

Long-term analysis of spatio-temporal patterns in population dynamics and demography of juvenile Pinfish (*Lagodon rhomboides*)



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ABSTRACT

In estuarine systems, proximity to the ocean has the potential to directly and indirectly drive patterns of fish distribution and population dynamics. To test this hypothesis, we conducted a comprehensive analysis of fisheries-independent data and quantified patterns of density, biomass, and growth rates of juvenile Pinfish (*Lagodon rhomboides*) across spatial and temporal scales in Tampa Bay, Florida, USA. Spatially, the highest density and biomass were found in the outermost regions (closest to the Gulf of Mexico) of the Bay, and these patterns were generally consistent temporally. Inter-annually, Pinfish density and biomass were the highest during periods coinciding with favorable oceanographic conditions (e.g., anomalously intense and prolonged upwelling) for across-shelf transport of larvae from spawning grounds in the Gulf to Tampa Bay. Intra-annually, density and biomass were the highest during spring and summer likely due to the combined effects of spawning timing (and delivery of new settlers), and high somatic growth fueled by increased secondary and primary productivity. Declines in density and biomass during the late summer through early winter were possibly due to high post-settlement mortality and egress to offshore habitats. Pinfish increased predictably in size across the months of the calendar year, and tended to be larger and grew faster in the innermost regions of the Bay, which were located farthest from the Gulf. Pinfish density was related to the proximity to the Gulf of Mexico, with the outermost regions of the Bay having greater seagrass cover, higher salinity, and being closer to the offshore larval pool where spawning occurs. Thus, this study provided evidence that distance to the ocean was an important driver of biotic and abiotic factors that influenced Pinfish demographic rates across spatial and temporal scales in the largest estuary in Florida.

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1. Introduction

The influence that proximity to the ocean can have on estuarine species has not been extensively studied despite its potential to directly and indirectly influence patterns of fish distribution and population dynamics. For example, oceanographic currents can affect dispersal of larval stages, resulting in spatial patterns in the delivery of competent larvae, settlement, population distributions, and species richness (Loneragan et al., 1986, 1987; Watson et al., 2011). Proximity of estuaries to the ocean can induce gradients in abiotic factors (e.g., salinity, nutrient input, temperature) that can influence predator-prey and competitive interactions (Breitburg et al., 1997; Chacin and Stallings, 2016), the presence of benthic

habitats (Marchand, 1993; Ley et al., 1999), physiological stress (Allen and Horn, 1975; Peterson and Ross, 1991; Menge, 1976; Araujo et al., 1999), and produce spatial and seasonal patterns of resource availability (Zimmerman and Minello, 1984). This continuum of environmental variation in estuarine systems in turn can structure patterns of abundance and composition of faunal assemblages (Loneragan et al., 1989; Cyrus and Blaber, 1992; Akin et al., 2003).

The Pinfish, *Lagodon rhomboides*, is one of the more abundant and common estuarine fish of the Gulf of Mexico and western Atlantic (Nelson et al., 2013; Stallings et al., 2015). They inhabit coastal waters from Massachusetts, USA to Florida through the Gulf of Mexico to the Yucatan Peninsula, Mexico (Hoese and Moore, 1977; Darcy, 1985; Nelson, 2002; Harter and Heck, 2006). Pinfish spawning typically takes place from late fall to late spring and occurs offshore, although the exact timing and location can vary geographically (Darcy, 1985). Larvae move into coastal estuaries

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from fall to late spring, with peak recruitment in January through March (Warlen and Burke, 1990). Once in the estuaries, the larvae and following life stages use various benthic habitats including seagrass (Meyer et al., 1999; Paperno et al., 2001), oyster reefs (Wenner et al., 1996), and salt marshes (Hettler, 1989; Meyer, 2006).

Pinfish play an important role in ecosystem dynamics for a variety of reasons. Their abundance is the highest among vertebrates found in seagrass beds of the northeastern Gulf of Mexico (Nelson et al., 2013; Stallings et al., 2015). Pinfish are prey to many piscivores including both fishes and birds (Seaman and Collins, 1983; Nelson, 2002; Stallings, 2010; Stallings et al., 2010). Their high abundance also results in important contributions to community production, respiration, and consumption (Darcy, 1985). During their time in the estuary, juvenile Pinfish consume a range of benthic invertebrates, influencing whole assemblages of benthic macrofauna (Young et al., 1976; Young and Young, 1977; Nelson, 1978, 2002; Stoner, 1980) before shifting ontogenetically to algae and plant matter (Stoner, 1982). Their biomass accrued from inshore-based production is carried offshore during their egress from estuarine habitats, serving as a nutrient subsidy for offshore food webs and creating an important link between primary and secondary production (Stoner, 1982; Weinstein et al., 1982; Seaman and Collins, 1983; Nelson, 2002; Stallings et al., 2010; Nelson et al., 2013). Pinfish are also an economically important species. Recreational and commercial fishermen use Pinfish as bait and larger individuals can be marketed as panfish for human consumption (Caldwell, 1957; Darcy, 1985). Additionally, Pinfish can be used for production of high-grade oil and can be ground up to be used as fish meal (Darcy, 1985).

In addition to their well-described ecological and economic roles, Pinfish also serve as an ideal study species given their aforementioned abundance, wide distribution, interactions with predators, competitors, and prey, and life-history similar to most of marine fishes that have a bipartite life cycle. Indeed, multiple population studies have focused on Pinfish in the western Atlantic (Hildebrand and Cable, 1938; Adams, 1976; Warlen and Burke, 1990), northern Gulf of Mexico (Hoese and Moore, 1977; Hellier, 1962; Cameron, 1969), and northeastern Gulf of Mexico (Caldwell, 1957; Hansen, 1970; Nelson, 1998, 2002). In this study we sought to investigate how the population dynamics and demography of Pinfish in an estuarine system can be structured spatially and temporally, including the potential role of proximity to the ocean.

During their juvenile stage, Pinfish are observed across a wide range of estuarine habitats within a seascape context, therefore, processes (e.g., competition, predation) at various spatial and temporal scales will likely influence population-level patterns. In this study, we conducted a long-term analysis on a multiyear dataset (2005–2012) in Tampa Bay, the largest estuary in Florida. Our goals were to (1) quantify spatio-temporal patterns in density and biomass of Pinfish, (2) quantify population-level growth across the estuary, and (3) characterize the relative importance of various habitat characteristics in explaining the observed demographic patterns. These analyses contribute to our general knowledge on the population ecology of Pinfish, and provide a detailed examination of habitat use and distribution by one of the more ecologically important fishes in the Gulf of Mexico and western Atlantic.

