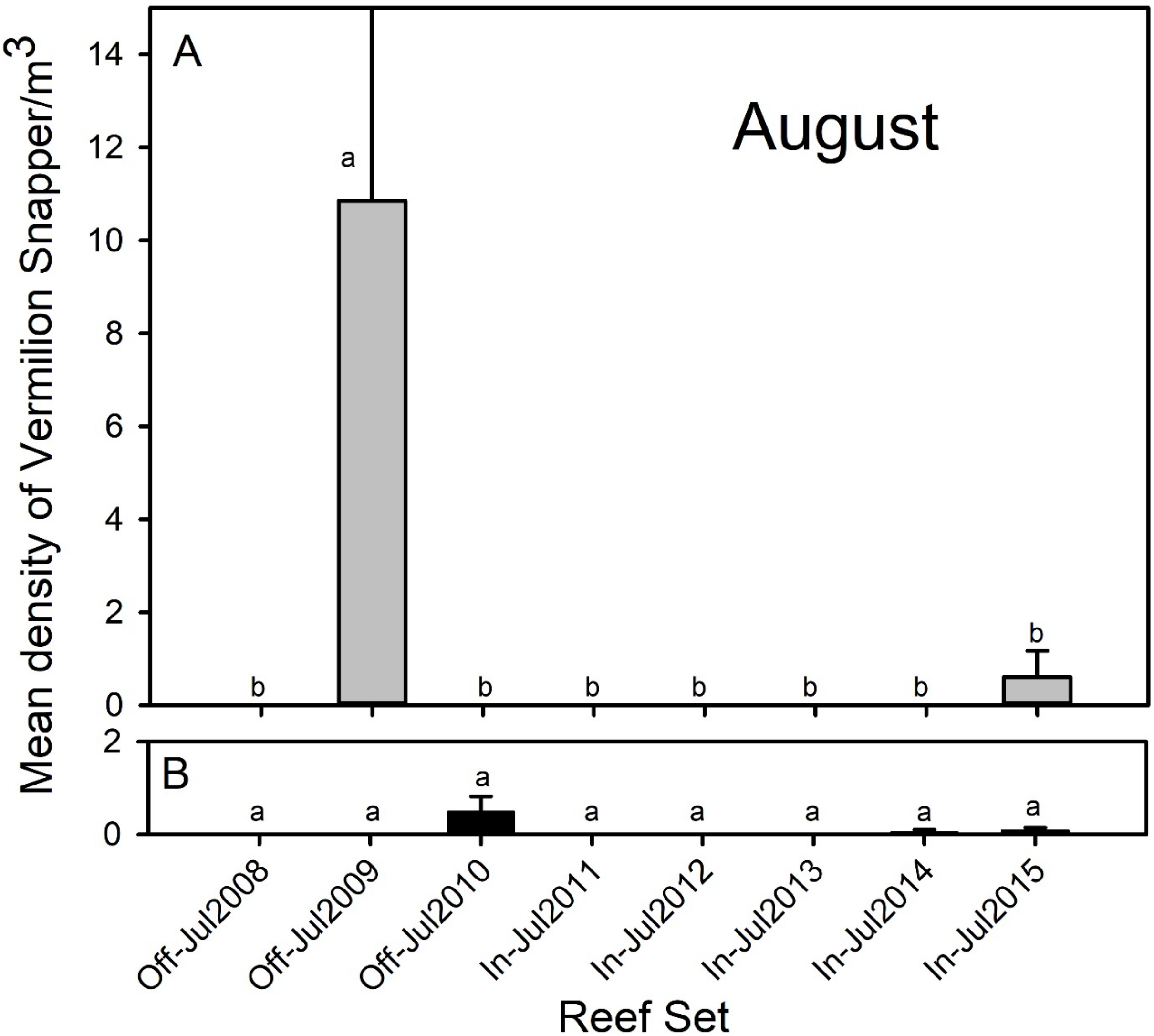

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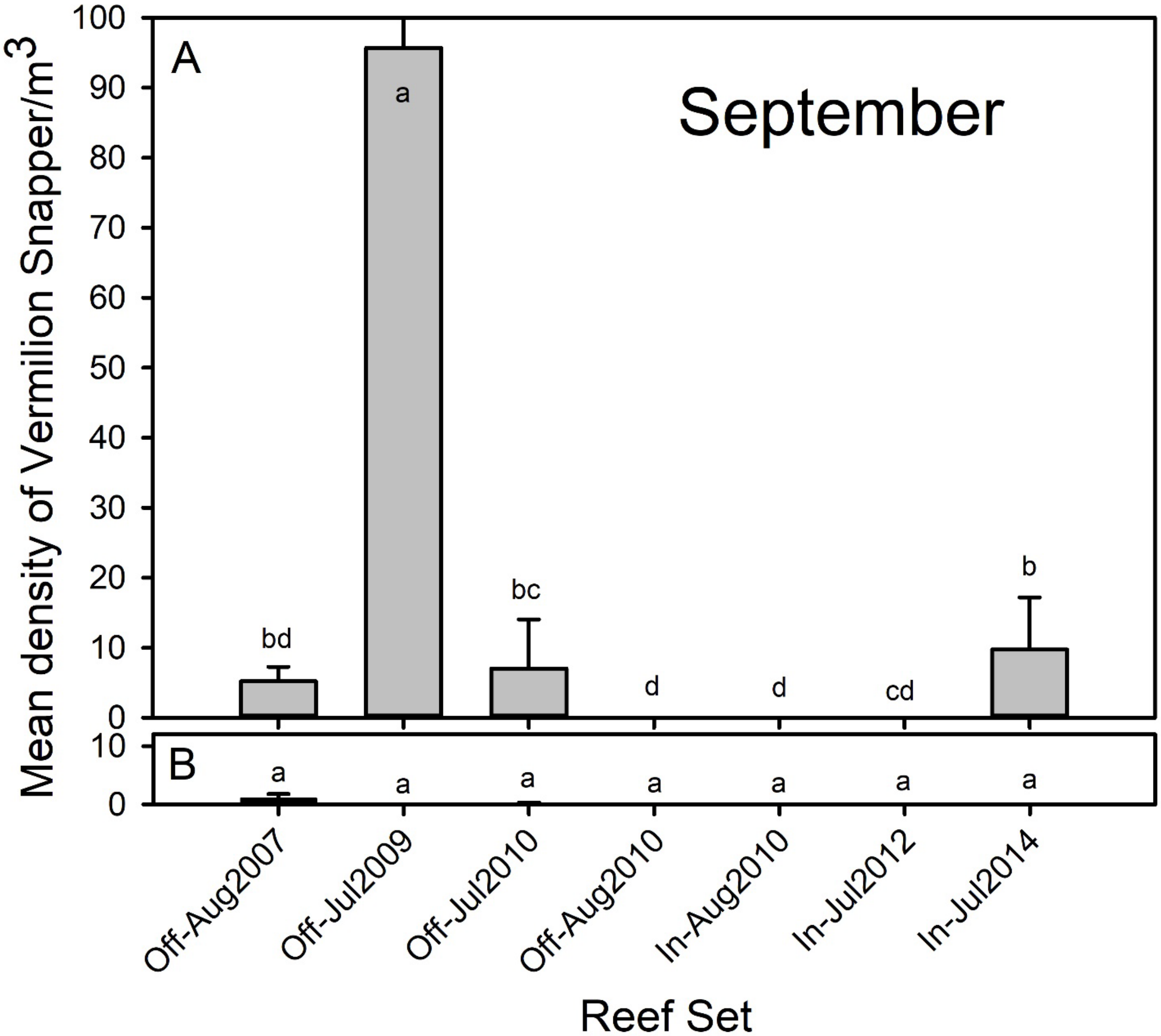

