Chapter 2

Salt Marsh Peat Dispersal: Habitat for Fishes, Decapod Crustaceans, and Bivalves

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Additional information is available at the end of the chapter

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Abstract

Salt marshes, especially those of *Spartina alterniflora*, are among the most productive habitats on Earth. The peat that is formed and accumulates there, as below-ground biomass, can be dispersed in a number of ways, through calving off the marsh edge along bays, in creeks, and other locations as occurs in the Mullica River – Great Bay estuary in southern New Jersey. Based on a variety of sampling approaches, including those collected by sidescan sonar and direct collection, we provide new insights into the ecological role of dispersed peat. Some of this is ice rafted on the marsh surface during storms. Elsewhere, and most commonly, it falls into the intertidal channels or flats where it may continue to support the growth of *Spartina*, and associated invertebrates such as *Geukensia demissa*. If it is deposited subtidally these may not be as likely, but in these situations the peat provides structured habitat for other animals such as fishes, crabs, shrimps, and bivalves.

Keywords: peat reefs, salt marshes, habitat complexity, fishes, macroinvertebrates

1. Introduction

Salt marshes are some of the most productive ecosystems on Earth. How that production is dispersed is a frequent focus, particularly in the form of detritus [1–3]. Other, unrecognized forms of dispersal, such as that for salt marsh peat, are infrequently studied. Peat in salt marshes results from the degradation of roots, stems and leaves of marsh plants, particularly *Spartina alterniflora* and *S. patens* [4, 5], and accumulates at a greater rate than decomposition.

This occurs in New Jersey east coast marshes as well, where estimates of the accumulation of this below ground have been determined [6–8]. Erosional processes in coastal salt marshes lead to peat breaking away from the marsh edge and falling into the channel to form peat reefs or being ice rafted from the edge to other locations. When ice dispersed salt marsh peat away from the edge of a channel, a large proportion of this peat was rafted to the lower intertidal while other pieces of peat were carried to the marsh surface [9]. The response of the marsh vegetation and associated fauna, such as *Geukensia demissa*, varied with the deposition site and the amount of ice that they were exposed to [10]. When deposited in the water, peat reefs are large pieces of live and decomposing plant material and associated sediments that separate from the marsh surface and form intertidal and subtidal structures of varying sizes in channels. While their existence, including as mud boulders [11], has been documented for many decades, it is only with new bottom imaging technology that it is possible to easily map these underwater structures.

One of the main causes of separation of marsh peat from the marsh platform is the bank being undercut by the current because the lower mud layer is less stable than the peat, and washes away first [12–14]. This leads to a peat overhang that then breaks off and falls away from the marsh edge into intertidal and subtidal waters. Three distinct forms of slump are observed during this process [15]. Rotational slump occurs when the peat slides down the bank on its side, with the marsh vegetation facing the bank. Non-rotational subsidence occurs when the block does not move, but sinks straight downwards, creating a ledge. Freefall slump occurs when the peat fractures cleanly from the bank and falls away from the marsh into the channel, as in peat reefs. The timing and size of bank failures is influenced by geological factors specific to each marsh, such as peat thickness and channel depth [14, 16]. High storm frequency leads to higher rates of erosion, which can cause seasonal and geographical variation among otherwise similar salt marshes [17]. Peat reef formation may be enhanced by eutrophication as well [18]. It has been shown that other marshes in the northeastern U.S. experience bank failure [14, 16, 19–21], but marshes there have not been observed to experience extreme channel migration [22]. A study in Sapelo Island, Georgia showed that the water volume of a coastal salt marsh had not changed significantly in 200 years, meaning erosion and deposition were in equilibrium in that system [17].

The subsurface peat reefs are fairly resilient. For example, a study conducted at Nauset Marsh in Cape Cod, Massachusetts established that a 2-meter long peat reef that had fallen into a tidal creek has a lifespan between 7.5 and 15 years before it erodes away [14], meaning there is enough time for it to be colonized by a variety of organisms [19]. Various crustaceans were found year-round on the peat reefs, including juvenile *Homarus americanus* and structure-seeking fish species. However, these sites have historically been difficult to survey. Long-term datasets of finfish populations throughout these marsh systems have been collected, but sites with peat reef bottom structure are seldom effectively sampled due to gear limitations. Thus, we know little of their structural and functional significance [23, 24] because peat reefs are difficult to detect in subtidal locations and even more difficult to sample. The purpose of this paper is to characterize patterns of marsh peat dispersal, i.e. peat reef formation and ice rafting, and faunal use in a relatively undisturbed estuary dominated by salt marshes. To accomplish this we used a number of techniques including subsurface sidescan surveys and in situ sampling during the summer and fall in 2017.

