

# Competitive interactions among juvenile and adult life stages of northern Gulf of Mexico red snapper *Lutjanus campechanus* and a tropical range-expanding congener

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**ABSTRACT:** Associated with regional warming, poleward species range expansions may have important consequences for biological communities. Within northern Gulf of Mexico (nGOM) offshore habitats, higher abundance of tropically associated lane snapper *Lutjanus synagris* is correlated with rising temperatures. Increased presence of juvenile and adult lane snapper could result in important competitive interactions with nGOM reef fishes, such as economically important red snapper *L. campechanus*, at multiple life stages and cause shifts in resource utilization and species composition of offshore fish assemblages. We investigated interactions between adult and juvenile lane and red snapper within experimental mesocosms. Although no significant effects on prey consumption were observed, interspecific competition between adults and juveniles was strongest, as adult lane snapper utilized habitats at higher rates than single juvenile red snapper in interaction trials. Additionally, adult red snapper most strongly displaced single juvenile lane snapper and increased their swimming activities in the presence of heterospecific juveniles. Adult red snapper also aggressively chased juvenile lane snapper and displaced them from habitats. However, less pronounced effects were observed for grouped juveniles in the presence of adults, especially juvenile red snapper, while adult lane snapper swam less in the presence of grouped juvenile lane and red snapper. Additionally, single juvenile red snapper swimming activities and prey consumption in the presence of adult snappers did not significantly differ from control values. Therefore, at small scales adult lane snapper may partially displace single juvenile red snapper, but clusters of red and lane snapper juveniles may be resilient to competitive effects of adult lane snapper and exert partial competitive pressures on them. As expected, we found that elevated aggressiveness by larger individuals resulted in dominance in space occupancy in one-on-one interactions. These findings suggest that prior occupation of preferred hard bottom habitat may be a determining factor for grouped juvenile red snapper competing against similar sized or larger individuals. Overall, our results indicate varying competitive vulnerabilities of red snapper to climate-related range expansions of tropical congeners.

**KEY WORDS:** Adult–juvenile interactions · Competition · Lane snapper · Mesocosm · Priority effects · Range shifts · Red snapper

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## 1. INTRODUCTION

Coincident with regional warming, numerous range expansions of both terrestrial and marine species into higher latitudes continue to be observed

(Parmesan & Yohe 2003, Hickling et al. 2006, Hollowed et al. 2013, Vergés et al. 2014). Increasing migrations of lower latitude fish species into temperate and subtropical regions are occurring, with growing likelihood of their permanent establishment in these

locations (Perry et al. 2005, Nakamura et al. 2013, Feary et al. 2014). Along with increases in regional species richness, compounding climate- and fishing-related changes in marine fish populations and communities have taken place (Cheung et al. 2009, Doney et al. 2012, Vergés et al. 2014), with potentially great implications for worldwide fisheries harvest (Roessig et al. 2004, Brander 2007, Stenevik & Sundby 2007). While range expansions alone do not necessarily alter community structure or ecosystem processes (Johnson et al. 2011), increased species richness could result in elevated rates of competitive exclusion (Mills et al. 2004, Olden et al. 2006, Harley 2011) and lead to localized extinctions (Cheung et al. 2009). Owing to their higher growth and metabolic rates, tropical species may be favored in competitive interactions with temperate residents (Ettinger & HilleRisLambers 2013).

Across the northern Gulf of Mexico (nGOM), large and historically unprecedented increases in the abundance of juvenile lane snapper *Lutjanus synagris* and other tropically associated fish species were observed within inshore seagrass meadows beginning in 2005–2006 (Fodrie et al. 2010). While tropical fishes have been seasonally observed in the nGOM (Lukens 1981), their more recent increased abundance has been correlated with regional warming trends (Fodrie et al. 2010). In the nGOM, the snapper/grouper complex is of great ecological (Pérez España 2003) and economic importance, as evidenced by the historically productive red snapper *L. campechanus* fishery (Rivas 1966, Goodyear 1995). Fodrie et al. (2010) suggested that overharvesting of ecologically and economically important red snapper (McAllister 2003) might have contributed to the recent increase in the abundance of nGOM lane snapper by lowering competition with red snapper and enabling increased spawning stocks. Given strong overlaps in life histories (Martinez-Andrade 2003, Patterson et al. 2014), diets (Franks & VanderKooy 2000, Wells & Cowan 2008), and habitat use (Gallaway et al. 2009), competitive interactions among late juvenile and adult red and lane snapper in the limited natural reef habitats of the nGOM (Parker et al. 1983) have the potential to occur, and if so, could have significant impacts on the ecology of nGOM reef fish assemblages.

Strong inter-cohort competitive interactions within red snapper populations have previously been observed both in the lab (Bailey et al. 2001) and in nature (Mudrak & Szedlmayer 2012). In both settings, larger juvenile and adult red snapper aggressively displaced smaller juveniles from structured reef habitats into nearby less structured habitats (i.e. sediment away from concrete blocks in laboratory

experiments and lower complexity artificial reef habitats in nature). Additionally, juvenile red snapper have been observed displacing juvenile lane snapper from structured habitats in experimental mesocosms (Marshak & Heck 2017). Following from these earlier observations, it seems likely that adult red snapper could displace adult lane snapper from reefs into less structured habitats, where these displaced adult lane snapper would overlap with juvenile red and/or juvenile lane snapper. Given the potential size advantage of earlier maturing lane snapper (Martinez-Andrade 2003), juvenile red snapper could be negatively affected by adult lane snapper. Likewise, larger adult lane snapper may impose competitive pressures upon juvenile lane snapper. Additionally, currently depleted numbers of adult red snapper caused by intense fishing pressure (Cowan et al. 2011) could favor successful colonization of lane snapper in habitats with low red snapper abundance.

Based on this background information, we designed a study whose objectives were to measure both intra- and interspecific competitive interactions between juveniles and adults of both red and lane snappers under current environmental conditions. Because of the well-known aggressive nature of red snapper (Bailey et al. 2001, Mudrak & Szedlmayer 2012, Marshak & Heck 2017), and a presumed competitive advantage of larger size in adults (i.e. enhanced ability to occupy larger space exploitatively, faster/greater access to and consumption of prey, greater effect of aggressive behaviors on and greater resilience to aggressions from smaller individuals), we hypothesized that even though adults of both snapper species would dominate juvenile red and lane snappers in prey consumption and habitat use, adult red snapper would outcompete juveniles of both snapper species more successfully than would adult lane snapper.

## 2. MATERIALS AND METHODS

Control and interaction mesocosm experiments to quantify inter- and intraspecific competitive intensities among juvenile and adult red and lane snapper were undertaken at the Dauphin Island Sea Lab indoor wetlab facility from 29 November 2013 to 27 January 2014. Following lengths at maturity ( $L_m$ ) defined for GOM red snapper ( $L_m$ : 350 mm total length [TL]; Collins et al. 1996) and lane snapper ( $L_m$ : 282 mm TL; Szedlmayer & Shipp 1994), fishes were classified as juveniles and adults. Juvenile (lane: 105–226 mm TL; red: 125–310 mm TL) and adult (lane: 430–451 mm

TL; red: 392–533 mm TL) red and lane snapper were collected in offshore natural and artificial reef habitats up to 65 km south of coastal Alabama and western Florida using buoyed small chevron traps (max. dimensions:  $0.7 \times 0.6 \times 0.29$  m; 0.635 cm mesh) and hooked lines. All fishes were transported live in aerated coolers from their collected offshore sites to the wetlab facility, and after introduction to holding tanks were allowed to acclimate for 2 wk prior to experiments. During acclimation and experimental periods, juvenile snappers were cumulatively fed 0.250 kg of squid *Loligo* sp. twice weekly, following Simmons & Szedlmayer (2018), while adult snappers were each given 0.250 kg of squid twice weekly. All individuals used in trials were starved 24 h prior to experiments. Wells et al. (2008b) and Franks & VanderKooy (2000) identified squid and crustaceans as a significant component in diets of juvenile and adult snappers.

Behavioral and consumptive interactions between adult and juvenile lane and red snapper were documented in mesocosms (1.82 m diameter, 0.76 m height) filled with saltwater to 0.5 m depth, lined with fine sediment, and containing 2 haphazardly placed concrete blocks (dimensions:  $0.39 \times 0.19 \times 0.19$  m) as simulated structural reef habitat. Given the high number of potential density combinations required to examine competition among species and life stages in a mixed or response surface experimental design, an additive design was employed to address inter- and intraspecific competitive interactions between adults and juveniles, and all experimental trials were executed in a randomized order. Although alternative experimental designs such as substitutive designs are capable of testing for the relative intensity of both intra- and interspecific competition, they are not appropriate for testing for either the occurrence or absolute magnitude of competition alone (Goldberg & Scheiner 2001).

Each experimental trial ( $n = 35$ ; Table 1) was video recorded with mounted cameras for 3 h. Trials were performed between 08:30 and 20:15 h. To approximate relative offshore adult and juvenile snapper frequencies in nGOM habitats (based on Wells et al. 2008a), 1 or 3 juvenile fish per snapper species and 1 adult snapper were used in each intra- and interspecific investigation between life stages, while corresponding uniformly stocked monospecific control trials of 1 adult, 1 juvenile, or 3 juvenile individuals were undertaken. Offshore surveys by divers and captures by hooked line suggest that multiple juvenile lane snapper are less likely to coexist with adult red snapper under current conditions (Mudrak & Szedlmayer 2012, Addis et al. 2013, Garner et al. 2014). There-

fore, interactions among adult red snapper and 3 lane snapper were not examined.

With the number of offshore lane snapper increasing in association with regional warming, we theorized that local prey resource limitation could occur at similar scales to those of our experimental mesocosms as predator species richness and density increased within and adjacent to limited natural reef habitat. A total of 10 juvenile blue crabs *Callinectes sapidus* (1.0–2.5 cm carapace width) were used as prey for each trial, independent of snapper density. This density of 1.1 crabs  $m^{-2}$  is much less than published densities of decapod crustacean prey adjacent to or within natural nGOM reef habitats (Darnell et al. 1987), and is a proxy for benthic prey limitation that may foster competitive interactions. Although field studies have demonstrated the importance of semi-continuous pelagic squid and crustaceans toward total reef fish food supply (Szedlmayer & Lee 2004), Marshak & Heck (2017) have additionally observed in laboratory trials that juvenile snappers can and do prey upon blue crabs of this size range, while Wells et al. (2008b) also documented major contributions of benthic crustaceans to the diets of juvenile and adult snapper in offshore nGOM habitats.

