Intensive use of an intertidal mudflat by foraging adult American horseshoe crabs *Limulus polyphemus* in the Great Bay estuary, New Hampshire

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**Abstract** Although concerns about harvesting levels of the American Horseshoe Crab, *Limulus polyphemus* have prompted increased research into its ecology, current understanding of the species’ foraging ecology is mostly limited to mid-Atlantic populations. This study elucidates the spatial and temporal pattern of *Limulus* foraging on an intertidal mudflat of a northern New England estuary. A novel survey method was used to monitor *Limulus* foraging activity without disturbing the sediment. A fixed 50 m × 2 m transect was monitored with monthly surveys of the number of *Limulus* feeding pits from June to October 2009, May and June 2010. Snorkelling surveys were also carried out to observe individual behavior and examine the spatial scale of activity of individual animals. Results showed frequent and intensive use of the mudflat by foraging *Limulus*. *Limulus* were actively foraging within the survey area during all months surveyed. Foraging patterns exhibited a seasonal pattern with activity levels peaking in August 2009 and increased significantly towards the end of the study in June 2010. It was also shown that *Limulus* intertidal foraging persisted and peaked after the spring breeding season. Observations of foraging *Limulus* revealed that individual predators dig multiple pits within a single high tide, with little disturbance to the sediment in between. In addition to altering the perception of *Limulus* as a subtidal predator outside of the breeding season, findings from this study suggests a segregation of spawning and feeding habitats, thus underscoring the need to consider a wider range of critical habitats in the management of *Limulus* populations [Current Zoology 56 (5): 611–617, 2010].

**Key words** Foraging, Epibenthic predator, Intertidal, Estuary, Disturbance

Concerns over sustainability of current levels of harvest of American horseshoe crab *Limulus polyphemus* (*Limulus* hereafter) by the eel and whelk fisheries for bait and biomedical industries have resulted in increased efforts to understand the ecology of exploited populations (Hooker et al., 2010). The majority of on-going monitoring and management strategies focus on the reproductive ecology and health of spawning habitats of the species (e.g. Smith et al., 2009, Hooker et al., 2010). However, there remains a lack of understanding of *Limulus* foraging ecology and habitats needed to support the trophic requirements of a *Limulus* population (reviewed by Botton et al., 2003, but see Carmichael et al., 2004, Moore and Perrin 2007 for recent studies), which is necessary for the development of a comprehensive management strategy.

*Limulus* is an epibenthic predator that feeds on buried infaunal prey in soft-bottom habitats with a preference for thin-shelled bivalves (Botton, 2009). *Limulus* feed by disrupting the sediment with their prosoma and digging with their legs (reviewed in detail by Botton et al., 2003). In the process, foraging *Limulus* create pits frequently observed on tidal flats along the east coast of the United States (e.g. Smith and Chin, 1951; Baptist et al., 1957; Woodin, 1978; Shuster 1982; Sickley, 1989; Botton et al., 2003; see Botton, 2009 for more references). However, the majority of the current understanding of foraging ecology of *Limulus* is based on work on mid-Atlantic and southern New England populations (Botton, 2009). Due to the relative isolation of populations across its range, it is important to investigate *Limulus* ecology across its distributional range. Intertidal foraging by *Limulus* along the mid-Atlantic coast is usually associated with the narrow seasonal window of the species’ spawning period spanning late spring till summer, after which they are thought to return to deeper waters (reviewed by Botton et al., 2003, Botton, 2009). However, the appearance of *Limulus*...
feeding pits after the spring breeding season has been reported elsewhere (Smith and Chin, 1951; Baptist, 1957; Woodin, 1978; Webster, 1991). In addition, recent studies on the movements of Limulus in enclosed bays and estuaries revealed that Limulus remain active in intertidal areas beyond the limited spawning season, with activity ceasing in the autumn (Moore and Perrin, 2007; Watson et al., 2009; Watson and Chabot, 2010). This evidence suggests that certain populations of Limulus utilize intertidal habitats beyond the mating season, but there remains a paucity of studies on Limulus behavior in intertidal habitats during the remainder of the year (Moore and Perrin, 2007).

