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Juvenile tarpon *Megalops atlanticus* use of natural and managed marsh habitats in coastal South Carolina

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Abstract There is a paucity of information on juvenile tarpon *Megalops atlanticus* habitat use at the northern edge of its distribution. Therefore, we investigated the timing of recruitment and the size distribution of juvenile tarpon in natural and managed marshes in coastal South Carolina. We monitored recruitment to salt marsh habitats during July through November 2019 in the North Inlet estuary, Kiawah Island, and Tom Yawkey Wildlife Center Heritage Preserve. One-hundred and two juvenile tarpon (36–333 mm standard length) were observed during July to November. Tarpon from natural marsh pools (North Inlet estuary; mean ± SD = 65.4 ± 20.2 mm) were smaller than those from managed impoundments (Kiawah Island and Yawkey Preserve; 253.9 ± 41.6 mm), with no overlap in size across habitats throughout the study duration. Mean tarpon length was relatively constant throughout the study in marsh pools (65 ± 20.2 mm SL), but mean tarpon length increased from 180 ± 9.9 mm SL in August to 290 ± 31.5 mm SL in October in managed impoundments. Peak catch-per-unit-effort occurred during August (marsh pools) into September (managed impoundments) across habitat types and declined as water temperatures decreased at the end of October to November. The absence of size overlap between habitats and increasing size of tarpon over time in marsh impoundments compared to the minimal change in length over time observed for marsh pools suggests that (1) tarpon are transient in marsh pools early in life, (2) tarpon do not enter impoundments until reaching a certain size, (3) small juvenile tarpon are cryptic in impoundments and larger juvenile tarpon are more susceptible to capture in those habitats, or (4) a combination of (1), (2), and (3).

Keywords Tarpon · Juvenile · Marsh pools · Impoundment · Recruitment · Salt marsh

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Introduction

Currently 40% of the US population lives within coastal counties, and the population in these coastal areas has increased by over 40% (~34.8 million people) since the 1970s (NOAA 2020a). A majority of these counties border or have intertidal salt marshes and mangroves, many of which are being altered or lost due to urban development, water control efforts, impounding, and dredging (Dahl 2006). Intertidal marsh and mangrove-dominated areas are impounded for various reasons including mosquito control, waterfowl management, and some aquaculture and erosion control (Harrington and Harrington 1982; DeVoe and Baughman 1986; Montague et al. 1987; Herke et al. 1992). Due to the increasing coastal population, coastal areas have more recently been developed for residential and commercial purposes (i.e., housing developments, golf courses, tourism attractions, infrastructure), resulting in the creation of more managed impoundments (e.g., stormwater retention ponds and golf course ponds).

Both natural and managed estuarine habitats, such as marsh pools and impoundments, are important for a variety of organisms, including but not limited to waterfowl, fishes, and reptiles (Miglarese and Sandifer 1982; DeVoe and Baughman 1986; McGovern and Wenner 1990, Weber and Haig 1996; Robinson and Jennings 2014; Carswell et al. 2015; Mace et al. 2018). Many impoundments within the southeastern USA are currently managed for waterfowl and migrating shorebirds; however, many fish species, such as Atlantic croaker *Micropogonias undulatus*, spot *Leiostomus xanthurus*, Atlantic tarpon *Megalops atlanticus*, and inland silverside *Menidia beryllina*, utilize these habitats at various points throughout their life, but particularly during early life stages (Gilmore et al. 1982; McGovern and Wenner 1990; Stevens et al. 2006; Robinson and Jennings 2014; Carswell et al. 2015). Thus, understanding how and when fishes use impoundments, how use of impoundments compares to natural habitats, and how use of impoundments affects other life history characteristics (e.g., recruitment, mortality, growth) is warranted.

