Competitive interactions between gray triggerfish (*Balistes capriscus*) and red snapper (*Lutjanus campechanus*) in laboratory and field studies in the northern Gulf of Mexico

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Competitive interactions between gray triggerfish (*Balistes capriscus*) and red snapper (*Lutjanus campechanus*) in laboratory and field studies in the northern Gulf of Mexico

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Abstract: Field removal and laboratory studies examined competitive interactions between gray triggerfish (*Balistes capriscus*) and red snapper (*Lutjanus campechanus*). In field studies, all gray triggerfish and red snapper were counted and sizes estimated on 24 reef sites. Gray triggerfish were then removed from half of these reef sites, resulting in significantly fewer gray triggerfish on the removal reefs at the start of the experiment. After 7 months the experiment ended and reef sites were resurveyed. Gray triggerfish decreased on both treatments, while the mean number of red snapper did not differ between treatments; however, there were significantly more small (<400 mm total length) red snapper on reefs where gray triggerfish were removed. In seven laboratory growth trials (30 to 35 days each), red snapper held with gray triggerfish had significantly lower growth rates and numerous bite marks compared with red snapper alone. These competitive interactions indicate that management efforts to rebuild and increase gray triggerfish populations may have unintentional negative effects on red snapper populations, particularly for smaller fish.

Résumé : Des retraits sur le terrain et des études en laboratoire ont été utilisés pour étudier les interactions concurrentielles entre balistes caprisques (*Balistes capriscus*) et vivaneaux rouges (*Lutjanus campechanus*). Dans les études de terrain, tous les balistes caprisques et vivaneaux rouges ont été comptés et leurs tailles estimées en 24 sites récifaux. Des balistes caprisques ont ensuite été retirés de la moitié de ces sites, réduisant ainsi de manière significative le nombre de balistes caprisques sur ces récifs au début de l'expérience. Après 7 mois, l'expérience a pris fin et les sites récifaux ont été évalués à nouveau. Le nombre de balistes caprisques avait diminué pour les deux traitements, alors que le nombre moyen de vivaneaux rouges ne différait pas entre les traitements; il y avait toutefois significativement plus de petits vivaneaux rouges (longueur totale <400 mm) sur les récifs dont avaient été retirés des balistes caprisques. Dans sept essais de croissance en laboratoire (de 30 à 35 jours chacune), des vivaneaux rouges maintenus en présence de balistes caprisques avaient des taux de croissance significativement plus faibles et de nombreuses marques de morsure comparativement aux traitements dans lesquels les vivaneaux étaient seuls. Ces interactions concurrentielles indiquent que les efforts de gestion visant à reconstituer et accroître les populations de balistes caprisques pourraient avoir des effets négatifs non intentionnels sur les populations de vivaneaux rouges, plus particulièrement en ce qui concerne les petits individus. [Traduit par la Rédaction]

Introduction

Competitive interactions between species can be substantial when resources are limited (Begon et al. 1996; Wootton 1998). Several studies have shown that shelter type and food can be limiting resources for fish on coral reefs (Shulman et al. 1983; Hixon and Beets 1989; Jones 1986), and field experiments have provided several examples of competition by removing one species and assessing change in abundance or growth of the other (Hixon 1980; Connell 1983; Schoener 1983).

Growth experiments have also examined interspecific competition between species confined in cages or in controlled laboratory conditions. Cage experiments demonstrate roach (*Rutilus rutilus*) suppressed the growth rate of age-0 European perch (*Perca fluviatilis*) (Persson 1987). Similarly, in a field removal study if either blackcap baslet (*Gramma loreto*) or fairy basslet (*Gramma melacara*) were removed from the study site, the other species had increased growth rates compared with control growth rates (Kindinger 2016).

Competition might be expected between gray triggerfish (*Balistes capriscus*) and red snapper (*Lutjanus campechanus*), because they are the most abundant co-occurring species on artificial reefs in the northern Gulf of Mexico (Kurz 1995; Lingo and Szedlmayer 2006; Simmons and Szedlmayer 2011). This competition may be due to overlapping diets (Blitch 2000; Ouzts and Szedlmayer 2003; Szedlmayer and Lee 2004) and limited suitable habitat that provides protection from predators (Piko and Szedlmayer 2007; Mudrak and Szedlmayer 2012; Herbig and Szedlmayer 2016). In the northern Gulf of Mexico, natural reefs are limited compared with artificial reefs and other structures such as oil and gas platforms (Parker et al. 1983; Gallaway et al. 2009).

Gray triggerfish are territorial and aggressive compared with many other reef fish species such as red snapper in the northern Gulf of Mexico. During the spawning season, male gray triggerfish defend a territory with one to three females on nests around the reef, while the nesting females also aggressively protect the eggs in the nest and chase off red snapper and other egg predators (Simmons and Szedlmayer 2012). In the present study, field removal and controlled laboratory experiments tested for competitive interactions between gray triggerfish and red snapper. Competition is defined as an interaction between individuals that results in

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the participants suffering a net loss of fitness such as reduced growth rate or even survival (Wootton 1998). We examined potential interspecific competition in field removal experiments, since previous studies have provided evidence for this competition by changes in abundance of one species when a competitor is removed (Hixon 1980; Schmitt and Holbrook 1986; Robertson 1996). Red snapper and gray triggerfish competitive interactions were also examined in laboratory growth rate experiments where food resources were not limited, and competition can be inferred by changes in survival and growth (Persson 1987; Olson et al. 1995; Fernandes et al. 2015). Growth rates are an overall integrator of other environmental factors as well as biological interactions (Sogard 1997; Lorenzen and Enberg 2001). As such, they can provide a measure of the competitive interactions between gray triggerfish and red snapper. The present study examines such competitive interactions between two commonly co-occurring species through both field and laboratory studies in the northern Gulf of Mexico.

