

Interactions between Northern-Shifting Tropical Species and Native Species in the Northern Gulf of Mexico

Rebecca L. Gericke · Kenneth L. Heck Jr. · F. Joel Fodrie

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Abstract Niche models applied in the context of future climate change predict that as regional temperatures increase, the distribution of tropical species will shift poleward. While range expansions have been documented for a number of species, there is limited information on the ecological impacts of shifts on native species. Recently, abundances of tropically-associated gray snapper (*Lutjanus griseus*) and lane snapper (*Lutjanus synagris*) have increased in seagrass nurseries in the northern Gulf of Mexico (GOM), concurrent with regional increases in sea surface temperature. We investigated effects of increased abundances of these species on abundance and growth of pinfish (*Lagodon rhomboides*), the dominant native species. Because juvenile pinfish and snappers share common prey, predators, and habitat, the high degree of niche overlap suggests an equally high potential for competition. We used a multiple before–after control impact design to determine whether increased snapper abundances significantly affected abundance or growth of pinfish. Trawl surveys at six locations in the northern GOM in summer and fall 2010 were used to calculate pinfish and snapper abundances. We identified three locations with high snapper abundances and three locations with no snapper and compared pinfish abundance and otolith-determined growth rates in these locations before and after snapper recruitment. Paired *t* tests and two-way analysis of

variance revealed no significant differences in pinfish abundance or growth in the presence of snappers compared to locations and seasons without snappers. We conclude that range expansions of tropically associated snappers have had no significant effect on abundance or growth of native pinfish in northern GOM seagrass habitats.

Keywords Range shift · Climate change · Pinfish · Snapper · Otolith microstructure analysis · Gulf of Mexico

Introduction

Global temperatures increased by 0.74 °C over the 100 years from 1906 to 2005 (Intergovernmental Panel on Climate Change (IPCC) 2007) and are predicted to continue warming in the future (Hiddink and Ter Hofstede 2008). Rising temperatures are predicted to have significant effects on the timing of seasonal activities of species and the structure and functioning of ecological communities (McCarty 2001), including poleward shifts in the distribution and range of tropical species (Perry et al. 2005).

A number of studies have documented cases of range expansion for both terrestrial and marine species. Perry et al. (2005) examined 36 species of fish in the North Sea and found that the mean latitude of the center of distribution for nearly half of the species shifted from 1977 to 2001. Of those that shifted, 13 species shifted northward, as predicted from climate change scenarios. Furthermore, they found that the southern range for 6 of 12 boreal species with a southern boundary in the North Sea shifted northward over the study period. Similarly, in a study of 35 species of European butterflies, Parmesan et al. (1999) found that 63 % of species showed range shifts of 35–240 km northward, while only 3 % of species shifted to the south. Other studies have shown similar shifts in the geographic ranges of birds (Thomas and

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R. L. Gericke · K. L. Heck Jr.
Dauphin Island Sea Lab, Dauphin Island, AL 36528, USA

R. L. Gericke (✉) · K. L. Heck Jr.
Department of Marine Sciences, University of South Alabama,
Mobile, AL 36688, USA
e-mail: rebecca.gericke@gmail.com

F. J. Fodrie
Institute for Marine Science, University of North Carolina at Chapel
Hill, Morehead City, NC 28557, USA

Lennon 1999), intertidal invertebrates (Sagarin et al. 1999), planktonic forams (Field et al. 2006), estuarine fishes (Nicolas et al. 2011), and mammals (Payette 1987; Fertl et al. 2004). These shifts are likely to have concurrent effects on species diversity and community ecology at sites receiving poleward-moving flora or fauna, although few studies have examined these dynamics (Sorte et al. 2010).

The Gulf of Mexico (GOM) is well suited for studying the ecological impacts of shifts in species distribution. The GOM is bisected by the Tropic of Cancer, which divides the GOM into two distinct climate zones characterized by tropical environments in the south and temperate/subtropical environments in the north (Fodrie et al. 2010). The northern edge of the GOM is bounded by the North American continent, restricting the geographic area available for range shifts of temperate aquatic species in response to climatic warming. For these reasons, the ecological impacts of climate-driven shifts in the distribution of tropical and subtropical species may be especially dramatic in the northern GOM, making this location a valuable site for studying the effects of climate change on marine communities via the collision of tropical and temperate fauna.

A number of recent studies have provided evidence of poleward shifts of tropical species from the southern to the northern GOM. For example, McKee (2004) documented the expansion of black mangrove (*Avicenna germinans*) in the mangrove–salt marsh interface in coastal Louisiana following the die-off of smooth cordgrass (*Spartina alterniflora*). Similarly, two common Caribbean corals have recently been observed north of their native range in areas where they were previously absent. North of Broward County, Florida, staghorn coral (*Acropora palmata*) and elkhorn coral (*Acropora cervicornis*) were first observed in 1998 and 2004, respectively (Precht and Aronson 2004; Vargas-Ángel et al. 2003), and elkhorn coral was first observed in the Flower Garden Banks National Marine Sanctuary off the coast of Texas in 2002 (Precht and Aronson 2004). In addition, reports of sightings of the West Indian manatee (*Trichechus manatus*) have increased substantially in recent years along the northern coast of the GOM, suggesting that migrations of this marine mammal from southwest Florida may be increasing (Fertl et al. 2004; Pabody et al. 2009).