2. Study site

The Mullica River - Great Bay estuary in southern New Jersey (**Table 1**, **Figure 1**) is dominated by tidal salt marshes [25, 26]. This system is relatively unaffected by urbanization due to the small

Sample Number	Location	Marsh seascape type	Dominant marsh vegetation	Approximate salinity (ppt)	Transect length (m)	Range of depths surveyed (m)	Range of depths for peat reefs (m)	Density of peat reefs (Reefs per 100 m of bank scanned)
1	Little Sheepshead Creek	Thoroughfare	*S. alterniflora*	25–32	1910	0.6–6.8	0.8–6.7	6.79
2	Big Sheepshead Creek	Thoroughfare	*S. alterniflora*	26–31	2350	0.0–4.3	0.7–3.4	0.70
3	Jimmies Creek	Thoroughfare	*S. alterniflora*	26–30	3680	0.3–3.9	0.5–3.7	0.76
4	Little Thorofare	Thoroughfare	*S. alterniflora*	26–30	2960	0.5–7.6	0.5–7.4	5.47
5	Big Thorofare	Thoroughfare	*S. alterniflora*	24–30	3440	0.0–5.8	0.6–4.6	0.74
6A	Seven Islands	Island Thoroughfare	*S. alterniflora*	28–30	1450	2.6–5.2	3.3–5.2	10.07
6B	Seven Islands	Island Thoroughfare	*S. alterniflora*	28–30	1560	0.5–3.5	1.4–3.5	1.15
6C	Seven Islands	Island Thoroughfare	*S. alterniflora*	28–30	1220	0.7–4.0	2.4–3.9	4.02
6D	Seven Islands	Island	*S. alterniflora*	28–30	1650	0.6–3.4	2.5–2.9	3.19
6E	Seven Islands	Island	*S. alterniflora*	28–30	1670	0.4–7.0	1.0–7.0	35.21
7A	Story Island	Island	*S. alterniflora*	28–31	5270	0.5–7.7	0.7–6.3	1.14
7B	Story Island	Island	*S. alterniflora*	28–31	1320	0.5–4.2	0.9–4.3	2.65
7C	Story Island	Island	*S. alterniflora*	28–31	1450	0.7–4.5	2.6–4.4	10.62
7D	Story Island	Island	*S. alterniflora*	28–31	4740	0.7–3.0	0.7–1.7	1.20
8	Motts Creek	Thoroughfare	*S. alterniflora*	16–25	5940	0.8–7.8	1.3–7.5	0.73
9	Nacote Creek	River	*S. alterniflora*	9–23	7040	1.4–7.5	2.0–6.9	0.12
10	Ballanger Creek	Creek	*S. alterniflora*	13–21	4450	0.6–7.8	0.8–7.2	0.12
11	Mathis Thorofare	Thoroughfare	*S. alterniflora*	13–21	5330	0.7–7.7	1.0–4.5	0.51

Sample Number	Location	Marsh seascape type	Dominant marsh vegetation	Approximate salinity (ppt)	Transect length (m)	Range of depths surveyed (m)	Range of depths for peat reefs (m)	Density of peat reefs (Reefs per 100 m of bank scanned)
12	Bass River	River	*S. alterniflora*	15–20	5210	1.0–8.3	2.2–7.2	0.47
13	Wading River (Lower)	River	*S. alterniflora*	7–12	4740	1.4–9.3	No Reefs	0.00
14A	Fence Creek	Creek	*Spartina/ Phragmites*	5–15	630	0.7–2.4	1.2–1.9	0.56
14B	Jerry Creek	Creek	*Spartina/ Phragmites*	5–15	1290	0.5–2.3	0.9–1.8	0.35
15	Teal Creek	Creek	*Spartina/ Phragmites*	0–7	1190	0.6–3.1	1.2–1.3	0.13

Sampling number corresponds to numbers on **Figure 1**. Marsh seascape types refer to Thoroughfares = open-ended connections through marshes with tidal flow in both directions along marsh edge; Creeks = dead end creeks with only one water access point; River = longer than creeks but with only one water access point; Island = water access to marsh edge at all points

Table 1. Sampling effort by location for determining distribution and abundance of peat reefs based on sidescan transects in the Mullica River – Great Bay estuary during summer and fall 2017.