Atlantic tarpon (hereafter tarpon) use natural and managed habitats as juveniles before emigrating to marine habitats and are frequently found in estuarine impoundments, ponds, and pools in and around South Florida and the Caribbean (Zerbi et al. 2005; Cianciotto et al. 2019; Wilson et al. 2019), as well as farther north in estuaries along the southeastern US Atlantic (i.e., South Carolina and Georgia; Nichols 1994; Robinson and Jennings 2014; Mace et al. 2018) and Gulf coasts (Stein et al. 2016). Managed marsh impoundments are designed to maintain consistent environmental conditions (e.g., depth), with water control structures limiting tidal influence and water flow according to seasonal operation protocols, but on occasion external forces (e.g., severe storms, drought) can combine with internal operations (e.g., low or no water flow) to create extreme water temperature, salinity, or dissolved oxygen conditions (McGovern and Wenner 1990; Robinson and Jennings 2014). Tarpon are capable of withstanding these variable and potentially harsh environmental conditions (Robins 1977; Crabtree et al. 1995; Geiger et al. 2000). Marsh impoundments offer juvenile tarpon an abundance of prey (Poulakis et al. 2002; Stevens et al. 2006; Robinson and Jennings 2014), and harsh environmental conditions may limit interspecific competition. Similar to marsh impoundments, natural marsh pools are typically shallow (< 0.5 m deep), isolated during low tide, and also experience extreme environmental conditions (Rickards 1968; Dahlberg 1972; Mace et al. 2019).

In South Carolina, 27% of the population lives within coastal areas (NOAA 2020b), where managed marsh impoundments and natural marsh pools are common estuarine features. These areas were traditionally developed for rice cultivation and mosquito control, converting natural salt marsh and tidal freshwater swamp habitats into impoundments by creating dikes with water control structures (Tiner 1977; DeVoe and Baughman 1986; McGovern and Wenner 1990); however, these areas and other coastal lands have recently been developed for stormwater retention and irrigation resulting in more than 14,000 storm water ponds along the South Carolina coast (Drescher et al. 2011; Smith 2012; Cotti-Rausch et al. 2019). About 28,000 ha of managed marsh impoundments still exist in South Carolina (Miglarese and Sandifer 1982; DeVoe and Baughman 1986), but the importance of these manmade habitats for juvenile tarpon occurring in southeastern US estuaries north of Florida, at the northern edge of their distribution, has received scant attention. Several nekton assemblage studies have documented tarpon in managed marsh impoundments across South Carolina (McGovern and Wenner 1990; Robinson and Jennings 2014), but only one study has examined their habitat use patterns in detail (Mace et al. 2018). To date, no studies have examined tarpon use of managed and natural salt marsh habitats concurrently during their period of estuarine residency in South Carolina (or elsewhere throughout their range); such an approach would allow for a better understanding of tarpon early life stage use of different habitats. For example, Mace et al. (2018) observed differences in size between tarpon in natural marsh habitats compared to managed marshes, but this analysis was restricted to one month (September). Therefore, to address the paucity of information on juvenile tarpon habitat use near the northern edge of their distribution, our study objectives were to (1) examine juvenile tarpon recruitment and arrival duration to three estuarine locations, one natural and two managed marsh sites, in South Carolina, and (2) compare size structure of tarpon between these habitat types. Information gained from this study will contribute to our understanding of juvenile tarpon estuarine habitat use and the role of natural and managed marshes as nursery habitats in this region.

Methods

Study sites

Study sites were located within the North Inlet estuary, Tom Yawkey Wildlife Center Heritage Preserve, and Kiawah Island (Fig. 1), spanning approximately 125 km of the South Carolina coast. We sampled five natural marsh pools in the North Inlet estuary (hereafter NIE; Fig. 1; Online Resource 1), which is a barrier island bounded system (3,300 ha in area) dominated by *Spartina alterniflora* marsh with creeks, intertidal flats, oyster reefs, and open water interspersed throughout (Allen et al. 2014). We sampled four