The abundances of several tropical fish species have also increased in seagrass habitats in the northern GOM in recent years. Fodrie et al. (2010) surveyed the ichthyofauna of seagrass beds in the northern GOM from 2006 to 2007 and compared their data to a trawl data set collected annually in the 1970s in northwest Florida (Livingston 1982). Several species of groupers, snappers, and parrotfishes showed marked abundance increases in the last 30–40 years consistent with the predictions of niche models. For example, gray snapper (*Lutjanus griseus*) increased nearly 105-fold to become the seventh most abundant species in 2006–2007, and lane snapper (*Lutjanus synagris*), which were absent in the 1970s,

increased to become the eighth most abundant species in 2006–2007. Concurrent with the ichthyofaunal surveys, Fodrie et al. (2010) also documented a regional increase in air and sea surface temperatures from the 1970s to 2007, with both the frequency and intensity of warm days and the nightly minimum sea surface temperature during the fall months increasing significantly over time. These trends in regional climate, coupled with the observed shifts in species abundance in local seagrass habitats, provide empirical evidence for climate-driven shifts in ichthyofaunal ranges in the GOM.

While it is evident that shifts in the range of non-native species have altered the composition of local ichthyofaunal communities, the effects of these shifts on community ecology are incompletely understood. In some regions, poleward expansion has increased local biodiversity (Hickling et al. 2006), with no obvious negative effects on the endemic populations. However, in the long term, range shifts of tropical species may have consequences similar to the invasion of introduced species, such as altering habitat utilization, modifying predator–prey dynamics, and increasing herbivory. In intertidal zones, for example, changes in water temperature have been shown to alter the direction and intensity of interspecific interactions (Sanford 1999; Leonard 2000; Harley 2011) demonstrating significant effects of climate change on food webs. Therefore, it is important to examine how modifications in fish assemblages in seagrass beds in the northern GOM described by Fodrie et al. (2010) may be impacting local community dynamics.

The purpose of this study was to examine whether negative, sublethal effects resulting from increased abundances of tropically-associated species could be detected on one of the most common native species in the northern GOM. Specifically, we examined whether higher occurrences of lane snapper and gray snapper in seagrass nursery habitats affected the abundance and/or growth rate of native pinfish (*Lagodon rhomboides*), the most abundant seagrass-associated species in collections from both the 1970s and 2006–2007 (Livingston 1982; Fodrie et al. 2010). Due to a high degree of overlap in preferred habitat, prey, and predators, it would be expected that increased abundances of juvenile snappers could have significant, sublethal effects on juvenile pinfish. We investigated these questions using a field-based, natural experiment in which we compared the abundances and growth rates of juvenile pinfish in areas either with or essentially without young-of-the-year snappers.

Materials and Methods

Experimental Organisms

Pinfish, *L. rhomboides*, are the numerically dominant fish species in seagrass beds in the northern GOM (Stoner 1980;

Livingston 1982; Fodrie et al. 2010). Pinfish are tolerant of a wide range of temperatures and salinities and their distribution extends from Massachusetts, USA to Yucatan, Mexico (Hoese and Moore 1977). Seagrass beds and salt marshes serve as important nursery grounds for juvenile pinfish (15–100 mm standard length (SL); Stoner 1980), where they grow in the spring, summer, and fall before migrating offshore in late fall (Weinstein et al. 1982). Pinfish diet shifts with age following ontogenic changes in dentition. Juvenile pinfish are omnivorous and feed primarily on amphipods and other small crustaceans (Carr and Adams 1973; Stoner 1979, 1982) but as they grow the diet becomes increasingly more herbivorous with pinfish larger than 110 mm SL feeding almost exclusively on plant material (Stoner 1979).

Lane snapper (*L. synagris*) and gray snapper (*L. griseus*) are common throughout the western Atlantic with a center of distribution in the Caribbean and extending from Brazil to North Carolina and Massachusetts, USA, respectively. Following offshore spawning, larval lane and gray snapper (approximately 10 mm SL; Stark and Schroeder 1971) migrate inshore where they occupy seagrass and mangrove habitats as juveniles (Lindeman et al. 1998) and feed predominantly on amphipods, decapods, and small fish (Orlando Duarte and Garcia 1999; Franks and VanderKooy 2000). The diets of juvenile lane snapper from Mississippi Sound, Mississippi, were found to consist of approximately 40 % amphipods, 48 % decapods, and 6 % fish, while juvenile gray snapper diets from the same region consisted of approximately 48 % amphipods, 40 % decapods, and 4 % fish (Franks and VanderKooy 2000). These data indicate a high degree of dietary overlap among juvenile lane snapper, gray snapper, and pinfish, suggesting a high potential for competitive interactions among these species.