Materials and methods

Study design

The present study tested for competitive interactions between red snapper and gray triggerfish in both field and laboratory experiments. Field studies tested for differences in red snapper abundance and sizes after removals of gray triggerfish from reef sites compared with reef sites without gray triggerfish removals. Laboratory studies tested for differences in red snapper growth rates and survival among treatments of red snapper held alone, gray triggerfish held alone, and red snapper held with gray triggerfish.

Field study

The study sites were located 24–50 km south to southeast of Dauphin Island, Alabama, USA, in the northern Gulf of Mexico. Divers (SCUBA) visually and video (Sony TR101 Hi–8 video camera; Tokyo, Japan) surveyed 24 public reef sites made from M60 army tanks (9.3 m × 3.6 m × 3.2 m, 51.3 tonnes). Diver surveys identified, counted, and placed into 25 mm size classes all gray triggerfish and red snapper. The census methods used by divers followed the methods described as the "point method" by Bortone et al. (1989). Two divers positioned over the reef counted the number of gray triggerfish and red snapper on and around each artificial reef for 15–20 min, but if visibility was low diver surveys were aborted. Divers estimated red snapper sizes based on total length (TL, mm) and gray triggerfish based on fork length (FL, mm) due to extended rays on their long caudal fins. After counting fish, the divers removed gray triggerfish on the same dive by spearfishing on 12 reefs (removal reefs). We conducted the visual surveys and removals from 13 October to 7 November 2005. After 7 months, the field removal experiment was ended, and divers resurveyed all reefs from 1 to 23 June 2006 for gray triggerfish and red snapper abundance and size class estimations.

Environmental parameters in the Gulf of Mexico can differ seasonally and among locations; therefore, at the start and end of the experiment, temperature (°C), salinity (‰), and dissolved oxygen ($mg \cdot L^{-1}$) were measured at each reef site with a remote recording YSI-6920 meter (Yellow Springs Instruments, Yellow Springs, Ohio, USA). Mean values of these measures were calculated from continuous vertical recordings (1 s intervals) as the instrument was slowly retrieved from the seafloor up to 9 m below the surface.

Depths were compared between treatments with a *t* test in the field removal experiment. Temperature, salinity, and dissolved oxygen were compared among treatments, surveys, and treatment–survey interactions with repeated measures ANOVA (rmANOVA). Before removals, the mean numbers and mean sizes of gray triggerfish were compared between treatments with separate *t* tests, and at the end of the experiment the mean sizes of gray triggerfish (FL, mm) were compared between treatments with a *t* test. After removals the mean numbers and mean sizes of red snapper (TL, mm) and mean numbers of gray triggerfish were compared among treatments, surveys, and treatment–survey interactions by rmANOVA, and a Student–Newman–Keuls test was used to show specific differences. Length–frequency distributions for red snapper were compared between treatments within each survey period with chi-square (χ^2) analyses. Differences were considered significant at $P \leq 0.05$.

Laboratory study

Competitive interactions between gray triggerfish and red snapper were assessed in a temperature- and salinity-controlled 14 800 L closed recirculating laboratory seawater system with nine attached experimental tanks, each 1240 L (1.5 m diameter × 0.7 m depth) with the same lighting. Each experimental tank contained two polyvinyl chloride refuge boxes (28.5 cm × 18.5 cm × 39.5 cm) with holes (14 cm × 14 cm) cut into each side. Every 2 days, temperature, salinity, and dissolved oxygen were recorded with a YSI-85 meter (Yellow Springs Instruments, Yellow Springs, Ohio, USA), and ammonia, nitrite, and nitrate levels were measured with LaMotte test kits (LaMotte Company, Chestertown, Maryland, USA).

Fish were caught by hook and line, returned to the laboratory, and species held separately at densities of 10–15 fish per tank prior to competition trials. To limit barotrauma, fish were collected from artificial reefs in depths ≤22 m. In the field, each fish was vented (release expanded gases) with a 12-gauge needle inserted into the swim bladder. Each fish was tagged with a passive integrated transponder (PIT) tag placed in the peritoneal cavity for individual measurement of growth rates over the trial periods (Biomark, Boise, Idaho, USA). All fish were acclimated to captivity for 3–4 weeks before starting experiments.

At the start and the end of a trial, all fish were anesthetized by 2 min immersion in 150 $mg \cdot L^{-1}$ of tricaine methanesulfonate (MS-222; Argent Chemical Laboratories, Redmond, Washington, USA), scanned for PIT tags, weighed to the nearest gram, and measured for standard length, FL, and TL (all in mm). Fish were randomly assigned to one of the following three treatments with a total of six fish per tank: six red snapper alone, six gray triggerfish alone, or mixed treatment of three red snapper and three gray triggerfish. Each trial had two replicate red snapper treatments, two replicate gray triggerfish treatments, and three replicate mixed treatments. Seven trials were completed with different fish for every trial, and each trial was 30 to 35 days. Fish were fed weighed rations of cut squid and shrimp typically ranging from 100 to 250 g per tank every 2 days to satiation. When feeding stopped, the remaining portion of food was removed and weighed to estimate mean daily ration consumed in each tank.

