2006

A Switch from Polyandry to Serial Monogamy: Results from a Three Year Tagging Study of Horseshoe Crabs in Long Island Sound

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ABSRACT

Part of an ongoing population study of the North American Horseshoe Crab, *Limulus polyphemus*, in Long Island Sound was completed during the 2003 – 2005 spawning seasons at Milford Point, in Milford, CT. Horseshoe crabs range more widely throughout Long Island Sound than expected and exhibit weak site fidelity. Animals originally tagged in Milford were found as far west as Stamford and as far east as Clinton, CT. during the 3 year study. Out of 522 female horseshoe crabs tagged in 2004 only 4 came back to spawn again at Milford Pt. in 2005. The sex ratios of tagged and recaptured horseshoe crabs are both skewed towards males (1:1.5 and 1:1.8, females to males, respectively). Only one percent of the horseshoe crabs that were observed to be mating at Milford Point were found in clusters consisting of one female and more than one male. In Delaware Bay, where horseshoe crab population density is higher, clustered mating behavior was reported to be 44% when counted in 1993 (Brockman, 1996). This difference in mating behavior may cause a decline in gene flow in the Long Island Sound population and could lead to the decline in health of the population. Harvest dates should be set for the last two weeks of June which would allow the majority of females to lay eggs before they are harvested and sanctuaries established, where no harvesting is allowed, in order to increase the Long Island Sound horseshoe crab population density.

INTRODUCTION

Horseshoe crabs (*Limulus polyphemus*) are well known for their lack of gross phenotypic variation in shell morphology throughout the fossil record, and have been classified as a "living fossil" because of this superficial stasis (Eldridge, et al. 1984). However, the population parameters and behaviors of extant horseshoe crabs are not static. For example, James-Pirri (2005), reported sex ratios to vary between bays in Cape Cod and over time from 1:2.4 (females to males) to 1:9. Similarly, in Delaware Bay and in Apalachee Bay, Florida adult spawning sex ratios were found to vary both between days within a season and from year to year by 1:1.5 to 1:5 (Rudloe, 1980; Shuster and Botton 1985; Brockman, 1996).

Spawning behaviors also vary. It has been found that horseshoe crabs spawn during particular lunar cycles and during particular tides (Barlow et al., 1986) and others report not (James-Pirri et al., 2005). It has been observed in Delaware Bay that between 40% and 50% of the spawning horseshoe crabs occur in mating clusters (Duffy et al. 2006). However, over a 3 year study Brockman (1996) found unequal distribution of males between spawning paired females. Some paired and actively spawning horseshoe crabs were ignored by roving satellite males others had as many as 22 satellite males. We report here the observations from a three year mark-recapture study conducted on Milford Point, Connecticut.

PROCEDURES

Study Site:
The study site includes the barrier beaches around Milford Point, including the area near the breakwater, at the mouth of the Housatonic River, a small area of Wheeler Marsh near the Connecticut Audubon Coastal Center and the sandbar that is exposed at low tide lying perpendicular to the breakwater.

Methods:
Starting in mid-May through the first week of July of each year, 2003-2005, approximately 1500 meters of beach at Milford Point was surveyed for the presence of spawning horseshoe crabs. In 2003 and 2004 these surveys were conducted 5 days a week. In 2005, the beaches were surveyed daily. We normally started observations a few hours after high tide and continued for 5 to 6 hours depending on the weather and other conditions. Most of the data collected took place during the hours of 5:00 A.M. and 9:00 P.M. A few late night surveys were attempted but generally did not prove to be productive (e.g. crabs were difficult to find; collecting data was more difficult at night).

For each individual encountered, the presence of a mate and number of mates was recorded. The individual's prosomal length and width were also measured and recorded utilizing a straight edged metal ruler with measures to the nearest half centimeter. Cylindrical, bright yellow cinch-up tags (model FT-4, 8": Floy Tag Inc., http://ww.floytag.com) were utilized for individual identification. The tag also contains contact information as well as a 5 digit tag number unique to every individual. A small hole was drilled into either side edge of the prosoma using a scratch awl #1 (Challenge Sailcloth Inc. Vernon-Rockville, CT). The tag was then cinched into place around the back edge of the shell and then the animal was released.