Blue crabs were collected offshore by trawling or within nearshore seagrass and marsh habitats by seining. Snappers and crabs were introduced to treatment tanks in a randomly determined direction of entry and sequence per treatment. Some adult and juvenile snappers and surviving crabs (~11%) were re-used in subsequent trials; however, this was done non-consecutively and at least 2 d after that individual's previous use in trials to allow for re-acclimation. Additionally, to minimize bias, individuals that were used for a given trial were not matched together more than once. Snappers were allowed to acclimate for 1 h in experimental tanks prior to trials, and blue crabs were haphazardly introduced to tanks at the onset of the experiment. Given the large size of the experimental tanks and haphazard placement of prey ( $n = 10$  crabs), snapper awareness of initial blue crab location was therefore minimized due to lowered probability of immediate encounter.

Prior to each trial, data for water temperature, salinity, dissolved oxygen, and time of day were recorded. To minimize parasite and disease outbreak within indoor facilities, holding tanks and experimental tanks were held at mesohaline salinities (~15). Snappers were allowed to slowly acclimate to mesohaline salinities during the 2 wk acclimation period, and no noticeable effects upon their behavior or consumption of rationed squid were observed

Table 1. Experimental mesocosm combinations assessing interactions between adult and juvenile (juv) lane and red snapper. Combinations are listed according to trials between juveniles (1 or 3 ind.) and 1 adult. In total, 17 trials were run for the paired species and life-stage combinations, in addition to 18 monoculture control trials to account for identity of snapper species and life-stage treatment<sup>-1</sup>. X: 3 replicates; Y: 2 replicates

Treatment	Density of fishes (no. per tank)				Total replicates
	1	2	3	4	
Juv lane snapper control	X		X		6
Juv red snapper control	X		X		6
Adult lane snapper control	X				3
Adult red snapper control	X				3
1 Juv lane – 1 adult lane		X			3
3 Juv lane – 1 adult lane				X	3
1 Juv lane – 1 adult red		Y			2
1 Juv red – 1 adult lane		Y			2
3 Juv red – 1 adult lane				Y	2
1 Juv red – 1 adult red		Y			2
3 Juv red – 1 adult red				X	3
Total = 35 replicates					

throughout the period of study. At the conclusion of each 3 h trial, the number of remaining crabs was recorded and all fishes were measured (TL) to the nearest mm and weighed to the nearest g. Carapace width of blue crab prey was measured to the nearest mm and divided by predator TL for a given trial to calculate relative prey size. Videos were downloaded from camera Secure Digital (SD) cards, and each video was analyzed in its entirety to quantify swimming activities at concrete blocks and throughout the mesocosm, adult and juvenile snapper interactions (i.e. time swimming together, interspecific approaches upon and retreats from fishes), consumption rates, time pursuing prey, predatory attacks, non-consumption prey approaches, retreats from prey, ignoring nearby prey by fishes, and aggressive interactions (i.e. chasing, nipping, biting, pushing, or actively displacing others from habitat) between adult and juvenile snappers during all experimental and control trials as defined in Table 2. The relevance of these variables toward demonstrating competitive advantage has been shown in the scientific literature, where increased swimming activity by fishes in the presence of other species or conspecifics has been strongly associated with social dominance and aggression in

behavioral interactions (Gomez-Laplaza & Morgan 2003, McDonald et al. 2011), and consumption success (Overli et al. 1998). All values were standardized per number of fish of each species used in each trial to account for varying fish densities. As quantified behavioral and consumption variables (Table 2) were not found to conform to parametric assumptions (i.e. homoscedasticity examined using Levine's *F*-test; normality examined using Shapiro-Wilk test), all behavioral and consumption variables were analyzed using 1-way Kruskal-Wallis tests ( $n = 13$ ) and post hoc Conover-Iman multiple comparisons. In addition, relations between behavioral variables of juveniles and adults, environmental parameters, time of day, and fish size were assessed using linear and non-linear multiple regressions (Zar 1999).

### 3. RESULTS

Average ( $\pm$ SE) environmental variables (temperature, salinity, and dissolved oxygen) for all trials were  $17.8 \pm 0.32^\circ\text{C}$ ,  $14.7 \pm 0.07$ , and  $15.1 \pm 0.54 \text{ mg l}^{-1}$ , respectively, and no significant differences among temperature or dissolved oxygen among trials were found (temperature: Kruskal-Wallis  $K = 18.275$ ,  $p = 0.108$ ; oxygen:  $K = 5.669$ ,  $p = 0.932$ ). Specific values for control and interaction trials are listed in Table 3, and little variation among measurements was observed. Although experimental adult–juvenile interaction trials were performed at cooler temperatures (max.  $3.6 \pm 0.33^\circ\text{C}$ ) than control monoculture trials, no significant difference was observed. While experimental salinities only ranged from 13.9–15.3, they differed significantly among trial types ( $K = 26.457$ ,  $p = 0.009$ ).

Average TLs (Table 4) and weight to length (W/L) ratios were similar for juvenile lane snapper in control and experimental trials (Mann-Whitney  $U_{\text{length}} = 97$ ,  $p = 0.514$ ;  $U_{\text{W/L}} = 110$ ,  $p = 0.189$ ), and, although larger than juvenile lane snapper, similar sized juvenile red snapper were used in control and experimental trials ( $U_{\text{length}} = 125$ ,  $p = 0.548$ ;  $U_{\text{W/L}} = 119$ ,  $p = 0.730$ ). Although significantly larger in length for control trials ( $U_{\text{length}} = 30$ ,  $p = 0.013$ ;  $U_{\text{W/L}} = 20$ ,  $p = 0.441$ ), average sizes among adult lane snapper in experimental and control trials differed only by  $12.9 \pm 0.5 \text{ mm}$ . However, no significant difference in size was observed among adult red snapper used in control or experimental trials ( $U_{\text{length}} = 17$ ,  $p = 0.133$ ;  $U_{\text{W/L}} = 17$ ,  $p = 0.183$ ). For all fishes used in trials, adult lane snapper were significantly larger than adult red snapper, despite only a 3 mm average

Table 2. Recorded fish behaviors in experimental mesocosms during adult and juvenile red and lane snapper control and interaction trials

Term (dependent variable)	Definition
Percent time spent interacting (% trial time)	Percent time of the entire 3 h trial in which fish(es) of one or more species overlapped in close proximity to each other (<20 cm), approached each other, or displayed aggressions to each other
Percent time swimming tank (% trial time swimming)	Percent time of the entire 3 h trial in which at least one fish of a given species swam beyond the boundaries of concrete block habitat and covered $\geq 25\%$ of the experimental mesocosm area in a given swim
Percent time swimming block (% trial time swimming)	Percent time of the entire 3 h trial in which at least one fish of a given species swam or shifted at or around the perimeter of concrete block habitat, not exceeding 25% of the experimental mesocosm area in a given swim
Percent time swimming at center (% trial time swimming)	Percent time of the entire 3 h trial in which at least one fish of a given species swam or shifted at or around the perimeter of the center of the mesocosm tank, not exceeding 25% of the mesocosm area in a given swim
Percent time huddling (% trial time huddling)	Percent time of the entire 3 h trial in which at least 2 fish of a given species aggregated together, but did not swim, at the edge, center, or at concrete block habitat of the experimental mesocosm.
Number of approaches (or retreats)	Number of times a fish of a given species directly approached (or retreated from) a fish of another species
Number of crabs consumed per fish	Number of blue crab prey observed partially or fully consumed by each fish of a given species
Number of predatory attempts per fish	Number of times each fish attacked blue crab prey
Percent time pursuing prey	Percent time of the entire 3 h trial in which fish of a given species were observed following, approaching, stalking, or attempting to consume blue crab prey prior to successful consumption
Number of prey approaches per fish	Number of times each fish followed, stalked, or actively moved within proximity of blue crab prey
Number of retreats from prey per fish	Number of times each fish retreated from approaching blue crab prey
Number of ignores of prey per fish	Number of times each fish did not respond to prey within close proximity, or to prey that passed directly in front of fish
Number of aggressions per fish (chases, bites, pushes)	Number of times each fish chased another fish, nipped at or bit another fish, or pushed its body against another fish to cause the fish to react by moving at or from its location; Both intra- and interspecific aggressions were examined

length and a 20 mm median length differential (lane:  $439.8 \pm 1.9$  mm [SE],  $440 \pm 8$  mm [inter-quartile range, IQR]; red:  $436.7 \pm 16.1$  mm SE,  $420 \pm 15$  mm IQR;  $U_{\text{length}} = 104$ ,  $p = 0.014$ ;  $U_{W/L} = 97$ ,  $p = 0.047$ ). Additionally, juvenile red snapper were significantly larger than juvenile lane snapper (lane:  $130.3 \pm 5.0$  mm [SE]; red:  $282.2 \pm 10.9$  mm;  $U_{\text{length}} = 51$ ,  $p < 0.0001$ ;  $U_{W/L} = 51$ ,  $p < 0.0001$ ). Relative blue crab prey sizes were similar across control and interaction trials species<sup>-1</sup>, while they were larger for juvenile lane snapper than juvenile red snapper.