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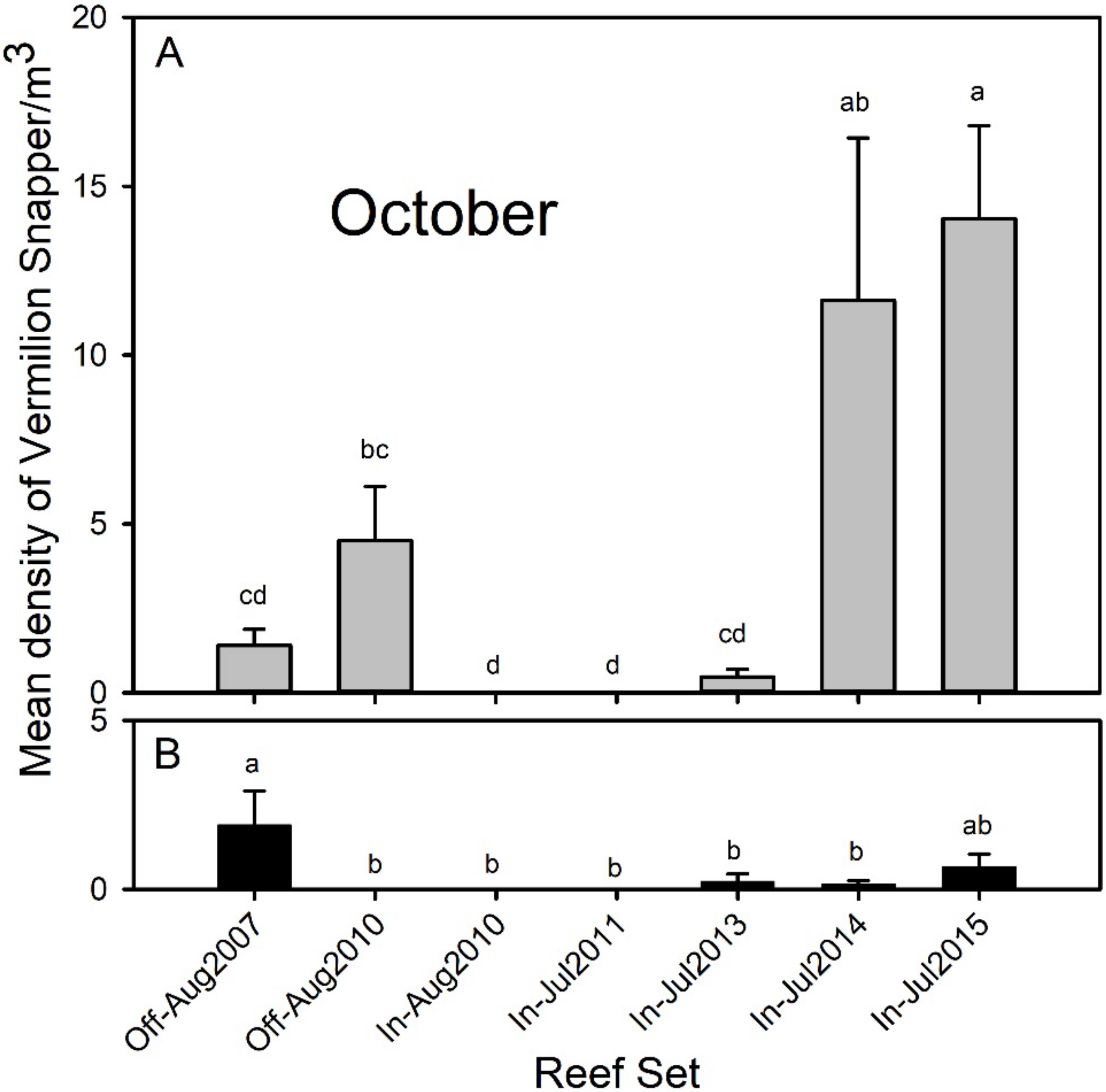

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