2. Methods

2.1. Study site description

Sampling of Pinfish was conducted by the Fishery Independent Monitoring Program (FIM) at Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute (FWRI). Monthly sampling was conducted in Tampa Bay, which is located on the

central west coast of Florida, USA, between latitudes 27°30' and 28°00' N (Fig. 1). Tampa Bay is Florida's largest open-water estuary (surface area, ~1000 km², average depth < 5 m) and is tidally mixed and connected to the Gulf of Mexico. Tampa Bay is characterized by having shallow and extensive soft sediment flats, which are often covered with submerged aquatic vegetation (SAV), principally seagrass beds composed of *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*, often mixed with algae (e.g., *Cladophora*, *Chaetomorpha*, *Boodileopsis*, *Vaucheria*, *Centroceras*). Shorelines are often populated with mangroves (i.e., *Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*) and saltmarsh grass (e.g., *Spartina alterniflora*, *S. bakeri*, *S. patens*; Winner et al., 2010).

2.2. Sampling design

The Tampa Bay estuary was divided into four sampling regions characterized by biological (e.g., submerged aquatic vegetation cover, species composition; Yarbro and Carlson, 2011) and hydrological homogeneity (e.g., salinity gradients, circulation patterns; Lewis and Estevez, 1988). Additionally, these regions vary in their distance to the mouth of the Bay and therefore to the larval pool of Pinfish located offshore in the Gulf of Mexico where spawning occurs (Darcy, 1985; Nelson, 2002). The Lower Bay (LB) is the southernmost region (and outermost portion, closest to the mouth of the Bay and the Gulf of Mexico) followed by the Middle Bay (MB), which is bounded to the north by the two innermost portions, Old Tampa Bay (OT) and Hillsborough Bay (HB; Fig. 1).

Stratified random sampling (strata defined by spatial zone and habitat type) was conducted monthly in Tampa Bay from January 2005 to December 2012. Sampling effort was allocated among the four zones each month and resulted in sampling locations comprising a mix of vegetated and unvegetated habitats. Each zone was further subdivided into 1 nautical mile² (nmi²) grids and stratified by depth. Prior to sampling each month, grids within each zone with a maximum depth of 1.8 m (the maximum depth the gear used can sample efficiently) were randomly selected. Within each grid, a 0.1 nmi² microgrid was then randomly selected as the starting point to search for appropriate habitat (e.g., presence or absence of submerged aquatic vegetation). For full survey details, see McMichael (2009). At each sampling site, environmental variables including salinity and water temperature were measured with a YSI handheld multiparameter water quality meter, and the percent cover of SAV was visually estimated in ten percent increments.

Sampling was conducted with a 21.3 m center-bag seine with 3.2 mm mesh netting. A sampling event consisted of deploying the seine net in either the Bay shoreline or offshore (sites ≥ 5 m from shoreline) and pulling it over a distance of 9.1 m. The net width was 15.5 m between seine poles, resulting in a sampled area of 140 m². After net deployment, the sample was retrieved by pulling the leads and tripping the bag. All Pinfish were counted and a subsample of ten randomly selected individuals was measured for standard length (SL) in millimeters (mm).

2.3. Data analysis

In order to examine population dynamics of Pinfish, we converted catch abundances to densities by dividing all fish collected in each sampling event by the total area covered by the gear. There were three separate analyses. First, we calculated density per sampling event and then averaged over all months and years for each region to examine patterns spatially. Second, we averaged density over all months and region per year to examine patterns inter-annually. Third, we averaged over years and region per month

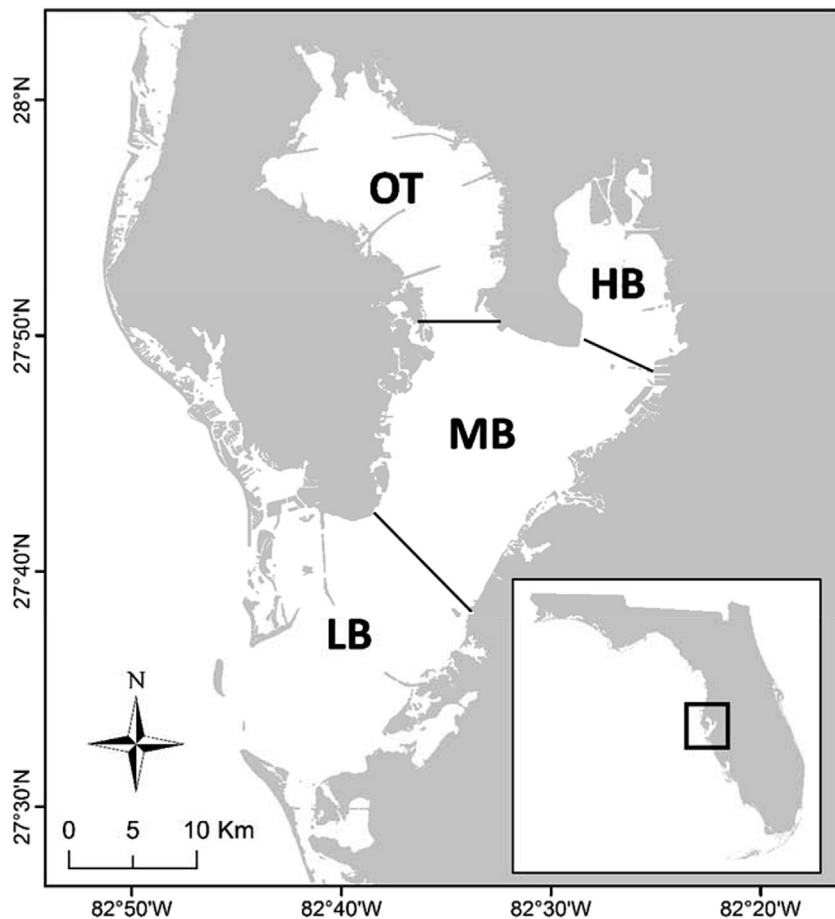


Fig. 1. Locations of the four regions sampled in the Tampa Bay estuary: Old Tampa Bay (OT), Hillsborough Bay (HB), Middle Bay (MB), and Lower Bay (LB). Inset is a map of Florida showing the relative location of the study.

to explore patterns intra-annually. We investigated regional patterns in density by conducting a non-parametric, distribution-free, permutation-based, one-way analysis of variance (npANOVA) followed by pair-wise comparisons of Pinfish density among the different regions of the Bay. We produced a dissimilarity matrix for the response variable (density) based on Euclidean distance using the Fathom toolbox for Matlab (Jones, 2014). Level of significance for all tests was based on an alpha value of 0.05.