Juvenile gray snapper, lane snapper, and pinfish also share many predators common in seagrass beds, including speckled trout, red drum, large blue crabs, and small sharks (Darcy 1985; Bortone and Williams 1986). An examination of stomach contents from juvenile lemon sharks found that teleosts comprised 98.4 % of lemon shark diets by weight with fishes from the family *Sparidae* representing 20 % and fishes from the family *Lutjanidae* representing 8.5 % of the total fishes consumed (Cortes and Gruber 1990). Due to the overlap in predators, an increase in the abundance of snappers may have either an indirect positive or indirect negative effect on pinfish abundance. High snapper abundances may result in increased abundances of juvenile pinfish if shared predators preferentially feed on snappers, thereby reducing predation on pinfish. On the other hand, high abundances of snappers may lead to apparent competition, whereby the increased abundance of snappers attracts predators to an area, resulting in higher predation on pinfish and lower pinfish abundances. Furthermore, juvenile snappers and pinfish may compete over refuge

space from predators. In this case, the increased presence of juvenile snappers would make pinfish more vulnerable to predation resulting in lower pinfish abundances.

Field Collections

Trawl surveys were conducted in summer (June and July) and fall (September–November), 2010, in seagrass beds in the northern GOM, from the Chandeleur Islands, LA, USA in the west, to St. Joseph Bay, FL, USA in the east (Fig. 1). All study sites were located within 1° latitude of one another. Ichthyofauna communities were sampled using a 5-m otter trawl (2.0-cm body mesh; 0.6-cm bag mesh; 0.3×0.7 m doors) towed for 2–7 min behind a research vessel traveling approximately 2.5 knots. Tows were conducted over both monospecific and mixed seagrass beds including turtlegrass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), widgeon grass (*Ruppia maritima*), and manatee grass (*Syringodium filiforme*), interspersed with unvegetated sand patches. All fishes collected in the trawls were identified to the lowest possible taxonomic unit and enumerated in the field. Trawl abundance data for each species was converted to catch per unit effort (CPUE), defined as the number of fish captured per minute trawled. At each site in each season, up to 30 young-of-the-year pinfish were collected, frozen, and transported on ice to the Dauphin Island Sea Lab for further analyses.

Using the trawl data, we identified three locations with seasonally high abundances of both gray and lane snapper (“impact” sites), and three locations with low or no snapper throughout the year (“control” sites; Fig. 1). From west to east, impact sites were Horn Island, MS, USA (30.230 and –88.616); Big Lagoon, FL, USA (30.324 and –87.327); and

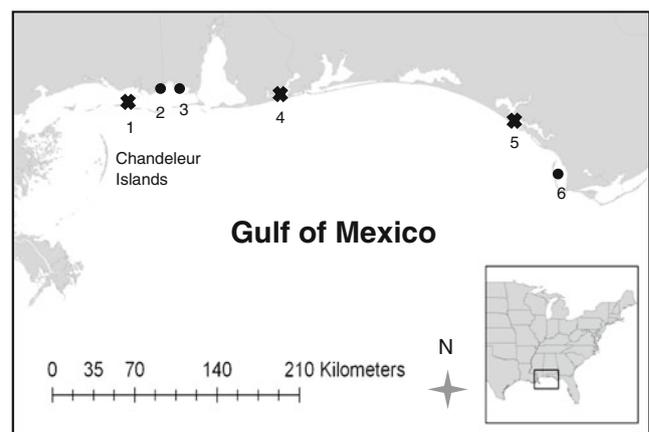


Fig. 1 Map of trawl sites from which pinfish were collected. 1 Horn Island, MS, USA; 2 Middle Bay, MS, USA; 3 Point aux Pins, AL, USA; 4 Big Lagoon, FL, USA; 5 St. Andrew Bay, FL, USA; 6 St. Joseph Bay, FL, USA. Sites marked with an *X* (sites 1, 4, and 5) indicate impact sites where snappers were present in the fall months and sites marked with a *circle* (sites 2, 3, and 6) denote control sites where snappers were absent in both the summer and fall months

St. Andrew Bay, FL, USA (30.114 and -85.682); and control sites were Middle Bay, MS, USA (30.387 and -88.406); Point aux Pins, AL, USA (30.380 and -88.311); and St. Joseph Bay, FL, USA (29.801 and -85.406). Pinfish were collected from all locations in the summer, before the arrival of snapper recruits (“before” samples) and again in the fall after the arrival of snapper recruits (“after” samples).

The Deepwater Horizon oil disaster occurred off the coast of Louisiana on 20 April 2010, less than 2 months before our trawl surveys commenced. Fortunately, none of our study sites were oiled and therefore experienced no direct effects of oiling. Because pinfish, gray snapper, and lane snapper spawn offshore, there was concern that larvae and presettlement juveniles would be susceptible to oil pollution (Kerr et al. 2010). Using a 5-year trawl data set from the northern GOM, Fodrie and Heck (2011) compared overall and species-by-species CPUE from 2006 to 2009 (pre-oil) to 2010 (post-oil). In 2010, pinfish and gray snapper CPUEs were significantly greater and lane snapper CPUE was not significantly different compared to 2006–2009. Thus, the Deepwater Horizon oil disaster had no immediate negative effects on the abundance of any of the species in this study and snapper–pinfish interaction strengths during 2010 trawl surveys were not expected to be anomalous. However, the long-term effects of the Deepwater Horizon oil disaster remain unknown and the potential long-term impacts facing fishes as a result of chronic exposure and delayed, indirect effects now require attention.