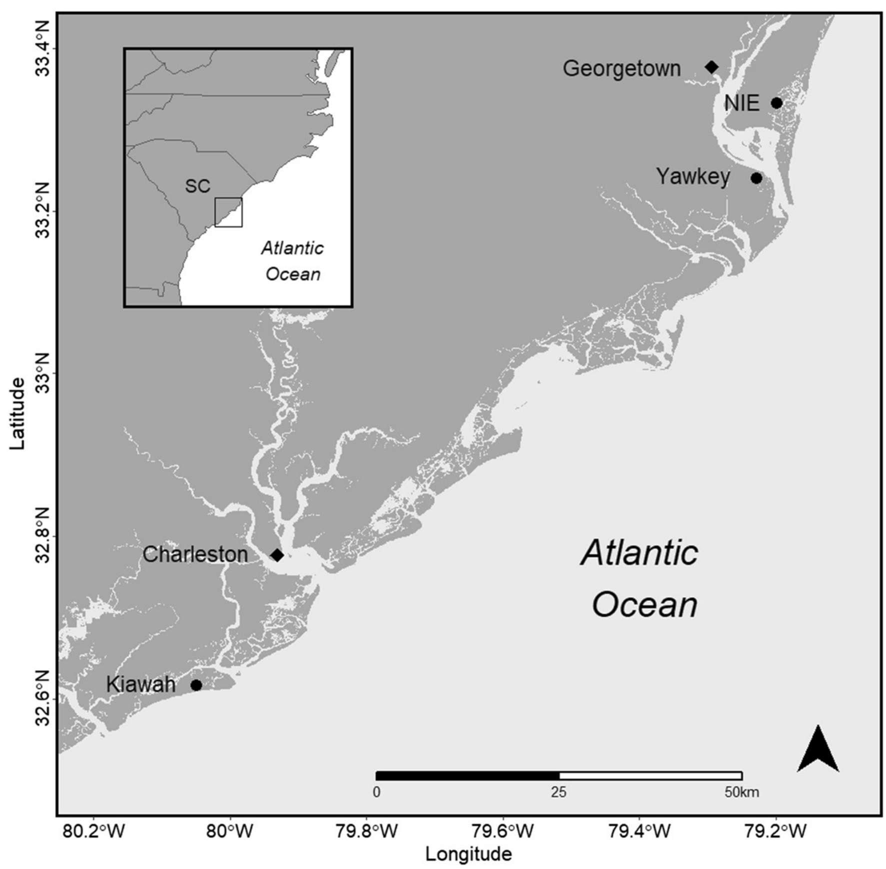

Fig. 1 Study sites (closed circles) from which tarpon were collected during July through November 2019 in the North Inlet estuary (NIE), the Tom Yawkey Wildlife Center Heritage Preserve (Yawkey), and Kiawah Island in South Carolina along the southeastern US Atlantic coast. The cities (closed diamonds) of Georgetown and Charleston are shown for reference

managed marsh impoundments at the Tom Yawkey Wildlife Center Heritage Preserve (hereafter Yawkey; Fig. 1; Online Resource 1), a 6,200-ha research area and wildlife refuge maintained by the South Carolina Department of Natural Resources with *Spartina alterniflora* marsh habitat consisting primarily of marsh impoundments managed seasonally for waterfowl migration and reproduction. The managed marsh impoundments at Yawkey are typically shallow (<1 m), except near water control structures, and have salinity profiles that range from fresh to saline. We sampled four managed marsh impoundments located on Kiawah Island (hereafter Kiawah), a 3,470-ha coastal barrier island with a mix of natural *Spartina alterniflora* marsh with creeks, intertidal flats, and managed marsh impoundments that are situated along roads within the highly developed residential communities and golf courses on the island. Two impoundments were surrounded by short *Spartina alterniflora* marsh, and two were surrounded by golf course fairways and residential development. The impoundments varied in size, depth (0.5–> 3m), salinity profiles, and shore vegetation. Salinities ranged from fresh to saline; however, most impoundments connect to one another forming a mosaic across the island, and all had direct connections to the bordering tidal marsh. Sampling in Kiawah and Yawkey was conducted near metal and wooden water control structures and access points of impoundments because fish are known to congregate near these areas (Kimball et al. 2015, 2017). These locations were chosen because NIE and Yawkey have juvenile tarpon (Mace et al. 2018), there is limited information on tarpon elsewhere in SC, access is limited in other areas where juvenile tarpon have been reported, and fishing guide services have reported juvenile tarpon within managed marsh impoundments on Kiawah Island (M. Kimball, unpublished data).