We also estimated mean biomass to investigate patterns spatially, inter-annually, and intra-annually. Lengths of the measured portion of Pinfish were extrapolated to the unmeasured remaining portion to estimate biomass. We calculated Pinfish biomass using the length-weight relationship:

$$W = a \times L^b,$$

where W is weight in grams, L is standard length in millimeters, and a and b are length-weight constants derived from a study on Pinfish conducted in Tampa Bay and the Gulf of Mexico (Nelson, 2002). We conducted a one-way, permutation-based ANOVA to explore spatial patterns in biomass.

We conducted a month-to-month comparison of mean standard lengths to estimate Pinfish growth rates. Instantaneous growth coefficients were additionally calculated for Pinfish annually. The assessment of growth coefficients in the Bay assumed limited migration of Pinfish among regions but we acknowledge the possibility that other factors could affect size class structure such as

size selective mortality and egress. Thus, growth rates were approximated with mean length data with an emphasis on months April through July in order to reduce biases related to settlement (January–March) and ontogenetic movements of juveniles (August–December). Following the approach of Nelson (1998), we estimated growth with the model:

$$\ln(L_t) = \ln(L_0) + G \times t,$$

where G is the instantaneous growth rate (per month), L_t is the monthly mean length (mm), L_0 the theoretical length at which Pinfish recruit to each Bay region, and t is time in months. We conducted *a posteriori* Pearson correlation tests between inter-annual mean density and growth within each region to explore potential density effects on growth. We also conducted *a posteriori* Pearson correlation tests between inter-annual mean temperature and growth within each region to investigate the potential effects of temperature on growth.

Last, we conducted a multiple regression analysis in order to explore which environmental variables were related to the observed variation in Pinfish density. We used a stepwise selection of explanatory variables via forward addition based on Akaike Information Criteria (AIC; Jones, 2014). AIC estimated the Kullback-Leibler information loss by having a “lack-of-fit” term and a penalty for the number of parameters. Then, an optimal subset of variables in terms of parsimony was achieved by minimizing the AIC (Legendre and Legendre, 1998; Anderson et al., 2000; Burnham and Anderson, 2001; Dray et al., 2006; Jones, 2014). Explanatory

variables included percent cover of submerged aquatic vegetation (SAV), water temperature, salinity, SAV² (to account for non-linear saturation effects of habitat structure), SAV-temperature interaction term, depth, and within-Bay region coded as a categorical variable.

3. Results

In total, 107,516 Pinfish from 1,918 seine-tows were collected from Tampa Bay during the study period (Table 1). Among the four regions of Tampa Bay, we observed spatial variation in both Pinfish density (Table 2, Fig. 2A) and biomass (Table 3, Fig. 2B). The posteriori, permutation-based, pair-wise comparisons indicated that Pinfish density was the highest in the Lower Bay, which was not different than the Middle Bay, but was greater than both Hillsborough Bay, and Old Tampa Bay (Table 2, Fig. 2A). Density in the Middle Bay was greater than that in both Hillsborough Bay and Old Tampa Bay (Table 2, Fig. 2A). Density in Hillsborough Bay was not different from Old Tampa Bay (Table 2, Fig. 2A). Biomass was the highest in the Lower Bay, which was greater than Middle Bay, Old Tampa Bay, and Hillsborough Bay (Table 3, Fig. 2B). Biomass in the Middle Bay was higher than both Hillsborough Bay and Old Tampa Bay (Table 3, Fig. 2B). Biomass in Old Tampa Bay was greater than that in Hillsborough Bay (Table 3, Fig. 2B).

Across the regions of the Bay, we observed inter-annual variation in Pinfish density and biomass (Fig. 3A–D). The highest mean (\pm standard error) densities observed in 2009 (73 ± 24 fish/100 m²) and 2010 (105 ± 16 fish/100 m²) were up to one order in magnitude greater than the lowest densities in 2005 (14 ± 4 fish/100 m²) and 2006 (9 ± 3 fish/100 m²; Fig. 3A). Similarly, Pinfish mean biomass was the highest during 2009 (113 ± 17 g/100 m²) and 2010 (147 ± 23 g/100 m²) and the lowest in 2005 (32 ± 8 g/100 m²) and 2006 (42 ± 11 g/100 m²; Fig. 3C). The extremely high densities and biomasses observed in 2009 and 2010 were largely driven by increased densities in the Lower and Middle regions of the Bay (Fig. 3B and D). We also observed relatively high density and biomass in Old Tampa Bay compared to Hillsborough Bay in 2010 (Fig. 3B and D). Furthermore, density and corresponding biomass (years 2005–2008) were generally lower in the Middle, Old Tampa, and Hillsborough Bay in comparison with the Lower Bay (Supplemental Figs. S1 and S2).

Intra-annual variation in mean density and biomass of Pinfish was qualitatively similar across the regions of the Bay, albeit with higher values in the outermost regions (Fig. 4B and D). Density increased in the early months of the year, peaked in March, and decreased in the later months (Fig. 4A). Pinfish mean biomass exhibited a similar pattern as density with a delay of two months, peaking in April through June (Fig. 4C).

The size distributions of Pinfish across the four regions changed predictably within years (Fig. 5A). Mean standard lengths were the

Table 2

Non-parametric one-way analysis of variance (npANOVA) results for differences in Pinfish density among four regions of Tampa Bay followed by pairwise comparisons. Catch abundances were converted to densities by dividing all fish collected in each sampling event by the total area covered by the gear. Values in bold indicate significant differences at the level $\alpha < 0.05$. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay.

