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Mark Beekey
Sacred Heart University, beekeym@sacredheart.edu

Jennifer Mattei
Sacred Heart University, matteij@sacredheart.edu

Barbara J. Pierce
Sacred Heart University, pierceb@sacredheart.edu

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Horseshoe crab eggs: A rare resource for predators in Long Island Sound

Mark A. Beekey *, Jennifer H. Mattei, Barbara J. Pierce

Department of Biology, Sacred Heart University, 5151 Park Avenue, Fairfield, CT 06825, United States

ABSTRACT

In Delaware Bay, the spawning of several million horseshoe crabs (*Limulus polyphemus*) coincides with the arrival of migratory shorebirds that feed on their eggs. High horseshoe crab spawning densities and resulting high egg densities drive egg availability and predation rates. At high spawning densities, female horseshoe crabs perturb previously deposited clutches causing eggs to rise to the sediment surface (surface egg densities average 100,000 eggs m^{-2}). At the surface (0–5 cm), the eggs are quickly depleted by shorebirds and other predators. This interaction between egg density and egg predation has not been explicitly explored on beaches with low spawning densities such as on the Connecticut (CT) shore of Long Island Sound (LIS). Spawning indices in LIS (range: 0.002 to 0.02 females m^{-2}) are two to three orders of magnitude less than in Delaware Bay (0.7–1.0 females m^{-2}). Given the low spawning density and correspondingly low subsurface egg density ($x = 1.5$ eggs cm^{-2}), we predicted that the frequency of egg predation would be rare. A series of exclosures was constructed on two known horseshoe crab spawning beaches to test the frequency and rate of predation on horseshoe crab eggs. There was no significant difference between egg masses initially placed in artificial nests and recovered at the conclusion of each experiment. While shorebirds were observed probing sediments within and outside of experimental plots, eggs were never observed at the surface during this study. Foraging by shorebirds for buried eggs may be energetically prohibitive given the lack of eggs on the surface and the low subsurface egg densities on CT beaches in LIS (range = 0.6–2.4 egg cm^{-2}). Limited egg predation by fish was observed but tidal scouring of eggs buried below mean tide primarily drove egg availability for these predators. We conclude that horseshoe crab egg predation is a rare occurrence in Connecticut due to low egg density as a direct result of low spawning densities.

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1. Introduction

Limulus polyphemus (Linnaeus), the American horseshoe crab, is an economically and ecologically important species. Economically, *L. polyphemus* is harvested and bled for the multi-million dollar biomedical industry that uses the blood-clotting compound *Limulus* Amoebocyte Lysate (LAL) to detect pathogenic endotoxins in vaccines and implantable medical devices (Berkson and Shuster, 1999). Additionally, horseshoe crabs are commercially harvested for use as bait in the eel and whelk fisheries (Ferari and Targett, 2003; Manion et al., 2000). Ecologically, horseshoe crabs are important members of food webs along the coast of the eastern United States and parts of the Gulf of Mexico and are biologically linked to many different species. They provide habitat for more than 20 epibiont species and are the sole host of ectoparasitic flatworm, *Bdelloura candida* (Dietl et al., 2000; Grant, 2001; Leibovitz and Lewbart, 2003; Turner et al., 1988). Horseshoe crabs are bioturbators (Commito et al., 1995; Kraeuter and Fegley, 1994; Smith, 2007) and are predators of benthic invertebrate species (Botton, 1984; Botton and Haskin, 1984; Botton and Ropes, 1989). Of particular importance is their tight ecological

link to shorebirds. *Limulus* eggs are a major food source for migrating shorebirds in the mid-Atlantic region (Botton et al., 1994; Castro and Myers, 1993; Clark et al., 1993).

Horseshoe crab eggs are a critical component of the diet of shorebirds on their northward migration (reviewed by Mizrahi and Peters, 2009) and as a result, horseshoe crabs in Delaware Bay are managed to provide for these dependent species (ASMFC, 2009). Horseshoe crab eggs are not immediately available to shorebirds and other predators. Amplexed females (posterior of female opisthosoma clasped by male) burrow into the sediment where they deposit eggs in nests 15–20 cm below the sediment surface (Shuster and Sekiguchi, 2003). Amplexed males along with or without any satellite males (unpaired males that cluster around the amplexed male and female) remain above the sediment surface and externally fertilize the eggs as they are released from the female. The eggs remain buried in the sediment where they develop and hatch as trilobite larvae. At this depth, eggs are unreachable by the majority of shorebirds due to their limited beak length (Tsipoura and Burger, 1999). As successive female horseshoe crabs excavate and push through the sediment to deposit their eggs, they can potentially disturb previously deposited clusters of eggs. This disturbance entrains eggs in the sediment where they are vertically transported to the surface (Jackson et al., 2002, 2005; Smith, 2007). As a result of this bioturbation, surface egg

* Corresponding author. Tel.: +1 203 371 7783; fax: +1 203 365 4785.
   E-mail address: beekeym@sacredheart.edu (M.A. Beekey).

densities have been reported to range from 430 to 115,000 eggs m^{-2} in Delaware Bay during mid May when migratory birds stopover (USFWS, 2003).