RESULTS

During the 2005 spawning season there are peaks of spawning activity after the full and new moons (see Figure 1.). However, additional peaks of spawning activity seemed to be correlated with calm, warm weather at a different phase of the moon (see June 2, 2005 on Figure 1.). In some years, there seemed to be little correlation with lunar cycles (Figure 1. for 2003). Since this tagging program started in 2003, the total of newly tagged individuals has increased progressively each year (Figure 2.). In 2005, 2,243 spawning adult individuals were tagged which is 40% more than in 2004 (1806 tagged), and 66% more than in 2003 (756 tagged).

The sex ratio for the tagged sample population was skewed towards males in all three years. Each year an increasing number of males came up on the beach. When the data from all three years is averaged the sex ratio is 1:1.7 females: males.

Recapture data:
With the annual increases of newly tagged individuals over the three years and the increase in the number of people on the beach making observations, a corresponding increase in the number of recaptures occurred in 2005. In 2005, 202 individuals were recaptured, compared to 76 in 2004 and 60 in 2003. The sex ratio of the recaptured sample population was 1:1.5 females: males, averaged over the three years.

Analysis of the 2005 recapture data showed that 78% of the total recaptures were originally tagged and recaptured during the 2005 season. Similar percentages were found in 2003 and 2004. The remaining 22% of recaptures from 2005 were tagged in years prior to 2005. One was originally tagged in 1999, three of the recaptures were originally tagged in 2001, one was from 2002, four were from 2003 and 29 of the recaptures were originally tagged in 2004.

Approximately 95% of the recaptures encountered during 2003, 2004, and 2005 were recaptured at the primary study site at Milford Point or within two miles of it. Table 1. lists a few examples of wider ranging horseshoe crabs. The distance record goes to a horseshoe crab that was originally tagged at Milford Point in 2002 and was recaptured in Narragansett Bay, RI. in 2006. Of the 522 female horseshoe crabs tagged in 2004, four came back to Milford Point to spawn in 2005. In 2003, 408 females were tagged at Milford Point and 3 were recaptured spawning at Milford Point in 2004.

TABLE 1. A sample of places tagged horseshoe crabs have been found outside of Milford Point.

Place Recaptured	Place originally Tagged	Date Originally Tagged	Date Recaptured
Stratford, CT	Milford Pt. CT	15-Jun-03	20-Jul-03
Clinton, CT	Milford Pt. CT	3-Jul-03	19-Oct-03
Narragansett Bay, RI	Milford Pt. CT	Jun-02	Sept. 2006
Silver Sands, CT	Milford Pt. CT	12-Jun-03	2-May-04
New Haven, CT	Milford Pt. CT	Jun-03	29-Jun-04
Stamford, CT	Milford Pt. CT	23-Jun-04	25-Apr-05

Mating Behavior:
Over the three years of the study, 99 % of the spawning behavior involved one male attached to the epistosoma of one female. There were ten observations of a female with one male connected to her epistosoma and an additional male attached to the epistosoma of the first male (i.e., forming a chain of three attached individuals). No mating clusters of a female laying eggs surrounded by three males were found. Four male – male pairings were also observed. In 2005, large numbers of single males (745) were found on the beach and were not associated with any particular female. There were also 231 single females found on the beach. Proportionally equivalent numbers of single animals were found in 2004 and 2003 (Figure 2.).