Field collections

Field collections for juvenile tarpon occurred weekly during July to November 2019 using cast nets (1.8-m radius, 6-mm mesh). Mace et al. (2018) demonstrated that cast nets were effective in sampling natural marsh pools and managed marsh impoundments because of the similar physical characteristics between habitat types, which also limit the use of other sampling gears (e.g., fyke nets, seines, gill nets) due to soft sediments, debris, or shallow water within the sampling areas. All locations within a study site were sampled on the same day during daylight hours. Sampling at NIE occurred during day-time low tide when marsh pools were hydrologically disconnected from adjacent habitats and water bodies. Marsh pools in NIE were sampled during multiple high tide events (these data were not used in further analyses) to test the assumption that tarpon were most vulnerable to sampling during low tide, and the size structure of tarpon in marsh pools did not vary based on tides (i.e., larger juveniles were not moving into marsh pools during high tide). Tarpon size structure did not vary between tidal stages at NIE during three paired sampling events, and the number of tarpon caught at low tide was twice the number caught at high tide (low tide [n = 29] mean SL ± SD = 68 ± 24 mm; high tide [n = 13] mean SL ± SD = 80 ± 30 mm), thus validating that sampling during low tide was sufficient for this study. Sampling at Yawkey and Kiawah was independent of tide stage because water levels were held constant, while allowing for some water exchange by the water control structures at each impoundment. Three replicate casts were made at each sampling location. If juvenile tarpon were caught, they were kept in an aerated holding cooler until all casts were thrown at a site and then standard length (SL, mm) was recorded prior to release. Water temperature and salinity were recorded using a YSI pro2030 at each sampling location after sampling was completed.

Data analyses

All juvenile tarpon data were analyzed using Microsoft Excel (Microsoft, Redmond, Washington) and R statistical software within RStudio (2020, version 1.3.1073; R Core Team 2019, version 3.6.1). For statistical purposes, all locations from a study site were considered subsamples and combined to calculate one mean catch-per-unit-effort (CPUE) and one set of water quality measurements for each sampling event (date). Data from the Yawkey and Kiawah sites were pooled to make comparisons between natural (NIE) and managed (Yawkey and Kiawah pooled) habitats. Descriptive statistics of tarpon lengths (mean ± standard deviation, minimum, maximum) were calculated for both habitat types. Weekly, CPUE was calculated by dividing the number of tarpon caught by the total number of cast nets thrown per habitat type, per weekly sampling event (e.g., the total number of tarpon caught divided by the total number of casts in high marsh pools in a given week). Analysis of covariance (ANCOVA; significance level = 0.05) was used to determine if tarpon length (mm SL) differed between habitat types over time. The response variable was tarpon length, and the independent variables were habitat type (natural or managed), Julian day, and the interaction between habitat type and Julian day. Residual and Q-Q plots were examined to determine if these data met the assumptions of linear models or if transformations were necessary.

Results

We collected 102 age-0 tarpon, ranging in size from 36 to 333 mm SL (Fig. 2). Tarpon were collected during July to November. However, the timing of tarpon collections differed between habitat types; peak tarpon catches in natural marsh pools occurred about a month earlier than in managed marsh impoundments (Fig. 3). Sixty-eight tarpon were collected during July 15 through November 6 within natural marsh pools at NIE, and 34 tarpon were collected during August 15 through October 24 within managed marsh impoundments at Yawkey and Kiawah. Tarpon from impoundments (Yawkey and Kiawah; mean ± SD = 253.9 ± 41.6 mm) were longer than those collected from marsh pools (NIE; mean ± SD = 65.4 ± 20.2 mm), and differences in length increased over time (interaction

