Chapter 13
The Life History Cycle of *Limulus polyphemus* in the Great Bay Estuary, New Hampshire U.S.A.

Helen Cheng, Christopher C. Chabot, and Winsor H. Watson III

Abstract The overall goal of this chapter is to provide an overview of the life history cycle of the American horseshoe crabs (*Limulus polyphemus*) that reside in the Great Bay Estuary, New Hampshire, U.S.A. Great Bay horseshoe crabs generally spawn during high tides in the spring. Based on recent work and studies, spawning appeared to be triggered by increases in water temperature, and animals seemed to prefer to spawn in the warmest sections of the estuary. However, in contrast to horseshoe crabs in some other areas of the U.S.A., peaks of spawning activity did not necessarily correspond with the new and full moons, or with the highest tides, and similar numbers of animals were observed spawning during day and night high tides. Once the eggs hatch, it is hypothesized that their planktonic larvae are likely transported to the upper regions of the estuary where they settle on the expansive mudflats that characterize most of the Great Bay Estuary. At ~9 years (about the 17th instar stage), males appear to reach sexual maturity, while it appears that females molt one more time before reaching sexual maturity. This difference, along with a tendency for males to approach mating beaches more often than females, may contribute to a sex ratio that is skewed towards males at most spawning beaches in the estuary.

Keywords *Limulus polyphemus* • Great Bay Estuary • Spawning • Juveniles • Mating • Thermal preferences • Estuary • Sex ratios • Tidal rhythms

13.1 Introduction

In this overview, our goal is to bring together the results of published and more recent unpublished studies to provide an overview of the life history cycle of the horseshoe crabs that reside in the Great Bay Estuary, New Hampshire, U.S.A.

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This estuary is located at the northern end of the range of horseshoe crabs and, perhaps as a result, there are both similarities and differences in the behavior and life history of this subpopulation of *Limulus* compared to other populations that have been extensively studied in other areas. We will begin this overview in the early spring, when overwintering adults begin to migrate to intertidal areas to spawn, and we will end with the juvenile horseshoe crabs that grow up in the estuary and reach sexual maturity after ~17 molts (Sekiguchi et al. 1988).

13.2   The Great Bay Estuary of New Hampshire, U.S.A.

The Great Bay Estuary is a complex, semi-enclosed, embayment near the New Hampshire-Maine border. It is separated into three different areas: the Piscataqua River, Little Bay, and Great Bay (Fig. 13.1). The rivers that flow into the Great Bay Estuary drain a watershed that extends more than 1,600 km², and this convergence of land and water shapes the features and uses of the ecosystem (Short 1992). There are five dominant aquatic habitats: eelgrass meadows, mudflats, salt marsh, channel bottom, and rocky intertidal. Additionally, the large quantities of water that move in and out of the estuary create some of the strongest tidal currents in North America
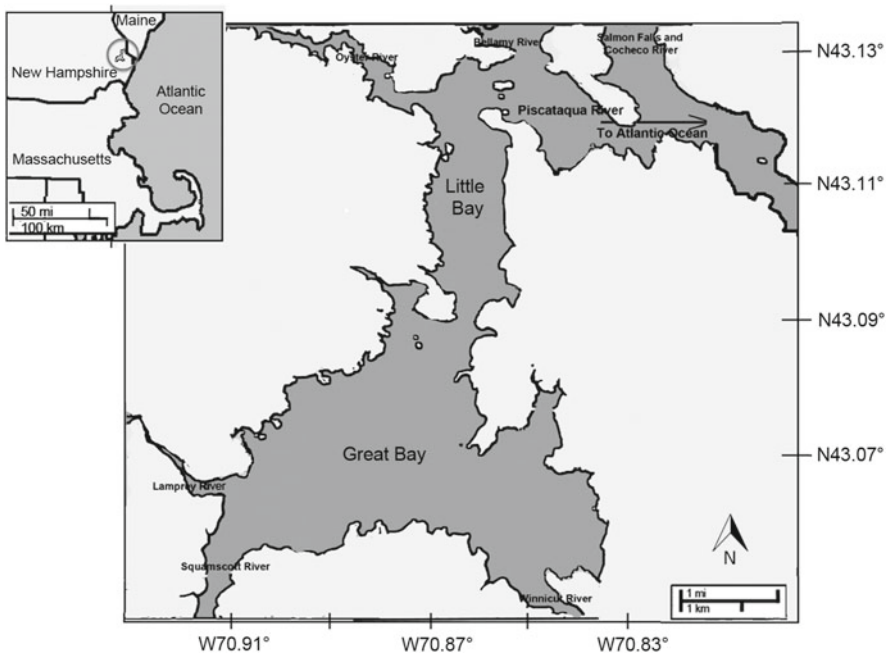

Fig. 13.1   Map of the Great Bay Estuary, New Hampshire, U.S.A. The Great Bay Estuary is 16 km inland from the Gulf of Maine and the Atlantic Ocean

(Short 1992). This tidal exchange structures the Great Bay Estuary ecosystem by affecting water quality, habitat extent, and species distributions.