Swimming activities (Fig. 1) by fishes around the entire mesocosm ( $K = 30.484$ ,  $df = 19$ ,  $p = 0.046$ ) significantly differed by species and life stages within and among control and interaction trials, while no significant difference was observed for swimming times at block structures ( $K = 19.777$ ,  $df = 19$ ,  $p = 0.408$ ). Most fishes swam predominantly around the entire tank, except single juvenile lane snapper and adult red snapper in control trials, which spent proportionally more time swimming near blocks than around the entire tank. Proportionally, fishes spent very little

Table 3. Observed measured environmental parameters (mean  $\pm$  1 SE) in experimental mesocosms during adult and juvenile (juv) lane and red snapper control and interaction trials

Treatment	Temperature ( $^{\circ}$ C)	Salinity	Dissolved oxygen (mg l $^{-1}$ )
Adult lane snapper control	18.5 $\pm$ 1.36	14.4 $\pm$ 0.25	15.7 $\pm$ 4.20
Adult red snapper control	17.7 $\pm$ 0.71	14.2 $\pm$ 0.22	15.1 $\pm$ 3.32
Juv lane snapper control	19 $\pm$ 0.57	14.7 $\pm$ 0.07	14.6 $\pm$ 1.43
Juv red snapper control	18.9 $\pm$ 0.50	14.5 $\pm$ 0.14	16.5 $\pm$ 0.89
Juv lane – adult lane	16.4 $\pm$ 0.45	15 $\pm$ 0.05	14.8 $\pm$ 0.79
Juv lane – adult red	15.4 $\pm$ 0.90	15.2 $\pm$ 0.10	14 $\pm$ 0.21
Juv red – adult lane	16.7 $\pm$ 1.39	15.1 $\pm$ 0.12	14.6 $\pm$ 0.60
Juv red – adult red	17.9 $\pm$ 1.00	14.9 $\pm$ 0.08	14.7 $\pm$ 1.06

Table 4. Observed total length (TL) and weight ( $\pm$  1 SE) of juvenile (juv) and adult lane and red snappers used in control and interaction trials. Ranges in the quotient of blue crab *Callinectes sapidus* prey size related to the average size of a given predator are also included

Treatment	Species	TL (mm)	Weight (g)	Relative prey size
Adult lane snapper control		449.7 $\pm$ 0.88	1326.7 $\pm$ 17.64	0.02–0.06
Adult red snapper control		491.7 $\pm$ 39.84	1768.7 $\pm$ 432.30	0.02–0.06
Juv lane snapper control		136.7 $\pm$ 9.11	49.4 $\pm$ 14.14	0.07–0.18
Juv red snapper control		292.1 $\pm$ 18.69	385.9 $\pm$ 50.61	0.03–0.08
Juv lane – adult lane	Juv lane	128.2 $\pm$ 5.01	34.4 $\pm$ 3.58	0.08–0.20
	Adult lane	438.7 $\pm$ 1.76	1273.3 $\pm$ 29.51	0.02–0.05
Juv lane – adult red	Juv lane	105.0 $\pm$ 0.00	17.5 $\pm$ 0.35	0.10–0.24
	Adult red	396.0 $\pm$ 4.00	880 $\pm$ 10.00	0.03–0.06
Juv red – adult lane	Juv red	272.5 $\pm$ 32.40	340.1 $\pm$ 69.32	0.04–0.09
	Adult lane	434.0 $\pm$ 1.63	1217.5 $\pm$ 28.39	0.02–0.06
Juv red – adult red	Juv red	278.5 $\pm$ 5.46	334.4 $\pm$ 16.39	0.04–0.09
	Adult red	420.0 $\pm$ 2.74	1086 $\pm$ 45.78	0.02–0.06

time swimming in the center of a tank or huddling, and no significant differences in values for these behaviors were observed across treatments (swim at center:  $K = 18.323$ ,  $df = 19$ ,  $p = 0.501$ ; huddling:  $K = 13.971$ ,  $df = 19$ ,  $p = 0.785$ ).

Across control and interaction trials, post hoc analyses demonstrated significant differences among swimming activities for adult red and lane snapper and grouped and single juveniles. In interaction trials, grouped ( $n = 3$ ) juvenile lane snapper were significantly more active (i.e. greater percentage of time swimming around the mesocosm) than adult lane snapper, although no significant difference in swimming activity was observed between grouped juvenile lane snapper interaction and control trials. Adult lane snapper were significantly less active than in control trials when paired with grouped juvenile red and lane snapper. When paired with adult lane snapper, however, single juvenile lane snapper were significantly more active than in control trials. When paired in interaction trials, single juvenile red snapper swam significantly less than adult lane snapper; this trend was not observed in their interactions with

adult red snapper. Additionally, no significant difference in single or grouped red snapper swimming activity was observed among control and interaction trials. In interaction trials, adult red snapper swimming activities did not significantly differ from those of juvenile red or lane snapper. However, adult red snapper demonstrated significantly higher swimming times around mesocosms when paired with single juvenile lane snapper than in control trials or other interaction trials. Cumulatively, within control trials, adult lane snapper, grouped juvenile lane snapper, and grouped juvenile red snapper were all significantly more active than single juvenile lane snapper and adult red snapper.

During experimental trials, adult and juvenile snappers often interacted (Table 5), with the highest percentage of interaction time per trial between juvenile red snapper and adult red and lane snappers. Juvenile lane snapper interacted significantly less with adult snappers than did juvenile red snapper ( $K = 13.142$ ,  $df = 6$ ,  $p = 0.041$ ), although single juvenile red snapper interacted very rarely with adult lane snapper and at similar duration as juvenile lane snapper.

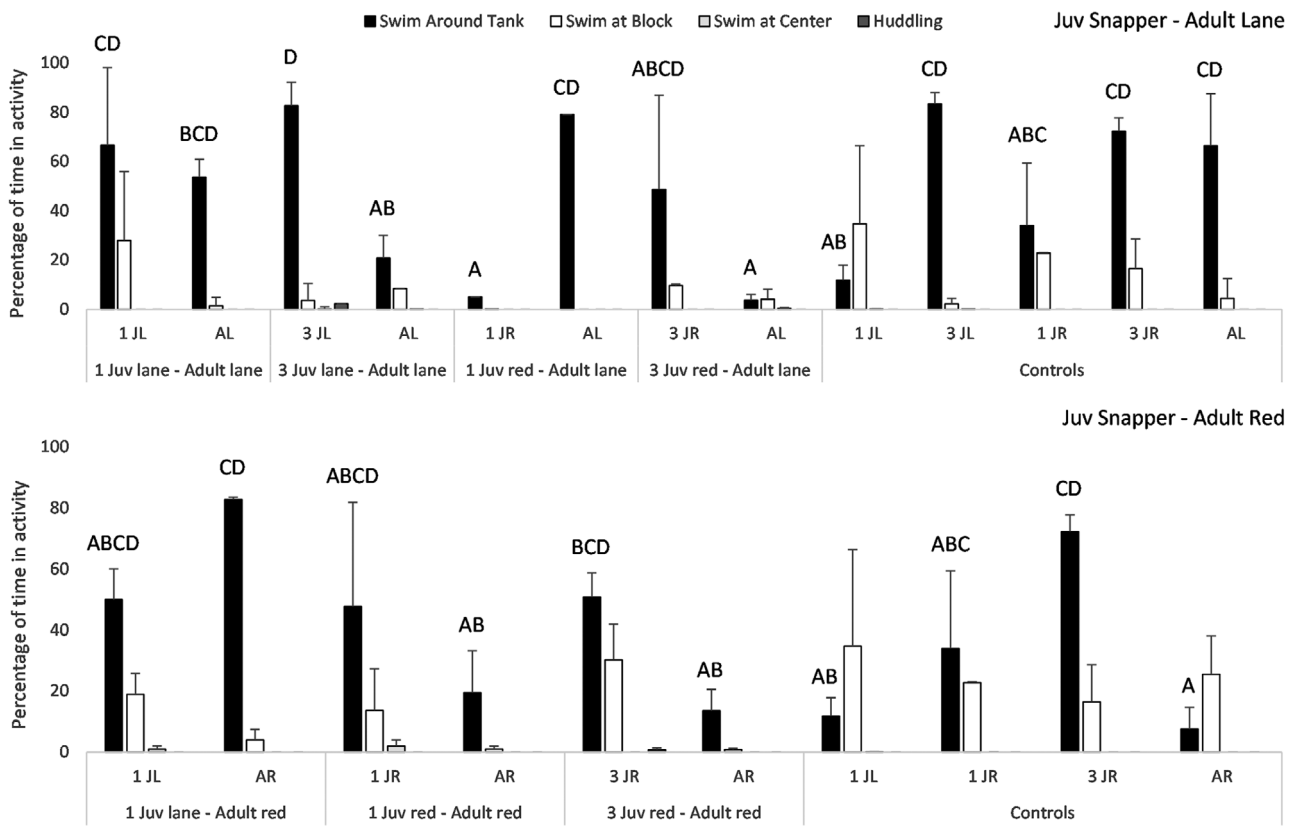


Fig. 1. Mean ( $\pm 1$  SE) percentage of time in activity spent swimming around the experimental mesocosm, at concrete blocks or edge of mesocosm, at the center of the mesocosm, or huddling at blocks by adult and juvenile lane and red snappers. Data from interaction trials with single (1 juv lane: 1 JL; 1 juv red: 1 JR) and grouped (3 juv lane: 3 JL; 3 juv red: 3 JR) juvenile snappers and adult lane snapper (adult lane: AL, top panel) or adult red snapper (adult red: AR, bottom panel), and monoculture control trials of single and 3 juvenile snappers and single adult snappers. Shared uppercase letters indicate groups that do not differ significantly (Kruskal-Wallis and post hoc Conover-Iman tests,  $p = 0.05$ )

Single juvenile lane snapper retreated from adult lane snapper significantly more often than they approached them ( $K = 44.916$ ,  $df = 27$ ,  $p = 0.017$ ), and were approached by adult lane snapper at equivalent values to their retreats (Fig. 2). Additionally, post hoc analyses showed that adult lane snapper approached single juvenile lane, and especially single juvenile red snapper, significantly more frequently than they were approached by juveniles. These trends were not observed between adult lane snapper and grouped juvenile snappers. Adult red snapper approached single juvenile lane snapper significantly more frequently, and were never approached by juvenile lane snapper. Single juvenile red snapper were observed retreating from adult red snapper significantly more often, but no significant difference was observed in their approaches. Both adult red snapper and grouped juvenile red snapper approached and retreated from each other at similar intensities, while they approached each other significantly more often.