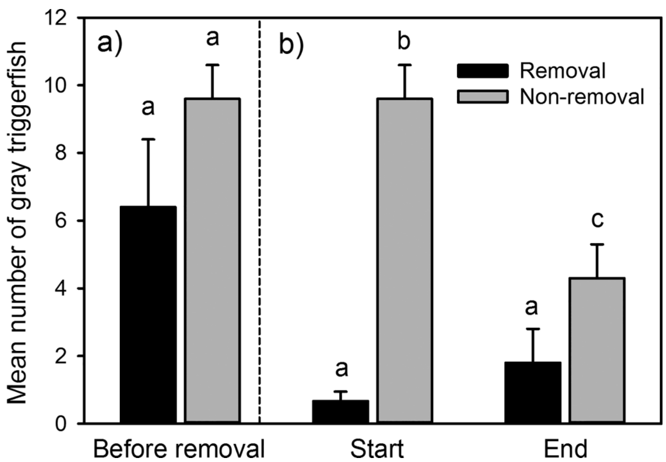
Specific growth rates (change in mass (g) · start mass $(kg)^{-1}$ · number of experiment $days^{-1}$) of individual fish and mean daily ration (food consumed in each tank (g) · total mass of six fish in the tank $(kg)^{-1}$ · number of experiment $days^{-1}$) were compared among treatments by ANOVA and a Student–Newman–Keuls test. Differences were considered significant at $P \leq 0.05$.

Results

Field study

Depths of reefs differed between removal (mean 25.2 m, range 20.7–29.6 m) and nonremoval treatments (mean 27.9 m, range 23.4–30.1 m; $t_{[22]} = 2.6$, $P = 0.015$). Salinity did not differ (mean 34.2‰, range 33.0–35.8‰; $F_{[1,16]} = 0.10$, $P = 0.76$), temperature did not differ (mean 24.7 °C, range 21.6–27.2 °C; $F_{[1,16]} = 0.06$, $P = 0.81$), and dissolved oxygen did not differ (mean 5.9 $mg \cdot L^{-1}$, range 5.0–7.2 $mg \cdot L^{-1}$; $F_{[1,16]} = 0.33$, $P = 0.57$) between treatments. There were significant differences in salinity (mean difference = 0.3‰), temperature (mean difference = 1.1 °C), and dissolved oxygen (mean

Fig. 1. Mean (+ standard error, SE) number of gray triggerfish per reef counted on removal (black bars) and nonremoval (gray bars) artificial reefs before removals (*a*) and after removals at the start (13 October – 7 November 2005) and the end (1–23 June 2006) of the field experiment (*b*). Significant differences ($P \leq 0.05$) are shown by different letters between treatments before removal (*a*) and after removal between start and end (*b*).



difference = 0.7 mg·L^{-1}) between start and end of the field experiment, but these differences were considered small and biologically unimportant. There were no significant treatment–survey interaction effects for salinity ($P = 0.38$), temperature ($P = 0.78$), or dissolved oxygen (rmANOVA, $P = 0.51$).

The mean number of gray triggerfish did not differ between treatments before removals ($t_{[22]} = 1.6$, $P = 0.126$). Divers removed 91% (77 of 85) of the gray triggerfish on removal reefs. After removals, gray triggerfish numbers were significantly lower on removal compared with nonremoval treatments ($F_{[1,22]} = 34.0$, $P < 0.001$), decreased between surveys (start and end; $F_{[1,22]} = 8.8$, $P = 0.007$), and showed a treatment–survey interaction effect where they decreased on nonremovals but did not differ on removal reefs between surveys ($F_{[1,22]} = 20.4$, $P < 0.001$; Fig. 1). The mean number of red snapper did not differ by treatments ($F_{[1,22]} = 0.01$, $P = 0.95$), surveys ($F_{[1,22]} = 1.9$, $P = 0.180$), or show a treatment–survey interaction ($F_{[1,22]} = 0.1$, $P = 0.77$; Fig. 2).

Size comparisons

Gray triggerfish were significantly larger on removal reef treatments before being removed at the start of the field experiment (removal: 316 ± 5.3 mm FL; nonremoval:, 271 ± 6.7 mm FL; $t_{[190]} = -4.9$, $P < 0.001$) and at the end of the experiment between treatments (removal: 298 ± 15.2 mm FL; nonremoval: 261 ± 5.8 mm FL; $t_{[71]} = -2.8$, $P = 0.007$). Red snapper mean lengths (±standard error, SE) did not differ between treatments (removal = 390 ± 4 mm TL; nonremoval = 395 ± 4 mm TL; $F_{[1,22]} = 0.57$, $P = 0.459$), surveys (start 393 ± 4 mm TL; end 392 ± 3 mm TL; $F_{[1,22]} = 0.05$, $P = 0.824$), or show a treatment–survey interaction ($F_{[1,22]} = 0.02$, $P = 0.882$).

Length–frequency distributions

Red snapper length–frequency distributions (100 mm bins, starting at 150 to 250 mm) did not differ between removal and nonremoval reefs at the start of the field experiment ($\chi^2_{[8]} = 12.9$, $P = 0.115$; Fig. 3*a*). After 7 months the length–frequency distribution of red snapper differed between treatments ($\chi^2_{[8]} = 20.1$, $P = 0.010$; Fig. 3*b*) with a higher frequency of smaller fish (<400 mm TL) on removal treatments.