Source	df	SS	MS	F	p
Pinfish density	3	8.05×10^5	2.68×10^5	8.13	0.001
Residual	1,914	6.32×10^7	3.30×10^4		
Total	1,917	6.39×10^7			
Comparison ^a		t		p	
OT versus HB		1.08		0.295	
OT versus MB		2.27		0.007	
OT versus LB		5.13		0.001	
HB versus MB		2.17		0.012	
HB versus LB		4.86		0.001	
MB versus LB		0.94		0.374	

^a Pair-wise *a posteriori* tests of density among Tampa Bay regions.

smallest in the beginning of the year, increased during the summer and early fall, peaked in September and October, and decreased or exhibited no change during the remaining calendar year (Fig. 5A). Pinfish from Old Tampa Bay and Hillsborough Bay were consistently larger than those from Middle and Lower Bay. Growth rates were the highest in Old Tampa Bay and Hillsborough Bay compared to the Middle and Lower Bay (Fig. 5B). Inter-annually, Pinfish growth rates were highly variable (0.125–0.380), but again tended to be the highest in the innermost regions of the Bay (Fig. 5C). There was no support of negative density dependent effects on growth rates from the Pearson correlation analyses: LB = -0.14 ; MB = 0.50 ; OT = 0.18 ; HB = -0.06 .

The salinity in Tampa Bay varied spatially with higher values in Lower Bay and Middle Bay (32 ± 0.1 ppt and 27.7 ± 0.2 ppt, respectively) compared to Old Tampa Bay (24.9 ± 0.2 ppt) and Hillsborough Bay (25.6 ± 0.2 ppt). There was no support for a region-specific effect of temperature on fish growth from the Pearson correlation analyses: LB = -0.05 ; MB = 0.26 ; OT = -0.26 ; HB = 0.50 . Variables selected during multiple regression model fitting accounted for 34.1% of the total variance of Pinfish density ($F = 248.8$, $p = 0.001$, 1000 permutations; Table 4). High Pinfish density was explained by increased percent coverage of SAV, higher salinity, and the two regions of the Bay closest to the Gulf of Mexico (Middle Bay and Lower Bay; Supplemental Fig. S3). The remaining variables (water temperature, SAV², SAV-water temperature interaction, and depth) did not contribute substantially to the variation of Pinfish density and thus were not selected by the AIC process.

4. Discussion

In this study we conducted a series of analyses on eight years of

Table 1

Catch statistics for Pinfish collected in four regions of Tampa Bay, Florida with a 21.3 m center-bag seine from January 2005 to December 2012. Catch abundances were converted to densities by dividing all fish collected in each sampling event by the total area covered by the gear. Catch per unit effort (CPUE; fish/100 m²) is reported as mean density (\pm SE). Densities were compared using a non-parametric, permutation-based, one-way analysis of variance (npANOVA) followed by pair-wise comparisons of Pinfish density among the different regions of the Bay. Densities with the same letter indicate the regions were not significantly different from each other (posteriori permutation-based multiple comparisons $\alpha = 0.05$). Min = minimum, Max = maximum standard length.

Bay region	Number of tows	Number of Pinfish	Standard length (mm)				CPUE (fish/100 m ²)	
			Mean \pm SE	Median	Min	Max	Mean density	SE
Old Tampa Bay	556	15,844	29.7 ± 0.13	56.8	11	158	20.3 a	4.62
Hillsborough Bay	284	4,941	29.4 ± 0.18	50.5	11	163	12.4 a	4.77
Middle Bay	466	32,623	27.9 ± 0.08	41.6	12	172	50.0 b	13.19
Lower Bay	612	54,108	22.7 ± 0.07	50.6	10	161	63.1 b	6.75
Total	1,918	107,516						

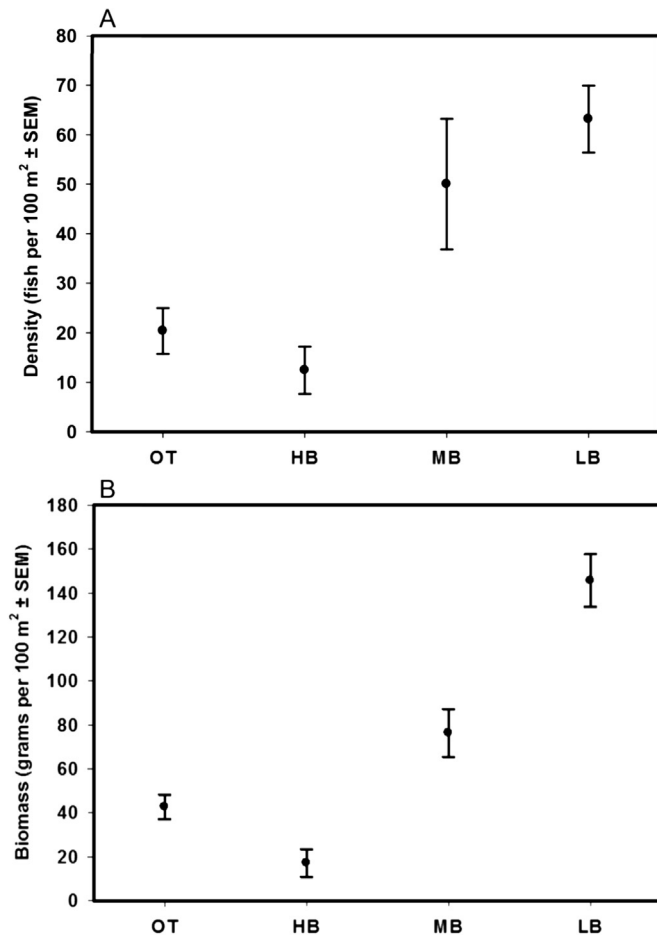


Fig. 2. Spatial analyses of mean (\pm standard error) Pinfish (A) density and (B) biomass, calculated for the four regions of Tampa Bay. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay. Catch abundances were converted to densities by dividing all fish collected in each sampling event by the total area covered by the gear. Pinfish biomass was calculated using the length-weight relationship $W = a \times L^b$, where W is weight in grams, L is standard length in millimeters, and a and b are length-weight constants derived from a study on Pinfish conducted in Tampa Bay and the Gulf of Mexico (Nelson, 2002).