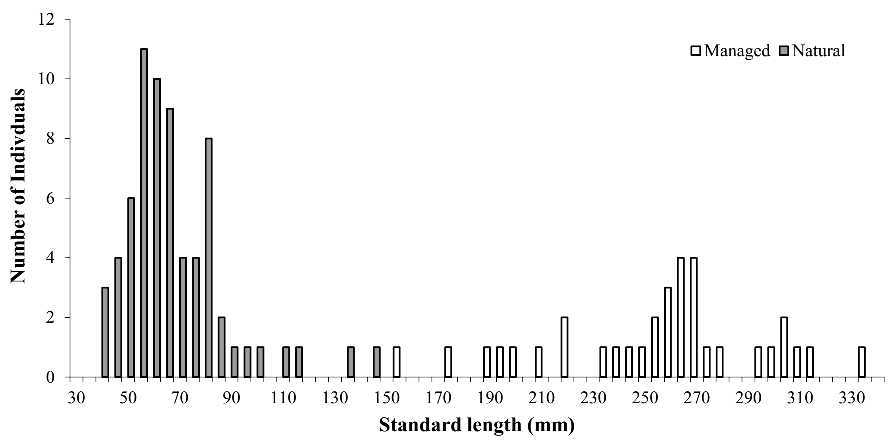

Fig. 2 Length-frequency distributions of early life stage Atlantic tarpon *Megalops atlanticus* collected during July through November 2019 in South Carolina from North Inlet estuary natural marsh pools (Natural, gray bars) and from managed marsh impoundments at Tom Yawkey Wildlife Center Heritage Preserve and Kiawah Island (Managed, open bars)

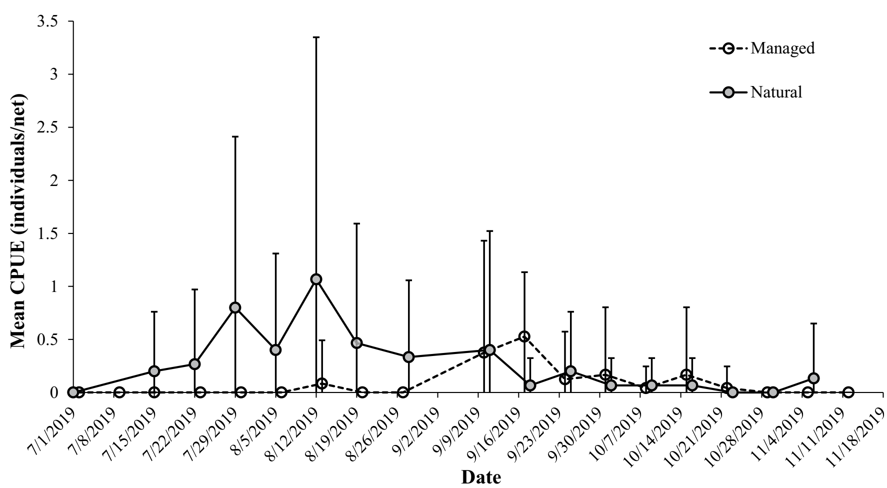

Fig. 3 Mean catch-per-unit-effort ± SD of early life stage Atlantic tarpon *Megalops atlanticus* collected during July through November 2019 in South Carolina from North Inlet estuary natural marsh pools (Natural, gray circles) and from managed marsh impoundments at Tom Yawkey Wildlife Center Heritage Preserve and Kiawah Island (Managed, open circles)