For control and interaction trials, overall trends in prey consumption were non-significant ( $K = 28.550$ ,  $df = 19$ ,  $p = 0.073$ ; Fig. 3). Of note however, no consumption was observed by adult lane snapper in interaction trials with single juvenile lane snapper

Table 5. Percentage of trial time spent interacting (mean  $\pm 1$  SE) between adult and juvenile (juv) red and lane snappers treatment<sup>-1</sup> during mesocosm experiments. Shared letters: groups that do not differ significantly (Kruskal-Wallis and post hoc Conover-Iman tests,  $p = 0.05$ )

Trial	Percentage of time in which species/stages interact
1 Juv lane – adult lane	3.5 $\pm$ 1.23 (b)
3 Juv lane – adult lane	0.7 $\pm$ 0.51 (a)
1 Juv red – adult lane	1.8 $\pm$ 0.00 (ab)
3 Juv red – adult lane	28.1 $\pm$ 6.06 (d)
1 Juv lane – adult red	2.2 $\pm$ 0.34 (b)
1 Juv red – adult red	22.2 $\pm$ 4.67 (cd)
3 Juv red – adult red	17.4 $\pm$ 1.35 (c)

and grouped juvenile red snapper. Additionally, adult lane snapper consumption was observed in interaction trials with grouped juvenile lane snapper and single red snapper, and in control trials. Similarly, no consumption was observed by adult red snapper in interaction trials with grouped juvenile red snapper, while adult red snapper consumption was observed in control and other interaction trials. Additionally, no significant trends were observed for predatory attempts per fish ( $K = 20.911$ ,  $df = 19$ ,  $p = 0.342$ ; Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m622p139\\_supp.pdf](http://www.int-res.com/articles/suppl/m622p139_supp.pdf)) within and among control and interaction trials.

Overall, low or zero-values were observed for the percentage of time that adult and juvenile snapper spent pursuing prey ( $K = 19.504$ ,  $df = 19$ ,  $p = 0.425$ ; Fig. S2) and for the number of non-consumptive approaches by fishes on prey ( $K = 15.934$ ,  $df = 19$ ,  $p =$

0.665; Fig. S3). No significant differences in values for either variable were observed. Retreats from crab prey were only observed twice (for single juvenile lane snapper and single juvenile red snapper) throughout all trials.

Prey ignored by fishes significantly differed among control and experimental treatments ( $K = 32.687$ ,  $df = 19$ ,  $p = 0.026$ ; Fig. 4). Across control trials, post hoc analyses revealed that adult lane snapper ignored prey significantly more often than adult and juvenile red snapper, or single juvenile lane snapper. Additionally, adult lane snapper ignored prey significantly more often in control trials than when paired with grouped juvenile lane snapper. Within interaction trials, adult lane snapper ignored prey significantly more often than single juvenile red snapper when paired together. Single juvenile lane snapper also ignored prey significantly

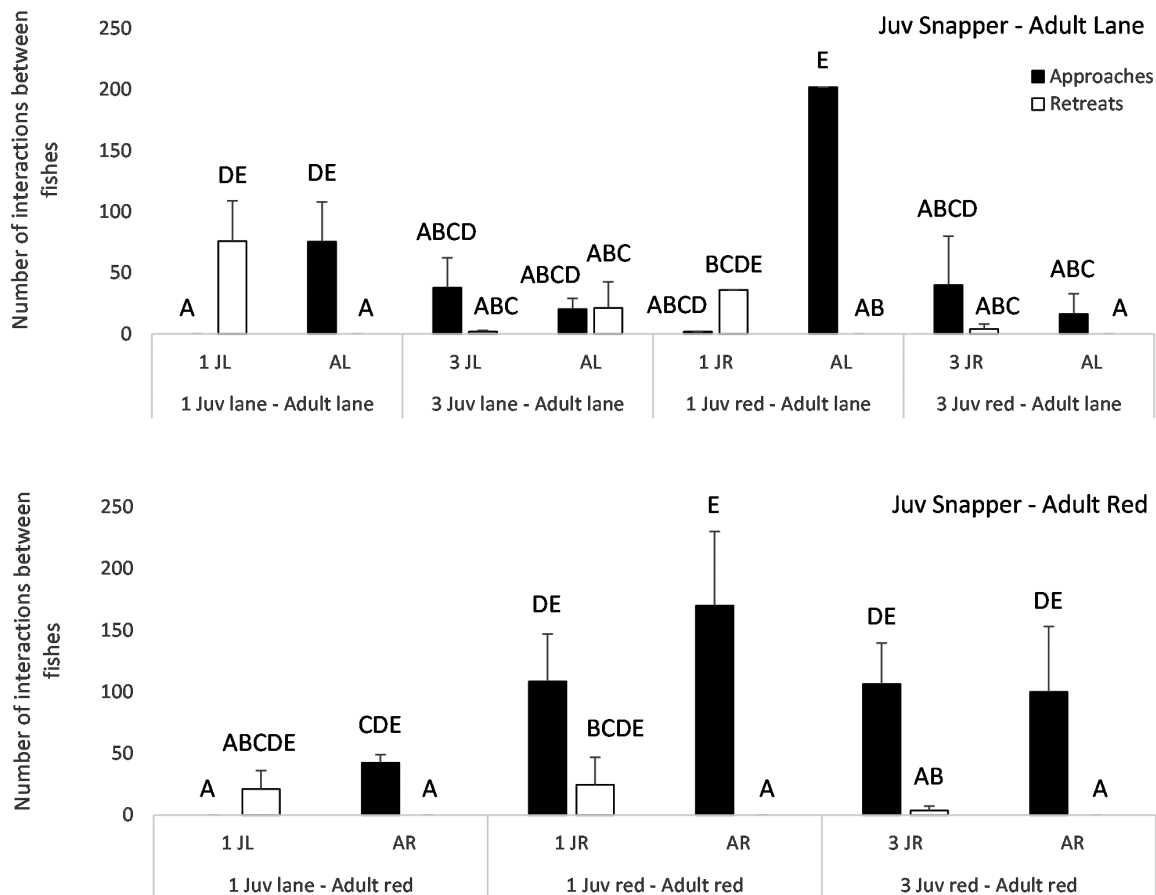


Fig. 2. Mean ( $\pm 1$  SE) number of interspecific approaches and retreats on other fish species between adult and juvenile lane and red snappers during interaction experiments. Data from interaction trials with single (1 juv lane: 1 JL; 1 juv red: 1 JR) and grouped (3 juv lane: 3 JL; 3 juv red: 3 JR) juvenile snappers and adult lane snapper (adult lane: AL, top panel) or adult red snapper (adult red: AR, bottom panel). Shared uppercase letters indicate groups that do not differ significantly (Kruskal-Wallis and post hoc Conover-Iman tests,  $p = 0.05$ )



more often when paired with adult lane snapper than in control trials, while single juvenile red snapper ignored prey significantly more often when paired with adult red snapper than in control trials.

Intraspecific and interspecific aggressions by adult red and lane snapper upon juveniles occurred during this study, while no aggressions by juveniles were observed (Fig. 5). Chasing behaviors by adult lane and red snapper, while not differing significantly among treatments ( $K = 19.056$ ,  $df = 13$ ,  $p = 0.121$ ), were observed by adult snappers upon single juvenile red and lane snapper, and by adult red snapper upon grouped juvenile red snapper. Habitat displacements of juveniles by adults were the most frequent aggressive interactions. While displacement behaviors among treatments were not significant ( $K = 20.310$ ,  $df = 13$ ,  $p = 0.088$ ), adult lane snapper displaced single juvenile lane snapper at highest frequencies. Additionally, adult red and lane snappers were frequently observed displacing single juvenile lane snapper from habitats, while adult lane snapper also frequently displaced single juvenile red snapper. No displace-

ments of grouped juvenile snappers by adults were observed. Adult lane and red snapper infrequently nipped at juveniles, and activity was significantly higher for adult red snapper acting upon single juvenile red snapper ( $K = 28.966$ ,  $df = 13$ ,  $p = 0.007$ ). Additionally, very few instances of pushing by adults upon juveniles were observed, and values did not differ significantly ( $K = 9.192$ ,  $df = 13$ ,  $p = 0.758$ ).

No significant relationship between temperature and any adult or juvenile fish behavior was observed (Table 6), while the strongest relationships were found for all 3 environmental factors (temperature, salinity, dissolved oxygen), average length, and percentage of time swimming together (adults  $R^2 = 0.83$ ; juveniles  $R^2 = 0.98$ ). Relationships were polynomial, parabolic, or inverse parabolic. Similarly, few strong, significant relationships were observed between fish behaviors, salinity, dissolved oxygen, or average size. For adults, significant relationships between salinity and percent time pursuing prey ( $R^2 = 0.55$ ,  $p = 0.031$ ; Fig. S4), and salinity and number of non-consumptive prey approaches ( $R^2 = 0.62$ ,  $p = 0.001$ ) were

