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Limulus polyphemus (Atlantic Horseshoe Crab) Habitats in a Small Estuary and the Adjacent Inner Continental Shelf: Linkages Across Mid-Atlantic Bight Seascapes

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Abstract - While there are numerous studies of *Limulus polyphemus* (Atlantic Horseshoe Crab) populations on the East and Gulf coasts of the US, especially for spawning adults in large estuaries such as Delaware Bay, there are fewer efforts relative to small estuaries in the Mid-Atlantic Bight. We determined, for the first time, the pattern of seasonal linkages between the Great Bay–Little Egg Harbor estuaries in southern New Jersey and the adjacent inner continental shelf with multiple gears over multiple years. Adults of both sexes are distributed along the inner continental shelf in all seasons, while large juveniles were most abundant in the fall. The seasonal occurrence of larvae, small juveniles, and spawning adults in high salinity, sandy, natural habitats in these small estuaries was consistent. Our findings suggest that these and other small estuaries may provide the same habitats, predators, prey, and fishery resources as larger estuaries, except at a smaller scale. Thus, small estuaries contribute by enhancing landscape and habitat diversity for this vulnerable species. Further clarification of the importance of estuarine habitats would benefit from an increasing emphasis on juveniles and their subsurface habitats in small and large estuaries.

Introduction

Limulus polyphemus (L.) (Alantic Horseshoe Crab, hereafter, Horseshoe Crab), is an important component of the ecosystems and economies of both coastal and estuarine areas of the Atlantic and Gulf coasts of the US (Botton 2009, Botton et al. 2003, Levin et al. 2003, Shuster et al. 2003). The Mid-Atlantic Bight (from Massachusetts to South Carolina), and especially Delaware Bay, supports the largest population of Horseshoe Crabs in the world (Pierce et al. 2000, Shuster 2015, Smith et al. 2017) and is their primary spawning site (Shuster and Botton 1985). The population was once thought of as a vast resource, but a decline in numbers became apparent in the 1990s (Shuster et al. 2003, Smith et al. 2017, Walls et al. 2002). The decline has been largely credited to 2 sources: first, the harvest of

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Horseshoe Crabs for fertilizer (late 1800s–early 1900s), and after some recovery, a second decline in the 1990s, when the species was harvested as bait for commercial *Anguilla rostrata* Lesuer (American Eel) and *Busycon* spp. (conch or whelk) fisheries (Berkson and Shuster 1999), and for use in the biomedical industry (Anderson et al. 2013, Atlantic States Marine Fisheries Commission 2013, Levin et al. 2003). In the last decade, the landings from both of these sources have stabilized at a lower level (Atlantic States Marine Fisheries Commission 2013), but the species has been listed as "vulnerable" by the IUCN Red List (http://www.iucnredlist.org/details/11987/0). A recent genetic evaluation throughout the Horshoe Crab's range indicates that there are 5 distinct subunits, 1 of which is the Mid-Atlantic Bight (King et al. 2005, 2015). This interpretation is supported by other meta-analyses (Smith et al. 2009b); thus, we place our studies in New Jersey in context relative to the Mid-Atlantic Bight population.

Most of what we know about the Mid-Atlantic Bight population has focused on adults in the ocean and in Delaware Bay (Botton 2009, Botton and Haskin 1984, Botton and Ropes 1987). Adults migrate from the ocean (Swan 2005) into the estuary in late spring, where females lay eggs on sandy estuarine beaches in the early summer. Following external fertilization, egg development is estimated at 2–4 weeks (Botton et al. 2010, Sekiguchi et al. 1988). These eggs have a high nutritional value and serve as a primary dietary component for shorebirds migrating during this time (Shuster 1982), fishes (Nemerson 2001, Nemerson and Able 2004), and other species (Burton et al. 2009).

We have a fairly thorough understanding of Horseshoe Crab habitat use and reproduction in Delaware Bay, but have a less comprehensive understanding of the role of habitats in smaller estuaries in the population status of this species, particularly for juveniles (Botton 2009). The exceptions include in the Gulf of Mexico, where the juveniles occur in sandy locations in the intertidal zone and subadults are found at the seaward limit of the same zone (Rudloe 1981); and in a Massachusetts estuary, where juveniles are inactive and buried in intertidal sand in winter and are more active on low tides in the summer (Meury and Gibson 1990). A few studies suggest that juveniles migrate to undefined deeper waters as they grow (Botton et al. 2003, Burton et al. 2009, Rudloe 1981). One primary reason for this lack of understanding of juvenile habitat use is their burial behavior (Rudloe 1979, 1980; Vosatka 1970), which makes them less available to most conventional sampling gears (Burton et al. 2009, Carmichael et al. 2003). The post-settlement juvenile stage is relatively long and requires an estimated 9 y for males and 10 y for females to achieve sexual maturity; Horseshoe Crabs have a maximum life span of 17–19 y (Botton and Ropes 1988, Sekiguchi et al. 1988, Swan 2005).

The purpose of this paper is to summarize, from recent studies over years to decades, the occurrence, abundance, and habitat use of larval, juvenile, and adult life-history stages in a small estuary in New Jersey and the linkages with the adjacent Atlantic Ocean inner continental shelf.