Watson and colleagues hypothesised that Limulus make repeated excursions to tidal flats after the spawning season to forage (Watson et al., 2009; Watson and Chabot, 2010). Studies of decapod predators have shown that tidal flats in estuaries are important foraging grounds, which are accessed at high tide (reviewed by Holsman et al., 2006). For these predators, the energetic cost of tidal migration is potentially outweighed by the abundance of infaunal prey in intertidal areas relative to subtidal habitats (reviewed by Holsman et al., 2006). Limulus are commonly found in highly productive estuaries with extensive soft-bottom intertidal zones (e.g. Anderson and Shuster, 2003; Carmichael et al., 2004; Moore and Perrin, 2007; Watson et al., 2009). In the spring, Limulus migrate to the upper intertidal zones to mate and spawn, and the animals are expected to exploit the food resources in adjacent intertidal habitats, as observed by previous studies (Anderson and Shuster, 2003; Botton et al., 2003; Botton, 2009). After the spawning season, abundant intertidal prey may still be energetically profitable for estuarine populations of Limulus to continue making tidal migrations, thus explaining their continued presence in intertidal habitats (Smith and Chin, 1951; Baptist, 1957 et al.; Woodin, 1978; Webster, 1991; Watson et al., 2009; Watson and Chabot, 2010).

While presence of Limulus feeding pits has been repeatedly reported by the aforementioned authors, there have been relatively few attempts to quantify the patterns of foraging behavior. Methodological difficulties are partly responsible for this information gap, as visibility is usually low while the predators are feeding at high tide. Prior work quantified intertidal foraging by Limulus by counting the number of animals found on the intertidal at low tide (Smith and Chin, 1951; Botton, 1984). However, as Limulus forage mostly at high tide, and retreat to the subtidal zone with the outgoing tide, the number of Limulus found exposed on tidal flats may be an underestimate of the level of foraging activity occurring at a particular tidal flat. Examination of predator tracks is a complementary method to assessing foraging activity (Hines et al., 1997, Schaubet et al., 2009), but disturbance to the benthos caused by researchers’ footprints on fine-grain habitats prohibit repeated monitoring of mudflats for Limulus feeding pits. To the best of my knowledge, only Woodin (1978) has quantified Limulus pit digging pattern by examining the percentage area covered by pits on a sandflat in Virginia. However, Woodin did not report on the density of pits which would measure the number of foraging attempts an area of tidal flat can support.

Using a novel non-invasive technique to observe the presence of Limulus feeding pits, this study examines temporal and spatial pattern of Limulus intertidal foraging of a northern estuarine Limulus population. In particular, I ask the following questions: (1) how intensively and frequently is a mudflat used as a foraging ground; (2) does Limulus forage intertidally beyond the spawning season; (3) what is the foraging behavior of individual Limulus?

1 Materials and Methods

1.1 Study site

This study was conducted at Adams Point in the Great Bay estuary, New Hampshire, U.S.A., which has a large population of Limulus (Watson et al., 2009) and extensive unvegetated fine-grained mudflats (>20% of 44 km²; Short et al., 1992; Jones, 2000). The study site is characteristic of unvegetated fine-grained mudflats commonly found in Great Bay, consisting of poorly sorted fine to medium silt (Webster, 1991). Limulus is the only epibenthic predator that creates large feeding pits (approximately 20 cm in diameter, Fig. 1) on the mudflats of Great Bay (Sickley, 1989; Webster, 1991, pers. obs.). Foraging Limulus have been observed to dig elliptical pits surrounded by a raised rim of sediment usually with a rim broken on one side (Committo, 1995; Shuster, 2001). Snorkeling surveys in Great Bay also found Limulus to excavate sediments while pivoting over one point, creating circular pits in the process (pers. obs.). Bivalve shell fragments and large volumes of sediment have been found in the guts of Limulus from Great Bay (Lee unpubl. data), which corroborates with previous studies on mid-Atlantic populations showing that they are generalist predators with a preference for bivalves (reviewed by Botton, 2009). Great Bay is close to the distributional northern limit of Limulus and is
characterised by large seasonal fluctuations in temperature and salinity typical of high latitudinal temperate estuaries (Watson et al., 2009).