Table 3

Non-parametric one-way analysis of variance (npANOVA) results for differences in Pinfish biomass among four regions of Tampa Bay followed by pairwise comparisons. We calculated Pinfish biomass using the length-weight relationship $W = a \times L^b$, where W is weight in grams, L is standard length in millimeters, and a and b are length-weight constants derived from a study on Pinfish conducted in Tampa Bay and the Gulf of Mexico (Nelson, 2002). Values in bold indicate significant differences at the level $\alpha < 0.05$. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay.

Source	df	SS	MS	F	p
Pinfish biomass	3	4.54×10^6	1.51×10^6	31.42	0.001
Residual	1,914	9.22×10^7	4.82×10^4		
Total	1,917	9.68×10^7			
Comparison ^a	t		p		
OT versus HB	2.82		0.007		
OT versus MB	2.87		0.003		
OT versus LB	7.54		0.001		
HB versus MB	4.00		0.001		
HB versus LB	7.10		0.001		
MB versus LB	4.15		0.001		

^a Pair-wise *a posteriori* tests of density among Tampa Bay regions.

results add to our understanding of the population dynamics and habitat use of one of the more abundant fish in the Gulf of Mexico by quantifying spatial, inter-annual, and intra-annual patterns of density and biomass. We found strong evidence of spatial patterns in both the population dynamics and demographic rates among four regions of Tampa Bay, which tended to be fairly consistent both inter- and intra-annually and highly influenced by the proximity to the Gulf of Mexico.

On average, the density and biomass of Pinfish were related to the proximity to the Gulf of Mexico, with higher values in the outermost regions (Lower and Middle Bay) which were characterized by having greater seagrass coverage (Yarbro and Carlson, 2011), higher salinity (Lewis and Estevez, 1988), and were located closer to the offshore larval pool (Nelson, 1998, 2002). The positive correlation between the extent of seagrass cover and densities of juvenile fishes has been well documented (see reviews by Heck and Crowder, 1991; Hemminga and Duarte, 2000; Gillanders, 2006). The outermost regions of Tampa Bay are characterized by having greater seagrass coverage (Yarbro and Carlson, 2011), which might have resulted in higher retention of Pinfish larvae compared to the innermost regions. Pinfish are one of the dominant fishes in vegetated habitats of the northeastern Gulf of Mexico (Hansen, 1970; Darcy, 1985; Nelson et al., 2013; Stallings et al., 2015); their association with these habitats was likely related to shelter and prey availability (Heck and Thoman, 1981; Heck and Crowder, 1991; Harter and Heck, 2006; Heck and Orth, 2006; Chacin, 2014). Chacin and Stallings (2016) experimentally demonstrated that survival of Pinfish increased with habitat complexity, suggesting that seagrass blades were used for refuge against their predators. Pinfish diet comprises epiphytes, seagrass blades, and benthic invertebrates (Darnell, 1958; Nelson, 1979; Stoner and Livingston, 1984), which indicates seagrass habitats also provide food resources for juveniles. Additionally, the outermost regions of the Bay had higher and more stable salinities than the innermost regions, which may have provided more suitable conditions for the early life stages of Pinfish. Studies have suggested that lower salinities, whether due to punctuated events (e.g., heavy rainfalls) or chronic conditions (e.g., proximity to freshwater input), can increase mortality and decrease shoreward transport of larval Pinfish, resulting in lower observed densities in response to osmotic stress (Cameron, 1969; Wang and Raney, 1971; Purtlebaugh and Allen, 2010). Additionally, the close proximity to the offshore larval pool and oceanic currents may have created a settlement gradient where competent larvae first intercepted suitable habitat in the outermost regions resulting in fewer larvae available to settle in the innermost regions (Gaines et al., 1985). This was especially evident in some years (2005–2008) where there was lower recruitment of Pinfish to the innermost regions of the Bay in comparison to the Lower Bay and emphasizes the importance of near-ocean estuarine habitats as settlement and juvenile grounds. Furthermore, Pinfish biomass, which is driven by the combined influences of density and size, tended to mirror the density patterns, despite larger mean sizes and higher growth rates in the upper regions, suggesting that disproportionately higher densities of Pinfish in the Lower Bay primarily drove biomass dynamics.

It is important to note that temperature and depth were not selected as important variables in the multiple regression analysis of Pinfish density. The increase in Pinfish density during settlement, and decrease during egress, both coincided with lower water temperatures. Thus, this might have obscured the relationship between temperature and Pinfish density. We also did not find depth to contribute substantially to the variation of Pinfish density. However, the gear used in this study has depth restrictions, which limited our sampling to cover mainly shallow-water habitats, thus potentially masking Pinfish relationship to depth if present.