The excavation and transport of horseshoe crab eggs to the sediment surface is density-dependent (Jackson et al., 2002). Simulation models supported by observational evidence demonstrate that up to 46% of nests are disturbed by subsequent spawning (Smith, 2007) under typical spawning densities, described by the Index of Spawning Activity (ISA) or number of females m^{-2} in Delaware Bay (0.73 to 0.90 females m^{-2}). Even at one third the baseline spawning density in Delaware Bay at least 20% of the nests were predicted to be disturbed. At extremely low spawning indices, the model predicts that few if any nests would be disturbed and consequently few if any eggs would be available to predators at the sediment surface.

Reported spawning densities for New England are extremely low compared to those for Delaware Bay. Spawning indices in New England range from 0.004 to 0.01 females m^{-2} on Cape Cod (James-Pirri et al., 2005) and 0.002–0.02 females m^{-2} on Connecticut beaches (Beekey and Mattei, 2008; Mattei et al., 2010). At these low spawning indices, Smith's simulation model predicts that there would be little to no exhumation of eggs from nests over the course of the spawning season. Therefore, horseshoe crab eggs would be a rare resource for foraging shorebirds or other predators. We tested this prediction by determining the rate and frequency of aquatic and/or terrestrial predation on deposited horseshoe crab eggs at two Connecticut beaches with annually consistent spawning activity but low spawning indices.

2. Methods

2.1. Study areas

Milford Point (MP), Milford, CT (41°10′21.05″N, 73°6′30.27″W) is part of an 8.4-acre barrier beach within the Smith-Hubbell Wildlife Refuge situated next to the 840-acre Charles E. Wheeler Wildlife Management Area at the mouth of the Housatonic River (Fig. 1). MP is managed by the U.S. Fish and Wildlife Service, State of Connecticut Department of Energy and Environmental Protection, and Connecticut Audubon Society. Wheeler Marsh, the sandbars, and barrier beaches around MP are some of the most important migratory shorebird stopover areas on Long Island Sound providing foraging areas and resting areas for tens of thousands of shorebirds each year and was designated an Important Bird Area in 2004 (National Audubon Society, 2010). MP provides nesting habitat for Piping Plovers (*Charadrius melodus*), Least (*Sternula antillarum*) and Common Terns (*Sterna hirundo*), and is a regionally important Clapper Rail (*Rallus longirostris*) and Willet (*Tringa semipalmata*) nesting area (National Audubon Society, 2010). Other notable species that frequent the area include Oystercatchers (*Haematopus palliates*), Black-bellied (*Pluvialis squatarola*) and Semipalmated Plovers (*Charadrius semipalmatus*), and Red Knots (*Calidris canutus*) (National Audubon Society, 2010).

Sandy Point (SP) (41°16′0.59″N, 72°55′31.21″W) is an approximately 66-acre city-owned (West Haven, CT) barrier beach (sand spit) system with a tidal creek that includes an area of tidal marsh
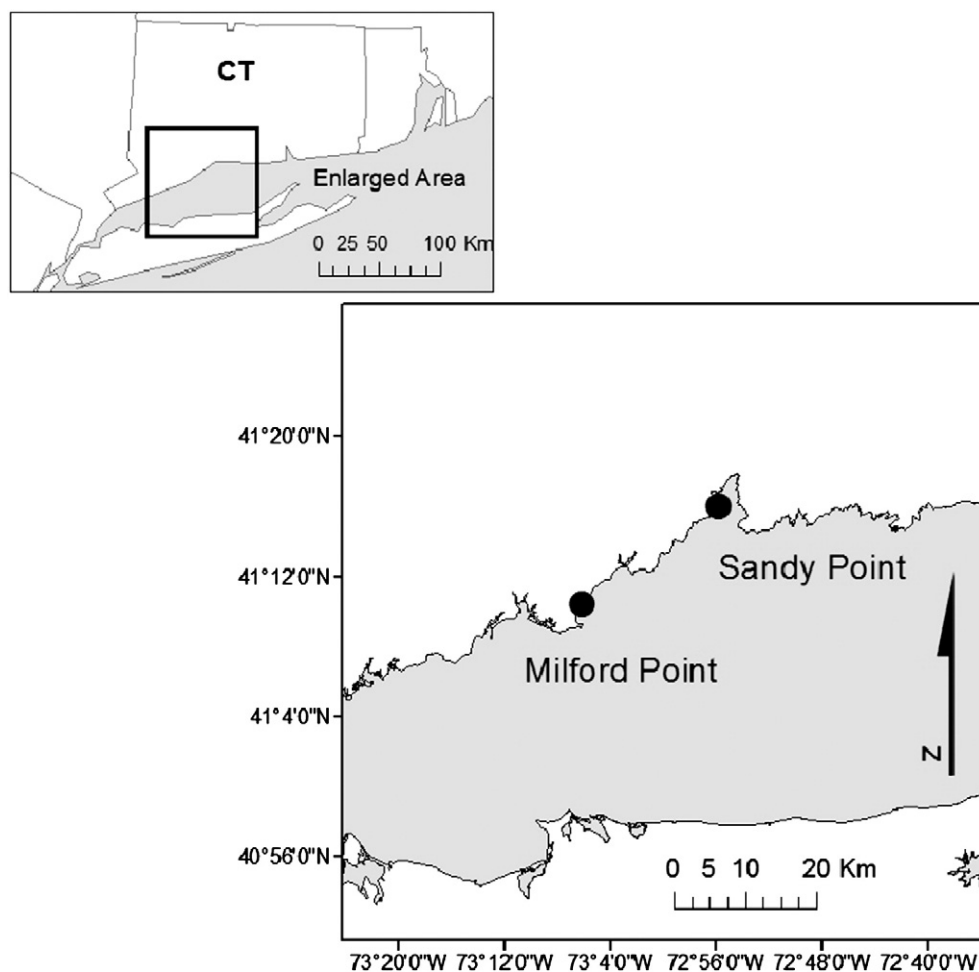