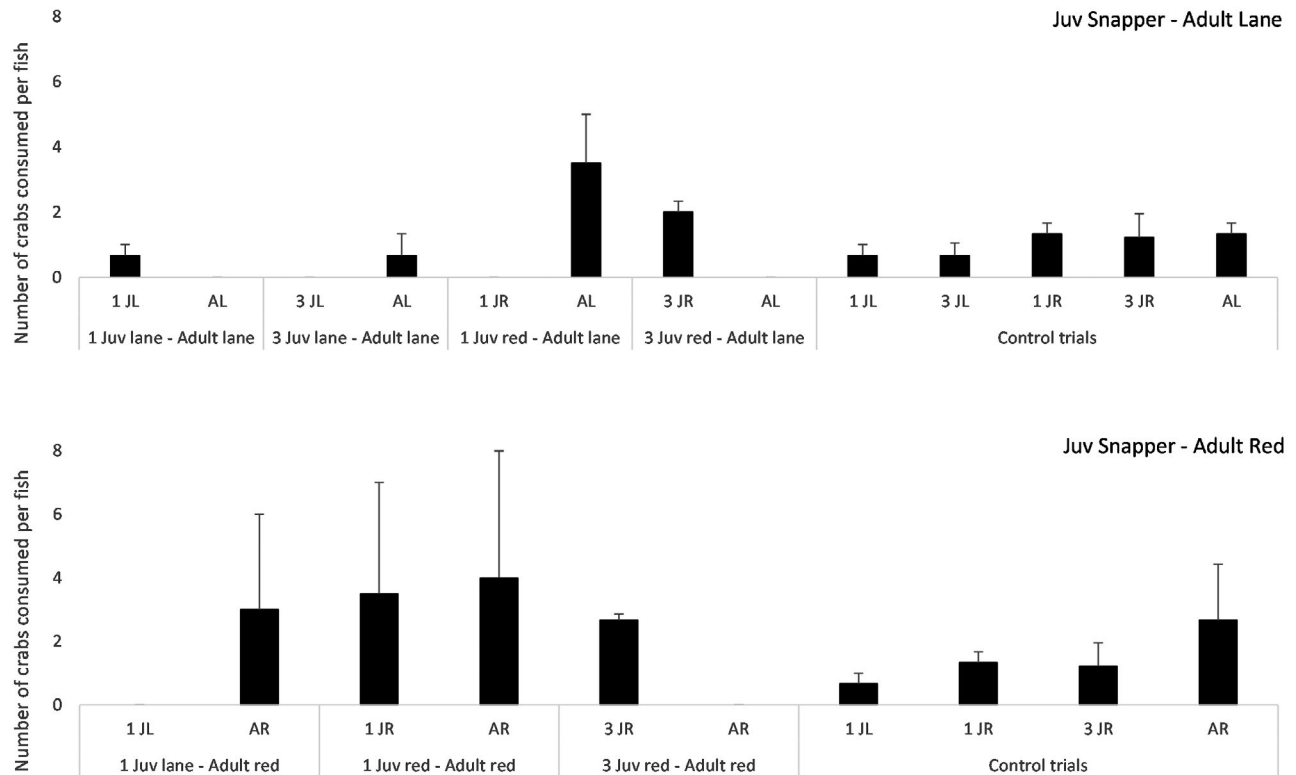


Fig. 3. Mean ( $\pm 1$  SE) consumption rates of blue crabs fish<sup>-1</sup> by adult and juvenile lane and red snappers. Data from interaction trials with single (1 juv lane: 1 JL; 1 juv red: 1 JR) and grouped (3 juv lane: 3 JL; 3 juv red: 3 JR) juvenile snappers and adult lane snapper (adult lane: AL, top panel) or adult red snapper (adult red: AR, bottom panel), and monoculture control trials of single and 3 juvenile snappers and single adult snappers

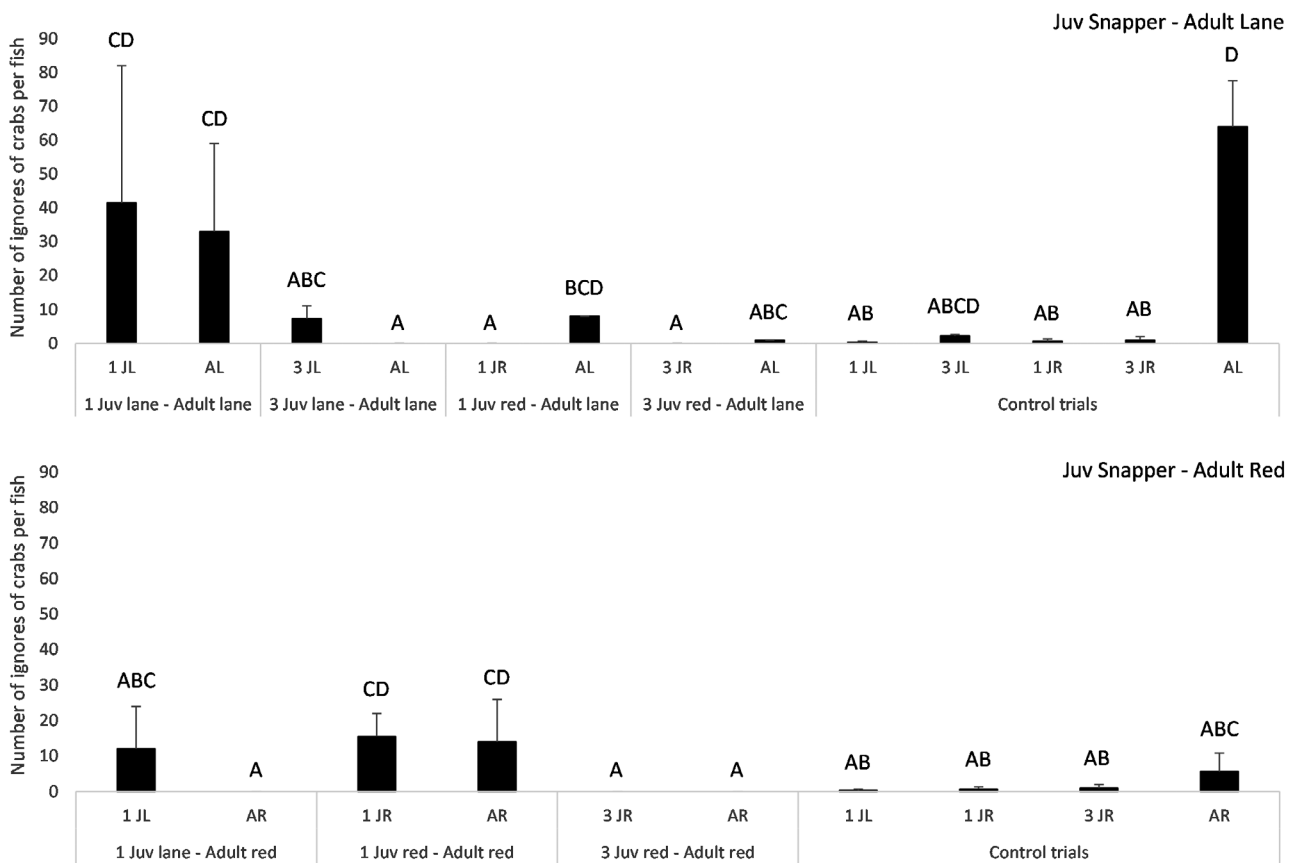


Fig. 4. Mean ( $\pm 1$  SE) number of ignores of nearby blue crab prey per fish by juvenile and adult lane and red snappers. Data from interaction trials with single (1 juv lane: 1 JL; 1 juv red: 1 JR) and grouped (3 juv lane: 3 JL; 3 juv red: 3 JR) juvenile snappers and adult lane snapper (adult lane: AL, top panel) or adult red snapper (adult red: AR, bottom panel), and monoculture control trials of single and 3 juvenile snappers and single adult snappers. Shared uppercase letters indicate groups that do not differ significantly (Kruskal-Wallis and post hoc Conover-Iman tests,  $p = 0.05$ )

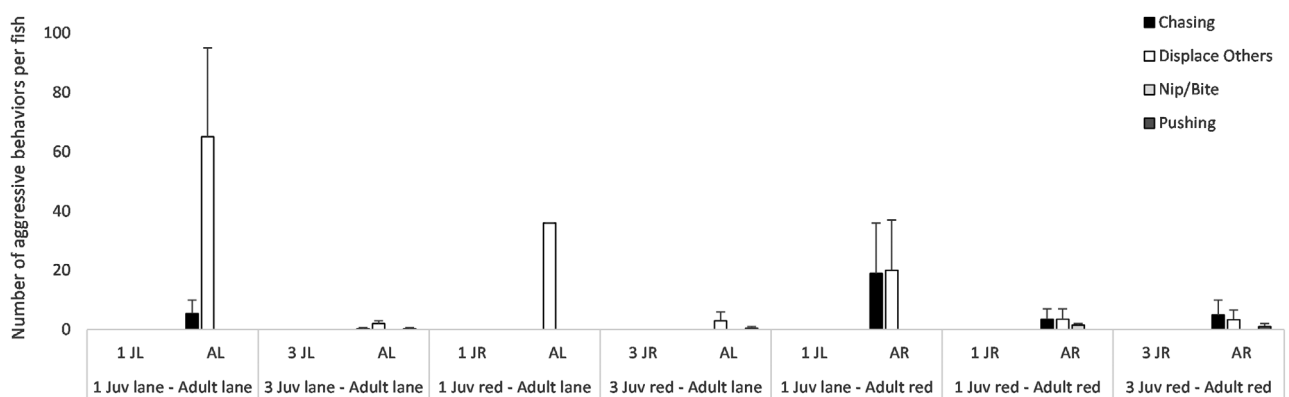


Fig. 5. Mean ( $\pm 1$  SE) number of inter- and intraspecific aggressive interactions per fish performed by single (1 juv lane: 1 JL; 1 juv red: 1 JR) and grouped (3 juv lane: 3 JL; 3 juv red: 3 JR) juvenile and adult lane and red snapper (adult lane: AL; adult red: AR)

observed. A significant relationship was additionally observed between average length and number of non-consumptive prey approaches ( $p = 0.006$ ). For juvenile behaviors, significant relationships were observed between dissolved oxygen and swimming

at concrete blocks ( $R^2 = 0.72$ ,  $p = 0.010$ ), and between average length and prey consumption ( $R^2 = 0.93$ ,  $p = 0.025$ ), predatory attempts ( $R^2 = 0.90$ ,  $p = 0.042$ ), and percentage of time swimming together ( $p < 0.0001$ ). For adult snappers, highest percentages of prey pur-

Table 6. Multiple regression relationships among environmental parameters, average fish total length (mm), and observed behaviors in adult–juvenile (juv) lane and red snapper control and interaction trials. Values in **bold** indicate significant relationships ( $p < 0.05$ ) among factors and behaviors