Materials and Methods

Study site

Two adjacent estuaries make up the estuarine portion of the study area within central–southern New Jersey on the east coast of the US (Fig. 1). The Great Bay–Mullica River estuary is a shallow (<2 m), salt marsh-fringed, drowned river valley (Fig. 1). Watershed protection makes it one of the least impacted systems in the northeastern US (Good and Good 1984, Kennish 2004). Water temperature regimes follow temperate seasonal patterns within the Mid-Atlantic Bight (<0 °C in winter to >30 °C in summer), and salinity corresponds to an upriver gradient from polyhaline regions near Little Egg Inlet to the freshwater–saltwater interface near Lower Bank, ~30 km upstream. The Mullica River–Great Bay rarely approaches the low dissolved oxygen levels of hypoxic estuaries (<4 mg/L). This estuary is dominated by sandy sediments in the lower portion and finer sediments in the upper portion (Kennish 2004). The adjacent Little Egg Harbor estuary is a lagoon-type barrier-island estuary of similar depths (<2 m at mean low water) and a narrow,

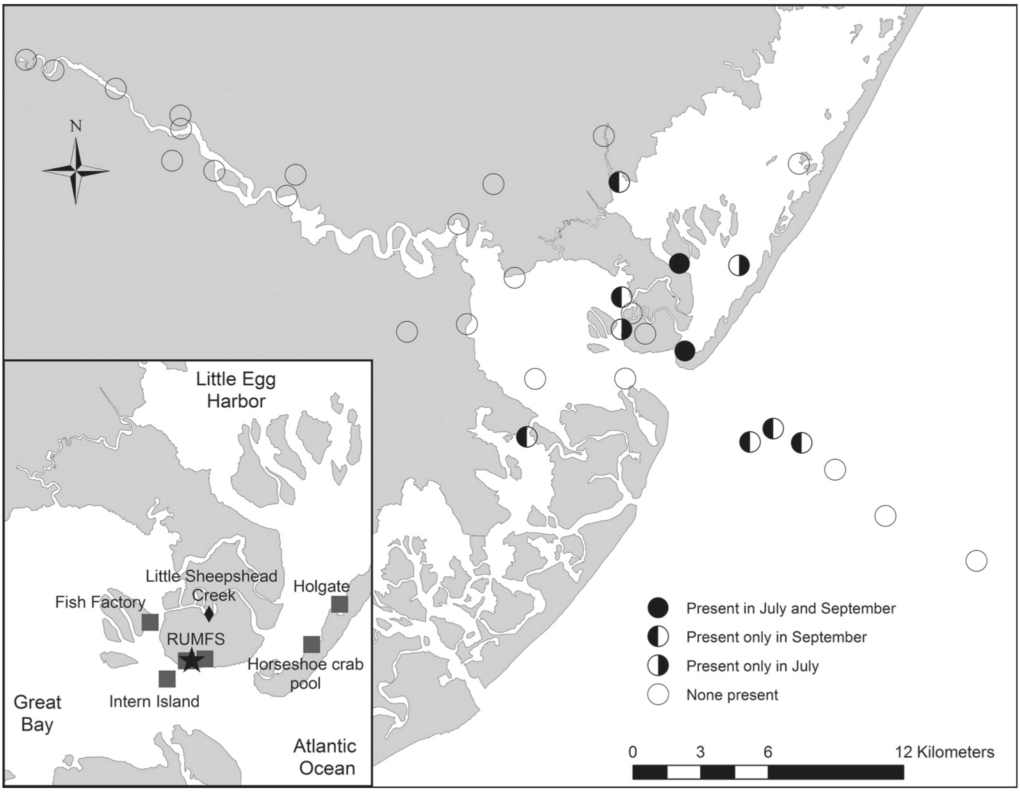

Figure 1. Horseshoe Crab study sites in the Great Bay–Mullica River estuary and the adjacent inner continental shelf. Occurrence of adult Horseshoe Crabs during 1988–2015 from the ocean to tidal freshwaters in the Mullica River–Great Bay estuary based on otter-trawl samples (circles) in July and September. Symbols in inset indicate the type of sampling conducted: push netting (■), plankton sampling (♦), and location of RUMFS (★).

semi-diurnal tidal range (<0.5–1 m), but fresh water input is limited to small creeks, and watershed development and human alterations are more extensive than for Mullica River–Great Bay (Kennish 2004).

The adjacent New Jersey inner continental shelf is characteristic of a passive margin, sloping gently to 100 m depth over ~80 km. The temperature of these and other Mid-Atlantic Bight shelf waters varies from approximately 1 °C to 26 °C, and salinity varies from 28 to 33, with tides and seasons controlling much of the variation (Chang et al. 2002, Steves et al. 1999). Nearshore habitats are less stable than those offshore, in terms of both temperature and salinity (Bowman and Wunderlich 1977, Steves et al. 1999).