The Great Bay Estuary appears to support a large population of horseshoe crabs (Watson et al. 2009; National Marine Fisheries Service 2010; Schaller et al. 2010; Watson and Chabot 2010). Using tag-recapture methods and the simplified Lincoln-Peterson Index calculation (Krebs 1998), preliminary population estimates in 2012 and 2013 indicated that there were approximately 122,430 horseshoe crabs that spawned along the shorelines of the Great Bay Estuary in the spring (Cheng, unpublished data).

13.3 Spawning Activity

Horseshoe crab spawning in the estuary generally occurs during the months of May and June, when both mature males and females approach spawning beaches. More than 95 % of the females approaching spawning beaches have a male attached (amplexed) to them (Cheng 2014), and interestingly, since we often observe male:female pairs while diving throughout the year, pair formation is not unique to the mating season. Beach approaches by single males are also common; however, amplexed pairs outnumber single males by ~3:1 (2.86 pairs to each single male).

13.3.1 Large-Scale Movements to Spawning Beaches

In the Great Bay Estuary, horseshoe crabs tend to overwinter in deep areas that are 2–5 km from where they spawn (Schaller et al. 2010; Watson and Chabot 2010). In contrast to reports from the mid-Atlantic States such as New York, New Jersey, Maryland, Delaware and Virginia (Shuster and Botton 1985; Botton and Ropes 1987; Walls et al. 2002), horseshoe crabs in northern bays and estuaries, such as the Great Bay Estuary, Taunton Bay, Maine and Pleasant Bay, Massachusetts, do not appear to move into coastal waters or offshore at any time of the year (Moore and Perrin 2007; James-Pirri 2010; Schaller et al. 2010). Based on high resolution tracking of animals equipped with ultrasonic transmitters, horseshoe crabs are very sedentary during the coldest months of the year (Schaller et al. 2010; Watson and Chabot 2010). Then, in the spring, as estuarine waters warm and exceed ~8–10 °C, they become active and migrate further up into the estuary where it tends to be warmer and the salinity is often lower. These data are consistent with similar telemetry studies in Taunton Bay and Pleasant Bay (Moore and Perrin 2007; James-Pirri 2010) and with laboratory investigations showing the close relationship between activity rhythms and water temperature (Watson et al. 2009; Chabot and Watson 2010; Chabot et al. 2011).

While this pattern of moving up estuary, or into bays, appears to be consistent at different locations, it is not clear what cues these animals use to find their spawning

beaches. While chemical, tactile, and visual cues likely aid their ability to locate each other (Barlow 1983; Barlow et al. 1984, 2001; Powers and Barlow 1985; Barlow and Powers 2003; Schwab and Brockmann 2007; Saunders et al. 2010) and suitable beaches for laying their eggs (Botton et al. 1988), these same cues are probably not useful for guiding them long distances to the general area where they spawn because odors would be rapidly diluted and dispersed in most locations; tactile cues only are effective in their immediate vicinity; and visual cues are only useful for distances of a few meters, especially in an estuary. Therefore, it is more likely that horseshoe crabs are detecting physical cues and gradients of things such as salinity and/or temperature. James-Pirri (2010) found that female horseshoe crabs were located in the shallow upper-regions of Pleasant Bay in the spring, moved towards the deeper portions of the bay in the fall, and then moved up to the upper regions again the following spring. Schaller et al. (2010) also found a similar trend in seasonal movements in the Great Bay Estuary and further reported that when temperatures exceeded 10–11 °C in the spring, horseshoe crabs started to become active and moved up-estuary. Then, when water temperatures became colder in the fall, the horseshoe crabs moved to deeper areas with more stable conditions where they spent the winter. Moreover, we find many spawning horseshoe crabs in the warmest parts of the estuary and up into the rivers that empty into the estuary, and our preliminary laboratory studies, described later in this overview, also suggest that horseshoe crabs might seek the warmest regions of bays and estuaries to spawn.