Fig. 1. Study area locations near Milford and New Haven, Connecticut.

and tidal flats (Fig. 1). The sand spit protrudes into New Haven Harbor from the west side. Spring and fall migrations bring multitudes of shorebirds such as terns, skimmers, plovers, sandpipers and gulls to the park (National Audubon Society, 2010). SP was designated an Important Bird Area in 2004 (National Audubon Society, 2010). In the summer, SP provides nesting habitats for Piping Plovers, Least and Common Terns, American Oystercatchers and Killdeer (*Charadrius vociferous*). Black Skimmers (*Rynchops niger*), herons, egrets, and gulls can also be seen throughout the summer months nesting within the marshes and tidal flats of the area (National Audubon Society, 2010). Strong tidal currents can occur across the unprotected sandy spits at both MP and SP and cause the sands to shift particularly during the spring tides of May and June (pers. obs. Beekey and Mattei). The Connecticut Department of Energy and Environmental Protection has declared both MP and SP off limits for the hand harvest of horseshoe crabs since 2007.

2.2. Egg predation experiment

To characterize the types of predators that may consume *Limulus* eggs and larvae at MP and SP, we conducted a series of exclosure experiments designed to separate effects of aquatic predators (mainly fish) from terrestrial predators (mainly shorebirds). We modeled our experimental design based on Quammen's study (1981, 1984), that was designed to examine the effects of fish predation separately from shorebird predation of marine invertebrates inhabiting intertidal shorelines. The exclosure experiments were set up in calmer backwater areas where horseshoe crabs were observed spawning and where shorebirds were observed foraging. Fresh nest depressions at each site prior to the start of the experiment indicated that horseshoe crabs were actively spawning at these sites. We also chose these sites to minimize wave action disruption of the exclosure treatments. At each site, four separate treatments were used to separate predation by predator type including: (1) a full exclosure excluding all terrestrial and aquatic predators, (2) a floating exclosure which excluded terrestrial predators during low tide but rose, with the aid of floats, with the incoming tide to allow fish and other aquatic predators to forage, (3) a half exclosure which allowed all predators to feed (used to test if there were cage effects on predator behavior), and (4) an open control marked only by four rebar stakes (Fig. 2). Full, floating, and half exclosures were constructed of 12.7 mm PVC tubing (0.5 m × 0.5 m × 0.3 m high). Full and floating exclosures were completely covered with high-density polyethylene mesh (6 mm opening) commonly used to construct oyster cultch bags. Half exclosures were covered in mesh so half the frame was open to predators. Exclosures were anchored in place with four pieces of rebar. At each site, the treatments were established in a randomized block design (Fig. 2) to control for tidal exposure and length of time the exclosures and control treatments were available for aquatic and terrestrial predators. The blocks extended outward from upper mean tide to the upper low tide line in an evenly spaced fashion (see Fig. 2) so that Block I was out of the water the longest with subsequent Blocks (II, III, IV, and V) having longer submergence times and Block VI submerged for the longest time. Block I was placed 5 m below the high tide line at both MP and SP. Since the distance between mean high tide and mean low tide was different at each site (31.3 m at MP versus 55.8 m at SP), the blocks were placed at different intervals (5 m at MP and 10 m at SP) to keep all treatments at both sites within the same intertidal area. Each treatment was replicated six times at each study site (Fig. 2). Our exclosures were set up identically at both sites during peak spawning activity in Connecticut. We conducted a short-term experiment from June 1 to 4, 2008 and a longer term predation experiment two weeks past peak spawning period from June 19 to 25, 2008. In this way we were able to measure the frequency or how often birds or other predators eat the eggs (i.e. throughout June or only once) as well as the rate of feeding (3 days vs. 6 days) by weighing the eggs before and after the treatment period.

To mimic horseshoe crab nests we buried an 8 cm × 8 cm plastic weigh boat containing 20 g of *Limulus* eggs 5–8 cm below the sediment surface in the center of each treatment. Eggs were collected from nests in areas adjacent to where the experiments were established, cleaned of sediment, and brought back to the lab for enumeration. Each experimental clutch had an initial egg mass of 20 g. The number of eggs in a 20 g sample was estimated by calculating the weight of eleven 100 egg aliquots ($\bar{x} = 0.59$ g ± 0.01 SE) and converting each individual weight to 20 g to give an average of 3382 ± 30.7 SE eggs per nest. The initial experimental clutch size is close to the average clutch size (3741 ± 3169.6 eggs/clutch, N = 24) measured in the field at Milford and Sandy Points (range; 1026–12,289 eggs/clutch) (unpublished data). Our experimental clutch size was near the low end of reported clutch sizes for Delaware Bay (3650 eggs/clutch, Shuster and Botton, 1985; 5836 eggs/clutch, Weber and Carter, 2009) but greater than the reported clutch sizes for Cape Cod (640–1280 eggs/clutch, (Leschen et al., 2006). Although clutches of eggs are typically deposited 15–20 cm below the surface, we buried the eggs 5 cm below the surface to artificially increase the likelihood of their discovery via probing or excavation by potential predators. Additionally, a concave hemispheric depression was made in the sand to mimic the look of a horseshoe crab nest and serve as a potential visual cue to predators that a resource reward was buried below the surface.