Sampling location and effort

Based on collections of over 33,000 individuals, we sampled larvae, juveniles, and adults (measured as prosomal width; PW) with multiple gears (Table 1) across inner shelf and estuarine locations (Figs. 1, 2). We determined seasonal distributions

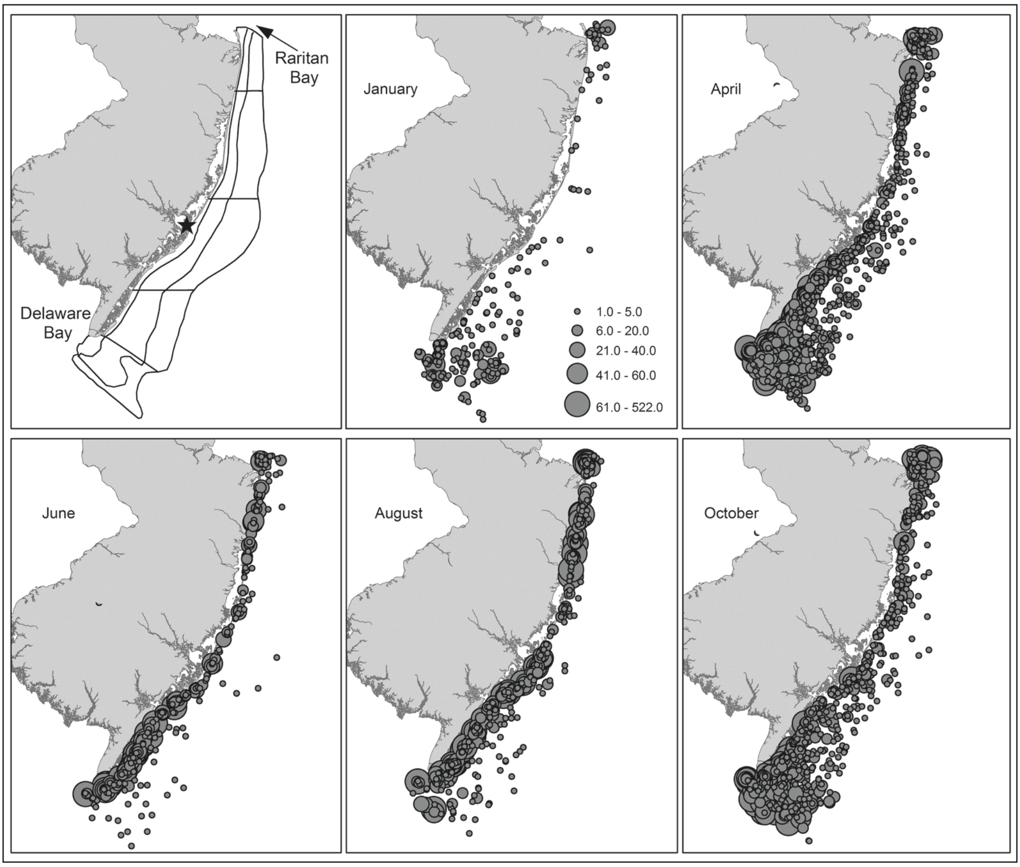

Figure 2. Sampling strata (upper left, depth contours of 9 m, 18 m, and 27 m) and seasonal distribution and abundance (expressed as number of individuals per minute of trawl tow for each sampling period) of Horseshoe Crabs on the New Jersey inner shelf, obtained from NJDEP otter trawl surveys (1988–2015). The star in the upper left indicates the location of Great Bay sampling sites in Figure 1.

Table 1. Sampling effort by location and gear for Horseshoe Crab larvae, juveniles, and adults in the Great Bay–Little Egg Harbor estuaries and the adjacent inner continental shelf (ocean) off the coast of New Jersey. Sources include RUMFS = Rutgers University Marine Field Station, and NJDEP = New Jersey Department of Environmental Protection. See Figure 1 for estuarine sampling locations. See Figure 2 for ocean sampling areas.

Location/Habitat	Sampling gear	Water depth (m)	Year	Months	# of stations	# of indiv.	Life-history stage(s)	Source
Inner Continental Shelf								
Ocean along coast of NJ	Otter trawl (<27 m, 6.4-mm bag liner)	2.0–36.0	1988–2015	February, April June, August, October	186	31,219	Juveniles, adults	NJDEP
Ocean at Beach Haven Ridge to Little Egg Inlet	Beam trawl (2 m, 3.0-mm mesh)	2.0–19.0	1991–1993, 1999–2001	All	43	135	Juveniles, adults	RUMFS
Ocean along Little Egg Inlet, Great Bay, Little Egg Harbor	Seine (330 m x 1.8 m, 6-mm mesh in wings, 2-mm bag)	0.0–2.0	2004–2006	May–October	9	23	Adults	RUMFS
Estuary								
Little Sheepshead Creek	Plankton net (1 m, 1-mm mesh)	3.0–4.0	2005–2014	All	9	1304	Larvae	RUMFS
Great Bay–Little Egg Harbor	Push net (1 m^2, 3-mm mesh)	0.0–2.0	2010–2011	May–September	6	101	Juveniles	RUMFS
Great Bay–Little Egg Harbor	Beam trawl (3.0-mm mesh)	0.6–5.0	1992–1996	All	50	91	Juveniles, adults	RUMFS
Great Bay–Little Egg Harbor	Gear comparison (seine beam, otter trawls)	1.0–5.0	1991	May–October	25	33	Juveniles, adults	RUMFS
Great Bay	Minnow trap (6.4-mm mesh)	0.25–2.0	1990–2015	All	1	2	Juveniles	RUMFS
Great Bay, Mullica River	Seine (6.1 m, 4-mm mesh)	0.3–1.5	1990–1991, 2012–2015	All	16	3	Juveniles, adults	RUMFS
Great Bay	Pop net (5-m x 5-m multi-mesh)	1.0–2.0	1995–1996	All	1	5	Juveniles, adults	RUMFS
Great Bay, Little Egg Harbor, Mullica River	Otter trawl (4.9 m, 6.0-mm mesh)	0.6–5.0	1988–2015	All	46	119	Adults	RUMFS
Great Bay, Mullica River	Multi–mesh gill net	0.0–2.5	2001–2002	June–November	5	1	Adults	RUMFS