Laboratory study

Mean ± SE temperature was 21.1 ± 0.1 °C and ranged from 18.8 to 24.8 °C ($n = 100$), mean salinity was 34.9 ± 0.1‰ and ranged from 32 to 38‰ ($n = 100$), and mean dissolved oxygen was 6.1 ± 0.1 mg·L^{-1} and ranged from 5.3 to 7.4 mg·L^{-1} ($n = 80$). Ammonia (NH_3) levels were <0.01 mg·L^{-1}, and nitrite (NO_{2-}) levels were <0.1 mg·L^{-1} throughout the laboratory experiments. Red snapper mean FL ± SE was 299 ± 2.6 mm and mean mass was 491 ± 10 g ($n = 161$), and gray triggerfish mean FL ± SE was 292 ± 2.8 mm and mean mass was 584 ± 20 g ($n = 156$). Specific rations consumed (g·kg^{-1}·day^{-1}) did not differ among red snapper alone, mixed treatments, and gray triggerfish alone ($F_{[2,764]} = 1.6$, $P = 0.1$; Fig. 4). Red snapper in the mixed treatments with gray triggerfish showed significantly slower growth rate (g·kg^{-1}·day^{-1}) than gray triggerfish alone, red snapper alone, and gray triggerfish in the mixed treatments ($F_{[9,291]} = 14.1$, $P = 0.001$; Fig. 5).

Fig. 2. Mean (+ standard error, SE) number of red snapper counted on removal (black bars) and nonremoval (gray bars) artificial reefs at the start (13 October – 7 November 2005) and the end (1–23 June 2006) of the experiment. Means did not differ among treatments ($P > 0.05$).

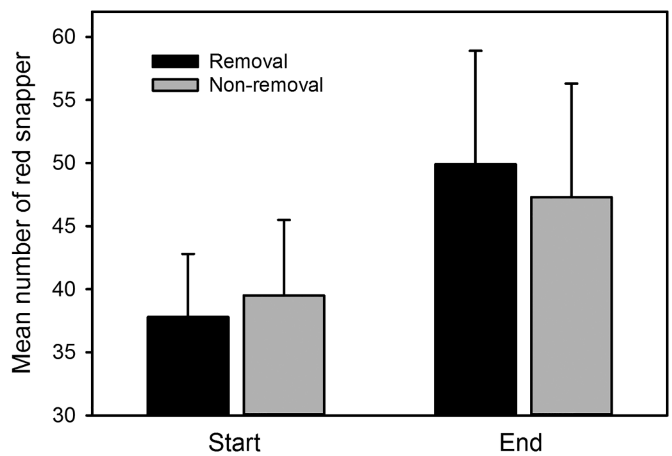
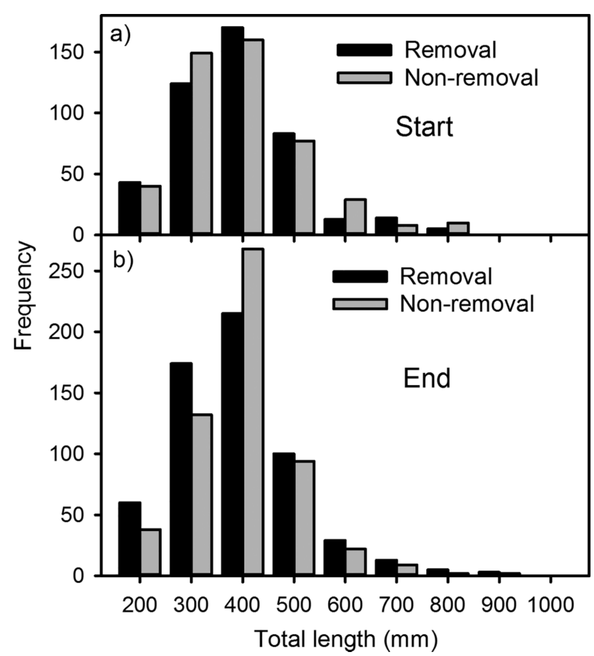


Fig. 3. Red snapper length distributions on removal (black bars) and nonremoval (gray bars) artificial reefs at the start (13 October – 7 November 2005) and the end (1–23 June 2006) of the experiment. Frequency distributions did not differ at the start (*a*), but differed at the end (*b*) ($P \leq 0.05$).



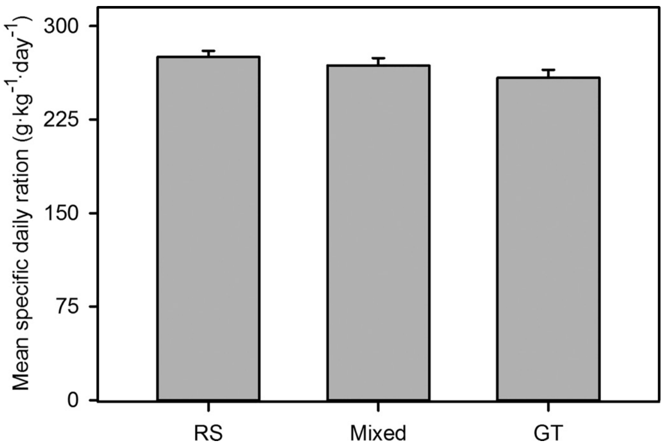


Fig. 4. Mean (+ standard error, SE) specific daily ration (g·kg^{-1}·day^{-1}) consumed by red snapper alone (RS), red snapper and gray triggerfish together (Mixed), and gray triggerfish alone (GT) in laboratory tanks. Means did not differ among treatments ($P > 0.1$).