For the short-term experiment, predators were allowed to feed for 72 h after which the buried trays were extracted without disturbing any sediment on top of the trays and shoveled into labeled Zip-lock™ bags. The eggs were separated from the sediment and weighed. For the long-term predation experiment, we allowed predators to forage for 144 h.

Comparison of treatments allowed us to address horseshoe crab egg predation by predator type (aquatic vs. terrestrial predation) (Quammen, 1981, 1984). Aquatic predators had access to eggs in the floating exclosures, half exclosures, and open control. Terrestrial predators had access to the half exclosure and open control, never the full or floating exclosures. Thus we predicted that the open control and half exclosure would contain the least amount of eggs. We predicted little difference between initial and final weight in the floating exclosure, since aquatic predators generally haven't been reported to excavate horseshoe crab nests, and in the full exclosure that excluded all predators.

2.3. Background egg density

We compared the density of eggs placed in the artificial nests to the background or natural egg densities in the sediment to ensure that the artificial egg density represented a true reward. We randomly core sampled the sediments to a depth of 10 cm between each of the four treatments within each of the six Blocks (Fig. 2). We placed a 3 m × 3 m quadrat subdivided into square meter quadrats between each treatment within each block and randomly sampled three one meter square subquadrats using a 10.2 cm diameter by 20 cm high PVC core for a total of 54 core samples. Each square meter quadrat was examined for any eggs on the surface. The contents of each core sample were placed in a Ziploc™ bag, returned to the lab, and frozen. Each sample was washed through a 1.0 mm sieve (James-Pirri et al., 2005) and the number of eggs (eggs, larvae, and trilobites) was enumerated.

2.4. Predator surveys

Prior to the start of the experiments, shorebird abundance was determined by counting the number and species of birds present at MP and SP during the first 3 h of incoming or receding tides three times a week from May 15th through May 30th. We also counted the number and species of birds present within the confines of the
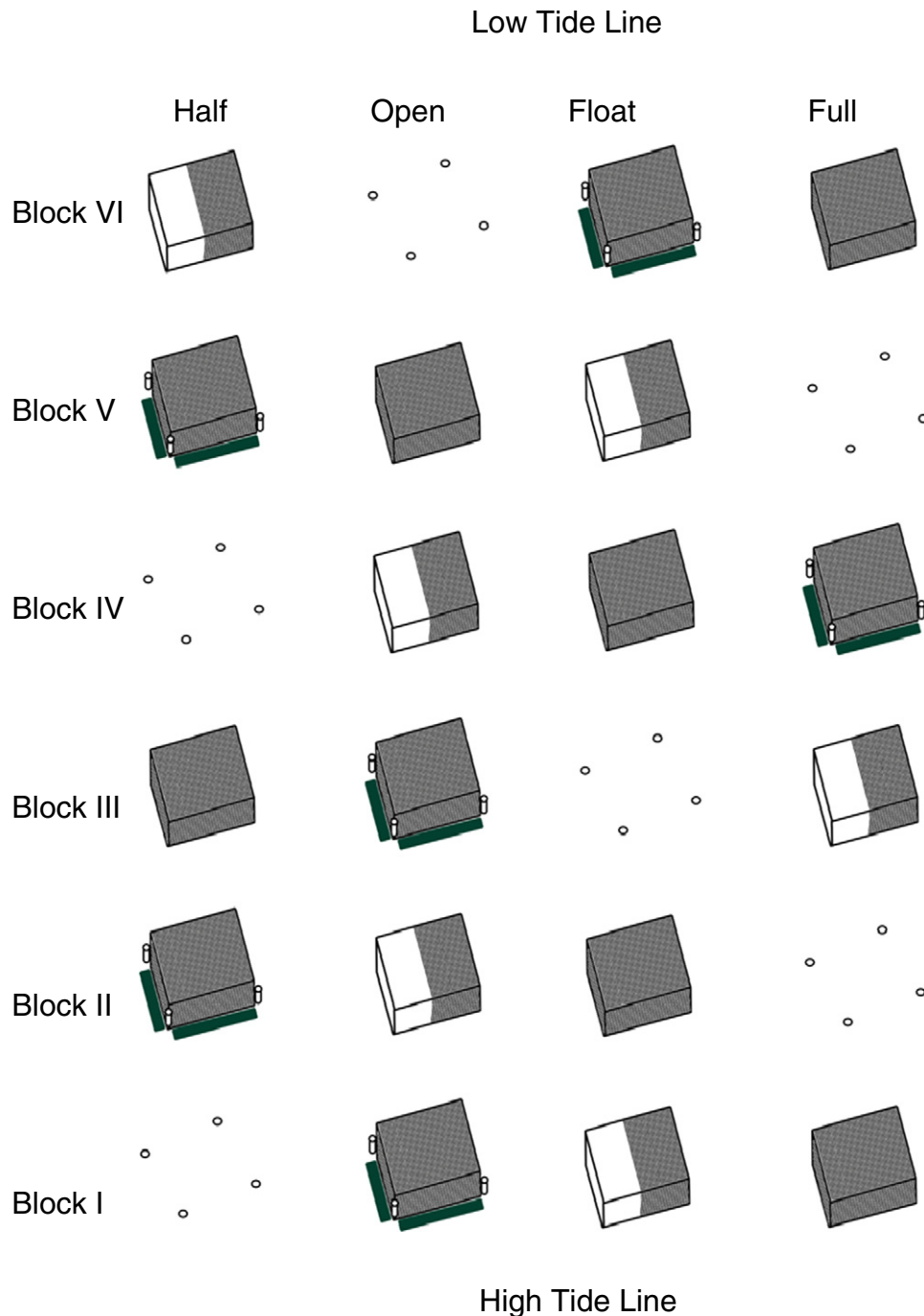
Fig. 2. Randomized block design depicting location of exclosure treatments for the predation experiment. A block design (Blocks I–VI) was used to control for tidal exposure of cages and amount of time available for foraging by aquatic and terrestrial predators. Blocks were established starting 5 m from the mean high tide line and extending outward to the mean low tide line. Blocks were spaced 5 m apart at MP and 10 m apart at SP. Exclosure treatments within each block were 5 m apart at both sites.