1.2 Spatial and temporal pattern in foraging activity

Intensity and frequency of intertidal foraging is defined as the level of activity of foraging *Limulus* over space and time respectively. Foraging intensity is measured by the number of feeding pits per unit area found at any one time, while the frequency is quantified by the rate of appearance of new feeding pits in a certain area over time. While feeding traces are useful indications of the use of a tidal flat by a predator population, its utility as a surrogate for predator abundance is not known (but see Schauber et al., 2009).

To examine the spatial and temporal pattern of *Limulus* intertidal foraging, the presence of feeding pits was quantified along a fixed 50 m × 2 m transect on a mudflat at Adams Point (43°5′29″N, 70°51′53″W) using a novel non-disruptive benthic survey method. Cohesive sediments at Adams Point are inhibitive to the development of *Limulus* eggs, and therefore the study site is unlikely to be a *Limulus* spawning habitat. In addition, previous surveys over the site found few *Limulus* buried in the sediment (pers. obs.). Therefore all pits found within the monitored transect are unlikely to be spawning or resting pits and were regarded as feeding pits. Repeated monitoring of the transect was carried out without disturbing the benthos by recording a video of the transect with a digital camera moving along a cable suspended 3 m above the mudflat (Fig. 2). The transect was located in the upper intertidal zone 5 m from...
the mudflat edge to reduce potential edge effects. The transect was monitored once a month during a daytime low tide from June to October 2009 after which the monitoring setup was taken down to prevent equipment damage by freezing winter temperatures. Monitoring resumed in May and June 2010. Each video was processed using Adobe Photoshop® CS5 Extended to extract still frames with approximately 90% overlap, which were aligned and overlaid to produce a mosaic of the transect. The images are scaled by measuring the distance between two fixed objects at two ends of the cable. The survey area was divided into 25 contiguous 2 m×2 m quadrats, and the number of Limulus pits present within each quadrat was quantified visually. Limulus feeding pits in Great Bay persist between one to two weeks (pers. obs.). In addition, comparisons of consecutive months’ mosaics showed that spatial arrangements and shapes of individual pits were unique to that particular month. Therefore, it was inferred that physical traces of feeding pits disappeared within a month, and pits found in each month’s transect were dug not more than one month earlier. It should be pointed out that pits dug between survey dates could have been ‘overwritten’ by more recent pits, therefore the number of pits observed per month reported here may be an underestimate.

1.3 Foraging behavior of individual Limulus

Snorkelling surveys were conducted at high tide over a mudflat near Adams Point (43°5’50″N, 70°52’3″W) to determine the rate of pit-digging by individual Limulus and the spatial extent of individual foraging activity. Surveys were carried out on 21 July and 6 August 2009. During each survey, the mudflat was searched visually in a haphazard pattern until individual or amplexed pairs of Limulus were found and subsequently followed. The locations where the predators excavated the benthos were marked with thin bamboo stakes. Individuals/pairs were tracked until the visibility and/or water depth made it impossible to continue observations. The distances between consecutive pits made by individual or pairs of Limulus were then measured at the subsequent low tide.

2 Results

2.1 Spatial and temporal pattern in foraging activity

Limulus feeding pits were found in all seven months surveyed between June 2009 to May 2010. Limulus foraging exhibited a seasonal pattern on Great Bay’s mudflats in 2009 (Fig. 3). The total number of pits differed significantly among months [ANOVA of SQRT(X+1) transformed data, \( F_{6, 168} = 25.35, P<0.001 \), Fig. 3]. Feeding pits were already present when the survey began in June 2009, and peaked in August 2009. Out of the five months surveyed in 2009, feeding pits were most abundant in August and September (Student-Newman Keuls’ test, \( P<0.01 \), Fig. 3). In the following year (2010), the activity level in May 2010 was similar to that in low-activity months of June, July and October 2009, but increased significantly one month later in June 2010, when the density of Limulus pits were as high as the density observed in August 2009 (SNK, \( P<0.05 \), Fig. 3).