Discussion

In the field experiment, the mean number of red snapper did not differ between removal and nonremoval treatments. However, a higher frequency of smaller size classes (<400 mm TL) of red snapper on removal compared with nonremoval treatments in the field provides evidence for competition between red snapper and gray triggerfish and was consistent with previous studies. These changes in size distributions were likely caused by gray triggerfish aggression having less effect on larger red snapper. Thus, after gray triggerfish removals, smaller red snapper were able to colonize these reef sites, which caused a shift in size class to smaller red snapper.

In the laboratory experiments, gray triggerfish presence negatively affected the growth rate of red snapper. Similar results were shown when age-0 European perch were mixed with roach in enclosed cages, which caused lower growth rates of perch that were sometimes negative (Persson 1987). Olson et al. (1995) also used enclosures and observed slower growth rate in age-0 largemouth bass (*Micropterus salmoides*) with high densities of bluegill (*Lepomis macrochirus*). Numerous bite marks on red snapper in mixed treatments (Fig. 6*a*) but not in red snapper alone treatments (Fig. 6*b*) suggest interference competition may have been a consequence of direct aggression by gray triggerfish excluding red snapper from ingesting food (Schoener 1983; Kindinger 2016).

These laboratory observations are consistent with previous behavioral field studies. For example, male and female gray triggerfish showed aggressive behavior during the spawning season (June–July) in the northern Gulf of Mexico, chasing away numerous other species of fish in the families Lutjanidae, Serranidae, and Carangidae (Simmons and Szedlmayer 2012). The males were especially aggressive and would attack any approaching fish and SCUBA divers. The only species not attacked by nesting and guarding gray triggerfish was a large (2 m) sandbar shark (*Carcharhinus plumbeus*) (Simmons and Szedlmayer 2012).

The lack of red snapper abundance differences from field removal experiments could indicate that competition in the open environment does not exist, but based on the laboratory growth rate effects and size frequency shifts, it is likely that other factors masked field abundance effects. Perhaps sample sizes were too low ($n = 12$) for both removal and nonremoval reefs, and further field experiments should attempt to increase sample size. For example, in the present study the pooled standard deviation = 30 and the sample size was $n = 12$ per treatment; thus, there needed to be a 37% difference in red snapper abundance between removal and nonremoval treatments for an 80% probability of correctly

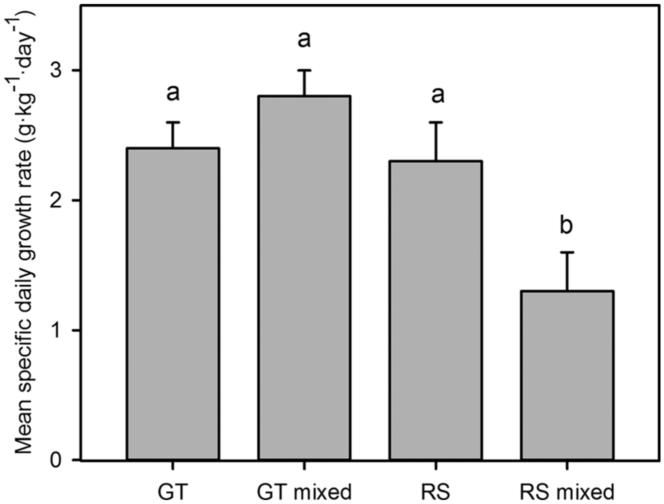
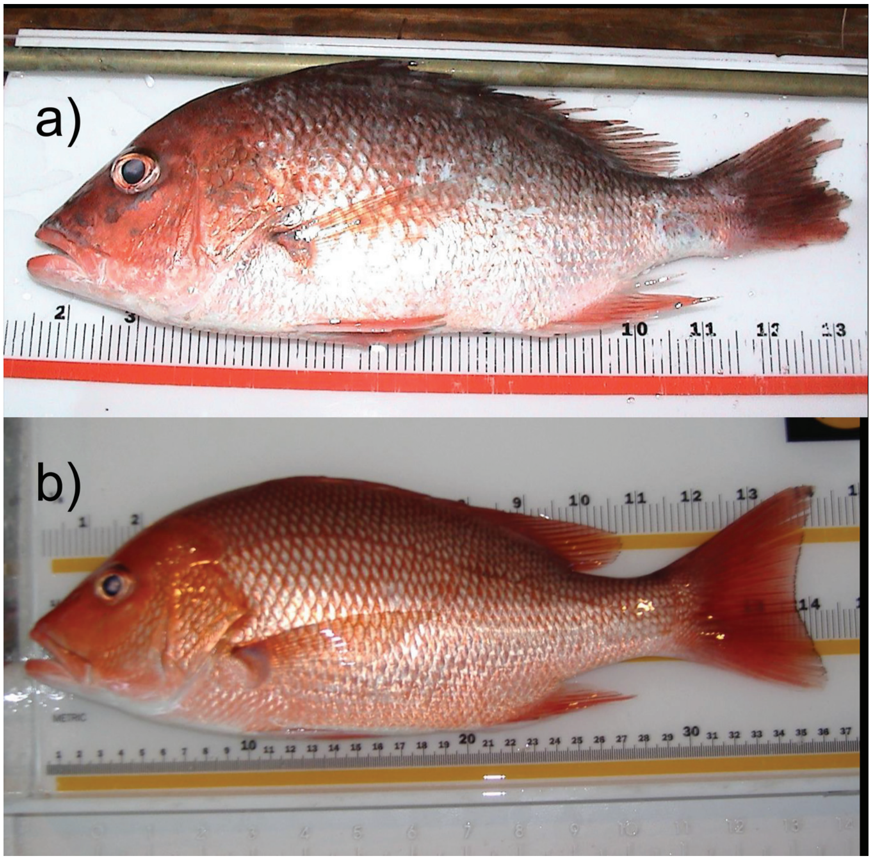