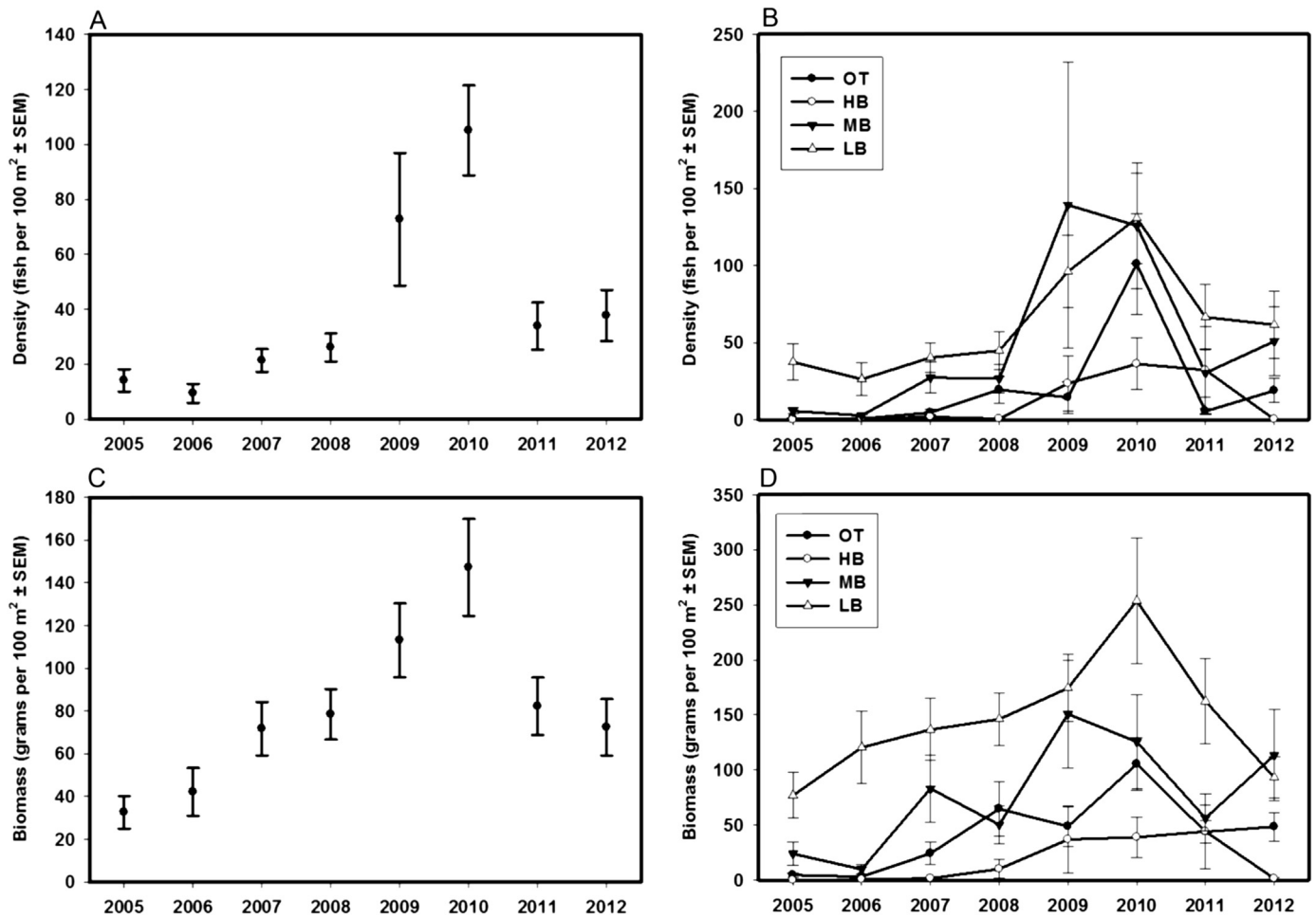


Fig. 3. Inter-annual analyses of mean (\pm standard error) Pinfish (A) density across regions, (B) density among regions, (C) biomass across regions, and (D) biomass among regions. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay. Catch abundances were converted to densities by dividing all fish collected in each sampling event by the total area covered by the gear. Pinfish biomass was calculated using the length-weight relationship $W = a \times L^b$, where W is weight in grams, L is standard length in millimeters, and a and b are length-weight constants derived from a study on Pinfish conducted in Tampa Bay and the Gulf of Mexico (Nelson, 2002).

High inter-annual variation in Pinfish density (and corresponding biomass) may have been influenced by changes in oceanographic dynamics. Local oceanographic forcing through Ekman-geostrophic spin-up primarily controls water circulation and upwelling over most of the inner West Florida Shelf (Weisberg and He, 2003; Liu and Weisberg, 2012). The year 2010 (when densities and biomass were extremely high) exhibited anomalously intense and prolonged upwelling on the West Florida Shelf. Such deep-ocean oceanographic conditions can influence the across-shelf transport of fish, invertebrate larvae, and the amount of inorganic nutrients used by phytoplankton and zooplankton, which can serve as food for the larval pool (Weisberg et al., 2014). Our Pinfish density model only explained 34% of the variation, thus other factors that we did not take into account influenced the patterns observed. Oceanographic conditions (e.g., sea surface temperature) occurring before settlement have been suggested to affect hatch success, growth, and transport mechanisms of larvae, thus possibly influencing annual variability in Pinfish density (Nelson, 1998).

In addition to the timing of spawning, oceanographic conditions likely played important roles in the observed intra-annual patterns of density (and corresponding biomass). The upwelling-favorable period, which can initiate primary production and food for larvae, predominantly occurs from fall to spring months on the West

Florida Shelf (Liu and Weisberg, 2012), coinciding with the steady increase in Pinfish density during the initial calendar months of the year. Previous studies have documented similar findings in that larval and post-larval Pinfish enter shallow waters from late fall to spring with density peaks in late winter and early spring (Tabb and Manning, 1961; Darcy, 1985). Furthermore, the life history of Pinfish has been linked to seasonal patterns of prey and macrophyte abundance (Stoner, 1980; Darcy, 1985). Thus, the continued high densities (and corresponding biomass) during late spring and early summer were likely further supported by increasing levels of primary and secondary productivity that occur in warm-temperate and subtropical seagrass beds during that time of year (Tukey and DeHaven, 2006; Stallings et al., 2015).

The observed decrease in Pinfish density during the summer through fall months could have been influenced by the individual or combined effects of post-settlement mortality, ontogenetic movements, and gear limitations. Juvenile fishes commonly experience high levels of mortality via predation during early life stages (Hixon, 1991; Sogard, 1997). Moreover, diet studies have demonstrated that Pinfish are a common prey for many piscivores in this ecosystem (Seaman and Collins, 1983; Nelson, 2002; Stallings, 2010; Stallings et al., 2010; Hall-Scharf and Stallings, 2014; Hall-Scharf et al., 2016). Thus, the decrease in Pinfish density was likely related to high predation during the juvenile stage. Another