for juveniles and male and female adults on the continental shelf along the coast from New Jersey Department of Environmental Protection daytime bottom-trawl surveys from 1988 to 2015, over an area of ~4660 km^2 (Fig. 2; Byrne 1994). This area was divided into 15 strata spanning 5–27 m with cross-shelf boundaries at ~9 m, 18 m, and 27 m depth (Fig. 2). Sampling sites within each stratum were randomly chosen during each sampling period. Each sample consisted of a ~20-min otter-trawl tow during daylight (Table 1). Since 1999, mature males were identified following Shuster and Sekiguchi (2003) and Smith et al. (2009a) based on presence of monodactylus pedipalps. For the purposes of this paper, we assumed that individuals >180 mm PW without monodactylus pedipalps were maturing or adult females. At smaller sizes, we could not distinguish the sexes and considered those without monodactylus pedipalps as immature females or males. This assumption might have resulted in the misclassification of a small number of female juveniles as adults (see Smith et al. 2009a).

Other individuals were obtained via a long-term, daylight otter-trawl program from a variety of stations/habitats located throughout the Mullica River–Great Bay–Inner Continental Shelf corridor (Table 1, Fig. 1; see Szedlmayer and Able 1996, Vasslides et al. 2011 for further details). We sampled other individuals with anchored multi-mesh gills nets (15 m x 2.4 m with 5 panels of 5 mesh sizes [2.5-cm, 3.8-cm, 5.1-cm, 6.4-cm, and 7.6-cm box] and 91 m x 2.4 m with 6 panels of 3 mesh sizes [1.3-cm, 1.9-cm, and 2.5-cm box]) in the Mullica River-Great Bay estuary (see Able and Fahay 2010 for additional details). We set gill nets during the day, at biweekly intervals, in the spring, summer, and fall in upper creek, creek mouth, and nearshore bay habitats; each set was for ~60 min. In an attempt to discern the seasonal occurrence of larvae, we sampled weekly on night flood-tides with plankton nets and flow meters suspended in Little Sheepshead Creek behind Little Egg Inlet in southern New Jersey; we expressed abundance as number per 1000 m^3 (Table 1, Fig. 1), with an approach identical to that presented in Able et al. (2017). For the purposes of this paper, we defined larvae as trilobite-stage individuals of 3 mm PW. We employed push nets (Tinsley et al. 1989) in intertidal and shallow subtidal habitats to sample in the estuary (Fig. 1 inset) for small juveniles (unsexed).

Telemetry

During 2009, we fitted 3 adult female (240–260 mm PW) and 3 adult male Horseshoe Crabs (190–210 mm PW) with Lotek CAFT-11-2 (92-day life) or CAFT-11-3 (229-day life) acoustic tags in a PVC sleeve glued with marine-grade moldable epoxy to a cleaned and sanded spot on the dorsal surface of the prosoma. We collected all of these adults along a spawning beach in Little Sheepshead Creek (Fig. 1, inset) on 11 June ($n = 4$) and 24 June ($n = 2$) of 2004; crabs were tagged and held in captivity 24–48 h to allow the epoxy to cure prior to release at the capture site. An array of 12 moored WHS_1000 hydrophones provided real-time monitoring of movement through the inlet to the inner continental shelf and adjacent estuaries and also to oligohaline or freshwater regions of the system (Grothues et al. 2005). Our weekly mobile tracking efforts, using the techniques of Sackett et al. (2008), covered the entire estuarine system and parts of adjacent estuaries and Little Egg Inlet through June and July.

During 2017, we fitted 5 male (PW = 200–230 mm) and 5 female (PW = 280–300 mm) Horseshoe Crabs with Lotek MM series (MM-M-11_28) transmitters (5-s interval, 90-day life) using a Velcro saddle fastened with thick formula cyanoacrylate to the cleaned carapace and transmitter. We collected the first 9 crabs in a single trawl-tow along a sandy beach off of the Fish Factory, and the last in Little Sheepshead Creek (Fig. 1). An array of 2 moored hydrophones monitored Shooting (adjacent to RUMFS) and Newmans (adjacent to the Fish Factory) thorofares. Fixed hydrophone batteries expired 25 August, and we recovered units in November. Weekly or subweekly mobile tracking occurred through August and into September.

Results

Seasonal distribution and reproductive phenology

Seasonal samples, stratified by depth along the inner continental shelf off New Jersey from 1988 to 2015, showed distinct patterns for adult male (>140 mm PW) and female abundance, but were much less clear for the less abundant juveniles. We detected juveniles in all strata from the northern to the southern limits of the sampling area (Fig. 2). There was a pronounced seasonality for adult males and females (Fig. 3). We collected relatively few individuals in the winter (January). From April to August, males and females were widely distributed over most depth strata; however, they were most abundant in the inshore strata. By October, males and females were most abundant in the inshore and midshore depth strata. Juveniles were scarce; their occurrence was largely limited to October and then primarily in the inshore depth strata (Fig. 3), with the smallest juveniles in these samples >80 mm PW (Fig. 4).