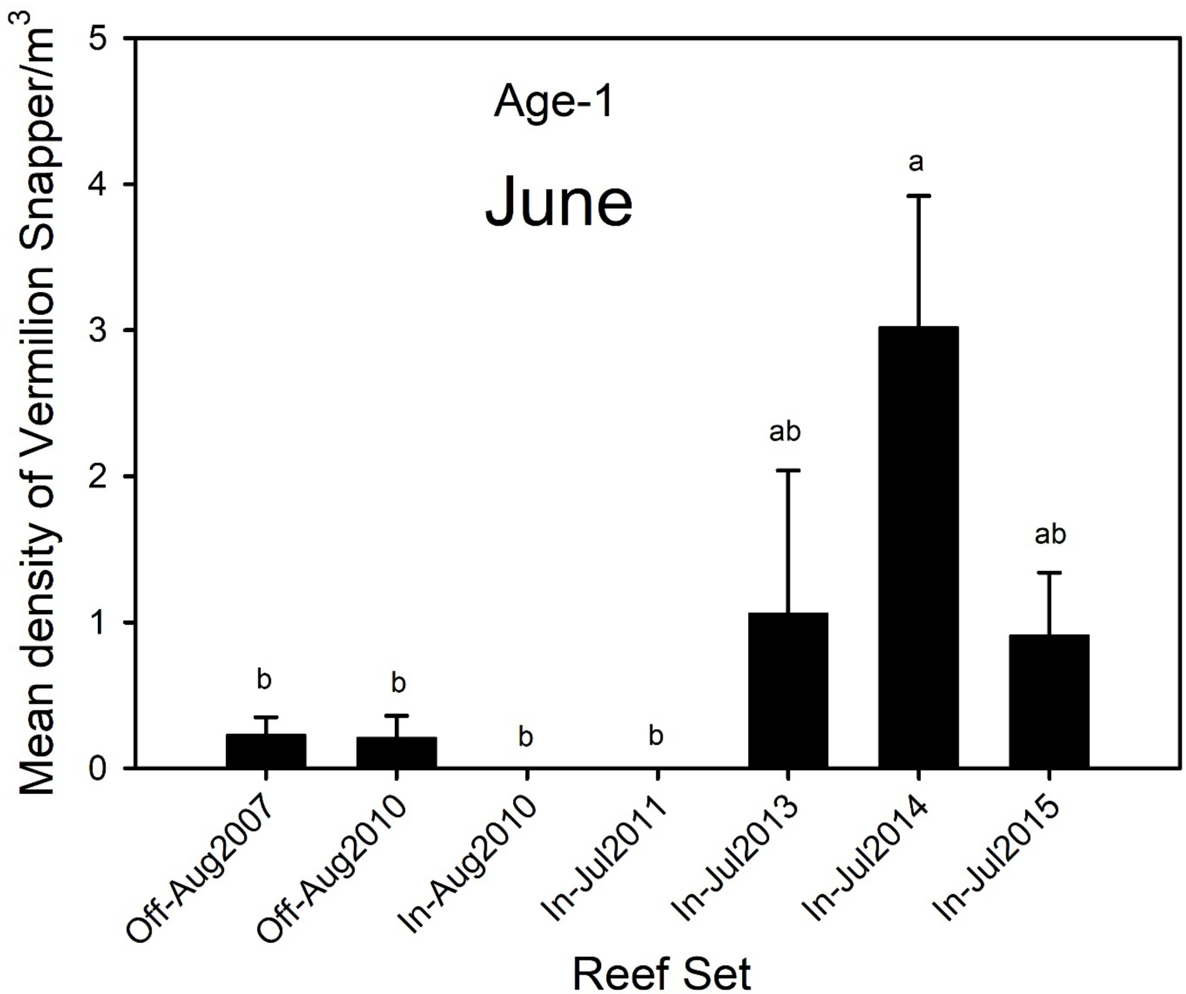

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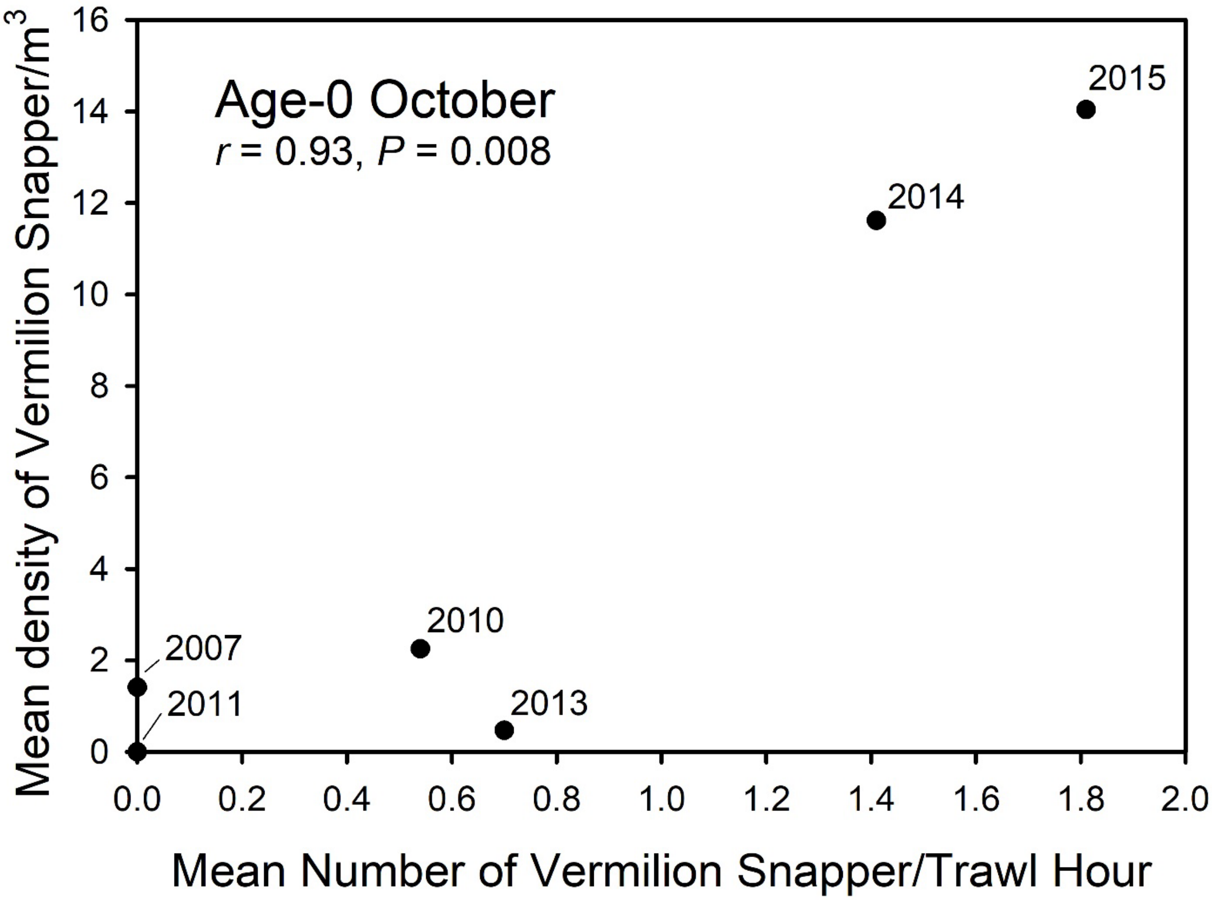