experimental plots on either the incoming or receding tide each day throughout the length of each experiment (i.e., June 1–4 and 19–25). Observers were concealed in the grasses above the experimental sites and were outfitted with binoculars so as not to disturb foraging birds. Exclosure areas were observed until all cages were covered by water (incoming tides) or until all cages were exposed (receding tides). We validated our bird species list with those reported on eBird (2009) for the same beaches and time period.

We sampled for potential aquatic predators using a 10 m long seine with 5 mm mesh during Experiment II. The sampling was conducted once at each site during the daytime peak high tide. We seined the 5 m width space between the treatments starting from Block VI and ending

at Block I (Fig. 2). Aquatic predators were frozen and returned to the laboratory for identification (genus/species) and stomach content analysis. Stomach contents were analyzed under a dissecting scope to enumerate *Limulus* eggs, larvae, and trilobites if present.

3. Results

3.1. Egg predation experiment

We found the frequency and rate of predation within and between sites on the artificial nests to be zero. Final egg weights in the short-term predation experiment at MP and SP exhibited some variation but

were not significantly different. Egg weights generally increased over time during the long-term predation experiment at both MP and SP (Fig. 3). There was no significant effect of tidal exposure (i.e., Block), (ANOVA, $F_{MP (5, 42)} = 0.539$, $p = 0.744$; $F_{SP (5, 47)} = 0.345$, $p = 0.880$), or treatment effects (ANOVA, $F_{MP (3, 42)} = 0.721$, $p = 0.552$; $F_{SP (3, 47)} = 0.178$, $p = 0.910$) or tidal exposure by treatment interaction (ANOVA, $F_{MP (15, 42)} = 0.354$, $p = 0.976$; $F_{SP (15, 47)} = 0.284$, $p = 0.993$) on change in egg weight at either MP or SP.

At the conclusion of the short-term predation experiment at MP, after the fall of a spring high tide, six egg trays were washed away from the sediment including two each from the full and half exclosure treatments, one from the floating exclosure treatment, and one from the open control from blocks V and VI (Fig. 2). One entire floating exclosure was lost from block IV. Two additional trays from the floating treatments were visible at the sediment surface at the conclusion of the experiment in Block IV. These visible trays lost 19.04 and 8.26 g of eggs, respectively contributing to the lower final average weight (Fig. 3A). One empty egg tray at MP was recovered from the high tide wrack line. All of the trays were recovered at SP from Experiment I and there was little variation in the initial versus final weight (Fig. 3B).

Overall change in egg weight in the long-term experiment, lasting 144 h, was positive at both MP and SP (Fig. 3C and D). All trays were recovered at MP and only one open control tray was not recovered at SP. While the full and floating exclosures gained more weight over time than the open control or half exclosure treatments at both sites, there was no significant difference between treatments.

3.2. Background egg density

Background egg density was significantly higher at MP compared to SP (ANOVA, $F_{(1,107)} = 6.96$, $p = 0.010$). The mean number of eggs per core at MP was 199.7 ± 44.4 SE (2.4 eggs cm$^{-2} \pm 0.5$ SE) compared to 45.2 ± 38.1 SE (0.6 eggs cm$^{-2} \pm 0.5$ SE) at SP. Background egg density (eggs, embryos, and trilobites combined) of individual sediment cores ranged from 0–15 eggs cm^{-2} (0–1227 eggs per core) at MP and 0–25 eggs cm^{-2} (0–2011 eggs per core) at SP. The majority of samples (51 of 54) at SP contained less than 1 egg cm^{-2} (approximately 83 eggs) whereas only half of the samples from MP (27 out of 54) contained less than 1 egg cm^{-2}. The average number of eggs (3467.2 ± 0.4 SE) placed in the artificial nests in each of the exclosure treatments (equivalent to 42.4 eggs cm$^{-2} \pm 0.002$ SE) was significantly greater than the background density at both MP (ANOVA, $F_{(1,106)} = 5218.5$, $p < 0.001$) and SP (ANOVA, $F_{(1,105)} = 8348.1$, $p < 0.001$).