The occurrence of adults in the estuary in March through June (Fig. 4) is consistent with egg laying on sandy beaches in the Great Bay–Little Egg Harbor estuaries (K.W. Able, pers. observ.). A lag time for egg hatching corresponds with the consistent occurrence of the larvae (3 mm) in year-round plankton samples during the 2004–2015 period inside Little Egg Inlet at Little Sheepshead Creek from May through September, with the highest values in July, when water temperatures were at their seasonal peak. Our findings indicate that adults continued to occur in the estuary into September, but some adults had migrated back into the ocean based on greater catches there at that time (Fig. 4).

Habitat use in the estuary

Horseshoe Crabs found in the estuary measured from 3 mm, for the planktonic larvae, to larger juveniles of up to 17–114 mm PW and adults up to 350 mm PW (Fig. 4). The size varied with sampling gear, with juveniles less than ~114–180 mm PW seldom collected in the estuary, while individuals of that size were frequently captured in most months by the surveys on the inner shelf, especially in October (Fig. 4). Perhaps the occurrence of smaller individuals on the inner shelf is part of a movement of juveniles from the estuary to offshore as they increase in size. We collected all juveniles and adults in the estuary in the lower portion, which is dominated by higher salinities and sandy substrates. We most frequently collected the post-settlement juveniles on the Little Egg Harbor side of Long Beach Island near Holgate in a natural area that is protected as part of the Forsythe National Wildlife Refuge (Fig. 1, inset). In this location, we found post-settlement juveniles moving over or buried in an intertidal–shallow subtidal sandy bottom along a series of coves found at prior storm-overwash points. Other areas with sandy substrates on the mainland side (mouth of Little Sheepshead Creek) and large sand bar inside the inlet (Anchoring Island) had no individuals.

Temporal and spatial use of the acoustically tracked adults varied substantially. Tagged Horseshoe Crabs utilized creeks, navigable channels (especially along emergent escarpments), and shallow open-bay habitat. There was no apparent difference between males and females in these patterns. Linear ranging distances were from 0.29 km to 0.83 km per week, but our range estimates could be biased by the period of time over which we detected an individual by mobile tracking because

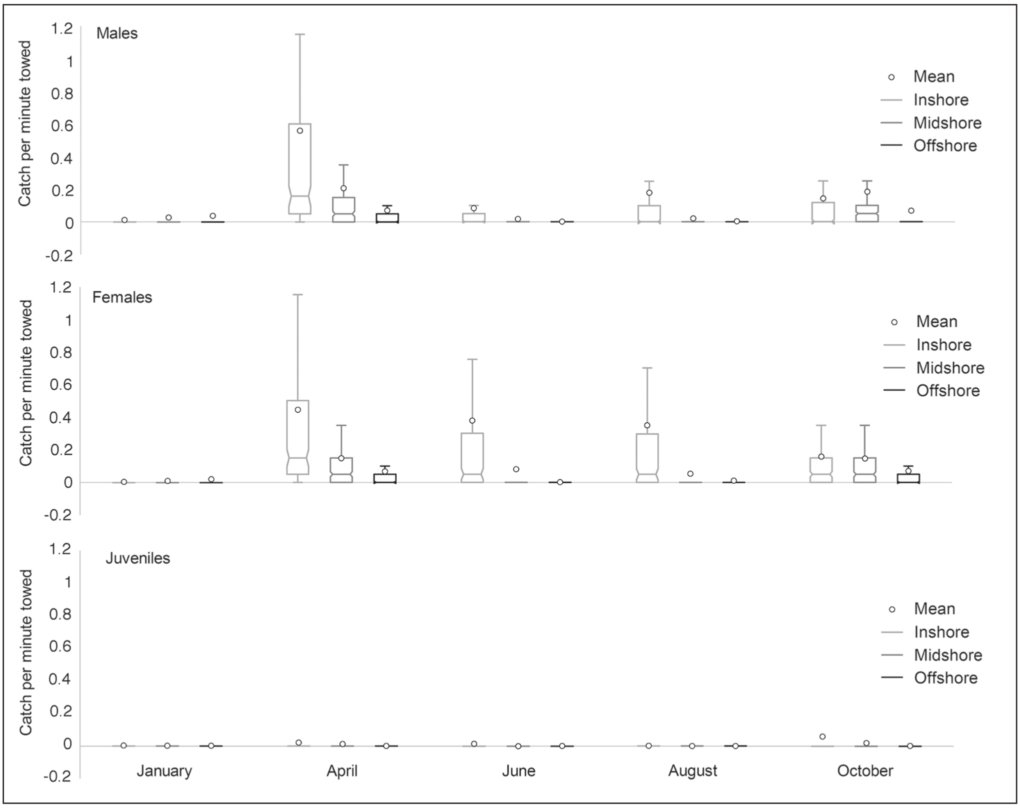

Figure 3. Horseshoe Crab abundance, expressed as catch per unit effort (catch per minute towed), by season and depth strata (across depth contours of less than 9 m [inshore], 18 m [midshore], and 27 m [offshore] from NJDEP otter-trawl surveys [1999–2015]; Fig. 1) for male, female, and juvenile Horeshoe Crabs. The notch displays the 95% confidence interval around the median, the box represents the interquartile range (IQR) or 50% of the data, and the circle is the mean.