Otolith Microstructure Analysis

Otolith microstructure analysis was used to calculate daily growth rates of pinfish. Daily growth increments have been shown to exist in other species in the family Sparidae (Francis et al. 1993) and previous studies have successfully measured pinfish growth rates using otolith increment widths as a proxy for somatic growth (Levin et al. 1997; Burfeind and Stunz 2007).

Prior to otolith removal, fish were thawed and the SL (in millimeter) and total length (TL, in millimeter) of each fish were recorded. The SL of pinfish used in the analysis ranged from 39.01 to 90.8 mm. The left and right lapillar otoliths of each fish were removed under a dissecting microscope following the methods of Secor et al. (1991). Care was taken to gently remove all attached tissue without causing damage to the otolith itself. Immediately following dissection, otoliths were rinsed in a 10 % bleach solution, rinsed with deionized water, and stored for approximately 24 h in standard microscopy immersion oil. This technique has been used in previous studies to enhance the clarity of daily increments without the need for sectioning (Burfeind and Stunz 2007) and preliminary tests indicated that 24 h was adequate for achieving desired clarity. Storage in immersion oil provided sufficient

resolution to distinguish between the opaque and translucent zones and no further processing was necessary. After 24 h, otoliths were removed from oil, dried, and glued to a microscopy slide under a dissecting microscope using Cytoseal liquid mounting medium.

All measurements were conducted on the margin of the left lapillar otolith of each fish. Otoliths were viewed using an Olympus BX41 compound microscope fitted with an Olympus SC30 digital camera, and images were processed using Olympus CellSens digital image enhancing software.

Pinfish otoliths display asymmetrical growth; therefore, it was necessary to standardize the location of increment measurements on otoliths from all fish (Campana 1992). To achieve this, a reference line was first drawn through the center of the primordium along the longest axis of the elliptical increments surrounding the primordium. The otolith radius was measured by drawing a line from the center of the primordium to the otolith margin, perpendicular to the reference line. The otolith radius line then served as a reference line for increment width measurements and all increment measurements were made nearby and parallel to this line. Increment widths were measured from the edge to the 10th increment in from the margin, corresponding to the most recent 10 days of growth. In many cases, the first one to three increments closest to the margin was unclear and could not be read; when this occurred, increment counts and measurements began at the first clearly defined ring. Preliminary tests indicated that these measurements were not significantly different than those beginning at the otolith margin.

Radius and increment widths were measured twice by the same reader. If the first two measurements did not agree within $\pm 5\%$, a third measurement was taken. If two of the three measurements did not agree within $\pm 5\%$, the otolith was excluded from statistical analyses. The two measurements with the closest degree of agreement ($\pm 5\%$ or less) were averaged to obtain an average radius measurement and an average increment width measurement for each otolith.

Statistical Analyses

The effect of treatment type (control vs. impact) and season (before vs. after impact) on pinfish abundance and growth was analyzed using a combination of *t* tests and analysis of variance (ANOVA, PASW Statistics 18). Data were tested for the assumptions of parametric statistics prior to analysis, and log transformations were applied when the data did not meet these assumptions. Log transformation achieved normality and homogeneity of variance for the growth data. Transformed CPUE data achieved homogeneity of variance but the distribution remained non-normal. However, ANOVA is robust to violations of normality (Quinn and Keough 2002), and this test was used. Results were considered significant at $\alpha = 0.10$.

We used a paired *t* test to investigate if the magnitude of the difference between control and impact sites was significantly different in the summer compared to the fall, while accounting for natural variation that existed among sites. Each pair consisted of one control site and one impact site, and sites were paired geographically with the assumption that environmental conditions would be most similar at closer sites. Pairs were (1) Big Lagoon, FL, USA (impact) and Point aux Pins, AL, USA (control); (2) Horn Island, MS, USA (impact) and Middle Bay, MS, USA (control); (3) St. Andrew Bay, FL, USA (impact) and St. Joe Bay, FL, USA (control). By pairing sites, we were able to assess whether the arrival of snappers had a significant effect on the impact sites relative to the controls, while accounting for natural variation that existed between control and impact sites.