DISCUSSION

While most people may view the horseshoe crab as morphologically static through millions of years of geologic history, its behavior and population parameters are the epitome of phenotypic plasticity. The 2005 spawning event was the only year that we observed the somewhat typical pattern of high horseshoe crab spawning densities after a full and new moon. In 2003, a very cool spring with intermittent storms prevented many horseshoe crabs from spawning normally. In 2004, there was more spawning activity during a half moon in June than on the full moon. In 2005, additional peaks of spawning activity seemed to be correlated with calm, warm weather during a quarter moon (see Figure 1., June 2, 2005). So clearly, peak spawning behavior changes based on multiple factors including water temperature, tide cycle, light, beach slope, intensity of wave action caused by storm events and/or wind speed (James-Pirri et al., 2005; Botton and Loveland, 1989; and Barlow et al., 1986).

The trend of more horseshoe crabs being tagged annually (2003-2005) is purely an artifact of the tagging effort (Figure 2.). In 2005, I had two undergraduates tagging everyday including weekends. In 2003 and 2004, tagging on weekends did not occur and in general only one person was tagging on the beach at any one time. An anomaly that was observed at Milford Point that has not been reported in the literature from Delaware Bay is the number of single females coming up on the beaches (231 in 2005). These lone females will not spawn successfully unless they find a mate. There were 745 single males roaming the Milford Point beach in 2005 also not involved in spawning. This phenomenon, of low population densities leading to a decline in successful spawning, is known as the “Allee Effect” (Berryman, 2003). With limitations on how far they can see to find a mate (both in and out of the water: Barlow et al. 2001, Barlow and Powers 2004) the population density may be too low for the males to display “satellite” behavior as seen in Delaware Bay (Brockman, 1990; Barlow et al., 1986; Botton, 1982; Smith et al., 2002). Brockman and co-authors (1994) found that satellite males may contribute up to 40% of the fertilizations of eggs of polyandrous nesting sites. The observed switch from polyandrous mating system to serial

monogamy at Milford Point may lead to a decrease in gene flow in the population and contribute to the decline in Long Island Sound.

CONCLUSION

To counter "Allee Effects" and increase horseshoe crab densities the legal harvest of horseshoe crabs should not begin until June 14th and end on June 30th. By this time, two thirds of the spawning population will have deposited eggs at least once before they are harvested. Late June is a time when lone males are most abundant thus allowing the majority of females to escape harvest. The current practice of harvesting horseshoe crabs in May takes out the female egg-bearing individuals before they have been able to lay at least some of their eggs. Spawning habitat preservation is important. The decline and near extinction of horseshoe crab species in Asia has been directly linked to the destruction of beach environments and pollution (Chiu et al., 1999). No harvesting should take place in the Milford Point area. Connecticut Audubon, and DEP volunteers monitoring the Piping Plover nests in the area could also help protect spawning horseshoe crabs. To promote higher density of *Limulus* populations, it is imperative that more beaches along Long Island Sound be protected. Parts of Delaware Bay are being considered for protection where no harvesting of horseshoe crabs may occur. Similar actions by the DEP in Connecticut should be considered in some areas to protect and increase the Long Island Sound *Limulus* population. More research is necessary to determine the effects of commercial harvesting of *Limulus* particularly illegal harvesting practices. More information is needed on egg density and larval survival in polluted versus less polluted beaches and shore areas. Additionally, DNA analysis would help to determine if the population of horseshoe crabs spawning in Connecticut has less genetic diversity than reported in other states.

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ACKNOWLEDGEMENTS:

Funding for this project was provided by Long Island Sound Fund administered by the Connecticut Department of Environmental Protection, through the sale of Long Island Sound license plates and contributions. I also received support from the Undergraduate Research Initiative, provided by the Dean of the College of Arts & Sciences, Sacred Heart University, Connecticut Audubon Coastal Center, and the Milford Marine Laboratory, NOAA. I am indebted to my colleagues in the Biology Department at SHU, particularly Mark Jareb, Kirk Bartholomew, and Mark Beekey for field and technical assistance. This work could not have been completed without the help of my undergraduate research assistants: Luc Bernacki, Gabriel Garcia-Ryan, Racelle Deschaies, Kayleigh Erazmus, William McKenzie, Dan Drew, Stefanie Basciano, and Meredith Baker. Data collection was also enhanced by numerous public school students from the Milford/Bridgeport area.