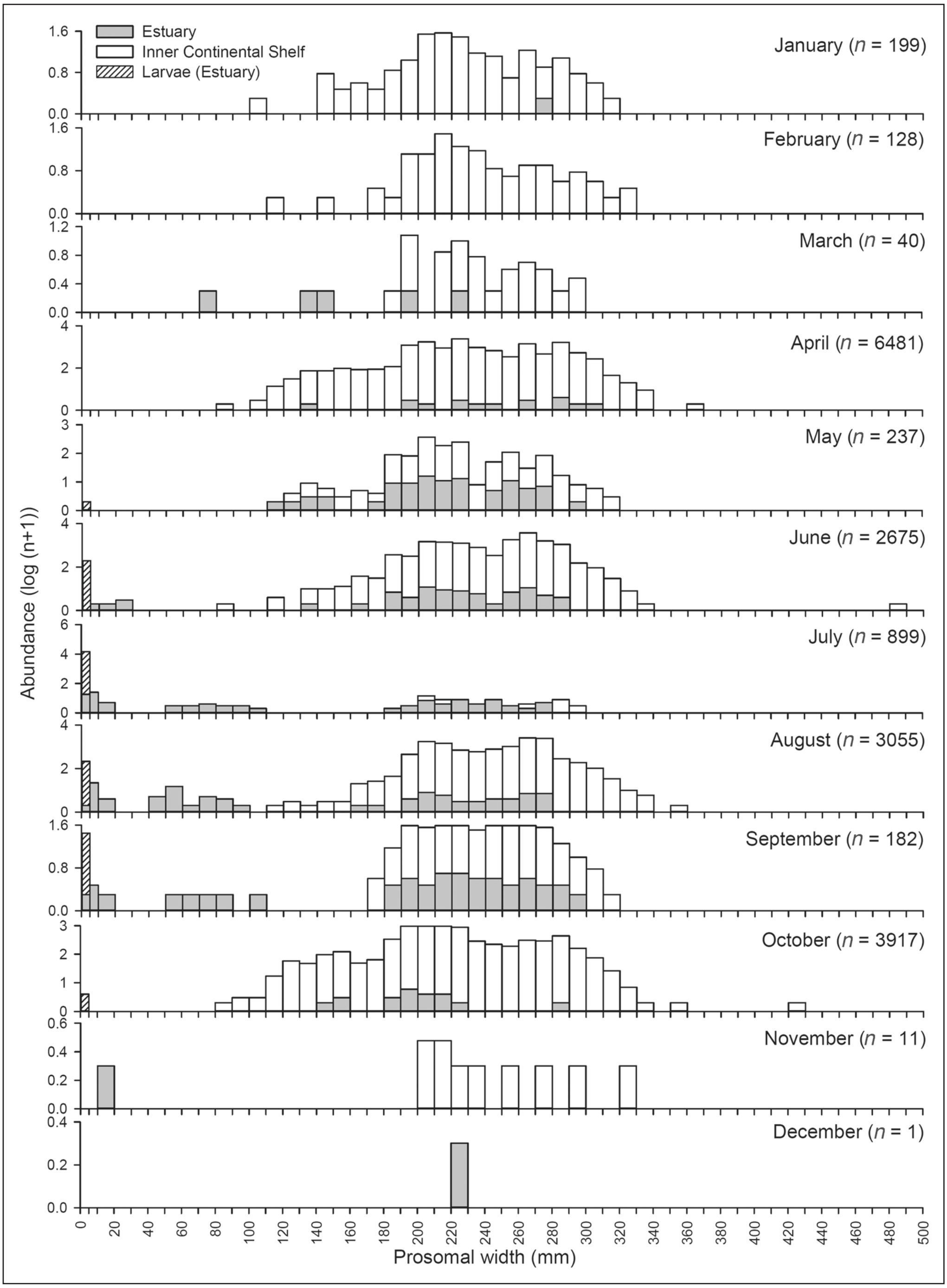

Figure 4. Monthly length frequencies (1988–2015) of Horseshoe Crabs across multiple gears in the inner continental shelf to estuary sampling area (Table 1). Larvae were collected with plankton nets; Inner Continental Shelf samples are from NJDEP otter-trawl surveys, and Estuary samples are a combination of RUMFS otter-trawls for larger animals, push-net surveys for juveniles, and others. Note the differences in the *y*-axis for each month.

movement was punctuated with quiescent periods of up to a month that included burial (as confirmed by diving).

Egress from estuary

Egress from the estuary to the inner continental shelf occurs at 2 stages in the Horseshoe Crabs life cycle in this small estuary. After a presumed long period of residence in the estuary, the juveniles, at sizes of <180 mm PW (Fig. 4), migrate onto the inner shelf. For many individuals, this movement occurs prior to achieving the size associated with sexual maturity. The smallest individuals detected on the inner shelf in our sampling were ~80 mm PW (Fig. 4). We detected individuals of this size in several months when extensive sampling occurred. The timing of egress for adults is likely in late summer or fall (September or October), based on the reduced number of adults collected in the estuary by the latter month (Fig. 4).