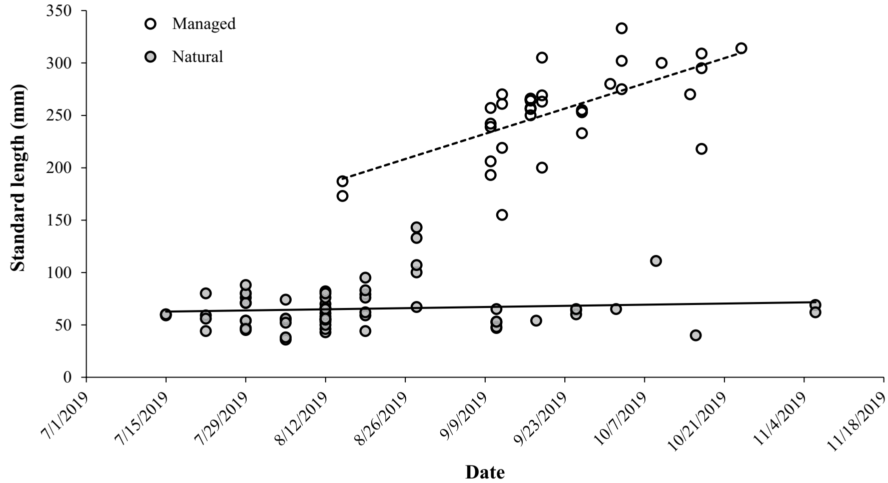

Fig. 4 Standard length of early life stage Atlantic tarpon *Megalops atlanticus* caught during July through November 2019 in South Carolina from natural marsh pools in the North Inlet estuary (Natural, gray circles) and from managed marsh impoundments at Tom Yawkey Wildlife Center Heritage Preserve and Kiawah Island (Managed, open circles)

of habitat type and Julian day $F = 31.35$, $df = 1$, $p < 0.001$; Fig. 4). Mean length ± SD of tarpon from impoundments increased from 180 ± 9.9 mm SL in August to 290 ± 31.5 mm SL in October, whereas the mean length ± SD of tarpon in marsh pools (65 ± 20.2 mm SL) was relatively consistent (Fig. 4).