3.3. Predator surveys

A variety of shorebird species, that are known to consume horseshoe crab eggs, were observed at MP and SP prior to the start of the exclosure experiments (Table 1). During both experiments (I & II), and at both sites, a number of predatory shorebird species were observed in the areas containing the exclosure treatments (Table 1). Shorebirds such as sandpipers and plovers were observed pecking nest depressions and sediments in and around the exclosure cages. Only one oystercatcher was observed actively probing a nest depression outside of the experimental plot. Bird tracks were observed in and around the experimental plots. No *Limulus* eggs were ever observed on the surface of the sand inside or outside of our experimental area.

Atlantic silverside (*Menidia menidia*), striped killifish (*Fundulus majalis*), mummichog (*Fundulus heteroclitus*) and broad striped anchovy (*Anchoa hepsetus*) were collected in seine hauls between the exclosure treatments. In general, horseshoe crab eggs were found in
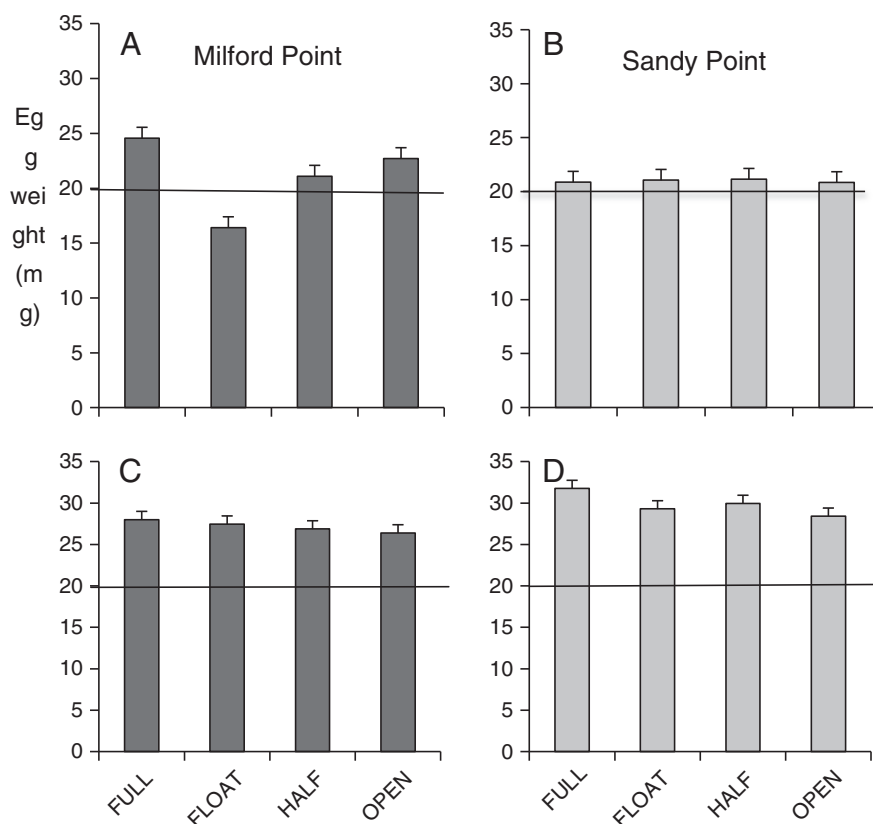
Fig. 3. The final average weight (g) for the eggs recovered from each treatment is plotted for Milford Point (MP) and Sandy Point (SP) for both Experiments I and II by cage type. Experiment I (6/1–6/4/2008) is plotted for MP (A) and SP (B). Experiment II (6/19–6/24/2008) is plotted for MP (C) and SP (D). N = 6 for all treatment combinations except for MP (A) where N = 4, 4, 5, 5, for the full, floating, half exclosures, and open control, respectively and for SP (B) where N = 5 for the open control. The solid line represents initial egg weight in each nest (20 g). No significant difference was found between Block or Treatment for Experiments I or II (ANOVA, p > 0.05).

Table 1

Bird species observed by researchers at Milford and Sandy Point from May through June, 2008. Total number of individuals observed, number of individuals observed during Experiments I and II, and number of individuals observed and reported to eBird during May and June of 2008 at Milford and Sandy Point (E-bird, 2009). Sample size (n) is shown for number of censuses.