Seasonal timing of egress from the estuary onto the inner shelf by acoustically tagged adults overlapped with that shown by captures during trawling on the inner shelf (Fig. 2). The last detection on the hydrophones of the 2009 fixed array occurred between 19 June and 21 July 2004, but we subsequently detected 2 individuals by mobile tracking until 31 July 2004, when that effort ended. One of these tagged individuals had moved into the adjacent estuary (Little Egg Harbor); another remained well inside Great Bay near the tagging location, and we did not detect it passing inlet hydrophones, possibly because the tag had expired before it finally left the estuary. Another individual detected leaving the estuarine hydrophone array on June 26 remained just inside the inlet until 8 July, as detected by mobile tracking.

In 2017, most individuals dispersed from the tagging/release site within 1 week, but 3 individuals remained within range of the loggers until August. Mobile searches of the bay showed that the tagged individuals were moving towards the inlet, and the last detection was of an individual in the inlet. However, during dives to recover the loggers on 11 November, we found 2 untagged adult Horseshoe Crabs in the vicinity of the loggers (1 each).

Discussion

Limitations of the study

Aspects of our understanding of the linkages between the estuary and the inner continental shelf for Horseshoe Crabs are likely compromised by the species' unavailability to many sampling approaches. This lack of detectability is, in part, due to burial as well as their seasonal migrations between these areas (Swan 2005). Of these, burial presents a general sampling problem (Able 1999, Able and Fahay 2010) given the ability to bury during their entire lives (Estes et al. 2015, Hata and Berkson 2003, Lockwood 1870, Meury and Gibson 1990, Vosatka 1970). The inclination of juveniles to bury may vary with tide (Meury and Gibson 1990, Rudloe 1981), day–night cycle, and season; thus, the behavior limits our understanding of this life-history stage, and perhaps of the adults as well due to an inadequate understanding of sampling efficiency (Cadrin et al. 2016, Jones 2011). Burial behavior also affects the ability to detect acoustically tagged individuals, and further, the ability to decode audible transmitters. In the case of moored logging hydrophones, an undecodable transmitter effects the study the same as total detection failure (Grothues et al. 2012). In the case of mobile tracking, a transmitter that is audible but cannot be decoded can at least be mapped and its identity interpreted based on movement on earlier or subsequent days. That was the case for 1 individual that we tracked as it was intermittently buried or crawling while crossing over a shoal and into Little Egg Inlet. These situations lead to extremely low signal-detectability. Further, the inability to confidently identify juvenile females, a complex issue at best (Smith et al. 2009a), limited our ability to follow their movements from the estuary to the inner continental shelf.

Linkages between estuary and the inner continental shelf

Our findings demonstrate that some populations of Horseshoe Crabs in the Middle Atlantic Bight, including those from the Great Bay–Little Egg Harbor estuaries, are linked, but the annual and seasonal patterns of estuarine–inner shelf movements are influenced by size/age at maturity and their long lives. We assume, based on indirect evidence, that Horseshoe Crabs live for 17–19 y (Botton and Ropes 1988, Sekiguchi et al. 1988, Swan 2005). This relatively long age-duration is supported by tag–recapture studies in which numerous adults were recaptured 9–10 years after tagging in the Mid-Atlantic Bight (Mattei et al. 2011, Swan 2005). If Horseshoe Crabs make their terminal molt in 9–11 y (Shuster 1950), then the duration of the juvenile stage may be relatively long, up to 9 y (males) or 10 y (females) (Sekiguchi et al. 1988) or slightly longer (Smith et al. 2009a). However, it is important to remember that aging based entirely on a size–age relationship could be erroneous because Horseshoe Crab instar duration can vary between the laboratory and the field (Botton and Ropes 1988, Kawahara 1982, Sekiguchi et al. 1988, Smith et al. 2009a).

Based on cumulative length frequencies in the study area, most individuals <100 mm are found in estuaries, and, at larger sizes, they are found on the inner continental shelf. This pattern is consistent with the general pattern that the larger juveniles migrate offshore and mature on the inner shelf. Smith et al. (2009a) cautioned that these patterns may be more complex, especially between different sexes and ages. The inshore–offshore linkages observed in this study are supported by an extensive tag–recapture study in the Mid-Atlantic Bight (Swan 2005). In that study, some adults had moved from spawning sites in Delaware Bay to areas on the continental shelf, mostly south of the bay but also to the north, over varying periods of time. Typically, these Horseshoe Crabs occurred 3.2–12.8 km from the shoreline, with the furthest at 48 km from shore (Swan 2005). Conversely, some individuals tagged on the inner continental shelf off Ocean City, MD, moved into Delaware Bay ($n = 48$). These inshore–offshore migrations are not surprising because they are also typical for fishes in the extreme, seasonally varying temperatures of the Mid-Atlantic Bight (Able and Fahay 2010, Able et al. 2014).

The seasonal inshore–offshore migratory patterns that are evident for Horseshoe Crabs in the Mid-Atlantic Bight based on our sampling in the estuary and inner continental shelf, and others (Botton and Ropes 1987), and our interpretation of tracking in this study are apparently not the case in the Gulf of Mexico (Rudloe 1980), the vicinity of Cape Cod (James-Pirri 2010, James-Pirri et al. 2005), or the Gulf of Maine (Moore and Perrin 2007, Schaller et al. 2010, Watson et al. 2009), where the adults apparently overwinter within estuaries, just in slightly deeper waters.