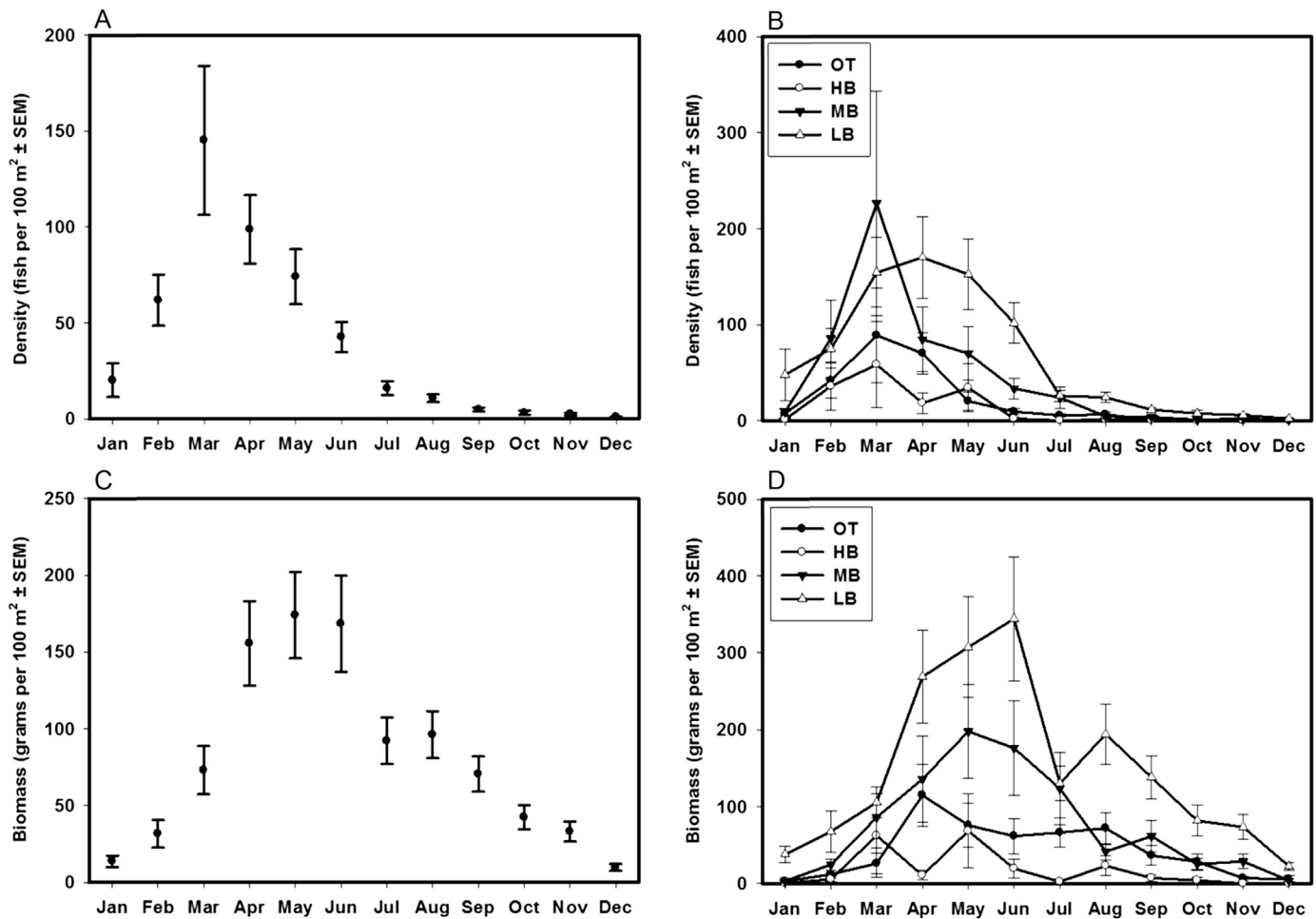


Fig. 4. Intra-annual analyses of mean (\pm standard error) Pinfish (A) density across regions, (B) density among regions, (C) biomass across regions, and (D) biomass among regions. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay. Catch abundances were converted to densities by dividing all fish collected in each sampling event by the total area covered by the gear. Pinfish biomass was calculated using the length-weight relationship $W = a \times L^b$, where W is weight in grams, L is standard length in millimeters, and a and b are length-weight constants derived from a study on Pinfish conducted in Tampa Bay and the Gulf of Mexico (Nelson, 2002).

potential mechanism is the migration of larger Pinfish into deeper waters, which could make them inaccessible to the sampling gear and thus influence monthly patterns of density and biomass (Cameron, 1969; Hastings, 1979). The exact reasons for this migration remain unclear, but speculations include shifts in feeding habitats, preparation for spawning, and inability to cope with metabolic extremes in shallow waters (Moe and Martin, 1965; Cameron, 1969). Further, the density patterns could have been also influenced by changes in size-specific capture efficiency of the gear used. For example, Pinfish size peaked in September and October (up to a mean SL of ~120 mm), followed by a period of no change, possibly suggesting decreased gear efficiency for larger individuals.

Growth of Pinfish in the different regions (although different in magnitude) was fairly consistent inter- and intra-annually and while the mechanisms underlying remain unclear, growth patterns may have been influenced by spatial patterns in nutrient concentration (Lewis and Estevez, 1988; Sherwood, 2012) and intraspecific competition. Nutrients can fuel epiphytic growth (Eminson and Phillips, 1978; Borum, 1985), which tends to be the primary basal resource in SAV food webs (Vizzini and Mazzola, 2003). Total nitrogen and phosphorus tend to be the highest in the innermost regions of the Bay, particularly in Hillsborough Bay (Feather Sound Seagrass Recovery Workgroup, 2004; Vaas and Janicki, 2010;

Peebles and Hollander, 2010), which might have influenced the increased growth rates and sizes of Pinfish we observed. The high densities of Pinfish in the outermost regions could have also caused food resource limitation, resulting in density-dependent effects thus lowering growth in those regions (Hixon and Webster, 2002; Craig et al., 2007). To further examine potential density dependent effects on growth, we conducted *a posteriori* Pearson correlation tests between inter-annual mean density and growth within each region, but did not find evidence of strong negative relationships. It is possible that the temporal scale of comparing inter-annual means may have obscured stronger negative relationships present at shorter periods. Furthermore, this non-experimental approach would have precluded us from directly inferring process and mechanism.

Water temperature, sampling artifacts, and deceleration of somatic growth could have influenced the apparent intra-annual patterns in growth rates. Pinfish growth rates have been shown to be dependent upon temperature, increasing during the warmest months and slowing during the coldest (Hildebrand and Cable, 1938; Caldwell, 1957). This coincides with our observations of greatest size increases during spring and summer, and a decrease of size during the later months of the calendar year. However, the decrease in mean size of Pinfish as the summer progressed may have been a mathematical artifact produced by a late settlers (i.e.,