Fig. 5. Mean (+ standard error, SE) specific daily growth rate (g·kg^{-1}·day^{-1}) for the four treatments: gray triggerfish alone (GT), gray triggerfish mixed (GT mixed), red snapper alone (RS), and red snapper mixed (RS mixed). Significant differences ($P \leq 0.05$) are shown by different letters among treatments.

rejecting the null hypothesis. If sample size is increased to $n = 38$ per treatment, detectable differences in abundance of red snapper decreases to 20% (Steidl et al. 1997). Another possibility for lack of significant differences in red snapper abundance between removal and nonremoval reefs at the end of the experiment may have been that too much time had elapsed (7 months) before ending the experiment. For example, other studies documented competitive interactions after much shorter time periods between surveys (i.e., 2 weeks; Hixon 1980; Sano 1990). A third reason was that experimental artificial reefs used during the present study were open to public fishing. It is likely that increased fishing mortality was responsible for the decrease in gray triggerfish on the nonremoval reefs due to the widespread destruction of artificial reefs from Hurricane Katrina in August 2005, when a majority of the private and public reefs were destroyed, buried, or moved in the northern Gulf of Mexico (Kaiser and Kasprzak 2008). For example, Hurricane Katrina displaced an offshore oil platform onto the beach at Dauphin Island, Alabama, USA. As a result of this reef loss, fishers concentrated their effort on the remaining army tanks used in the present study, one of the few types of artificial reef that survived Hurricane Katrina due to large size and heavy weight (51 tonnes). Further, this fishing mortality effect was only detectable on the nonremoval reefs, because they had higher abundances available for capture, while the removal reefs had most (91%) gray triggerfish already removed. In addition, high fishing mortality ($F = 0.41$) of red snapper has been documented on artificial reefs in the same study area (Williams-Grove and Szedlmayer 2016). These uncontrolled variables may mask any competitive interaction effects between gray triggerfish and red snapper abundance. Future removal studies should attempt to use experimental reef sites with locations that are not released to sport and commercial fishers and reduce the time period between surveys.

The present field removal study only used artificial habitats, but both species are also associated with natural rock–reef structure in the Gulf of Mexico (Frazer and Lindberg 1994; Kurz 1995; Lingo and Szedlmayer 2006). Ecologically, artificial reefs are temporary compared with natural reefs and provide different structure, biotic communities, and ecological functions compared with natural habitats (Simon et al. 2013; Cresson et al. 2014; Ferrario et al. 2016). In fact, artificial reefs may be considered disturbed habitat when compared with naturally occurring sand–mud substrates

Fig. 6. Example of red snapper showing bite marks from the laboratory when held with gray triggerfish (*a*) compared with red snapper held alone (*b*).



and scattered natural rock reefs in the northern Gulf of Mexico (Dufrene 2005; Gallaway et al. 2009; Schroeter et al. 2015). The time-stability hypothesis suggests that competition may be greater on artificial reefs compared with natural reefs, because species have more time to evolve greater specialization and reduced competition on natural reefs (Hessler and Sanders 1967; Sanders 1968; McClain and Schlacher 2015). Thus, in the present study the competitive interaction of gray triggerfish and red snapper could be the result of a disturbed habitat, and interactions may not be detected on more stable natural habitats. Studies that address these ecological functions of artificial habitats are limited (Smith et al. 2015), and future studies comparing gray triggerfish and red snapper interactions between natural and artificial habitats are needed.

At the time of the present study, red snapper and gray triggerfish were considered overfished, and management strategies were separately focused on increasing stocks of both species by reducing fishing mortality rates in an effort to rebuild these stocks (SEDAR 31 2015; SEDAR 43 2015). Questions remain as to the importance of food or habitat limitation, but gray triggerfish and red snapper showed competitive interactions based on significant differences in red snapper length frequencies in field removal treatments and lower growth rates of red snapper when held with gray triggerfish in laboratory experiments. Considering that these interactions may negatively affect one species over another, management strategies may need to be altered. For example, increasing gray triggerfish stocks that aggressively chase smaller red snapper (<400 mm TL) off critical habitats could cause increased natural mortality from predators and result in unintentional declines in red snapper stocks due to competitive exclusion on reefs (Lorenzen and Enberg 2001; Kindinger 2016). Managers could use this ecological information in the design and placement of artificial structures that might help protect smaller red snapper from gray triggerfish aggression. In addition, the direct gray triggerfish effect that caused reduced growth rates in red snapper would likely further decrease red snapper abundance (Lorenzen and Enberg 2001). Estimating such sources of natural mortality for younger age classes becomes increasingly more important as managers move towards ecosystem-based management strategies (May et al. 1979; Agnew et al. 2000; Coleman et al. 2011).