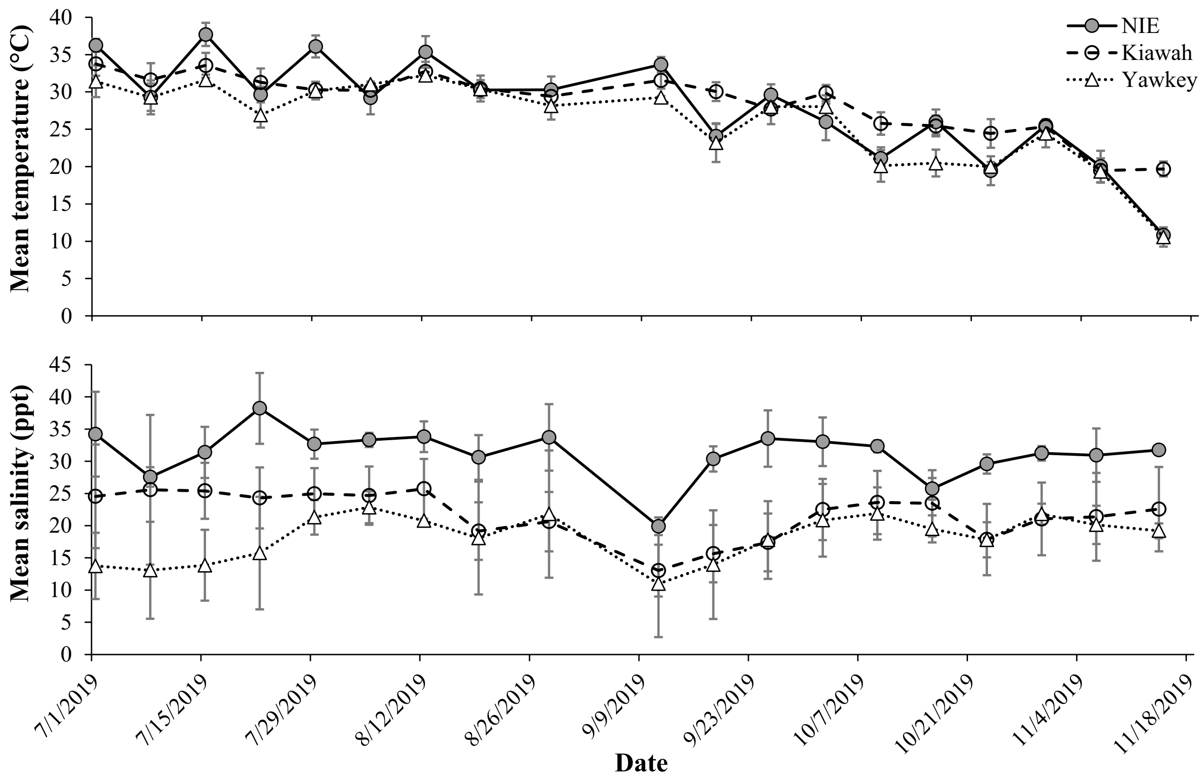

Fig. 5 Water temperature (mean ± SD) and salinity (mean ± SD) in South Carolina for North Inlet estuary (NIE, gray circles), Kiawah Island (Kiawah, open circles), and Tom Yawkey Wildlife Center Heritage Preserve (Yawkey, open triangles) during July through November 2019, the months which early life stage tarpon *Megalops atlanticus* were collected

Water quality varied among sample locations but followed seasonal patterns typical of the study region (Fig. 5). Temperatures ranged from 10.8 to 37.7 °C at NIE, 10.6 to 32.2 °C at Yawkey, and 19.5 to 33.8 °C at Kiawah (Fig. 5). Salinity also varied among study sites, with the highest salinities at NIE (19.9–38.2 ppt), lower salinities at Kiawah (13.0–25.7 ppt), and the lowest salinities at Yawkey (11.0–22.9 ppt; Fig. 5). Throughout the study duration, NIE had the highest salinity (~38 ppt) during summer, and Yawkey had the lowest (~7 ppt) during late spring (Fig. 5).

Discussion

Peak densities of juvenile tarpon in both natural marsh pools and managed impoundments were observed during mid-summer through fall, which is common for this species. The timing of these peak densities matches those observed in an earlier study by Mace et al. (2018) in some of the same NIE marsh pools and Yawkey impoundments, where tarpon were collected during September 2015 through November 2016. However, Mace et al. (2018) did not sample marsh impoundments during July through August and thus could not make comparisons between habitat types related to the timing of juvenile tarpon presence. The peak juvenile tarpon densities observed in this study also coincide with peak densities observed in Puerto Rico (Zerbi et al. 1999) and Louisiana estuaries (Stein et al. 2016); however, recruitment duration in Puerto Rico is more protracted (Zerbi et al. 1999). The timing of peak densities appears to be later in the western Atlantic compared to the eastern Atlantic (i.e., Nigeria), where juvenile tarpon recruitment is reported to peak earlier (February to April; Anyanwu and Kusemiju 2008). The difference in peak densities may be a factor of latitudinal differences in water temperature and photoperiod between locations, which may affect the timing of recruitment. We did not capture any tarpon during sampling for this study in late November, but tarpon were observed in late November while sampling for other ongoing tarpon work in managed marsh impoundments at Kiawah and Yawkey (M. Kimball, unpublished data). The decrease in juvenile tarpon presence in November in South Carolina is likely due to decreases in water temperature (Mace et al. 2017, 2018) and suggests that tarpon leave for warmer waters, which has also been observed in Louisiana (Stein et al. 2016).

We believe the juvenile tarpon collected during this study were all age-0 for multiple reasons. Winter water temperatures in most of South Carolina are below the minimum threshold for survival except in unique habitats which provide thermal refuges (e.g., thermally stratified upland pond; Mace et al. 2020). In addition, no tarpon were collected at any sites until mid- to late summer (suggesting no overwintering). Only one tarpon >age-0 has been collected from a natural marsh pool in NIE or Yawkey (that fish was a tagged fish that migrated from a unique habitat where overwintering does occur). Further, despite extensive sampling and examination of scales and otoliths from tarpon collected from natural marsh pools in NIE and managed marsh impoundments at Yawkey, we have never observed a tarpon >age-0 in these habitats (excluding the one fish mentioned above; G. Elmo, unpublished data). However, increases in winter water temperatures in coastal South Carolina, corresponding with climate change, may allow for increased overwintering of age-0 and older juvenile tarpon and in locations outside of rare and unique habitats (e.g., thermal discharges and stratified ponds). For example, Kiawah water temperatures were substantially warmer in November compared to NIE and Yawkey and never dropped below 19.5 °C during this study (~6 °C greater than the mean lower lethal limit for tarpon; Mace et al. 2017). Tarpon may potentially take advantage of the warmer water temperatures in southern South Carolina compared to northern South Carolina resulting in a year-round northward shift of the species range, which is not a unique phenomenon and has been predicted or documented for other tropical fish species such as lionfish *Pterois* spp. (Grieve et al. 2016) and common snook *Centropomus undecimalis* (Purtlebaugh et al. 2020). Although we are confident that all fish collected during this study were age-0, reports from local guide services and videos and photographs of juvenile tarpon that are >age-0 (based on large body size) suggest overwintering of tarpon in managed marsh impoundments on the southern coast of South Carolina. Winter water temperatures are consistently too low for overwintering of tarpon in NIE marsh pools and Yawkey impoundments (Mace et al. 2017), but given the warmer water temperatures of impoundments at Kiawah, it is possible that tarpon are able to overwinter in them and that we did not collect these older individuals due to our use of cast nets. Given the tropicalization of ecosystems associated with warming winter temperatures in temperate regions (Osland et al. 2021), studying the ecology of tropical and subtropical organisms at edge of their distribution is important for understanding these rapidly changing environments. If tarpon experience range expansion due to climate change, the importance of both natural and managed marsh habitats for this species will increase, impacting local estuarine management strategies.