The apparently greater abundance of Horseshoe Crabs in the southern and northern extremes of the New Jersey coast (Fig. 1) is likely due to proximity to estuarine spawning sites in large bays such as Raritan Bay/New York Harbor and particularly Delaware Bay (Botton and Haskin 1984, Botton and Ropes 1987, Shuster 1982, Smith et al. 2009b). The latter supports the largest spawning population documented for the species (Hata and Berkson 2003, Shuster and Botton 1985, Smith et al. 2010), as is evident from tag–recapture studies (Swan 2005). The consistent occurrence of Horseshoe Crabs along the rest of the coast, based on this and related studies (Botton and Haskin 1984, Botton and Ropes 1987), implies that migration inshore to and spawning in estuaries all along the coast may be common, as our data indicates for the Great Bay–Little Egg Harbor estuaries.

Habitat use in the estuary

Horseshoe Crabs in the Mid-Atlantic Bight may spend numerous years in estuaries as juveniles, yet we know relatively little about their patterns of habitat use because their habit of burying in the substrate often precludes them from frequent capture. Thus, these estuarine "nurseries" deserve the attention often afforded to fish, shrimp, etc. (Beck et al. 2001, Dahlgren et al. 2006, Nagelkerken et al. 2015) due to the economic and ecological importance of Horseshoe Crabs. Further, if we assume that Horseshoe Crabs live at least 11–19 ys (Botton and Ropes 1988), then they are resident in estuaries for at least one third of their lifespan and intermittently as long as they continue to reproduce. Thus, estuaries are essential habitat across all life-history stages.

The frequent occurrence of Horseshoe Crab larvae at our long-term plankton sampling site over most of the years sampled verifies that spawning occurs in this small estuary. These larvae are likely from this estuary because larval dispersal is limited (Botton and Loveland 2003) and egg deposition has been observed over many years in several sandy beaches, including one 10–20 m from the plankton collecting site. These nighttime collections may be optimal because the larvae are more active at night when they migrate into the water column (Cheng et al. 2015, Ehlinger and Tankersley 2006, Rudloe 1979).

Despite the common occurrence of larvae, the juveniles are infrequently captured. In this study, the juveniles were most abundant on natural, sandy, intertidal beaches on the bay side of barrier islands. This occurrence on sandy substrates and sand flats is consistent with observations in Delaware Bay (Botton and Loveland 2003, Botton et al. 2003), the Gulf of Mexico (Rudloe 1981), and in the vicinity of Cape Cod (Meury and Gibson 1990).

The distribution into deeper, subtidal estuarine waters increases with size of juveniles in some populations (Rudloe 1981, Shuster 1982). However, deeper subtidal habitats are seldom sampled effectively. An exception was sampling with a suction dredge at depths of 1–4 m in Delaware Bay, which found juveniles (peaks of 12.5-mm, 17-mm, and 24-mm carapace width) in the fall (Burton et al. 2009). Our efforts in the Great Bay–Little Egg Harbor estuaries found juveniles most consistently in the intertidal zone. In addition, extensive sampling (*n* = 600 grab samples) over 3 y (2012–2014) throughout subtidal areas (1–14 m) of Barnegat Bay, including Little Egg Harbor, collected only 2 juvenile Horseshoe Crabs (G. Taghon, Rutgers University, New Brunswick, NJ, pers. comm.).

The collection of relatively few juveniles collected in this small estuary is likely due to 2 factors. First, as previously indicated, burial behavior prevents effective sampling. Second, the population size may be small relative to an estuary like Delaware Bay. The Delaware Bay population might be larger because Delaware Bay is larger and has numerous sandy beaches for spawning and very large sand flats with numerous troughs that provide nursery habitat for juveniles, thus supporting large population sizes (Botton and Loveland 2003, Botton et al. 2003). The same kind of nursery habitat, extensive tidal flats, is also available in a frequently studied area in the Gulf of Mexico near Turkey Point near Carrabelle, FL (Rudloe 1980, 1981). Similar sand flats are also evident in the sandy substrates in the vicinity of Cape Cod (Carmichael et al. 2003). Other species of horseshoe crabs, such as *Tachypleus tridentatus*, also use sandy intertidal habitats as juveniles (Almendral and Schoppe 2005, Hsieh and Chen 2009, Hu et al. 2009, Shuster and Sekiguchi 2009).

In summary, despite the potentially reduced population sizes in the Great Bay–Little Egg Harbor estuaries, these and other small estuaries may contribute significantly by providing additional landscape and habitat diversity for all life-history stages of Horseshoe Crabs. In addition, Horseshoe Crabs also contribute to estuarine food webs in small estuaries all along the coast in the Mid-Atlantic Bight (Millard et al. 2015, Nemerson 2001) and the fisheries that depend on them (Millard et al. 2015). This same pattern occurs for fishes in other small estuaries (Able and Fahay 2010, Cardoso et al. 2011). In addition, the natural shorelines in the study area, with little or no human alteration such as shoreline armoring, suggests that these nearly natural habitats may provide spawning and nursery habitats for Horseshoe Crabs into the future even as sea levels continue to rise (Loveland and Botton 2015).

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