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References

Agnew, D.J., Nolan, C.P., Beddington, J.R., and Baranowski, R. 2000. Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. Can. J. Fish Aquat. Sci. **57**(2): 429–440. doi:10.1139/f99-264.

Begon, M., Harper, J.L., and Townsend, C.R. 1996. Ecology, individuals, populations, and communities. 3rd ed. Blackwell Science, Cambridge, Mass.

Blitch, K.M. 2000. The feeding habits of gray triggerfish, *Balistes capriscus* (Gmelin), from the northeast Gulf of Mexico. M.Sc. thesis, Department of Fisheries and Allied Aquacultures, University of Auburn, Auburn, Alabama.

Bortone, S.A., Kimmel, J.J., and Bundrick, C.M. 1989. A comparison of three methods for visually assessing reef fish communities: time and area compensation. Northeast Gulf Sci. **10**: 85–96. Available from http://goms.disl.org/assets/goms_disl/uploads/toc/1977_1990/Vol10No2P85-96.pdf [accessed 1 June 2017].

Coleman, F.C., Scanlon, K.M., and Koenig, C.C. 2011. Groupers on the edge: shelf edge spawning habitat in and around marine reserves of the northeastern Gulf of Mexico. Prof. Geog. **63**: 456–474. doi:10.1080/00330124.2011.585076.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. **122**(5): 661–696. doi:10.1086/284165.

Cresson, P., Ruitton, S., and Harmelin-Vivien, M. 2014. Artificial reefs do increase secondary biomass production: mechanisms evidenced by stable isotopes. Mar. Ecol. Prog. Ser. **509**: 15–26. doi:10.3354/meps10866.

Dufrene, T.A. 2005. Geological variability and Holocene sedimentary record on the northern Gulf of Mexico inner to mid-continental shelf. M.Sc. thesis, Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana.

Fernandes, W.P.A., Griffiths, S.W., Ibbotson, A.T., Bruford, M.W., and Riley, W.D. 2015. The role of density and relatedness in wild juvenile Atlantic salmon growth. J. Zool. **295**(1): 56–64. doi:10.1111/jzo.12188.

Ferrario, F., Ivesa, L., Jaklin, A., Perkol-Finkel, S., and Airoldi, L. 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. J. Appl. Ecol. **53**: 16–24. doi:10.1111/1365-2664.12533.

Frazer, T.K., and Lindberg, W.J. 1994. Refuge spacing similarly affects reef-associated species from three phyla. Bull. Mar. Sci. **55**(2–3): 388–400. Available from http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1994/00000055/F0020002/art00013 [accessed 19 December 2016].

Gallaway, B.J., Szedlmayer, S.T., and Gazey, W.J. 2009. A life history review for red snapper in the Gulf of Mexico with an evaluation of the importance of offshore petroleum platforms and other artificial reefs. Rev. Fish. Sci. **17**(1): 48–67. doi:10.1080/10641260802160717.

Herbig, J.L., and Szedlmayer, S.T. 2016. Movement patterns of gray triggerfish, *Balistes capriscus*, around artificial reefs in the northern Gulf of Mexico. Fish. Manage. Ecol. **23**: 418–427. doi:10.1111/fme.12190.

Hessler, R.R., and Sanders, H.L. 1967. Faunal diversity in the deep sea. Deep-Sea Res. Oceanogr. Abstracts, **14**: 65–78. doi:10.1016/0011-7471(67)90029-0.

Hixon, M.A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. Ecology, **61**(4): 918–931. doi:10.2307/1936761.

Hixon, M.A., and Beets, J.P. 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. **44**(2): 666–680. Available from http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1989/00000044/00000002/art00012 [accessed 19 December 2016].

Jones, G.P. 1986. Food availability affects growth in a coral reef fish. Oecologia, **70**(1): 136–139. doi:10.1007/BF00377123. PMID:28311299.

Kaiser, M.J., and Kasprzak, R.A. 2008. The impact of the 2005 hurricane season on the Louisiana artificial reef program. Mar. Pol. **32**(6): 956–967. doi:10.1016/j.marpol.2008.02.006.

Kindinger, T.L. 2016. Symmetrical effects of interspecific competition on congeneric coral-reef fishes. Mar. Ecol. Prog. Ser. **555**: 1–11. doi:10.3354/meps11836.

Kurz, R.C. 1995. Predator–prey interactions between gray triggerfish, *Balistes capriscus* (Gmelin), and a guild of sand dollars around artificial reefs in the northeastern Gulf of Mexico. Bull. Mar. Sci. **56**(1): 150–160. Available from http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1995/00000056/00000001/art00009 [accessed 19 December 2016].

Lingo, M.E., and Szedlmayer, S.T. 2006. The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. Environ. Biol. Fish. **76**(1): 71–80. doi:10.1007/s10641-006-9009-4.

Lorenzen, K., and Enberg, K. 2001. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. B Biol. Sci. **269**: 49–54. doi:10.1098/rspb.2001.1853.

May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J., and Laws, R.M. 1979. Management of multispecies fisheries. Sci. **205**(4403): 267–277. doi:10.1126/science.205.4403.267.

McClain, C.R., and Schlacher, T.A. 2015. On some hypotheses of diversity of animal life at great depths on the sea floor. Mar. Ecol. **36**: 1–24. doi:10.1111/maec.12288.