We observed no overlap in size of tarpon collected throughout their entire first growing season in natural marsh pools and managed marsh impoundments in coastal South Carolina. Similarly, Mace et al. (2018) documented little overlap in the size of tarpon collected in marsh pools and managed impoundments in the North Inlet-Winyah Bay estuarine ecosystem, but their analysis was limited to one month (September). The absence of size overlap between habitats and increasing length of tarpon over time in managed marsh impoundments compared to the minimal change in length over time observed for natural marsh pools suggests that (1) tarpon are transient in marsh pools early in life, (2) tarpon do not enter impoundments until reaching a certain size, (3) small juvenile tarpon are cryptic in impoundments and larger juvenile tarpon are more susceptible to capture in these habitats, or (4) a combination of (1), (2), and (3). Size differences of juvenile tarpon across habitat types have also been observed outside of South Carolina (Rickards 1968, Zerbi et al. 1999, Navarro-Martínez et al. 2020). Juvenile tarpon may utilize natural marsh pools and managed impoundments at different life stages, and future studies should investigate if size differences between habitat types are due to differential growth or ontogenetic shifts in habitat use.

This study demonstrated that multiple estuarine habitat types are important for juvenile tarpon. The results will be used to inform future South Carolina tarpon conservation efforts and devise management plans that protect important juvenile tarpon nursery habitats statewide. Managers will be able to utilize the information from this study to target specific marsh areas for future conservation and restoration efforts or use these results to aid current efforts establishing why certain marsh areas need protection. This study will also aid in locating other areas within South Carolina and along the southeastern US Atlantic coast that tarpon may be utilizing as estuarine nursery habitats. Such information will provide a starting point for scientists to study the ecological benefits of the different natural and managed habitats tarpon utilize. However, there is still a lack of knowledge regarding habitat use by older juveniles, the timing of tarpon habitat use shifts, and how South Carolina estuaries contribute to the global tarpon population. For example, there is a paucity of information about larger juvenile tarpon (>300 mm) estuarine habitat use in South Carolina. In areas of South Carolina where water temperatures are adequate, individuals may overwinter, reach larger sizes, and contribute to local fisheries. However, managed impoundments may be a potential sink for larger fish if water levels do not permit egress to marine environments used by adults or other warmer waters during periods of extreme cold. This lack of knowledge highlights the need for specific examination of tarpon emigration from managed marsh impoundments and other nursery areas to deeper estuarine waters where they can migrate to warmer waters and eventually recruit to adult populations.

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Data availability Not applicable.

Code availability Not applicable.

Declarations

Ethics approval This research was conducted in accordance with the guidelines set forth in the Coastal Carolina University IACUC Animal Care and Use Protocols #2018.04.

Consent to participate Not applicable.

Consent for publication All authors have read this manuscript and consent for publication.

Conflict of Interest The authors declare no competing interests.

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