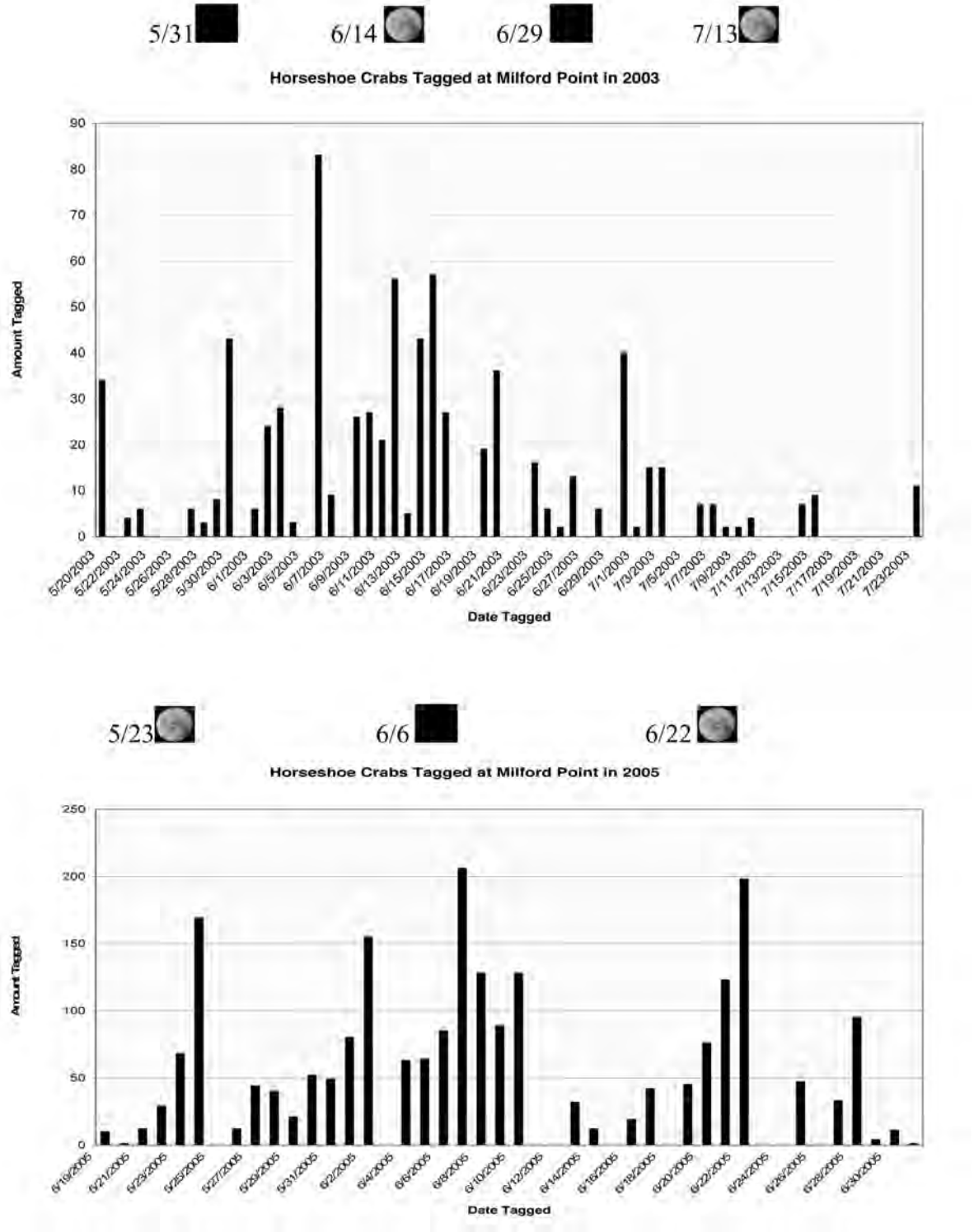

FIGURE 1. The number of individual horseshoe crabs tagged per day from May 20 – July 23, 2003 and May 19 — July 2, 2005. The phase of the moon placed above the graph is in the proximity of the date that it occurred.