Visual inspection of the spatial pattern of pits in the months of low activity (June, July and October 2009 and May 2010) suggested a clustered distribution. This clustering was less apparent during the months of high foraging activity (August, September 2009 and June 2010) where many 2 m×2 m quadrats were completely occupied by pits. In August 2009 and June 2010, pits appeared to be distributed evenly throughout the transect at high densities (Fig. 1). The maximum number of pits found within the 2 m×2 m quadrats was 21. This density was observed in six of the twenty quadrats surveyed in August 2009 and one of the quadrats in June 2010. Examination of the spatial arrangement of pits in these quadrats showed that 21 pits might be the upper limit of the pit density, as the areas between adjacent pits are smaller than those of individual pits (Fig. 1).

![Fig. 3](image-url)  Density (mean±SE) of Limulus pits on 7 dates

Letters a-c indicate results of Student-Newman-Keuls test.
2.2 Foraging behavior of individual Limulus

A total of ten Limulus individuals/amplexed pairs were observed on 6 August and 22 July 2009. Unattached males and females and amplexed mating pairs were not differentiated during the snorkeling surveys. However, all three types of predators were found actively foraging and each individual/pair was observed to dig more than one pit. The distances between consecutive pits dug by the same foraging individuals/pairs ranged from 1.3 m to 17.6 m. The mean distance between pits was 6.2 (±1.56 SE) m and the median distance was 5.0m. Disturbance to the benthos was minimal in between pits, except for small shallow tracks made by trailing Limulus tails and walking legs. Moving Limulus also left small perforations in the sediment, which appeared to be made by legs probing into the sediment.

3 Discussion

This study presents the first quantification of Limulus polyphemus foraging activity by measuring the spatial and temporal patterns of foraging excavations. The results revealed intense and frequent use of an intertidal habitat by foraging Limulus. While Limulus foraging occurs throughout a tidal flat at high tide, Limulus typically mate and spawn along the shoreline at high tide (Brockmann, 1990). A census of Limulus along the shore of five sites in Great Bay (including Adams Point – this study’s location) at high tide from May to July 2009 found Limulus only in May and June (NMFS 2010). It is likely that spawning ceases by July (Watson pers. comm.). While spawning activity in Great Bay usually peaks in June, intertidal foraging observed in this study peaked in August. This study shows that Limulus intertidal foraging activity not only persisted but increased, after the May-June breeding season. While this study examined only one site in Great Bay, presence of feeding pits on other mudflats in Great Bay (pers. obs.), together with the results of this study show that Limulus are actively foraging on Great Bay’s tidal flats from late spring till at least early autumn. These findings contrast with studies of mid-Atlantic Limulus that suggest that they forage intertidally and are significant agents of physical disturbance only during the spawning season (Kraeuter and Fegley, 1994; Botton, 2009)

Intertidal foraging by Limulus at Adams Point exhibited distinct seasonality. Seasonal movements such as foraging excursions into the intertidal zones are common among mobile estuarine species (Watson et al., 2009). My findings support Watson et al.’s (2009) and Watson and Chabot’s (2010) reports of high Limulus locomotory activity between subtidal and intertidal zones in Great Bay from May till August, and their hypothesis that Limulus are making foraging excursions on tidal flats. Tidal flats in Great Bay where Limulus foraging is evident are separated between >1km to >10km apart (pers. obs.). It is not known whether Limulus foraging activity peaks at the same time at all locations or forage in other parts of the estuary at different times. The latter is possible as Limulus were found to move downstream in Great Bay in the autumn (Watson et al., 2009; Schaller et al., 2010). On the other hand, the area surveyed in this study was repeatedly used as a foraging ground during the study period. Sixteen of the 20 quadrates monitored contained feeding pits on all the sampling dates, while three and one quadrates contained no pits in one and two months respectively. Therefore, it appears that the study site is an important feeding ground that is repeatedly utilized by Limulus on the scale of months and possibly years. Temporal persistence of foraging ‘hot spots’ has also been reported in other systems (Schauber et al., 2009). However, it is not known whether the same individuals are returning to the same site to feed within the duration of this study – although Watson et al.’s (2009) study at the same location reported Limulus returning to the site within days during the spawning season.