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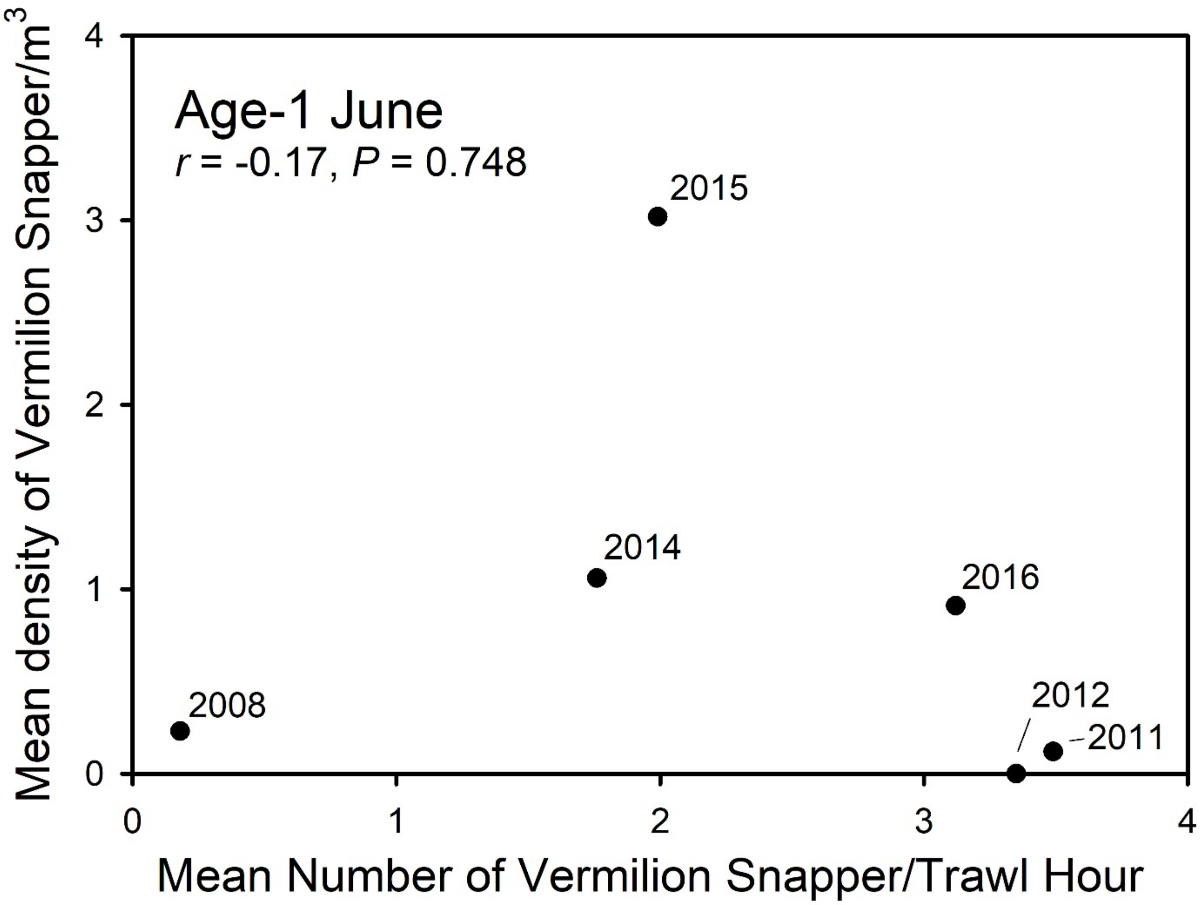

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