13.3.2 Timing of Mating Activity

While there is some evidence from certain study locations that horseshoe crabs tend to mate during the days that coincide with the new and/or full moons (Rudloe 1980; Cohen and Brockmann 1983; Barlow et al. 1986; Smith et al. 2002; Brockmann 2003; Table 13.1), in our study location there was no clear bias towards increased

Table 13.1 Comparison of major factors found to influence spawning activity among locations, including the Great Bay Estuary (Cheng 2014)

	Apalachee key (Florida)[a]	Seahorse key (Florida)[b]	Delaware Bay (New Jersey, Delaware)[c]	Mashnee Dike (Massachusetts)[d,e]	Great Bay Estuary (New Hampshire)
Lunar cycle	More spawning animals during full moon than new moon	More spawning animals during full moon than new moon	Only first half of spawning season, more spawning animals during full and new moon	Spawning occurred throughout May and first week of June, regardless of moon phase[d] More spawning animals during full and new moon[e]	Spawning occurred throughout May and June, regardless of moon phase

Table 13.1 (continued)

	Apalachee key (Florida)[a]	Seahorse key (Florida)[b]	Delaware Bay (New Jersey, Delaware)[c]	Mashnee Dike (Massachusetts)[d,e]	Great Bay Estuary (New Hampshire)
Highest high tides	Spawning only occurred on spring tides	Spawning only occurred on spring tides; more observed during high tides of full moon than high tides of new moon	Poor indicator alone of spawning activity	More spawning animals observed during spring tides, though significant numbers spawn on neap tides (lowest high tides)[e]	No relationship of spawning animals to highest high tides (spring tides); spawning occurred on spring tides and neap tides (lowest high tides)
	[f][Mean high tide height during full and new moon ~1.1 m; ↑ ~ 23.2 % from neap high tides (quarter moons)]	[f][Mean high tide height during full and new moon ~1.1 m; ↑ ~ 20.3 % from neap high tides (quarter moons)]	[f][Mean high tide height during full and new moon ~1.6 m; ↑ ~10.4 % from neap high tides (quarter moons)]	[f][Mean high tide height during full and new moon ~1.2 m; ↑ ~7.28 % from neap high tides (quarter moons)]	[f][Mean high tide height during full and new moon ~2.1 m; ↑~ 6.80 % from neap high tides (quarter moons)]
Day versus night	More spawning animals observed at night	More spawning animals observed at day than at night		Spawning only observed at night[4]	In 2012, more spawning animals observed at day; in 2013, no difference between day and night
	[Day tides height higher than night]	[Day tides higher than night by ~ ≤0.2 m]		Spawning observed day and night (dependent on highest tide of a given day)	[Night tides higher than day by ~0.5 m during spring tides, ~0.1 m during neap tides]
				[Daily tide difference depends on lunar phase, varies during spring tides by ~1 m][e]	

[a]Rudloe (1980)
[b]Cohen and Brockmann (1983)
[c]Smith et al. (2002)
[d]Cavanaugh (1975)
[e]Barlow et al. (1986)
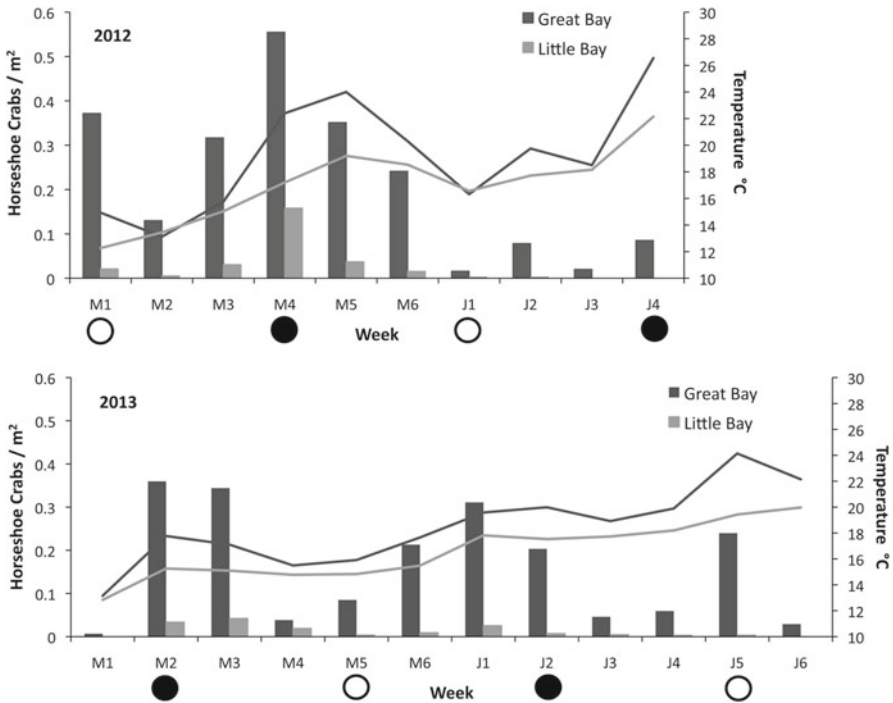[f]Tide heights were gathered from May 2014 NOAA Tide Predictions