Traditional before–after control–impact (BACI) designs study one impact and one control location and do not replicate sites. Underwood (1992) stressed the importance of sampling multiple control sites and multiple impact sites when logistically possible to increase the likelihood that observed differences are due to the impact in question. This study was replicated at three control and three impact sites, following a multiple before–after control–impact (MBACI) design (Keough and Mapstone 1997, and references therein). Results from an MBACI study can be analyzed using a partly nested ANOVA with a modified *F* ratio for the critical test. For both the abundance and growth data, we ran a two-way-nested ANOVA with season (two levels) and sites (six levels) nested within treatment (two levels) as our factors. The final ANOVA model included these terms: season, treatment, treatment × season, site (nested within treatment), and site (nested within treatment × season). This test is based on the hypothesis that temporal changes at the impacted sites before and after the onset of the impact should be significantly different from temporal changes that occur at unimpacted control sites (Underwood 1994). The ANOVA term of most interest is treatment × season, which is tested using the mean square error of site (treatment × season) as the denominator in the *F* ratio (Keough and Mapstone 1997; Underwood 1992).

Results

Snapper Abundance

No gray or lane snappers were collected at any of the control or impact sites in the summer (Table 1). The absence of snappers at all sites in the summer months allowed us to designate samples from this time as “before” samples in the MBACI design. In the fall, snapper abundances were significantly greater at the impact sites compared to the control sites ($t = -3.36$, $df = 2.12$, $p = 0.07$), confirming our distinction between control (few or no snapper) and impact (relatively

Table 1 Mean CPUE (fish per minute) of pinfish and snappers at all sites in both seasons. Sites with seasonally high abundances of snappers were designated “impact” sites, and sites with low or no snappers in both seasons were designated “control” sites. Samples collected in the summer before the recruitment of juvenile snappers were designated “before” samples, and those collected in the fall after the arrival of snapper recruits to the impact sites were designated “after” samples

Treatment	Site	Time	Mean pinfish CPUE	Mean snapper CPUE
Control	Middle Bay, Mississippi	Before	14.4	0
		After	0.7	0.4
	Point aux Pins, Alabama	Before	29.3	0
		After	11.6	0
	St. Joe Bay, Florida	Before	31.4	0
		After	194.2	0.1
Impact	Horn Island, Mississippi	Before	4.0	0
		After	4.3	1.7
	Big Lagoon, Florida	Before	138.7	0
		After	186.5	3.7
	St. Andrew Bay, Florida	Before	56.8	0
		After	125.9	1.8

abundant snapper) sites. The seasonal increase in snapper abundances at the impact sites in the fall allowed us to designate fall samples as “after” samples in the MBACI design.

Pinfish Abundance

In the summer, pinfish CPUE (mean ± SE) averaged 36.1 ± 15.8 fish per minute trawled at control sites and 50.8 ± 34.1 fish per minute trawled at impact sites. In the fall, pinfish CPUE averaged 69.7 ± 59.6 fish per minute at control sites and 106.3 ± 57.7 fish per minute at impact sites where snappers were present.

The results of a paired sample *t* test comparing the magnitude of the difference in pinfish CPUE between impact sites and control sites in summer versus fall was not significant ($t = -2.49$, $df = 2.84$, $p = 0.82$; Fig. 2). In addition, the direction of the change was counter to what would be expected if there was strong antagonism among species. This suggests that the arrival of snapper did not have a significant effect on the abundance of pinfish at impact sites (at the scale of our trawl samples), compared to control sites where snapper were absent. Furthermore, the data indicate that pinfish abundance was more different between impact and control sites in the fall, after the arrival of snapper to the impact sites.

A partly nested two-way ANOVA revealed no significant interaction between treatment and season on pinfish CPUE ($F_{1,2} = 0.013$, $p = 0.920$; Table 2). Similar to the results of the paired *t* tests, this suggests that the temporal change in snapper abundance from summer to fall that occurred at the impact

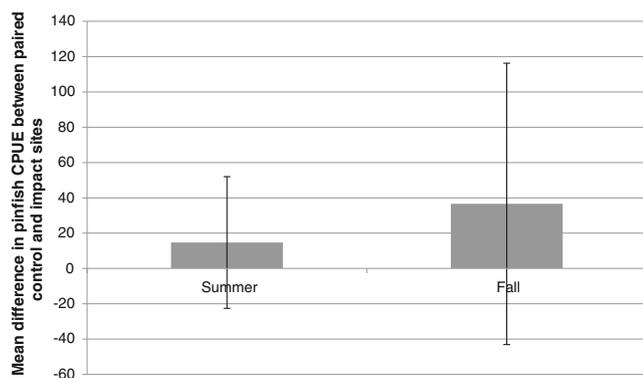


Fig. 2 Average difference in pinfish CPUE between paired impact and control sites in summer and fall. Error bars are $\pm 1SE$. Positive values indicate greater CPUE at impact sites compared to control sites. There was no significant effect of season on the magnitude of the difference in CPUE between impact and control sites ($p=0.82$)

sites was not significantly different from the temporal change in snapper abundance that occurred at the control sites during the same time. Thus, high abundances of juvenile gray and lane snapper at impact sites in the fall months had no significant effect on pinfish abundance.

Pinfish Growth

A total of 254 otoliths were read (Fig. 3c); 22 were subsequently discarded from further statistical analyses due to inconsistent measurements or unclear images that could not be analyzed. A regression analysis of otolith increment widths (corresponding to daily growth rates) on fish standard length indicated that among the fishes we investigated growth rates were not significantly related to fish size ($r^2=0.018$, $n=220$, $p=0.15$; Fig. 3a). In other words, smaller fish did not grow at a faster rate than larger fish or vice versa. Therefore, fish size

was not included as a covariate in any analyses of otolith increment width.