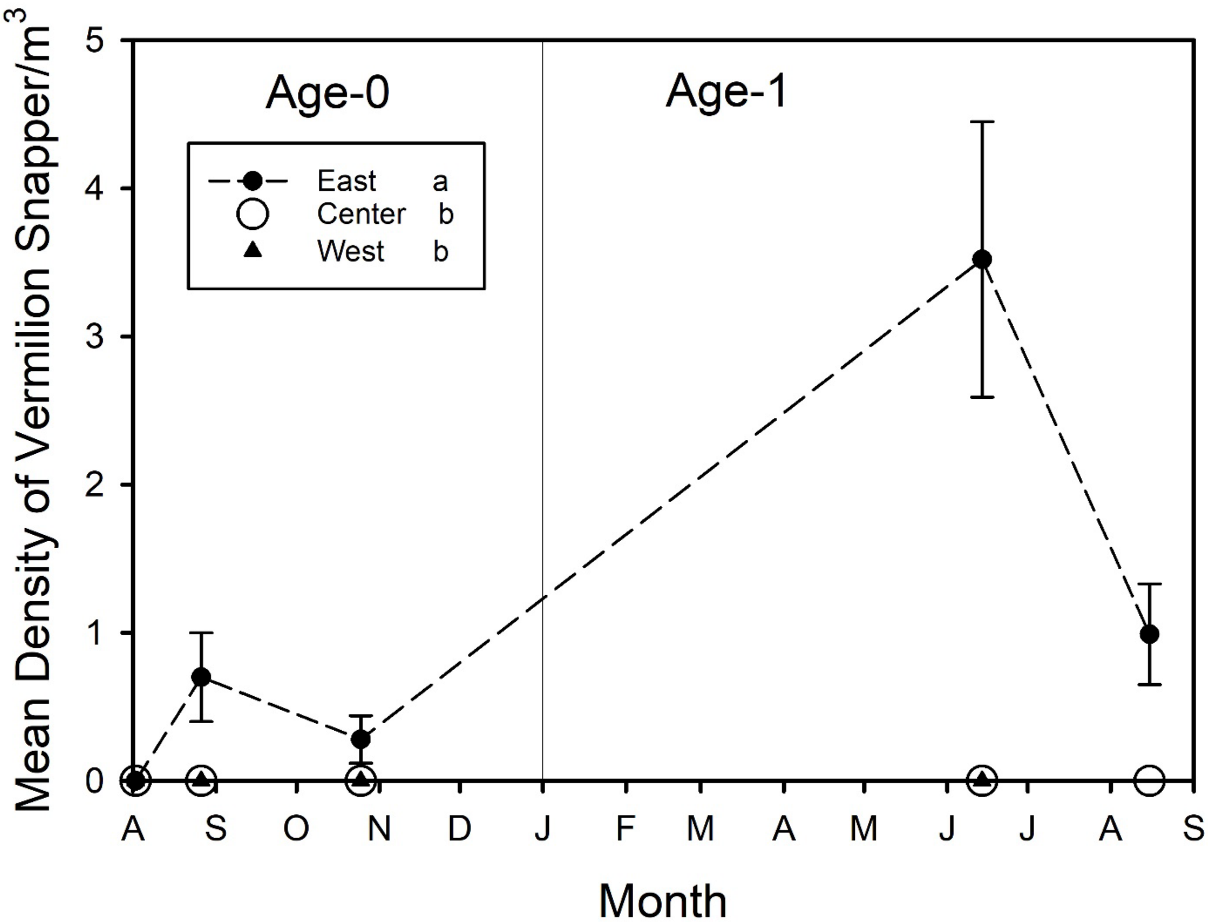

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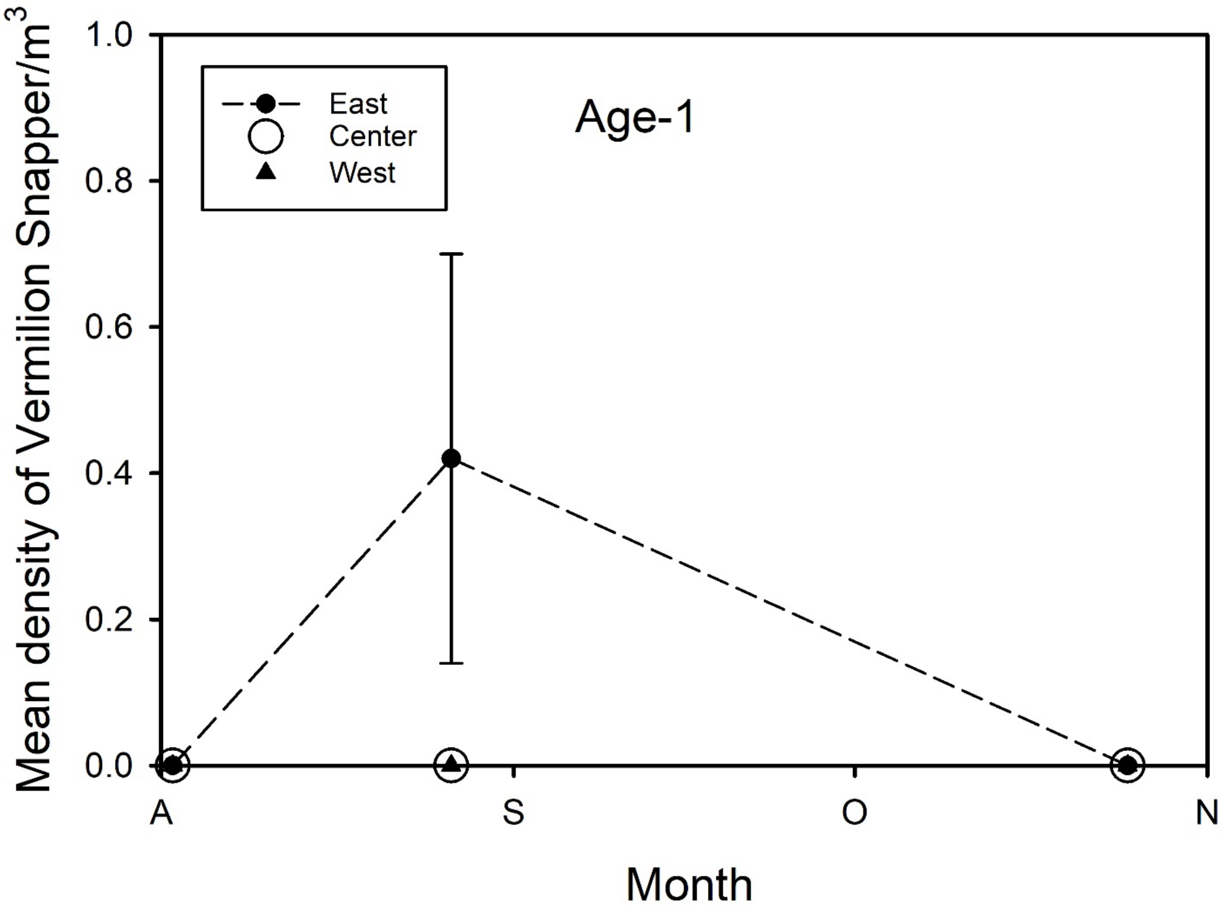