Fig. 13.2 The relationship between spawning horseshoe crab density (number of animals per square meter) and mean temperature per 5-day interval for May (*M*) and June (*J*) of 2012 and 2013. Five-day intervals when the full moon (*open circle*) and new moon (*darkened circle*) occurred are indicated

spawning at these times or during the highest high tides (Fig. 13.2; Table 13.1; Cheng 2014). There was no significant difference in the densities of spawning horseshoe crabs during the days around the new moon, full moon, and equivalent time periods outside of the moon cycles for both 2012 and 2013 combined ($p = 0.430$; Kruskal-Wallis test). This could be due to the characteristics of the tidal system and spawning beaches in the Great Bay Estuary. For example, certain well-studied Florida beaches (such as north and west of Apalachee Key and Seahorse Key; Table 13.1) have minimal tides throughout most of the month, except during the full and new moons. Therefore, if horseshoe crabs use water depth as a cue for the occurrence of high tides (and this appears to be the case; Watson et al. 2008), and thus for aggregating on spawning beaches, these might be the only times of the month when that cue might be above their detection threshold. In contrast, tide heights outside the full and new moons (neap tides) in the Great Bay Estuary are always large enough to entrain horseshoe crabs to the tidal rhythm (Chabot and Watson 2010), and the small increases in tide height that occur around the new and full moons (6.8 % increase from neap tide to spring tides; Table 13.1) might not be significant enough to cause a change in their behavior.

Another difference between the spawning beaches surrounding the Great Bay Estuary and those in some other areas along the East Coast is that the Great Bay beaches are generally shallow and not very long. Therefore, during a large high tide,
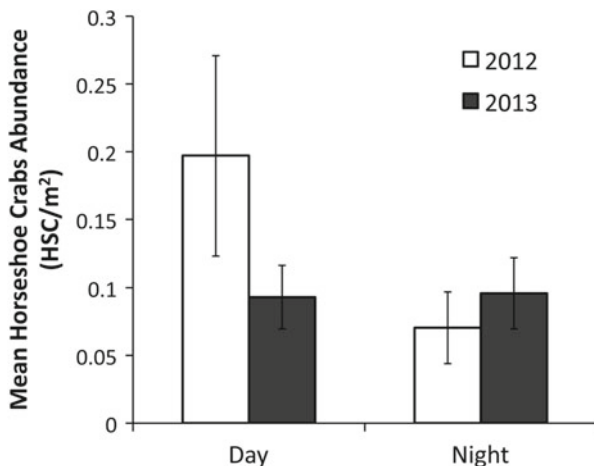
Fig. 13.3 Mean spawning horseshoe crab densities during day and night high tides in 2012 ($n = 12$ survey dates) and 2013 ($n = 39$ survey dates). *Bars* represent standard error of the means

the water can completely submerge a spawning beach, leaving little room for mating where the water meets the beach. This might actually lead to fewer animals mating during these higher tides and thus might, in part, explain why we did not find a close relationship between tide height, or a lunar cycle, and the number of mating horseshoe crabs (Fig. 13.2; Cheng 2014).

In contrast to a number of previous reports from studies conducted in other parts of the geographic range of *Limulus*, there was no clear tendency for horseshoe crabs to spawn during the night high tides in comparison to daytime high tides (Table 13.1; Fig. 13.3; Cheng 2014). In fact, in 2012 there were significantly more crabs spawning during the day ($p = 0.016$, Wilcoxon matched-pairs signed-ranks test, $n = 12$ survey dates; Fig. 13.3). Powers et al. (1991), Chabot et al. (2007), and Watson et al. (2008) proposed that horseshoe crabs evolved the ability to increase their visual sensitivity at night so they could effectively mate during either, or both, day and night high tides, which they appear to do in many locations. However, even though horseshoe crabs might be able to see well at night, due to the turbidity of many estuaries and the low amount of contrast and color difference between horseshoe crabs and the substrate, it might be somewhat more advantageous for them to mate during the day when they can probably see each other and other objects better (Barlow 1983; Barlow et al. 1984, 2001; Krutky et al. 2000).

13.3.3   Temperature

In the Great Bay Estuary both the timing and location of horseshoe crab mating are closely correlated with water temperature. For example, while spawning typically commences each year in May, in 2012, as the result of a warm winter and an unusual

warm spell in March and April, horseshoe crabs moved towards spawning areas sooner and spawned about 2 weeks earlier than usual (Fig. 13.2; Cheng 2014). In contrast, in 2013 spawning activity started at the more typical time in mid-May, when water temperatures began to warm and surpassed 11–13 °C (Fig. 13.2), and then continued into June. This is consistent with reports that the greatest spawning activity generally occurs at this time at other locations within their geographic range (Shuster 1979, 1982; Shuster and Botton 1985; Barlow et al. 1986).