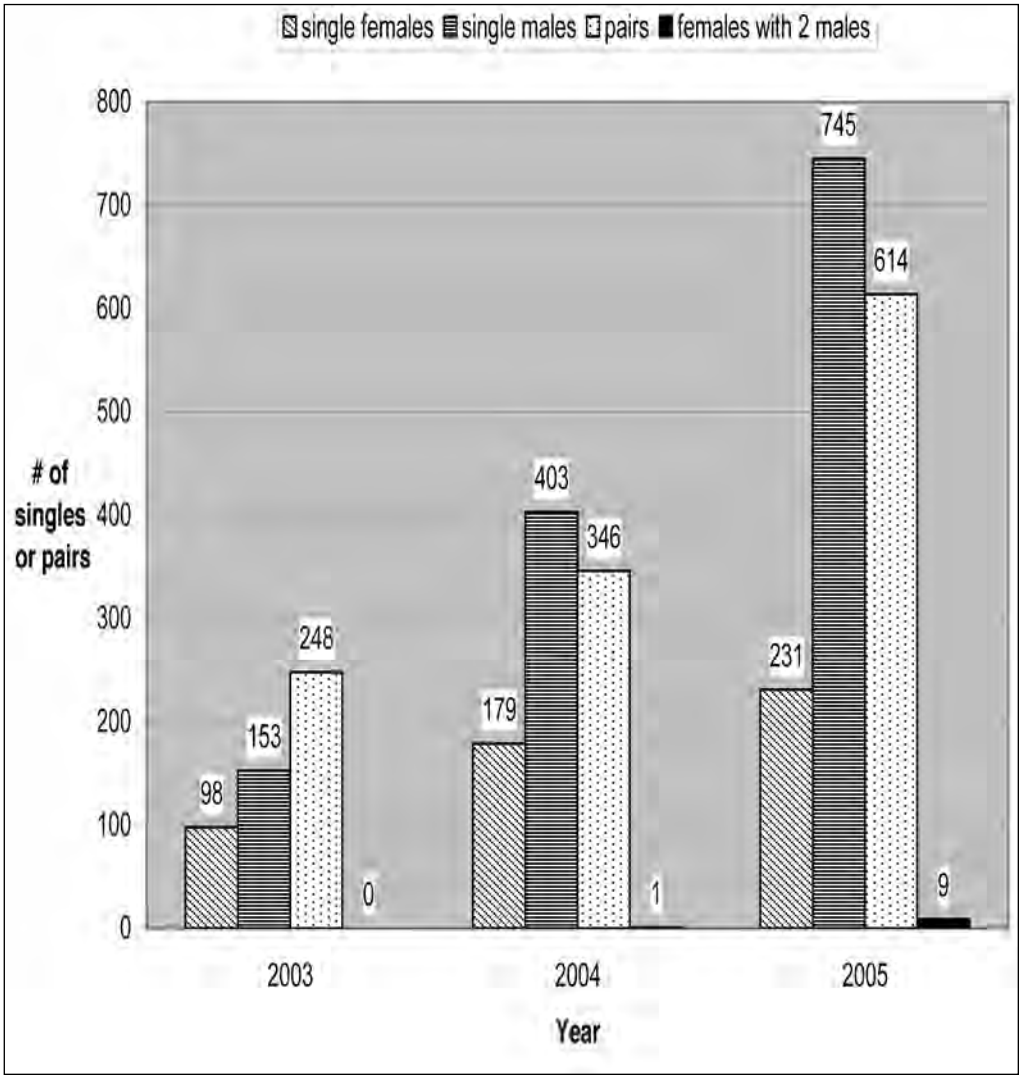

FIGURE 2. The distribution of observed mating behaviors of tagged horseshoe crabs in 2003, 2004, and 2005 at Milford Point, CT. The number of individuals found on the beach as singles, mated pairs, and clusters one female with two males.