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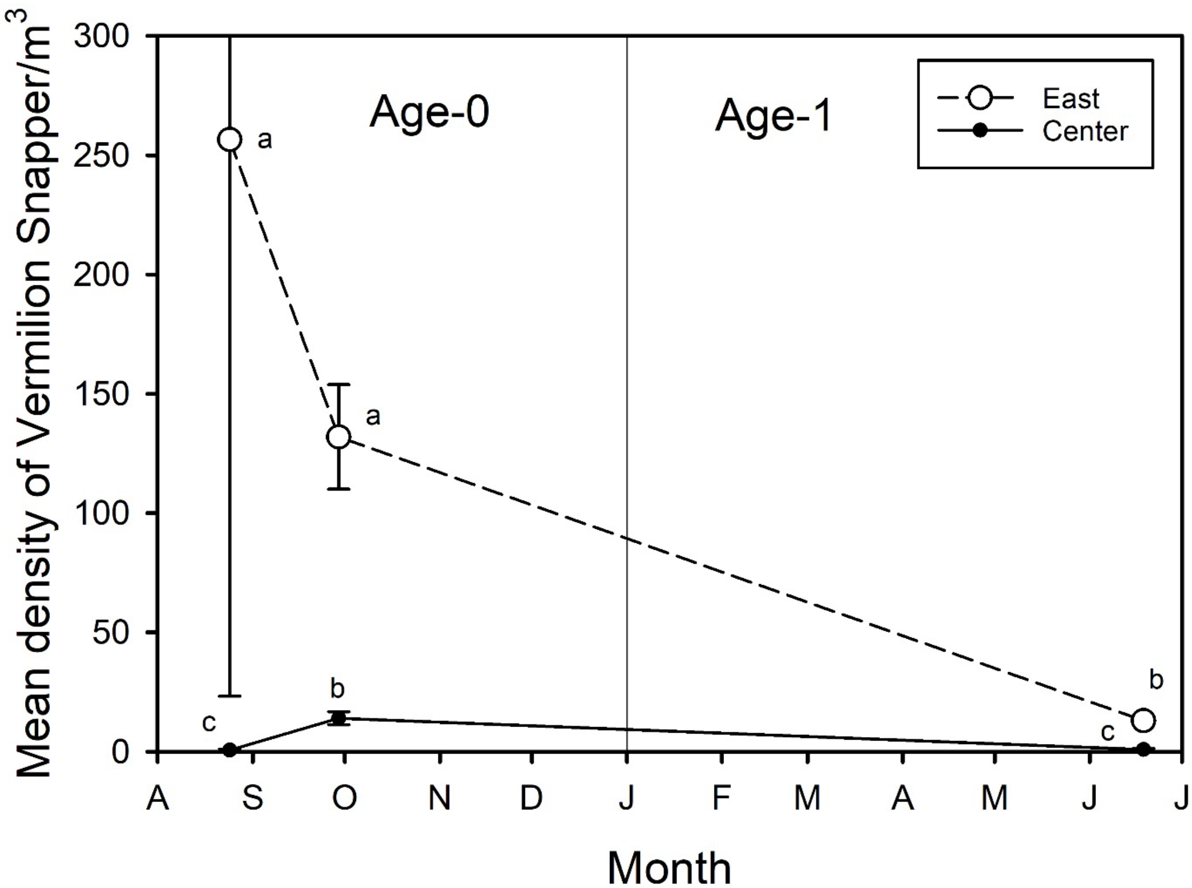

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