The first large surge in spawning activity in the Great Bay Estuary is usually followed by two to three more peaks, which are separated by 2–8 days, and these peaks are generally associated with rising water temperatures. Thus, spawning may be modulated by the rate of increase in water temperature, rather than just higher temperatures. An additional factor causing the periodic peaks in spawning activity might be a physiological refractory period during which female horseshoe crabs need to recharge their ability to produce and extrude mature eggs. Thus, even in the absence of higher tides associated with the full and new moons, or peaks in water temperature, there will be oscillations in the number of females spawning through-out the season.

The greatest numbers of spawning animals were always observed at the beaches that were located furthest up into the estuary, where the water temperature was also significantly warmer (Fig. 13.4; these beaches do not appear to differ in any obvious way from other beaches in the estuary; Cheng 2014). This observation is consistent with recent behavioral assay laboratory studies demonstrating that horseshoe crabs significantly spend more time on the warmer side than the colder side of a Y-maze ($p = 0.023$; unpaired t-test, Fig. 13.5; Cheng 2014). Thus, at least in the Great Bay Estuary, seasonal and daily changes in water temperature appear to be the primary drivers of mating activity and strongly influence both when and where animals mate.

Fig. 13.4 Graduated bubble map of spawning horseshoe crab density (horseshoe crabs/m^2) at each survey site, along with the mean temperatures at each site in 2012 (**a**) and 2013 (**b**)
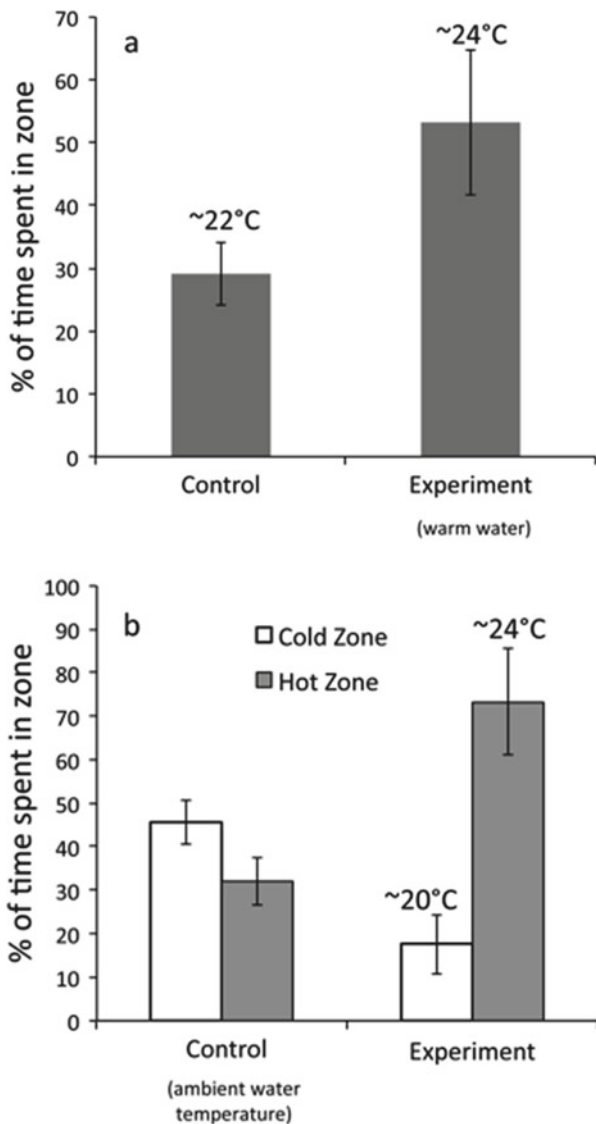
Fig. 13.5 The mean percent time spent by horseshoe crabs in the experimental zone (warm water) during control and experiment phases of Y-maze behavioral studies. Each experiment included a 1-h control period and a 1-h experimental period. In the first experiment (**a**), animals were given a choice between ambient water and warmer water ($n = 6$), while in the second experiment (**b**), animals were given a choice between ambient and ambient (Control), and then cold and warm water (Experiment; $n = 7$). *Bars* represent the standard error of the means

13.4 Growing Up in the Great Bay Estuary

13.4.1 Juvenile Horseshoe Crabs and the Location of Nursery Habitats

The extensive mudflats of the Great Bay Estuary appear to be important horseshoe crab feeding habitats for adults and juveniles (Lee 2010). These areas are generally characterized by an abundance of meiofaunal and infaunal prey and the absence of predators, which are usually restricted to deeper, subtidal habitats (Gunderson et al. 1990; Morrison et al. 2002; Holsman et al. 2006). During SCUBA surveys carried out at times of high tides on mudflats throughout the Great Bay Estuary, we found the most juvenile horseshoe crabs in the upper regions of the estuary, in Great Bay proper, and in areas that were not exposed to air at low tide. Juveniles were found both adjacent to adult horseshoe crab spawning beaches, as well as in areas that were at least 0.5–2.5 km from a known breeding beach (Fig. 13.6; Cheng 2014). Interestingly, there were no juvenile horseshoe crabs found during any of the surveys in Little Bay, despite surveying adjacent to documented spawning beaches. This may be due to the way larvae are carried by tidal currents, and perhaps the way that larvae move up and down in the water column (Rudloe 1979; Shuster 1982; Sekiguchi 1988; Botton and Loveland 2003; Ehlinger and Tankersley 2006).