Stage	Fish behavior	R <sup>2</sup>	p-value					
			Model	Temperature	Salinity	Oxygen	Average length	
Adult	Swimming around tank	0.39	0.378	0.339	0.452	0.554	0.678	
	Swimming at block/edge	0.64	0.196	0.695	0.122	0.081	0.804	
	Swimming at center	0.60	0.611	0.138	0.767	0.503	0.999	
	Huddling							
	Approaches on other fishes	0.64	0.517	0.317	0.455	0.775	0.658	
	Retreats from other fishes							
	Total aggressions	0.48	0.937	0.966	0.469	0.737	0.919	
	Consumption of crabs	0.38	0.469	0.950	0.221	0.292	0.213	
	Predatory attempts	0.39	0.209	0.780	0.106	0.227	0.067	
	<b>Percent time pursuing prey</b>	0.55	0.184	0.727	<b>0.031</b>	0.498	0.054	
	<b>Prey approaches</b>	0.62	<b>0.007</b>	0.140	<b>0.001</b>	0.125	<b>0.006</b>	
	Retreats from prey							
	Percent time swimming together	0.83	0.802	0.899	0.638	0.300	0.917	
	Number of times fish ignored prey	0.49	0.310	0.197	0.284	0.324	0.491	
	Juv	Swimming around tank	0.60	0.504	0.359	0.882	0.109	0.491
		<b>Swimming at block/edge</b>	0.72	0.077	0.908	0.938	<b>0.010</b>	0.761
Swimming at center		0.78	0.904	0.921	0.419	0.570	0.657	
Huddling		0.83	0.282	0.070	0.249	0.748	0.344	
Approaches on other fishes		0.88	0.360	0.379	0.273	0.622	0.084	
Retreats from other fishes		0.86	0.331	0.480	0.426	0.615	0.325	
Total aggressions								
<b>Consumption of crabs</b>		0.93	0.077	0.146	0.286	0.299	<b>0.025</b>	
<b>Predatory attempts</b>		0.90	0.156	0.274	0.423	0.323	<b>0.042</b>	
Percent time pursuing prey		0.51	0.583	0.902	0.442	0.362	0.204	
Prey approaches		0.44	0.324	0.377	0.158	0.081	0.310	
Retreats from prey		0.32	0.451	0.985	0.527	0.229	0.180	
<b>Percent time swimming together</b>		0.98	<b>0.0003</b>	0.918	0.587	0.172	<b>&lt;0.0001</b>	
Number of times fish ignored prey		0.57	0.689	0.890	0.525	0.711	0.501	

suit time and number of non-consumptive prey approaches were observed in low- to mid-salinities and by medium sized lane snapper. Increased swimming activities at concrete block habitat were observed with dissolved oxygen, with little differentiation between juvenile lane or red snapper. Higher interaction times were observed with juvenile average length, which were highest for juvenile red snapper, while prey consumption and predatory attempts were highest for medium sized juvenile red snapper. Additionally, no significant relationship was observed between time of day (3 h blocks of time) and behavioral variables ( $K = 0.715-7.074$ ,  $df = 2-3$ ,  $p = 0.063-0.699$ ).

#### 4. DISCUSSION

Examining inter- and intraspecific interactions between adult and juvenile red and lane snapper has revealed that competitive interactions in these fishes are complex, species-specific, and differ when in-

volving single versus grouped juveniles. Overall interactions for mutual prey and habitat were strongest among inter- and intraspecific adult snappers and single juveniles, and among intraspecific adult snappers and grouped juveniles. Inter- and intraspecific interference and exploitative interactions were observed as adult lane snapper frequently displaced single juvenile red snapper and lane snapper from habitats and as adult red snapper displaced and chased single juvenile lane snapper. Although single juvenile red snapper were less active in the presence of adult lane snapper, and were frequently displaced by them, overall they do not appear to be strongly affected by adult lane snapper as they did not significantly retreat in their presence nor did their swimming times and prey consumption significantly differ from control observations. Similar interspecific effects were also observed between single juvenile lane snapper and adult red snapper. Adult red snapper were more active in the presence of juvenile lane snapper than in control trials but did not cause juvenile

lane snapper to significantly retreat or significantly affect their prey consumption. Although our experimental design did not factor for prey depletion, Juliano (2001) highlighted the value of holding prey constant to inform about stochastic predation, which may be more likely to occur with increasing predator richness and density and from cohorts co-occurring in limited habitat (Wittmer et al. 2014). While increasing overlap of juvenile and adult snappers leads to a higher abundance of predators in a given area, competitive dominance among predators can cause species-specific predation intensities to vary. Competition may lead to differential predator abundance and to more specialized or stochastic predatory frequencies from rarer or less competitively dominant species (Festa-Bianchet et al. 2006).

Intraspecific interactions between cohorts were more pronounced between adult and juvenile lane snapper, where juveniles retreated from approaching adults at significant rates, displayed increased swimming activities in their presence, and adults displaced and chased juveniles from habitats. Additionally, single juvenile lane snapper were more active in the presence of an adult conspecific, while single juvenile red snapper were not significantly affected by the presence of adult red snapper. Among juvenile and adult snappers, however, grouped juvenile red snapper approached adults more readily. Adult lane snapper were also significantly less active in the presence of grouped juvenile lane and red snapper. Therefore, our data suggest limited effects of adult lane snapper on single juvenile red or lane snapper at small scales. Additionally, clusters of juveniles appear to be more resilient to competitive pressures by adult lane snapper while more strongly enacting competitive pressures on them. Inter- and intraspecific schooling associations among snapper species and cohorts are likely to occur while fishes are targeting mutual prey and space or mutually avoiding predation (Lukoschek & McCormick 2000). Under natural conditions, the behaviors observed in our study are more reflective of the former scenario. However, if more than one cohort or species is co-occurring in the presence of a predator, then enhanced interspecific associations and competitive interactions for shelter and prey may occur (Persson 1993). In more structurally complex habitats that could favor greater resource partitioning and differential predatory pressures, competition may be less intense and potentially mediated (Gilliam & Fraser 1988, Persson 1993).

Marshak & Heck (2017) found that juvenile red snapper were able to displace juvenile lane snapper, which could strongly affect adult lane snapper popu-

lation size. However, there may be greater potential for juvenile and early adult lane snapper to overlap with red snapper in structurally complex habitats (Wells & Cowan 2008, Mudrak & Szedlmayer 2012, Marshak 2016, Marshak & Heck unpubl. data). Interspecific interactions between solitary adult and juvenile snappers partially support our initial hypotheses that adults would dominate juvenile snappers in prey consumption and habitat use. However, grouped juveniles were often at a greater advantage than solitary adults, which suggests certain competitive resistance of juvenile and adult red snapper to both juvenile and adult lane snapper. Our data additionally show that adult lane snapper swimming activities and prey consumption when paired with juvenile snappers did not significantly differ from those observed for adult red snapper, which did not align with our initial hypotheses. In the presence of grouped juveniles, significant effects on swimming activity and ignoring prey were only observed for lane snapper and not for red snapper, while the opposite was observed for swimming activity in the presence of single intraspecific juveniles.

#### 4.1. Juvenile–adult interactions

In nature and the laboratory, intraspecific competition between adult and juvenile red snapper has been observed, with larger individuals excluding and displacing juveniles from priority habitats (Bailey et al. 2001, Mudrak & Szedlmayer 2012, Szedlmayer & Mudrak 2014), and older red snapper excluding young-of-the-year individuals from structures (Workman et al. 2002). Additionally, Robertson (1995) suggested that interspecific competition would be stronger and more size-determinant, with one species taking space from a smaller but not a larger heterospecific neighbor. Our study suggests that adult lane snapper may exert certain competitive pressures on juvenile red snapper at small scales, but not multiple red snapper. Our study likewise demonstrates that clusters of juveniles may be better able to resist adults than when alone, enhancing their successful transition from juvenile to adult, and potentially favoring later adult populations (Connell & Jones 1991). Juvenile and adult snappers are often found schooling with similar sized individuals (Mudrak & Szedlmayer 2012, Szedlmayer & Mudrak 2014); however, solitary individuals or smaller numbers of snapper of different species may also be observed among these clusters (Mudrak & Szedlmayer 2012). While red snapper is the dominant snapper

species in the nGOM, and often the dominant snapper in reef fish aggregations, its relative abundance may vary according to habitat (Wells & Cowan 2008, Marshak 2016, Marshak & Heck unpubl. data). Habitat overlap of juvenile age-0 and age-1 snappers and larger adult snappers has also been observed in nature (Mudrak & Szedlmayer 2012), with larger sized age-1 juvenile red snapper dominant in certain structured habitats.

Although overlapping with red snapper, lane snapper throughout their life histories do not currently appear to have major effects on red snapper populations (Marshak & Heck 2017). Similar to suggestions by Munro & Williams (1985) that resident populations may not necessarily affect recruitment of other species, ultimately it does not appear that under current conditions the increased presence of juvenile and adult lane snapper will strongly affect large-scale red snapper recruitment. Dominance of larger red snapper at artificial reef structures, and red snapper juveniles at lower-relief inshore habitats, suggests that red snapper may more strongly affect juvenile lane and adult snapper instead and limit their propagation. However, in deeper, more complex habitats where coexistence of lane and red snapper has been observed, and where refuge and prey may be more available, lane snapper can thrive and grow at faster rates than red snapper (Marshak 2016, Marshak & Heck unpubl. data), which could allow adult lane snapper to displace occasional juvenile red snapper. Although displaced snappers may still feed on benthic or pelagic prey (Szedlmayer & Lee 2004, Wells et al. 2008b), their vulnerability to predators while foraging away from preferred or limited natural structures may be enhanced. Alternatively, lane and red snapper may be favored to coexist in more structurally complex habitats. Additionally, localized depletions of red snapper by fishing may also favor propagation of larger lane snapper (Lindberg et al. 2006, Geange & Stier 2009).