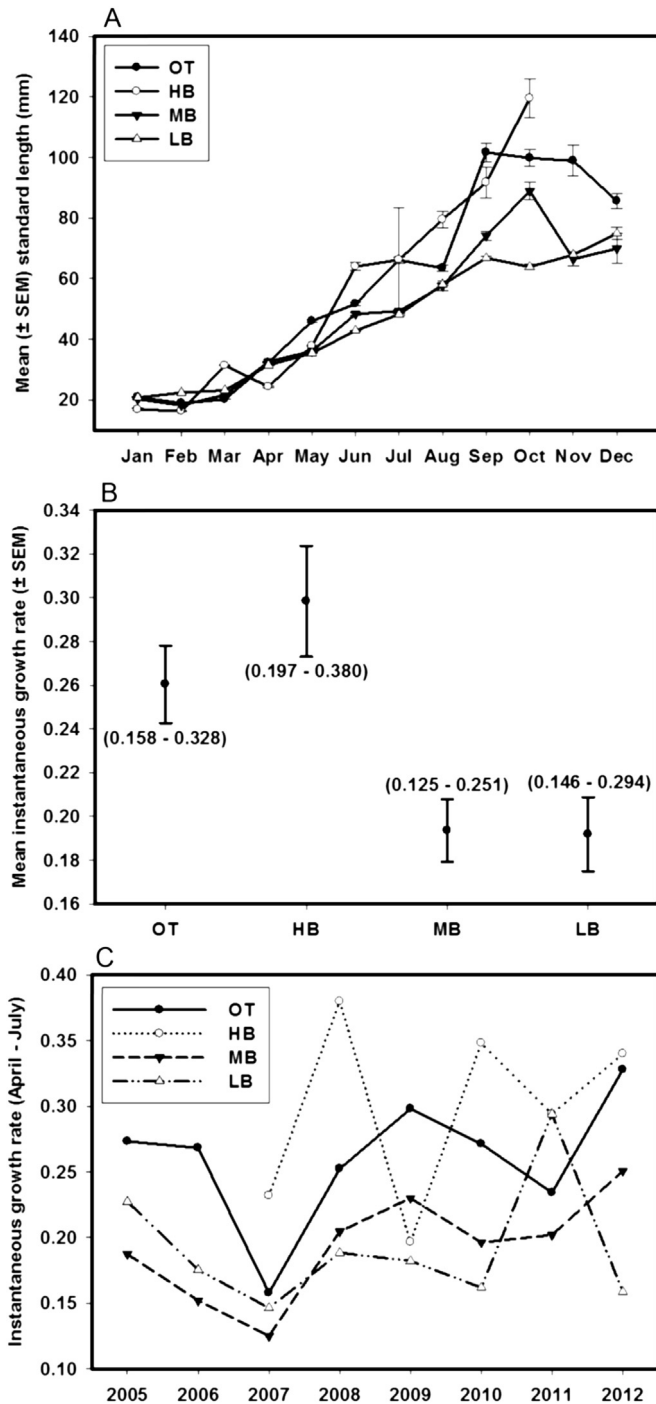


Fig. 5. Spatio-temporal variation of mean Pinfish (A) length among regions intra-annually, (B) growth rates among regions, (C) growth rates inter-annually among regions. OT = Old Tampa Bay, HB = Hillsborough Bay, MB = Middle Bay, and LB = Lower Bay.

small fish) remaining in the sampling area, b) larger individuals moving out (sexually-mature fish undergoing egress to offshore spawning habitats), and/or c) due to the efficiency of the sampling gear decreasing with increasing fish size. We did not find evidence of temperature affecting growth rates of Pinfish in the different regions of the Bay, possibly due to fairly similar temperatures occurring across the regions during the fastest period of growth. Furthermore, Pinfish might also undergo a true deceleration in

Table 4

Results from marginal tests using a stepwise selection of explanatory variables via forward addition based on Akaike Information Criteria (AIC) and multiple regression analysis on selected variables that substantially contributed to explaining Pinfish density. Abbreviations are: R^2 = coefficient of multiple determination, RSS = residual sum of squares, wts = weights, b = partial coefficient, SAV = submerged aquatic vegetation, LB = Lower Bay, MB = Middle Bay.

R ²		R ² adjusted			F-stat
0.343		0.341			248.8
Variable	RSS	R ²	AIC	wts	<i>b</i>
SAV	2393.8	0.290	432.9	0.986	0.015
Salinity	2255	0.331	320.6	1.000	0.034
LB	2231.8	0.338	302.9	1.000	0.423
MB	2216.1	0.343	291.4	0.991	0.238

somatic growth. In fishes this can occur from decreased feeding due to either prey reductions or metabolic inefficiency. Slowing of somatic growth can also be due to increased allocation of energy into reproduction and storage following an early post-settlement period of fast growth (Post and Parkinson, 2001). This characteristic allows juvenile fish to first reach a size beyond which predators become gape-limited followed by building energy reserves for future phases when resources can become scarce. Achieving a larger size in advance of food becoming insufficient can also be beneficial since per-mass metabolic demands decrease with increasing size in fishes (Shuter and Post, 1990; Schultz and Conover, 1999). While most of the evidence for this strategy has been shown in cold-temperate fishes, similar patterns have recently been observed in juvenile fishes at warm-temperate and subtropical latitudes (Stallings et al., 2010).

5. Conclusion

The results from this study provided valuable insights into the population dynamics of juvenile Pinfish in Tampa Bay, the largest estuarine system in the eastern Gulf of Mexico. This study emphasizes the importance of near-ocean estuarine locations as settlement and juvenile habitats of Pinfish given the high recruitment and densities observed in comparison to habitats located farther away from the Gulf. Nevertheless, higher densities of fish in particular habitats (such as the outermost regions of the Bay for Pinfish) may result in increased intraspecific competition due to limited resources with ensuing density-dependent effects on growth and mortality. In fact, Chacin and Stallings (2016) found higher mortality rates of Pinfish in the outermost regions of Tampa Bay (where higher densities were found) compared to the innermost regions. Greater competition can be deleterious and decrease the input of individuals into the adult stage of the population and their contribution to the next generation. It is possible that fish in habitats that may appear to be suboptimal due low densities of individuals or high nutrient loads (e.g., the innermost regions of the Bay for Pinfish) experience higher survival rates, less crowding leading to higher growth rates, and ultimately a high chance of making it to the spawning stage of the population. However, additional studies should be conducted to determine whether this is the case. Future studies should also evaluate whether similar patterns in population dynamics of estuarine fishes occur across a broader geographic range. This study lays the foundation for further efforts to examine the complicated interplay among spatial and temporal aspects in the population dynamics of juvenile Pinfish, and more broadly for further understanding the influence of ocean dynamics on the life history of estuarine-dependent species.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.ecss.2016.10.015>.

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