At low tide, Limulus individuals are extremely rare on Great Bay’s tidal flats relative to the abundance of pits present (per. obs.). Therefore, most of the animals that dug the pits described here migrate between subtidal and intertidal zones within a high tide. Watson et al. (2009) suggested that an endogenous tidal clock, which can be triggered by an increase in temperature in spring, drives such movements. The positive relationship between tidal migratory behavior and temperature may explain the spike in foraging activity observed in June 2010. Higher than average ambient temperatures in the spring of 2010 in New Hampshire (USDA Forest Service, 2010) might have caused the early increase of the Limulus intertidal foraging. 21 pits per 4 m² appears to be the upper limit of density for Great Bay’s Limulus population. The size of feeding pits is likely to correlate with prosomal width. As prosomal widths of northern Limulus populations tend to be smaller than those found on the mid-Atlantic, density of feeding pits found on mid-Atlantic habitats are predicted to be lower.

Predator activity has also been found to correlate positively with prey density (e.g. Seitz et al., 2001). Consequently, the drop in Limulus foraging rate at Adams Point might have been due to prey depletion. In
addition, foraging activity can vary within a single mudflat as shown by the presence of clustering of pits in months of low activity, and such aggregative response might be caused by the spatial variability in prey density (Sutherland, 1996). The apparently uniform distribution of high pit density in August 2009 and June 2010 follows the prediction of the Ideal Free Distribution of predators, where consumers will move into patches with lower prey density as predator density or activity increase (Fretwell and Lucas, 1970). Though the spatial pattern of prey density at the study site remains to be determined, Smith (1953) reported a *Limulus* detecting and excavating into plots of enriched *Mya arenaria* located 1 m apart, suggesting that *Limulus* are able to detect patches of high prey densities on a small spatial scale. While it is not known whether *Limulus* can detect cues from infaunal prey in the water column, probing of sediment observed in this study and reported by earlier work (Caster, 1938; Shuster, 2001) showed that *Limulus* probably detect prey on a small spatial scale with chemical and tactile cues.

Observations of individual *Limulus* behavior at Adams Point showed that individual and attached pairs dig multiple pits within a single intertidal excursion. In the course of this study, some animals were found to dig multiple pits in quick succession (<10 min per pit) before digging a pit for an extended period of time (up to 15 min). At spring low tides, Great Bay’s mudflats typically span hundreds of meters along the shore and between the high and low water line. The distances between pits made by foraging individuals/pairs located during snorkelling surveys indicated that *Limulus* foraged on a spatial scale smaller than that of individual mudflats. As a result, individual/pairs of *Limulus* might have dug multiple pits observed within the 50 m×2 m transect monitored in this study. However, because the minimum distance between pits was 1.3 m, the tightly clustered pattern of pits shown in Fig. 1 is the result of multiple predators foraging adjacent to each other or previous excavations. *Limulus* located during snorkeling surveys were at least 100 m away from the spring low water level. Regular tidal migration on this scale is possible given the movement rates of Great Bay *Limulus* reported by Watson and Chabot (2010), while Dungeness crabs *Cancer magister* have been found to carry out 1.2 km roundtrips to the littoral zones (Holsman et al., 2006). Display of energetically expensive migratory behavior by *Limulus* outside of the spawning season, provided strong support for the hypothesis that the benefits of exploiting intertidal food sources outweighs the cost of tidal migrations (Holsman et al., 2006).

In addition to evidence of frequent and intensive *Limulus* intertidal foraging activity presented here, the absence of *Limulus* eggs at the study sites (Lee unpubl. data) suggest a segregation of spawning and feeding habitats. Current *Limulus* management practices emphasize the quality of spawning habitats (Hooker et al., 2010), but an effective management plan needs to consider habitats used by the species at other stages of its life history. The potential use of different parts of the intertidal zone at different stages of *Limulus*’s life history in Great Bay underscores the importance of healthy diverse littoral habitats to support the reproductive and trophic requirements of resident estuarine populations. Consequently, findings of this study have important implications on the management of this economically and ecologically valuable species in estuarine systems. It is especially critical to include protection of intertidal habitats in management efforts because of the increasing impacts of anthropogenic influences on estuaries (PREP, 2009). Holsman et al. (2003) speculated that loss of intertidal habitats in San Francisco Bay might explain the decline in Dungeness crab production in the region, which rely on intertidal areas as foraging grounds. Similarly, recent declines of *Limulus* populations should also be examined within the context of foraging habitat quality.

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