	Milford Point				Sandy Point			
	Total # observed	# Observed in Exp. I	# Observed in Exp. II	E-bird total for May and June	Total # observed	# Observed in Exp. I	# Observed in Exp. II	E-bird total for May and June
Species	(n = 26)	(n = 4)	(n = 6)		(n = 26)	(n = 4)	(n = 6)	
Actitis macularius — Spotted Sandpiper	2			1 (1)	35			19 (6)
Arenaria interpres — Ruddy Turnstone	34			18 (5)	61			28 (4)
Calidris alba — Sanderling	10			21 (4)				2 (1)
Calidris alpina — Dunlin	25	5		187 (9)	35			7 (4)
Calidris canutus — Red Knot				2 (2)	3			3 (1)
Calidris fuscicollis — White-rumped Sandpiper	3			3 (3)				5 (3)
Calidris minutilla — Least Sandpiper	50			31 (8)	72	2		33 (2)
Calidris pusilla — Semipalmated Sandpiper	119	26		368 (6)	155	19	5	145 (4)
Charadrius melodus — Piping Plover	77	3	8	17 (6)	135	5	8	34 (6)
Charadrius semipalmatus — Semipalmated Plover	40			60 (9)	2			20 (4)
Charadrius spp. — Plover spp.	72							
Charadrius vociferus — Killdeer				1 (1)				1 (1)
Haematopus palliatus — American Oystercatcher	16	2	5	56 (15)	38	13	4	23 (7)
Larus delawarensis — Ring-billed Gull	2		2	174 (9)	43	2	2	35 (4)
Larus marinus — Great Black-backed Gull	6		3	78 (9)	22	2	4	18 (5)
Larus smithsonianus — Herring Gull	13		4	535 (11)	127	3	4	58 (5)
Leucophaeus atricilla — Laughing Gull				465 (9)				
Limnodromus griseus — Short-billed Dowitcher				5 (1)				7 (2)
Pluvialis squatarola — Black-bellied Plover	4			83 (8)	9	2		9 (3)
Tringa melanoleuca — Greater Yellowlegs				11 (3)				1 (1)
Tringa semipalmata — Willet	3		2	28 (12)	1			13 (5)

every species (1–83 eggs individual^{-1}) with the exception of broad striped anchovy ($N = 1$) (Fig. 4).

4. Discussion

Given the results of this study, it is clear that predation of horseshoe crab eggs buried in nests is negligible in Long Island Sound. Egg predation, when it occurs, is likely opportunistic and infrequent, such as when eggs are deposited in nests that are disturbed by

Fig. 4. The average number of eggs present in the stomachs of Atlantic silverside (*Menidia menidia*), striped killifish (*Fundulus majalis*), and mummichog (*Fundulus heroclitus*) collected by seining from within the exclosure area at MP and SP are plotted. N = 116 and 67 for *M. menidia*, 16 and 36 for *F. majalis*, 2 and 0 for *F. heroclitus* at MP and SP, respectively.

turbulence from severe storms or subject to strong tidal currents as we observed in Experiment I at Milford Point (Fig. 3A, Floating treatment). Based on the lack of disturbance observed among the cages within the experimental areas as well as a general lack of probe holes in nests surrounding the experimental cages, predators at Milford Point and Sandy Point rarely spend time excavating nests in search of deposited eggs.

The increase in egg mass over the course of the experiments is the result of the natural progression of development of horseshoe crab embryos. Over the course of development in the sediment the perivitelline fluid inside the developing eggs becomes hyperosmotic to the ambient seawater causing them to swell when inundated (Ehlinger et al., 2003). The eggs we used in this experiment were not freshly laid eggs and were already showing signs of development. Thus the swelling of the eggs was not unexpected.

Nest disturbance and egg availability to predators are driven by horseshoe crab density during the spawning season. Spawning density, described by the Index of Spawning Activity (ISA) or number of females per square meter, for Milford Point and Sandy Point is extremely low compared to values reported for Delaware Bay. Yearly spawning indices in Delaware Bay from 1999–2005 ranged from 0.7–1.0 females m^{-2} (Smith and Michaels, 2006), whereas the yearly ISA's at Milford Point and Sandy Point in 2008 were one to two orders of magnitude less at 0.002 and 0.058 females m^{-2}, respectively (Mattei et al., 2010). Correspondingly, both Milford Point and Sandy Point have relatively low egg densities compared to reported egg densities for beaches in Delaware Bay. Botton et al. (1994) observed egg densities ranging between 1 and 50 eggs cm^{-2} from 7 Delaware Bay beaches in 1990. Smith et al. (2002) observed egg densities ranging from 0 to 133 eggs cm^{-2} in 1999 from 16 beaches and Pooler et al. (2003) reported an average density of 23.6 eggs cm^{-2} from 32 beaches in Delaware Bay. Egg density averaged 2.4 eggs cm^{-2} at Milford Point and 0.6 eggs cm^{-2} at Sandy Point. These egg densities are more similar to egg densities reported from Cape Cod by James-Pirri et al. (2005) who found an average egg density of 1 egg cm^{-2}. Levels of disturbance, background egg density, and egg availability at the sediment surface are not high enough at either Milford Point or
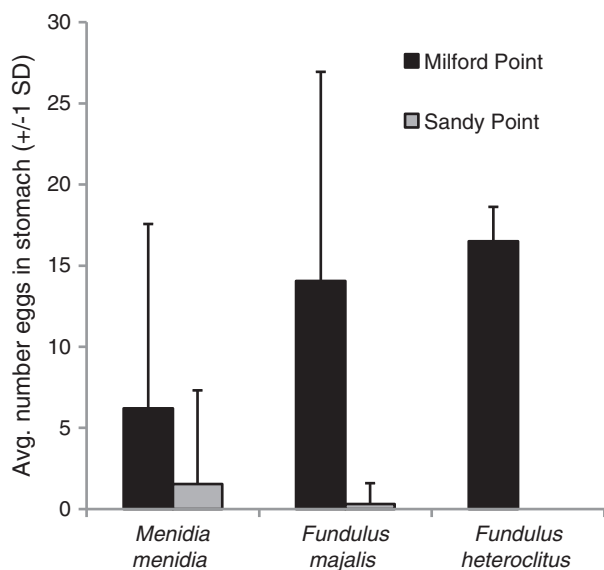
Sandy Point to attract or serve as a reliable and sufficient food resource to migratory and resident shorebirds.