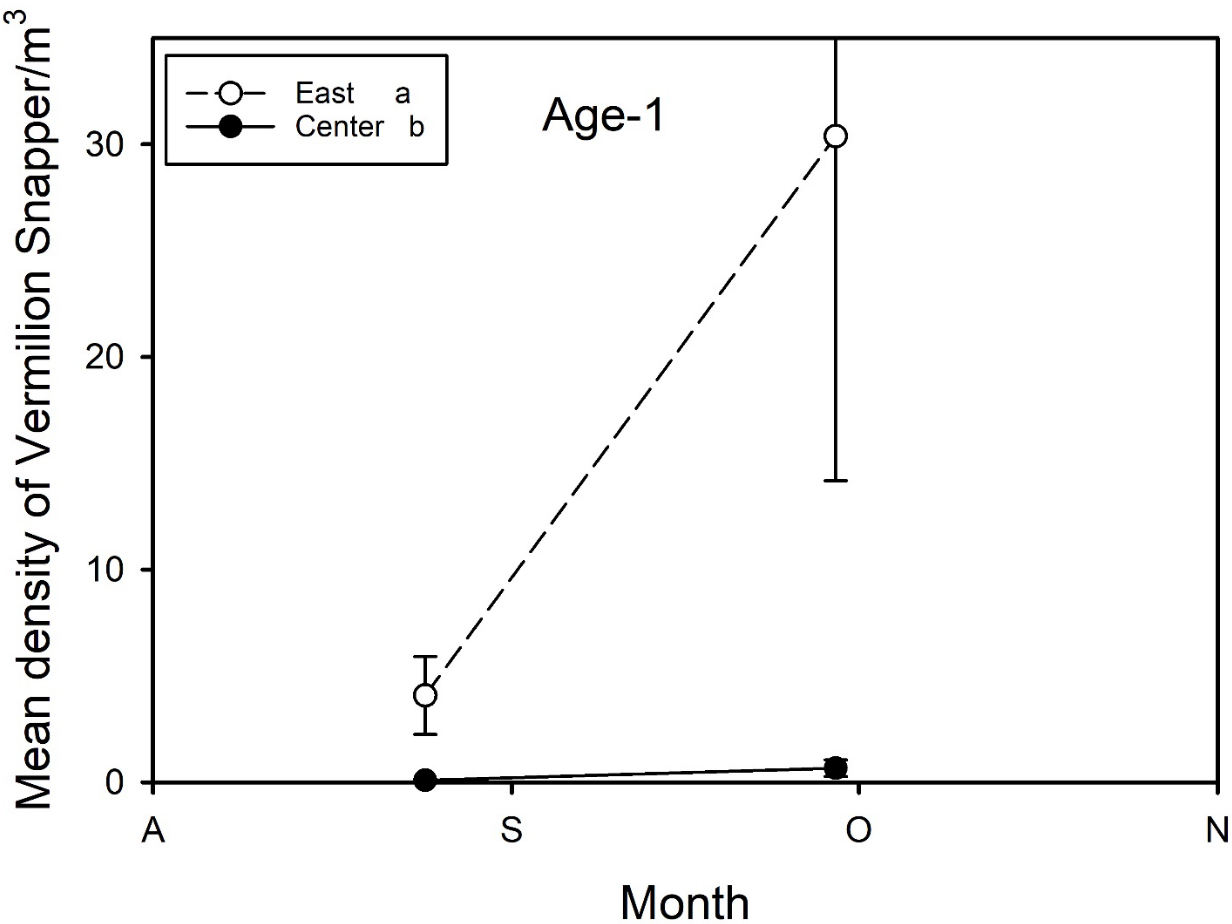

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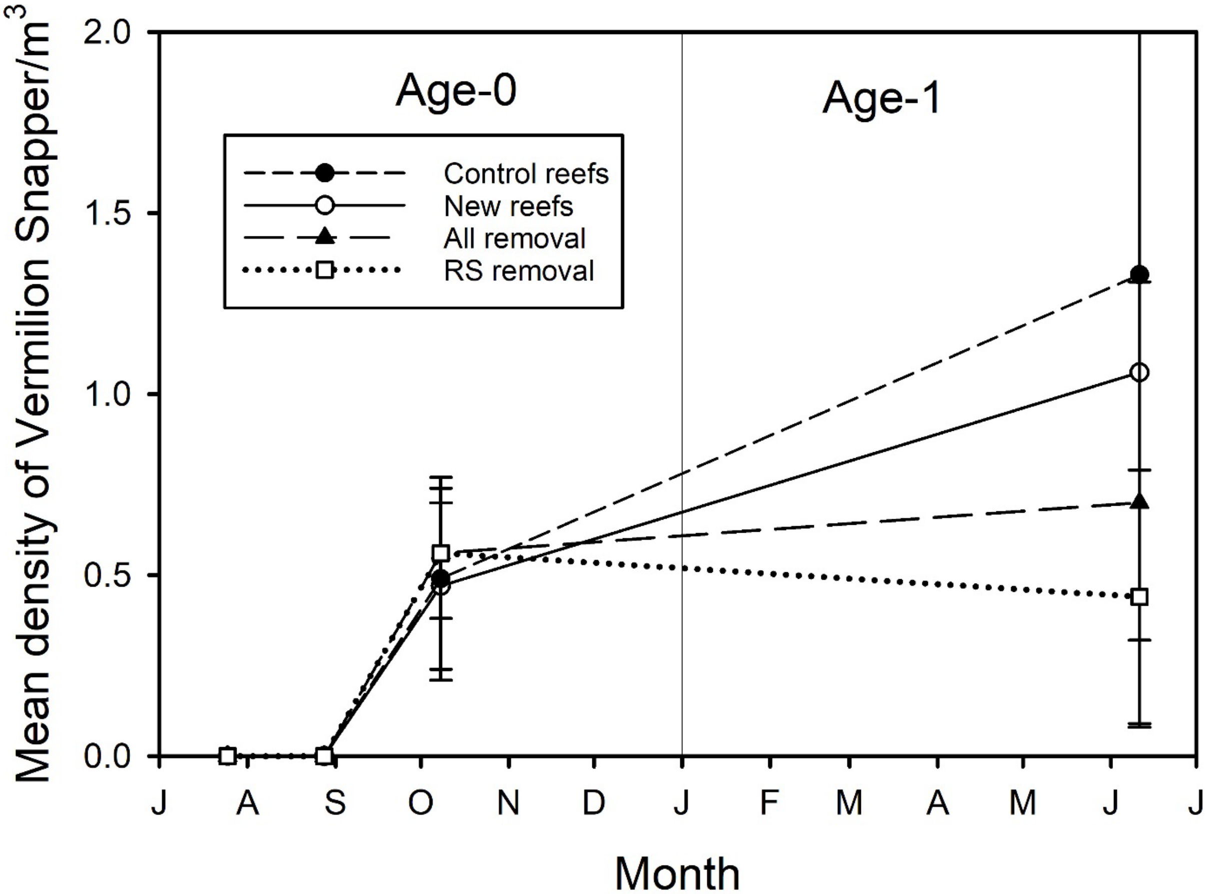