There was a significant positive relationship between pinfish SL and otolith radius (radius= $3.111 \times SL + 194.23$, $r^2=0.5996$, $p<0.001$; Fig. 3b). Thus, otolith increment widths were used as a proxy for somatic growth. Using this regression equation, otolith increment widths over the most recent 10 days were converted to pinfish daily growth rates (in millimeters per day).

In the summer, pinfish grew at an average rate (mean \pm SE) of 0.48 ± 0.01 mm day $^{-1}$ at control sites and 0.47 ± 0.01 mm day $^{-1}$ at impact sites. Daily growth rates in fall averaged 0.48 ± 0.01 mm day $^{-1}$ at control sites and 0.46 ± 0.01 mm day $^{-1}$ at impact sites.

To account for natural variation among sites and between seasons, the difference in average growth rates between impact and control sites was calculated for the three pairs of locations in both seasons, and the average difference between sites in summer was compared to the average difference between sites in fall using a paired samples t test. This test was used to assess whether the difference in growth rates between control and impact sites was affected by the arrival of snapper, relative to the difference in growth rates between control and impact sites prior to snapper arrival. In both seasons, the difference in otolith increment measurements between paired impact and control sites was negative, indicating higher growth rates in control sites relative to impact sites. Results of a paired samples t test indicated that the difference in otolith increment measurements between control and impact sites was not significantly different between seasons ($t=0.498$, $df=2$, $p=0.668$; Fig. 4).

A partly nested two-way ANOVA revealed no significant interaction between treatment type (control vs. impact) and season (summer vs. fall) on pinfish daily growth

Table 2 Results of a partly nested two-way ANOVA using log transformed CPUE of pinfish as the response variable. The critical term in this analysis is treatment \times season, which is tested using the mean square error (MS) of the site (treatment \times season) term as the denominator in the F ratio. This effect is not significant

Source		Type III sum of squares	Degrees of freedom	Mean square	F	p
Intercept	Hypothesis	66.281	1	66.281	31.786	0.000
	Error	19.000	9.112	2.085		
Treatment	Hypothesis	1.987	1	1.987	0.945	0.356
	Error	19.215	9.138	2.103		
Season	Hypothesis	0.005	1	0.005	0.004	0.953
	Error	2.707	2.206	1.227		
Treatment \times season	Hypothesis	0.015	1	0.015	0.013	0.920
	Error	2.707	2.206	1.227 ^a		
Site (treatment)	Hypothesis	27.769	8	3.471	3.119	0.234
	Error	2.618	2.353	1.113		
Site (treatment \times season)	Hypothesis	2.931	2	1.466	5.059	0.008
	Error	24.625	85	0.290 ^b		

^a 0.797 MS (site(treatment \times season))+ 0.203 MS (error)

^b MS (error)