13.4.2 Interactions Between Larval Behavior and Tidal Currents

Many estuarine, benthic invertebrates produce planktonic larvae that have evolved strategies to increase their chances of either being retained in the estuary or carried out of the estuary. This is accomplished using tidal-influenced vertical migration or selective tidal-stream transport (Forward and Tankersley 2001; Forward et al. 2003). After hatching, horseshoe crabs become planktonic (Rudloe 1979; Shuster 1982; Sekiguchi 1988; Botton and Loveland 2003) and often migrate vertically within the water column (Ehlinger and Tankersley 2006). However, it is unclear how long they stay planktonic, or if they time their excursions into the water column in a manner that would influence their transport within the estuary.

Tidal currents vary throughout the Great Bay Estuary, with fast moving currents ranging from 0.75 to 1.5 m/s in some areas of Little Bay to currents less than 0.5 m/s in the vast expanses of Great Bay (Short 1992). Drifter studies, using devices designed to mimic the passive drift of larvae, have been conducted in the Great Bay Estuary to investigate American lobster (*Homarus americanus*) larval transport (Goldstein 2012) and in all cases the drifters were retained within the estuary, regardless of whether they were released on a flood or ebb tide. Moreover, those released in Little Bay ended up in Great Bay ("upstream"). Recently, we repeated some of these drifter studies, releasing them adjacent to selected mating beaches in Little Bay and Great Bay, and most of them, as predicted from Goldstein's (2012)
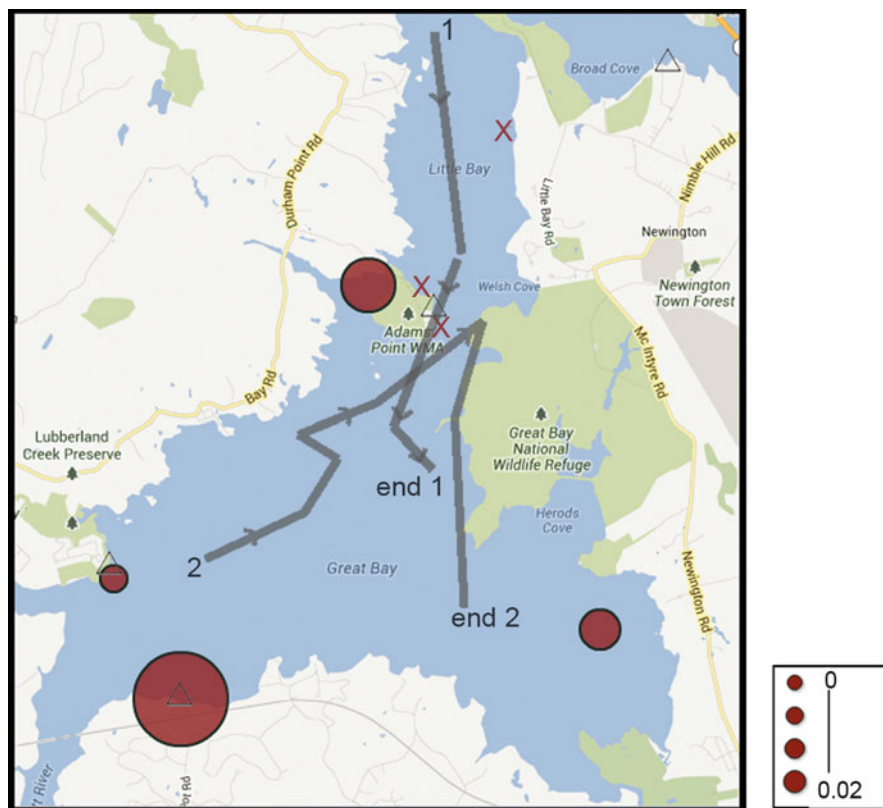
Fig. 13.6 Graduated bubble map of juvenile horseshoe crab densities (horseshoe crabs/m²) in Great Bay and Little Bay, based on dive surveys in 2012 and 2013 combined. Adult spawning survey beaches (Cheng 2014) are indicated by Δ's (also, refer to Fig. 13.4). X's indicate that no juveniles were found during surveys in these areas. The *gray lines* show the paths taken by two drifters that were released in Little Bay (*1*) and Great Bay (*2*) in 2014. Note that there is a tendency for the drifters to move up into Great Bay

work, were transported up into Great Bay (Fig. 13.6; Watson et al. unpublished data). Thus, it would appear that planktonic larvae are rarely exported out of the system and may, in fact, use these currents to increase their retention in the estuary. Specifically, horseshoe crab larvae that are hatched in spawning grounds in Little Bay are likely transported to areas in Great Bay where the current speeds are reduced in magnitude, and then they settle on appropriate soft bottom sediments.