Mudrak, P.A., and Szedlmayer, S.T. 2012. Proximity effects of larger resident fishes on recruitment of age-0 red snapper in the northern Gulf of Mexico. Trans. Am. Fish. Soc. **141**(2): 487–494. doi:10.1080/00028487.2012.667045.

Olson, M.H., Mittelbach, G.G., and Osenberg, C.W. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecol. **76**(6): 1758–1771. doi:10.2307/1940708.

Ouzts, A.C., and Szedlmayer, S.T. 2003. Diel feeding patterns of red snapper on artificial reefs in the north-central Gulf of Mexico. Trans. Am. Fish. Soc. **132**: 1186–1193. doi:10.1577/T02-085.

Parker, R.O., Colby, D.R., and Willis, T.D. 1983. Estimated amount of reef habitat on a portion of the U.S. Atlantic and Gulf of Mexico continental shelf. Bull. Mar. Sci. **33**: 935–940. Available from http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1983/00000033/00000004/art00012 [accessed 14 June 2017].

Persson, L. 1987. Competition-induced switch in young of the year perch, *Perca fluviatilis*: an experimental test of resource limitation. Environ. Biol. Fishes, **19**(3): 235–239. doi:10.1007/BF00005353.

Piko, A.A., and Szedlmayer, S.T. 2007. Effects of habitat complexity and predator exclusion on the abundance of juvenile red snapper. J. Fish. Biol. **70**(3): 758–769. doi:10.1111/j.1095-8649.2007.01336.x.

Robertson, D.R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology, **77**(3): 885–899. doi:10.2307/2265509.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Nat. **102**(925): 243–282. doi:10.1086/282541.

Sano, M. 1990. Patterns of habitat and food utilization in two coral-reef sandperches (Mugiloididae): competitive or noncompetitive coexistence? J. Exp. Mar. Biol. Ecol. **140**(3): 209–223. doi:10.1016/0022-0981(90)90128-Y.

Schmitt, R.J., and Holbrook, S.J. 1986. Seasonally fluctuating resources and temporal variability of interspecific competition. Oecologia, **69**(1): 1–11. doi:10.1007/BF00399030. PMID:28311677.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. **122**(2): 240–285. doi:10.1086/284133.

Schroeter, S.C., Reed, D.C., and Raimondi, P.T. 2015. Effects of reef physical structure on development of benthic reef community: a large-scale artificial reef experiment. Mar. Ecol. Prog. Ser. **540**: 43–55. doi:10.3354/meps11483.

SEDAR 31. 2015. Stock Assessment Update Report of Red Snapper in the Gulf of Mexico: 1872–2013, with Provisional 2014 Landings [online]. Southeast Data Assessment and Review. Available from http://sedarweb.org/docs/suar/SEDARUpdateRedSnapper2014_FINAL_9.15.2015.pdf [accessed 19 December 2016].

SEDAR 43. 2015. Stock Assessment Report. Gulf of Mexico Gray Triggerfish. Southeast Data Assessment and Review. Available from http://sedarweb.org/docs/sar/S43_SAR_FINAL.pdf [accessed 19 December 2016].

Shulman, M.J., Ogden, J.C., Ebersole, J.P., McFarland, W.N., Miller, S.L., and Wolf, N.G. 1983. Priority effects in the recruitment of juvenile coral reef fishes. Ecology, **64**: 1508–1513. doi:10.2307/1937505.

Simmons, C.M., and Szedlmayer, S.T. 2011. Recruitment of age-0 gray triggerfish to benthic structured habitat in the Northern Gulf of Mexico. Trans. Am. Fish. Soc. **140**: 14–20. doi:10.1080/00028487.2011.545002.

Simmons, C.M., and Szedlmayer, S.T. 2012. Territoriality, reproductive behavior, and parental care in gray triggerfish, *Balistes capriscus*, from the northern Gulf of Mexico. Bull. Mar. Sci. **88**(2): 197–209. doi:10.5343/bms.2011.1012.

Simon, T., Joyeux, J.C., and Pinheiro, H.T. 2013. Fish assemblages on shipwrecks and natural rocky reefs strongly differ in trophic structure. Mar. Environ. Res. **90**: 55–65. doi:10.1016/j.marenvres.2013.05.012. PMID:23796542.

Smith, J.A., Lowry, M.B., and Suthers, I.M. 2015. Fish attraction to artificial reefs not always harmful: a simulation study. Ecol. Evol. **5**(20): 4590–4602. doi:10.1002/ece3.1730. PMID:26668725.

Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. **60**(3): 1129–1157. Available from http://www.ingentaconnect.com/contentone/umrsmas/bullmar/1997/00000060/00000003/art00029 [accessed 14 June 2017].

Steidl, R.J., Hayes, J.P., and Schauber, E. 1997. Statistical power analysis in wildlife research. J. Wild. Manage. **61**(2): 270–279. doi:10.2307/3802582.

Szedlmayer, S.T., and Lee, J.D. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. Fish. Bull. **102**(2): 366–375. Available from http://fishbull.noaa.gov/1022/1022toc.htm [accessed 19 December 2016].

Williams-Grove, L.J., and Szedlmayer, S.T. 2016. Mortality estimates for red snapper, *Lutjanus campechanus*, based on ultrasonic telemetry in the northern Gulf of Mexico. N. Am. J. Fish Manage. **36**(5): 1036–1044. doi:10.1080/02755947.2016.1184197.

Wootton, R.J. 1998. Ecology of teleost fishes. 2nd ed. Kluwer Academic, Dordrecht, the Netherlands.