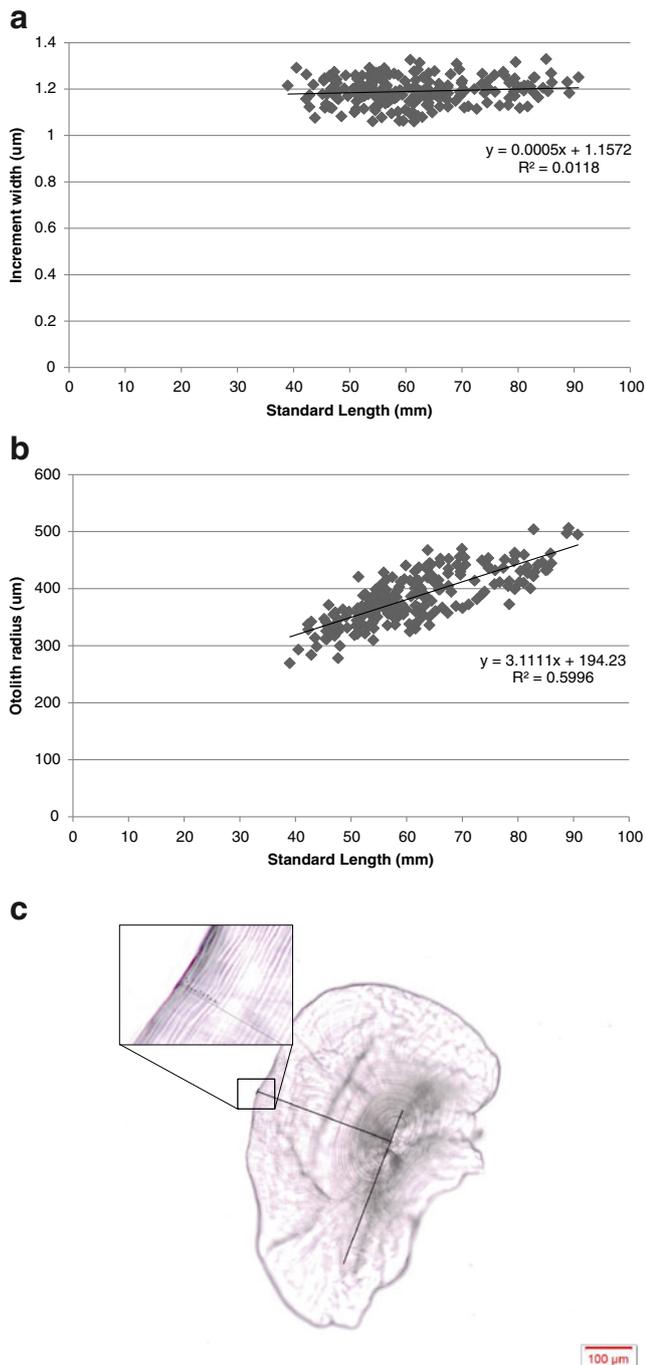


Fig. 3 Relationship between standard length of fish and **a** otolith increment width and **b** otolith radius. Increment widths were measured over the 10 most recent days of growth prior to capture (see inset in **c**). Data are from fish from all sites in both seasons

rates ($F_{1,4}=0.391$, $p=0.565$; Table 3). These results indicated that the temporal change in pinfish growth from summer to fall was not significantly different at the impact sites compared to the control sites suggesting that high abundances of tropical snappers at the impact sites in the fall did not have a significant effect on pinfish growth rates.

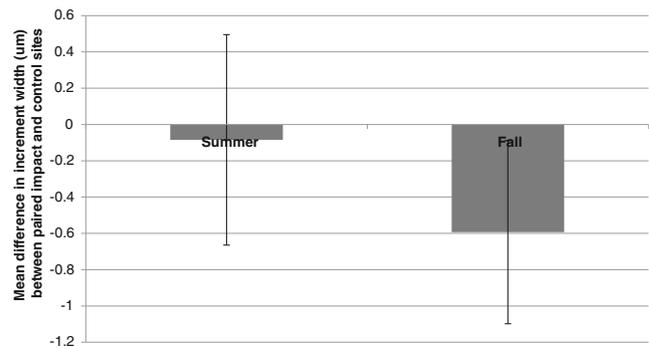


Fig. 4 Average difference in increment width between paired impact and control sites in summer and fall. Error bars are ± 1 SE. Negative values indicate larger increment widths at control sites compared to impact sites. There was no significant difference between summer and fall ($p=0.668$)

Discussion

The difference in pinfish abundance between paired control and impact sites was not significantly different between seasons, suggesting that the recruitment of tropically associated gray and lane snappers to the control sites in the fall did not have a significant effect on pinfish abundances. There was, therefore, no evidence of significant competition among juveniles of the species over shared habitat and prey resources, which would manifest as a decline in pinfish abundance in areas where snapper abundances were high. This indicates that habitat and prey resources were not limiting pinfish abundance. We also observed no indirect effects, either positive or negative, of increased snapper abundances on pinfish abundance due to the overlap in shared predators. The data collected in this study suggest that tropical snappers shifting north into the northern GOM have filled a niche in the local communities with no significant impacts on the population size of the numerically dominant native species.

Although increased snapper abundances were not associated with a decline in pinfish populations, it is possible that the increased presence of snappers may have negatively impacted other less dominant species. Our study focused on the effects of snappers on pinfish because pinfish are abundant across all sites and seasons. Furthermore, because pinfish are the dominant species in these communities, significant changes in pinfish population sizes would lead to greater impacts on local community ecology. The effect of increased snapper abundances may be detectable on less dominant species that could easily be outcompeted for shared resources, but the resulting impacts on overall community ecology would not be as severe. Nevertheless, the effect of snapper range shifts on additional species, including both tropically equivalent species, prey species, and predators, remains an interesting avenue for exploration and demands future attention.

The daily growth rates calculated in this study (means ranging from 0.46 to 0.48 mm SL day⁻¹) are consistent with previously reported growth rates for pinfish in the northern

Table 3 Results of a partly nested two-way ANOVA using log transformed values of average increment width of pinfish otoliths as the response variable. The critical term in this analysis is treatment \times season, which is tested using the mean square error (MS) of the site (treatment \times season) term as the denominator in the F ratio. This effect is not significant

Source		Type III sum of squares	Degrees of freedom	Mean square	F	p
Intercept	Hypothesis	305.553	1	305.553	33110.753	0.000
	Error	0.037	4.012	0.009		
Treatment	Hypothesis	0.006	1	0.006	0.603	0.481
	Error	0.037	4.012	0.009		
Season	Hypothesis	0.001	1	0.001	0.130	0.737
	Error	0.024	4.019	0.006		
Treatment \times season	Hypothesis	0.002	1	0.002	0.391	0.565
	Error	0.024	4.019	0.006 ^a		
Site (treatment)	Hypothesis	0.037	4	0.009	1.519	0.348
	Error	0.024	4	0.006		
Site (treatment \times season)	Hypothesis	0.024	4	0.006	2.103	0.082
	Error	0.603	208	0.003 ^b		

^a 0.995 MS (site(treatment \times season)) + 0.005 MS (error)

^b MS (error)

GOM. For example, Levin et al. (1997) measured pinfish growth at a rate of 0.41 mm SL day⁻¹ in March near Galveston Island, TX, USA. Similarly, Spitzer et al. (2000) calculated daily growth rates of pinfish ranging from approximately 0.45 to 0.60 mm TL day⁻¹ from July to October in Big Lagoon, FL, USA. The close agreement between the growth rates calculated in this study and those reported previously provide further validation for the use of otolith daily growth increments to calculate juvenile pinfish growth rates.