13.4.3   Growth and Maturation

The majority of the juvenile horseshoe crabs found SCUBA diving were 45–85 mm in prosomal width (Fig. 13.7). Smaller juveniles were either in different areas or not captured because they were hard to see due to their size and cryptic coloration. It is
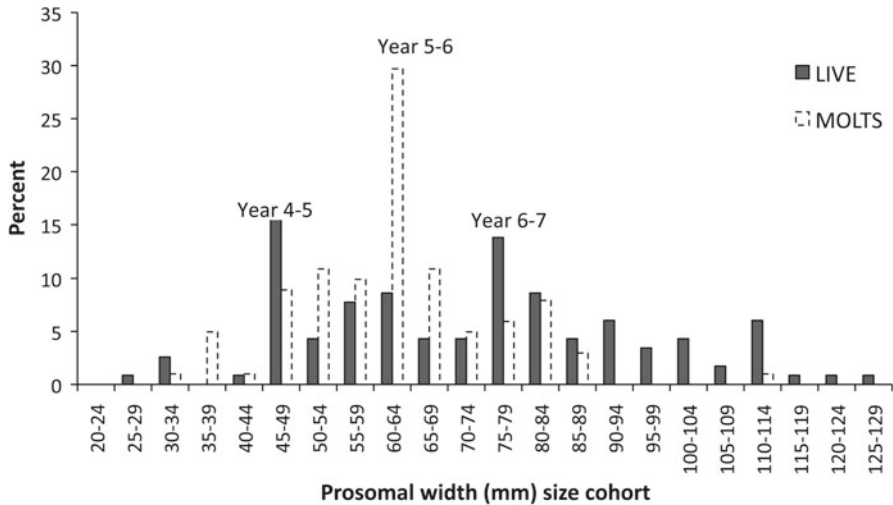
Fig. 13.7 Size-frequency distribution of live juveniles ($n=116$) and molts ($n=101$) collected diving and on beaches. Estimated ages of horseshoe crabs (According to Sekiguchi 1988) are indicated for the most abundant size cohorts

also likely that many could have been buried in the sediment at the time the surveys were conducted. Based on size frequency plots, it appears as if juveniles in the Great Bay Estuary increase in size by about 30 % with each molt (Fig. 13.7), which is consistent with previous studies (Carmichael et al. 2003; Burton et al. 2009). Carmichael et al. (2003) measured the growth of juvenile horseshoe crabs in Pleasant Bay, Massachusetts and also found that horseshoe crabs grew ~25–35 % larger with each molt. Based on the sizes of juveniles collected in the Great Bay Estuary, these horseshoe crabs were likely 1–8 years old (according to Table I from Sekiguchi et al. 1988 and Figure VI-44 from Sekiguchi 1988).

During shoreline surveys on nearby spawning beaches, the most abundant small males were 120 mm in prosomal width, and the most abundant small females were 150 mm (Fig. 13.8; Cheng 2014). Thus, we rarely saw horseshoe crabs that were 100–115 mm in either our dive surveys or spawning surveys. It is likely that this "missing" cohort of juveniles were beginning to move into areas that were deeper than where the smaller juveniles were found and yet were not sexually mature, so they were also not observed on the mating beaches.