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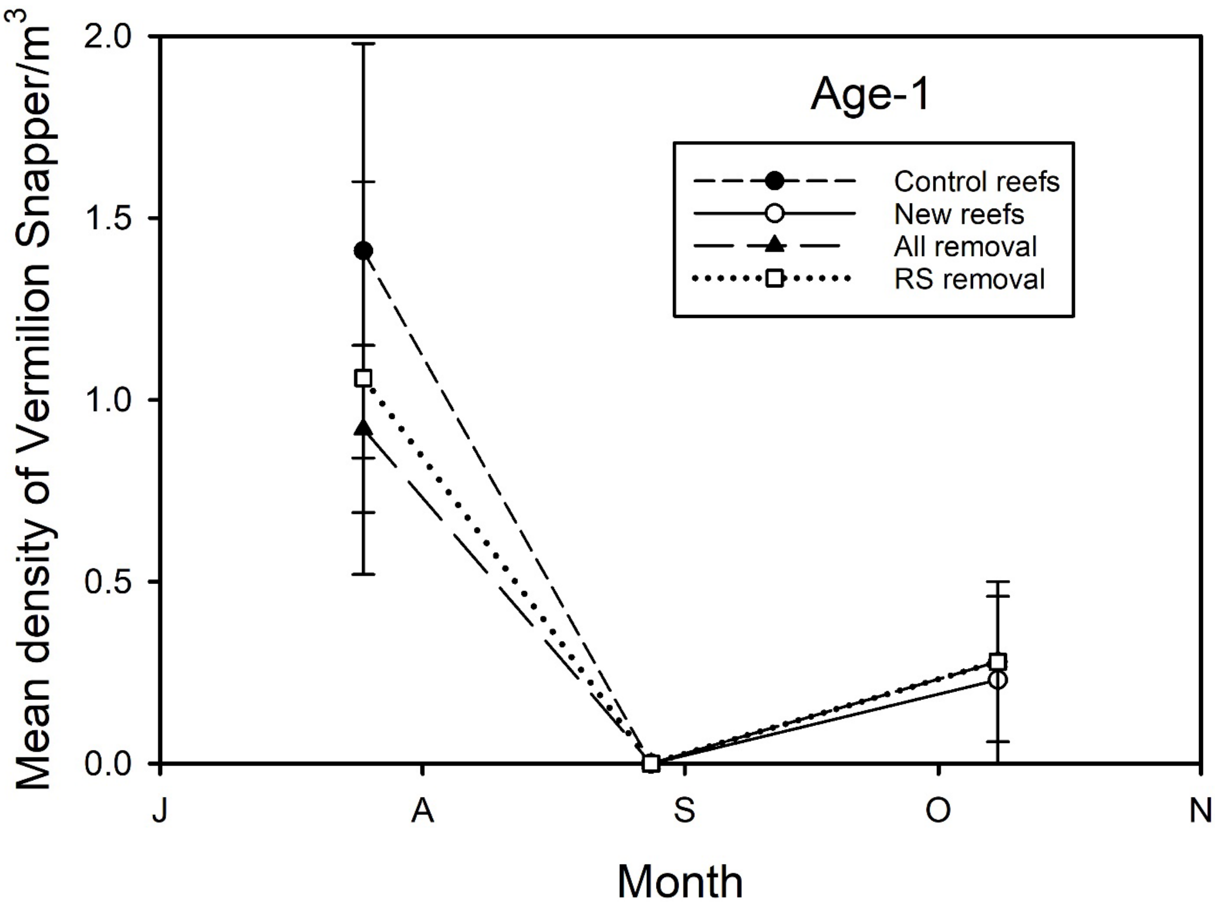

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