Because the daily growth rates of pinfish calculated in this study fall within previously reported ranges for fish in the study area, our growth data from 2010 were not considered anomalous. We detected no immediate, negative effects of the Deepwater Horizon oil disaster on local pinfish growth rates, although long-term direct and indirect effects of the disaster on the growth of pinfish and other species are unknown.

The difference in pinfish growth rates between impact and control sites was not significantly different between seasons. Thus, seasonal increases in snapper abundance at impact sites in the fall had no significant effect on pinfish growth. Overall, the lack of significant effects of increased snapper abundance on both pinfish abundance and growth suggest that shared resources, such as habitat and prey, are not limiting the size of these populations in seagrass beds in the northern GOM. The data indicate that, although the degree of niche overlap suggests high potential for interspecific competition, no significant competition occurred. Within northern GOM seagrass habitats, pinfish and snappers are able to coexist at their current population sizes as they often do in other regions where their ranges overlap, such as the Florida Keys (Acosta et al. 2007).

Climate-driven range shifts have been compared to anthropogenically driven species introductions because both processes involve the movement of one or more species from a donor community within their natural range to a recipient

community outside of their established range (Sorte et al. 2010). Consequently, impacts of climate-influenced range shifts may be predicted by studying exotic species literature. On a global scale, species invasions and introductions in recent decades have been shown to increase the similarity of species composition in once distinct regions, through a process known as biotic homogenization (Olden et al. 2004). However, on a local scale, our findings are consistent with recent studies of anthropogenically driven species invasions which suggest that invasions by non-indigenous species often lead to an increase in local biodiversity and/or species richness in the recipient community with few significant negative effects on native species (Cohen and Carlton 1995; Hickling et al. 2006; Hiddink and Ter Hofstede 2008; Parker et al. 1999; Sagoff 2005; Sax and Gaines 2003; Sax et al. 2002).

In a recent review, Sax et al. (2007) suggested that many communities are not saturated with species, and thus introductions of non-native species may lead to an increase in local biodiversity. For example, in New Zealand, species richness of vascular plants has doubled in the last few hundred years due to invasions (Sax et al. 2002). Similarly, vascular plant richness has increased nearly 20 % in regions of both the USA and Australia (Sax et al. 2002; Sax and Gaines 2003). In Hawaii, no native freshwater fish species went extinct following the introduction of 40 exotic species, leading to an 800 % increase in local species richness (Sax and Gaines 2003).

We predict that the effects of snapper range shifts on native species would be less severe and more difficult to detect than the effects of species invasions, despite the similarities in the two processes. Sorte et al. (2010) suggested that impacts of species whose ranges have expanded would be weaker and less frequent than the effects of introduced or exotic species, making community-level effects of shifting species difficult to detect. Furthermore, in the southern GOM, the distribution of juvenile pinfish and snappers overlap, and these species are

known to coexist in some areas (Acosta et al. 2007). Additionally, it is likely that abundances of juvenile snappers in the northern GOM were greater in the warmer 1920s and 1930s, and their populations have fluctuated with changing temperatures (Fodrie et al. 2010). These species, therefore, are not completely novel to one another and likely share some of their evolutionary history. This may explain the lack of statistically significant effects of increased snapper abundances on pinfish, despite the high likelihood for competition among the species.

This study is unique in that it focuses on the indirect effects of an expanding species on a trophically equivalent species. Although these species are known to coexist in some areas (Acosta et al. 2007), they are recently novel to one another in the northern GOM, making the ecological outcomes of climate-driven range expansion difficult to predict. Additionally, this study is unique in that it was conducted on highly mobile species, whereas many previous impact studies focus on one or more benthic species. This study used a novel approach to investigate the ecological impacts of climate-related shifts in tropical species distributions using field observations and a natural experiment.

To our knowledge, this study is one of the few studies investigating the community-level impacts of species introduced by climate-related range expansions (Sorte et al. 2010). As evidence of climate-related shifts in faunal distributions becomes more abundant, a key question to investigate next is how these species impact local community ecology. In fact, studies of the impacts of shifting species have been called the “next frontier” in climate change research (Kintisch 2008). We conclude by suggesting that it is possible that the impacts of lane and gray snapper range expansions may be more pronounced in the future, as regional temperatures continue to increase and tropically associated snappers establish larger resident populations in the northern GOM; therefore, future studies will be useful in elucidating these outcomes.

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