Beaches exposed as the tide recedes at Milford Point and Sandy Point are typically pockmarked with depressions left by nesting females during the horseshoe crab spawning season. We did observe and photograph footprints from foraging shorebirds along with obvious probe-holes made by the probing bills of shorebirds. Many of the species we observed (e.g. sandpipers) rely primarily on eggs near or at the surface of the sand (Mizrahi and Peters, 2009; Tsipoura and Burger, 1999). The only species that would be candidates for efficient probing of buried eggs would be American oystercatchers and Dunlins. During one bird census, we observed two oystercatchers pecking and disturbing spawning horseshoe crabs as they were in the process of depositing eggs in a nest on a receding tide but did not probe the nest depression after the amplexed pair of horseshoe crabs returned to subtidal waters.

Throughout the course of both experiments, we observed a number of shorebird species pecking sediments and nest depressions inside the confines of the exclosure experiment (Table 1). Based on our observations, we assumed that the exclosure cages did not disrupt or change shorebird feeding behavior and thus were not responsible for a lack of egg predation in the open and half open exclosures. Additionally, the timing of these experiments was based on peak horseshoe crab density and egg availability in CT, which occurs in early June (Mattei et al., 2007). The bird census data and additional data from eBird (2009) demonstrate that many shorebird species were in the vicinity during the experiments (Table 1). The timing of the experiments also represents the peak time when shorebirds would have the highest probability of finding eggs. However, we found no evidence that shorebirds were successful at finding eggs or removing them from the artificial nests in this study.

The presence of *L. polyphemus* eggs in Atlantic silversides, mummichog, and striped killifish, all opportunistic omnivores, suggests that horseshoe crab nests are disturbed at both Milford Point and Sandy Point. It is unlikely that these fish were excavating nests to forage on eggs. Most likely, the eggs were scoured out of the sediments by tidal currents. Interestingly, more eggs were found in fish from Milford Point than Sandy Point even though spawning indices and egg densities are greater at Sandy Point. One explanation is that the experiment at Milford Point was located at the tip of a point of land extending into a tidal river whereas the experiment at Sandy Point was located in a protected tidal lagoon. Thus currents were generally higher at Milford Point than Sandy Point and likely resulted in greater tidal scouring of nests at Milford Point than Sandy Point. In fact, our experimental results confirm this in that six out of 24 egg trays we buried at Milford Point were not recovered where as only one tray was not recovered at Sandy Point. The loss of an entire floating exclosure at Milford Point indicates the potential for tidal currents to scour nests and expose eggs. Given the low spawning density in LIS, it is highly probable that any eggs found in fish stomachs is primarily due to scouring rather than conspecific nest disturbance.

High spawning densities in Delaware Bay and successive nest disturbance and exhumation of eggs clearly explain why Delaware Bay is such an important migratory stopover for shorebirds reliant on horseshoe crab eggs as their primary food source (Smith, 2007). Previous studies have questioned whether current egg densities in New England could sustain migratory shorebirds (Botton, 2009; Leschen et al., 2006). While infrequent reports of shorebird predation of horseshoe crab eggs have been noted as far north as Plymouth Bay, Massachusetts (Mallory and Schneider, 1979), our results indicate that horseshoe crab eggs are not a significant food resource for predators in Long Island Sound. We attribute the lack of egg predation to low spawning densities and consequently low conspecific nest disturbance that would result in the availability of *Limulus* eggs at the sediment surface where predators could easily forage on them. Predators are more likely to forage on epifaunal and infaunal invertebrates such as polychaetes and small bivalves.

Our findings with regard to the limited horseshoe crab egg predation at Milford Point and Sandy Point have implications for the overall management of horseshoe crabs in Long Island Sound. In 2007, the Connecticut Department of Energy and Environmental Protection established no harvest zones at three Important Bird Areas (National Audubon Society, 2010): Milford Point, Sandy Point, and Menunketesuck Island in Westbrook. The objective of setting aside the no harvest zones was to increase recruitment of horseshoe crabs by increasing the current number of horseshoe crabs allowed to spawn on beaches and ultimately increase egg densities to support foraging by migratory shorebirds. The effects of this management strategy on the Sound's horseshoe crab population will not be measurable until at least 2016 given their 9–10 year maturation period (Shuster and Sekiguchi, 2003). As a result, it is unlikely that egg densities will increase sufficiently to provide a reliable resource for migratory shorebirds well into the future. The practice of hand harvesting spawning horseshoe crabs from other beaches around Long Island Sound will only continue to limit the potential recovery of the horseshoe crab population. Thus, the ecological services that other species derive from higher densities of spawning horseshoe crabs and the corresponding higher egg densities remain limited. In order to ecologically reconnect *Limulus* to other species in Connecticut, a change in harvest regulations is warranted. We suggest that the next step should be limiting the harvest of females in New England.

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