In this study we did not test for interactions among grouped juvenile lane snapper and adult red snapper because this occurrence was beyond the scope of investigation, and as they are generally not observed co-occurring in nature (Mudrak & Szedlmayer 2012, Addis et al. 2013, Garner et al. 2014). This pattern is potentially due to documented competitive aggression between adult and juvenile red and lane snapper (Mudrak & Szedlmayer 2012, Marshak & Heck 2017). When paired with juvenile lane snapper, exploitative dominance by juvenile red snapper has been observed (Marshak & Heck 2017), while habitat differentiations among interspecific adult and juve-

nile red and lane snapper appears to be less distinct for adult red snapper (Dance et al. 2011, Marshak 2016, Marshak & Heck unpubl. data). Additionally, single juvenile lane snapper have been observed coexisting with occasional solitary adult red snapper (Mudrak & Szedlmayer 2012). However, as regional warming in the nGOM continues to favor the migrations of multiple species and cohorts into deeper waters with limited naturally occurring reef habitat (Schroeder et al. 1988, Gallaway et al. 1999, Pinsky et al. 2013), higher overlap among grouped juvenile and adult red and lane snapper in more complex habitats may occur and result in more pronounced interactions. Ongoing research into the effects of habitat complexity and regional warming on inter- and intraspecific adult and juvenile interactions remains warranted, particularly as it can help predict outcomes of these potential habitat shifts.

#### 4.2. Size and priority effects

Size is suggested to be more important in influencing competitive success than residence in a given habitat (Geange & Stier 2009, Poulos & McCormick 2014). Studies examining reef fishes (Poulos & McCormick 2014) have demonstrated that size-based aggression plays a larger role in space occupation, while residence history may be important when competitors are of a similar size. Our study demonstrated that adult snapper do have partial size-based advantages against single intra- and interspecific juveniles, while Marshak & Heck (2017) found that similar sized juvenile red snapper have a competitive advantage against juvenile lane snapper, which may also be reflective of priority. Given the partial inshore life history of lane snapper, red snapper may have a priority advantage in some offshore habitats, but adult lane snapper are able to establish themselves in offshore shelf habitats <40 m depth, and with differing degrees of overlap with red snapper (Marshak 2016, Marshak & Heck unpubl. data). Overall, our findings affirm that aggressive interactions by larger individuals can produce competitive dominance and, together with these aforementioned studies, suggest that prior residence may be more important in interactions among smaller individuals.

Although a relationship among fish size and number of non-consumptive prey approaches was observed for adults, there was only one non-zero observation observed in total, which was for a single adult lane snapper. Nor was there a significant difference among trials observed for this behavior, suggesting

little overall biological effect. Additionally, relationships among fish size and juvenile fish behaviors showed influence of size on percentage of time swimming together, which may have influenced red snapper gregariousness with adult snappers. Medium sized juvenile red snappers more frequently attempted to prey upon and consume crabs, also suggesting lowered effects of adults on these mid-size individuals. While relative blue crab prey size was highest for juvenile lane snapper, no significant differences in swimming activities, approaches, retreats, consumption, or predatory attempts were observed among juvenile snappers in trials, suggesting no major effect of prey size on juvenile lane snapper. In interaction trials, solitary and grouped juvenile red snapper were equally able to consume prey as adult snappers, and their swimming activities were not diminished. Juvenile lane snapper did not appear to compensate in feeding ability as observed in other interaction studies (Marshak & Heck 2017), but they increased their swimming activities in the presence of adult lane snapper. This suggests that intraspecific competition may affect both red and lane snapper more strongly than interspecific competition, as observed at natural and artificial habitats (Dance et al. 2011, Mudrak & Szedlmayer 2012, Syc & Szedlmayer 2012).

### 4.3. Role of temperature, dissolved oxygen, and salinity

Although red snapper appear to be stronger competitors under current conditions, models (Poloczanska et al. 2008) and empirical studies have illustrated reversals in the competitive dominance of salmonid fishes (Taniguchi & Nakano 2000) with altered temperatures. In addition, warming has been demonstrated to exacerbate interspecific interactions between labrids (Milazzo et al. 2013). We observed juvenile lane snapper and adult red snapper interactions at temperatures reflective of winter temperatures at which red snapper exist (~14°C; Gallaway et al. 1999, Turner et al. 2017) and at which lane snapper appear able to overwinter (Fodrie et al. 2010). No significant effect of temperature on adult or juvenile red or lane snapper behaviors was observed in this study. Juvenile lane snapper were active at a range of temperatures, suggesting that warmer temperatures might lead to an increase in lane snapper activity and competitive ability. To date, however, empirical evidence on the role of warming in modulating the strength and direction of species interactions remains limited (Nagelkerken & Simpson 2013).

Additionally, while dissolved oxygen values in our experiments were indicative of supersaturation, swimming activities and behaviors by juvenile red and lane snapper were similar to those found by Marshak & Heck (2017), suggesting minimal effect of oxygen. The only significant effect of oxygen on fish behavior observed was on percentage of time swimming at concrete block habitat by juveniles; no other effects of oxygen on swimming activities were observed for juveniles or adults. Similarly, while salinity differed significantly among trials, and regressions found relationships with salinity and adult lane snapper prey pursuit and number of non-consumptive prey approaches, together these findings did not appear to have biological significance or to demonstrate strong influences of observed temperatures, salinity, and oxygen concentrations on snapper activities and behavior. This assertion is supported by the lack of significant differences for these values among species and life stages in interaction and control trials.

Szedlmayer & Shipp (1994) and Gallaway et al. (1999) suggested that little variation in temperature is observed in offshore nGOM snapper habitats, especially at depths of >25 m where juveniles are found. Additionally, Fodrie et al. (2010) and Whitfield et al. (2014) proposed that deeper-water individuals are mostly influenced by minimum winter temperatures and that increasing sea surface temperatures will more heavily influence inshore community composition. As warming in deeper snapper habitats is not likely to be as strong as in nearshore habitats, differential degrees of competitive ability may occur with depth, and be especially important in shallower areas with limited structural habitats. Thus, shifts toward juvenile and early adult lane snapper advantage in warmer waters may be concentrated in shallower offshore habitats where structural natural reef habitats are generally limited (Patterson et al. 2005). However, migrations by adults into deeper waters may additionally result in differential competitive interactions between red and lane snapper populations.

### 4.4. Management implications

Ongoing study of biological interactions of range-shifting and resident species throughout their life stages will provide enhanced understanding of their differential vulnerabilities to climate change and of reef fish ecology. Findings from such studies will also improve understanding of multi-species interactions that can be applied to ecosystem-based fisheries management, integrated ecosystem assessments (Cowan

et al. 2012, Karnauskas et al. 2017), and lead to more complex species-specific and ecosystem-level climate vulnerability assessments (Hare et al. 2016). For example, our observations that grouped juvenile snappers demonstrate lesser effects from tropically associated lane snapper adults compared to single individuals reinforces the importance of ongoing stock rebuilding and conservation efforts to enhance snapper populations as they are affected by regional warming and range expansions of confamilials. As displacement potential may strengthen with predicted overlap between species and cohorts in limited natural habitats, occupation of preferred hard bottom habitat by abundant juvenile and adult red snapper may lead to enhanced resiliency against additional warming-related species shifts and stressors. Additionally, as management efforts broaden, incorporation of these species' interactions into holistic managerial approaches can enhance management of vulnerable fish stocks, and ground-truth and build upon models that investigate the impacts of regional warming upon marine ecosystems. Ultimately, examining differential vulnerabilities to climate change can allow adaptive strategies to mitigate effects upon historically overfished commercially important species, such as red snapper.

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#### LITERATURE CITED

- Addis DT, Patterson WF, Dance MA, Ingram GW (2013) Implications of reef fish movement from unreported artificial reef sites in the northern Gulf of Mexico. *Fish Res* 147:349–358
- Bailey HK, Cowan JH, Shipp RL (2001) Experimental evaluation of potential effects of habitat size and presence of conspecifics on habitat association by young-of-the-year red snapper. *Gulf Mex Sci* 2:119–131
- Brander KM (2007) Global fish production and climate change. *Proc Natl Acad Sci USA* 104:19709–19714
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish* 10: 235–251
- Collins LA, Johnson AG, Keim CP (1996) Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. In: Arreguín-Sánchez F, Munro JL, Balgos MC, Pauly D (eds) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf Proc 48:174–188
- Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J Exp Mar Biol Ecol* 151:271–294
- Cowan JH, Grimes CB, Patterson WF, Walters CJ and others (2011) Red snapper management in the Gulf of Mexico: Science- or faith-based? *Rev Fish Biol Fish* 21:187–204
- Cowan JH, Rice JC, Walters CJ, Hilborn R and others (2012) Challenges for implementing an ecosystem approach to fisheries management. *Mar Coast Fish* 4:496–510
- Dance MA, Patterson WF, Addis DT (2011) Fish community and trophic structure at artificial reef sites in the northeastern Gulf of Mexico. *Bull Mar Sci* 87:301–324
- Darnell RM, Kleypas JA, Defenbaugh RE (1987) Eastern Gulf shelf bio-atlas: a study of the distribution of demersal fishes and penaeid shrimp of soft bottoms of the continental shelf from the Mississippi River Delta to the Florida Keys. MMS 86-0041. Minerals Management Service, Gulf of Mexico OCS Region, US Department of the Interior, New Orleans, LA
- Doney SC, Ruckelshaus M, Duffy JE, Barry JP and others (2012) Climate change impacts on marine ecosystems. *Annu Rev Mar Sci* 4:11–37
- Ettinger AK, HilleRisLambers J (2013) Climate isn't everything: competitive interactions and variation by life stage will also affect range shifts in a warming world. *Am J Bot* 100:1344–1355
- Feary DA, Pratchett MS, Emslie MJ, Fowler AM and others (2014) Latitudinal shifts in coral reef fishes: why some species do and others do not shift. *Fish Fish* 15:593–615
- Festa-Bianchet M, Coulson T, Gaillard JM, Hogg JT, Pelletier F (2006) Stochastic predation events and population persistence in bighorn sheep. *Proc R Soc B* 273:1537–1543
- Fodrie FJ, Heck KL Jr, Powers SP, Graham WM, Robinson K (2010) Climate related, decadal-scale assemblage changes of seagrass associated fishes in the northern Gulf of Mexico. *Glob Change Biol* 16:48–59
- Franks JS, VanderKooy KE (2000) Feeding habits of juvenile lane snapper *Lutjanus synagris* from Mississippi coastal waters, with comments on the diet of gray snapper *Lutjanus griseus*. *Gulf Caribb Res* 12:11–17
- Gallaway B, Cole JG, Meyer R, Roscigno P (1999) Delineation of essential habitat for juvenile red snapper in the northwestern Gulf of Mexico. *Trans Am Fish Soc* 128:713–726
- Gallaway BJ, Szedlmayer ST, Gazey WJ (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* 17:48–67
- Garner SB, Patterson WF, Poch CE, Tarnecki JH (2014) Experimental assessment of circle hook performance and selectivity in the northern Gulf of Mexico recreational reef fish fishery. *Mar Coast Fish* 6:235–246
- Geange SW, Stier AC (2009) Order of arrival affects competition in two reef fishes. *Ecology* 90:2868–2878
- Gilliam JF, Fraser DF (1988) Resource depletion and habitat segregation by competitors under predation hazard. In:

- Ebenman B, Persson L (eds) Size-structured populations: ecology and evolution. Springer, Berlin, p 173–184
- Goldberg DE, Scheiner SM (2001) ANOVA and ANCOVA: field competition experiments. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Oxford University Press, New York, p 77–98
- ✦ Gomez-Laplaza LM, Morgan E (2003) The influence of social rank in the anglerfish, *Pterophyllum scalare*, on locomotor and feeding activities in a novel environment. *Lab Anim* 37:108–120
- Goodyear CP (1995) Red snapper in US waters of the Gulf of Mexico. Stock assessment report MIA-95/96-05. Southeast Fisheries Science Center, Miami, FL
- ✦ Hare JA, Morrison WE, Nelson MW, Stachura MM and others (2016) A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. *PLOS ONE* 11:e0146756
- ✦ Harley CD (2011) Climate change, keystone predation, and biodiversity loss. *Science* 334:1124–1127
- ✦ Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distribution of a wide range of taxonomic groups are expanding polewards. *Glob Change Biol* 12:450–455
- ✦ Hollowed AB, Barange M, Beamish RJ, Brander K and others (2013) Projected impacts of climate change on marine fish and fisheries. *ICES J Mar Sci* 70:1023–1037
- ✦ Johnson CR, Banks SC, Barrett NS, Cazassus F and others (2011) Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J Exp Mar Biol Ecol* 400:17–32
- Juliano SA (2001) Non-linear curve fitting: predation and functional response curves. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, 2<sup>nd</sup> edn. Oxford University Press, Oxford, p 178–196
- Karnauskas M, Kelble CR, Regan S, Quenée C and others (2017) Ecosystem status report update for the Gulf of Mexico. NOAA Tech Memo NMFS-SEFSC-706
- ✦ Lindberg WJ, Frazer TK, Portier KM, Vose F and others (2006) Density-dependent habitat selection and performance by a large mobile reef fish. *Ecol Appl* 16:731–746
- Lukens RR (1981) Ichthyofaunal colonization of a new artificial reef in the northern Gulf of Mexico. *Gulf Caribb Res* 7:41–46
- Lukoschek V, McCormick MI (2000) A review of multi-species foraging associations in fishes and their ecological significance. *Proc 9<sup>th</sup> Int Coral Reef Symp*, Bali 1:467–474
- Marshak AR (2016) Ecological impacts of climate-related ichthyofaunal shifts and invasive lionfish upon the northern Gulf of Mexico red snapper population and reef fish community. PhD dissertation, University of South Alabama, Mobile, AL
- ✦ Marshak AR, Heck KL Jr (2017) Interactions between range-expanding tropical fishes and the northern Gulf of Mexico red snapper *Lutjanus campechanus*. *J Fish Biol* 91:1139–1165
- Martinez-Andrade F (2003) A comparison of life histories and ecological aspects among snappers (Pisces: Lutjanidae). PhD dissertation, Louisiana State University, Baton Rouge, LA
- McAllister MK (2003) Analysis of total fishing mortality for Gulf of Mexico red snapper contributed by shrimp trawl bycatch and commercial and recreational fisheries (including discards). SEDAR7-DW-37. South Atlantic Fishery Management Council, North Charleston, SC
- ✦ McDonald MD, Gonzalez A, Sloman KA (2011) Higher levels of aggression are observed in socially dominant toadfish treated with the selective serotonin reuptake inhibitor, fluoxetine. *Comp Biochem Physiol C Toxicol Pharmacol* 153:107–112
- ✦ Milazzo M, Mirto S, Domenici P, Gristina M (2013) Climate change exacerbates interspecific interactions in sympatric coastal fishes. *J Anim Ecol* 82:468–477
- ✦ Mills MD, Rader RB, Belk MC (2004) Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. *Oecologia* 141:713–721
- ✦ Mudrak PA, Szedlmayer ST (2012) Proximity effects of larger resident fishes on recruitment of age-0 red snapper in the northern Gulf of Mexico. *Trans Am Fish Soc* 141:487–494
- Munro JJ, Williams DD (1985) Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. *Proc 5<sup>th</sup> Int Coral Reef Congr*, Tahiti 4:544–580
- ✦ Nagelkerken I, Simpson SD (2013) Who's hot and who's not: ocean warming alters species dominance through competitive displacement. *J Anim Ecol* 82:287–289
- ✦ Nakamura Y, Feary DA, Kanda M, Yamaoka K (2013) Tropical fishes dominate temperate reef fish communities within western Japan. *PLOS ONE* 8:e81107
- ✦ Olden JD, Poff NL, Bestgen KRL (2006) Life history strategies predict fish invasions and extirpations in the Colorado River basin. *Ecol Monogr* 76:25–40
- ✦ Overli O, Winberg S, Damsgard B, Jobling M (1998) Food intake and spontaneous swimming activity in Arctic char (*Salvelinus alpinus*): role of brain serotonergic activity and social interactions. *Can J Zool* 76:1366–1370
- Parker RO, Colby DR, Willis TD (1983) Estimated amount of reef habitat on a portion of the US South Atlantic and Gulf of Mexico continental shelf. *Bull Mar Sci* 33:935–940
- ✦ Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42
- Patterson WF, Wilson CA, Bentley SJ, Cowan JH and others (2005) Delineating juvenile red snapper habitat on the northern Gulf of Mexico continental shelf. *Am Fish Soc Symp* 41:277–288
- ✦ Patterson WF III, Barnett BK, Sluis MZ, Cowan JH, Shiller AM (2014) Interspecific variation in juvenile snapper otolith chemical signatures in the northern Gulf of Mexico. *Aquat Biol* 21:1–10
- ✦ Pérez España H (2003) Ecological importance of snappers in the stability of modeled coastal ecosystems. *Ecol Modell* 168:13–24
- ✦ Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308:1912–1915
- ✦ Persson L (1993) Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos* 68:12–22
- ✦ Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine taxa track local climate velocities. *Science* 341:1239–1242
- ✦ Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modeling the response of populations of competing species to climate change. *Ecology* 89:3138–3149
- ✦ Poulos DE, McCormick MI (2014) Who wins in the battle for space? The importance of priority, behavioural history and size. *Anim Behav* 90:305–314
- Rivas LR (1966) Review of the *Lutjanus campechanus* complex of red snappers. *Q J Fla Acad Sci* 29:117–136



- Robertson DR (1995) Competitive ability and the potential for lotteries among territorial reef fishes. *Oecologia* 103: 180–190
- Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Rev Fish Biol Fish* 14:251–275
- Schroeder WW, Shultz AW, Dindo JJ (1988) Inner-shelf hardbottom areas, northeastern Gulf of Mexico. *Trans Gulf Coast Assoc Geol Soc* 38:535–541
- Simmons CM, Szedlmayer ST (2018) Competitive interactions between gray triggerfish, *Balistes capricus*, and red snapper, *Lutjanus campechanus*, in laboratory and field studies in the northern Gulf of Mexico. *Can J Fish Aquat Sci* 75:1313–1318
- Stenevik EK, Sundby S (2007) Impacts of climate change on commercial fish stocks in Norwegian waters. *Mar Policy* 31:19–31
- Syc TS, Szedlmayer ST (2012) A comparison of size and age of red snapper (*Lutjanus campechanus*) with the age of artificial reefs in the northern Gulf of Mexico. *Fish Bull* 110:458–469
- Szedlmayer ST, Lee JD (2004) Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fish Bull* 102:366–375
- Szedlmayer ST, Mudrak PA (2014) Influence of age-1 conspecifics, sediment type, dissolved oxygen, and the *Deepwater Horizon* oil spill on recruitment of age-0 red snapper in the northeast Gulf of Mexico during 2010 and 2011. *N Am J Fish Manage* 34:443–452
- Szedlmayer ST, Shipp RL (1994) Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. *Bull Mar Sci* 55:887–896
- Taniguchi Y, Nakano S (2000) Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology* 81:2027–2039
- Turner RE, Rabalais NN, Justi D (2017) Trends in summer bottom-water temperatures on the northern Gulf of Mexico continental shelf from 1985 to 2015. *PLOS ONE* 12: e0184350
- Vergés A, Steinberg PD, Hay ME, Poore AG and others (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc R Soc B* 281:20140846
- Wells RJD, Cowan JH (2008) Video estimates of red snapper and associated fish assemblages on sand shell, and natural reef habitats in the north-central Gulf of Mexico. *Am Fish Soc Symp* 60:39–57
- Wells RJD, Boswell KM, Cowan JH, Patterson EF (2008a) Size selectivity of sampling gears targeting red snapper in the northern Gulf of Mexico. *Fish Res* 89:294–299
- Wells RJD, Cowan JH, Fry B (2008b) Feeding ecology of the red snapper *Lutjanus campechanus* in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 361:213–225
- Whitfield PE, Muñoz RC, Buckel CA, Degan BP, Freshwater DW, Hare JA (2014) Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Mar Ecol Prog Ser* 509:241–254
- Wittmer HU, Hasenbank M, Elbroch LM, Marshall AJ (2014) Incorporating preferential prey selection and stochastic predation into population viability analysis for rare prey species. *Biol Conserv* 172:8–14
- Workman I, Shah A, Foster D, Hataway B (2002) Habitat preferences and site fidelity of juvenile red snapper (*Lutjanus campechanus*). *ICES J Mar Sci* 59(Suppl):S43–S50
- Zar JH (1999) *Biostatistical analysis*, 4<sup>th</sup> edn. Prentice-Hall, Upper Saddle River, NJ

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