After undergoing approximately 17 molts, in the span of 7–11 years, horseshoe crabs reach their terminal molt and stop growing (Shuster 1950; Walls et al. 2002). Given the sizes of the smallest males and females observed spawning in the Great Bay Estuary (Fig. 13.8), it appears as if males reach sexual maturity one molt sooner than females. This was also been observed in laboratory studies (Sekiguchi 1988; Sekiguchi et al. 1988). They suggest that males reach sexual maturity at year 9, at
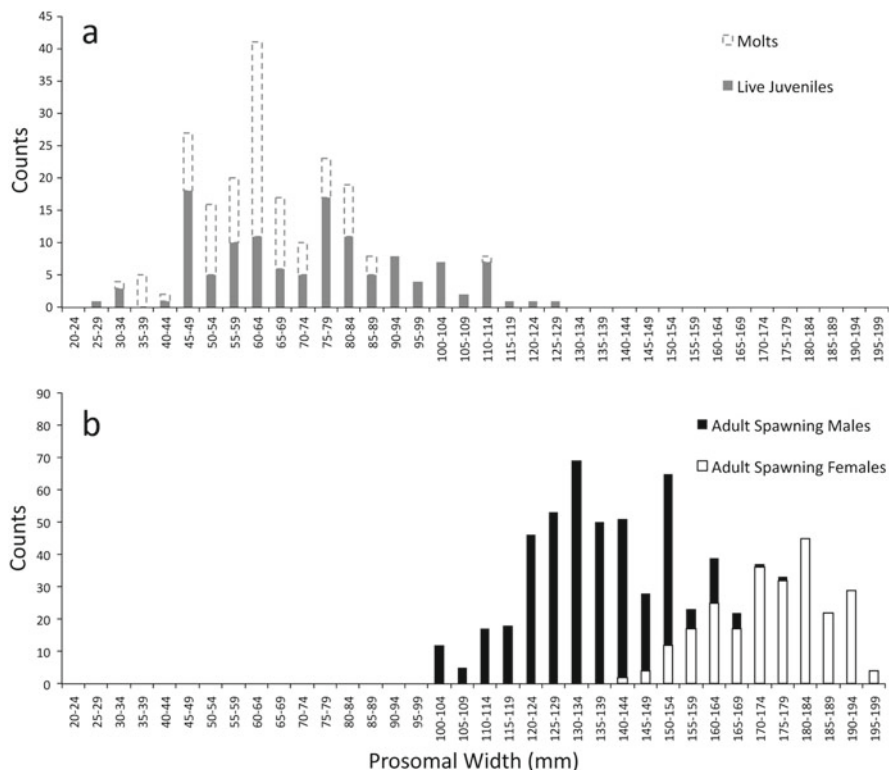
Fig. 13.8 A comparison of the size frequency distribution of (**a**) molts and live juvenile horseshoe crabs (*n* = 225), and (**b**) adult spawning horseshoe crabs (*n* = 668)

the 17th instar stage, and females reach sexual maturity at year 10, at the 18th instar stage. If males reach sexual maturity one molt sooner than females, this might explain both their size differences and, in part, the male-skewed sex ratios observed on mating beaches, both in New Hampshire (1.4 males to 1 female; Cheng 2014) and elsewhere (Rudloe 1980; Cohen and Brockmann 1983; Smith et al. 2002; Carmichael et al. 2003; James-Pirri et al. 2005). For example, in Florida, Rudloe (1980) and Cohen and Brockmann (1983) observed sex ratios of four males to one female (4:1), and in Delaware Bay, sex ratios have been reported to reach up to 5:1 (Shuster and Botton 1985; Smith et al. 2002). In some areas the sex ratio is even more skewed, but this might be the result of harvesting for the larger females by the biomedical and bait industries (James-Pirri et al. 2005). Data gathered from Pleasant Bay, a location where horseshoe crabs historically are harvested in large numbers for biomedical purposes (Rutecki et al. 2004; James-Pirri et al. 2005), showed nine males for every one female (James-Pirri et al. 2005).

13.5 Final Comments

The results from these collective studies on the American horseshoe crabs that reside in the Great Bay Estuary shed new light on this northern population. The Great Bay Estuary is characterized by large seasonal fluctuations in temperature and salinity, typical of high latitudinal temperate estuaries (Watson et al. 2009). Maximum temperatures occur during mid-summer through the fall. In addition, tidal cycles cause temperature and salinity fluctuations, with ebb tide water temperatures being warmer than flood tides, and flood tides bringing more saline waters into the estuary (Short 1992). All of these environmental factors play a role in the activities of horseshoe crabs in this location, and thus the behaviors and distributions observed in this study may be a result of local adaptations to the Great Bay Estuary.

The overall numbers of adult horseshoe crabs that return to spawn year after year along the shorelines, embayments, and estuaries of the U.S. Atlantic Coast are decreasing, or have decreased, in a number of regions. Though there are populations, such as those in Delaware Bay, that have shown annual fluctuations (Smith and Michels 2006) and are reported to be stable or increasing in recent years, populations in New York and Massachusetts show continuing declines and have not recovered (ASMFC 2009, 2010, 2013). Additional pressure from coastal development is reducing the quality of spawning beaches and possible nursery habitats where juvenile horseshoe crabs can develop. The Great Bay Estuary could serve as an important baseline for comparisons of horseshoe crab population health across the entire U.S. Atlantic coast since there has been little to no reported commercial harvest for horseshoe crabs in recent years (J. Carloni 2013 personal communication) and no history of biomedical company activity (State of New Hampshire 2001, 2002). Continued monitoring and assessments of the Great Bay horseshoe crab population might be useful in determining whether shifts in sex ratios, distribution, abundance, growth rates and other characteristics are the result of climate change or harvesting.

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