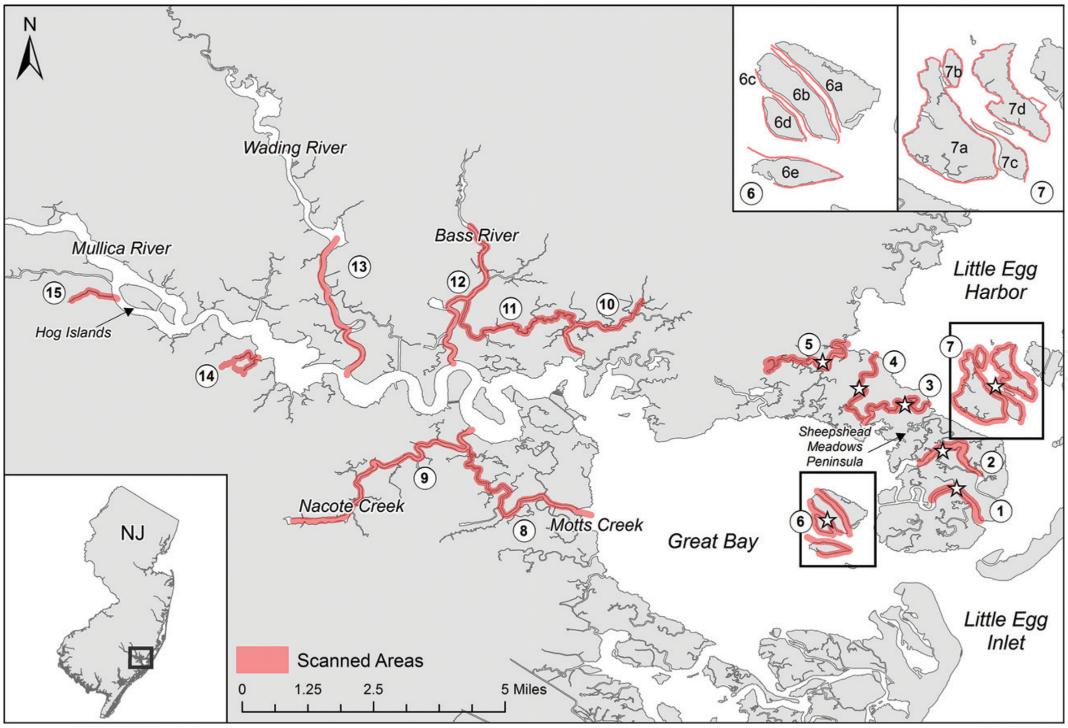

Figure 1. Sidescan sonar sampling locations in the Mullica River – Great Bay estuary in southern New Jersey, USA (see inset). Numbers correspond to location names: 1 = Little Sheepshead Creek, 2 = Big Sheepshead Creek, 3 = Jimmies Creek, 4 = Little Thorofare, 5 = Big Thorofare, 6A - E = Seven Islands (see inset), 7A - D = Story Island (see inset), 8 = Motts Creek, 9 = Nacote Creek, 10 = Ballanger Creek, 11 = Mathis Thorofare, 12 = Bass River, 13 = Wading River, 14 = Jerry and Fence Creeks, 15 = Teal Creek. Stars indicate locations of peat reef faunal sampling.

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human population living in the watershed [23, 25, 27], so it can be assumed that human impact on the natural processes here is minimal. The marsh surface in the lower estuary, at higher salinities, is dominated by *Spartina alterniflora* cordgrass, including the Sheepshead Meadows peninsula [28], which builds up on the marsh surface to form a 0.5 m deep layer of peat [6].

Within these marshes the morphology of channels can vary along the salinity gradient and presumably along a creek development gradient. Dead end creeks dominated by *Spartina alterniflora* in the lower, higher salinity estuary and *Spartina cynosuroides* in the upper estuary are the most common. In the upper estuary, at lower salinities, the marshes are dominated by invading *Phragmites* [26, 29, 30] and have a more diverse freshwater flora. Thoroughfares connecting bays and other waterways are most common in the lower estuary, such as in Sheepshead Meadows, and the channels through the flood tidal delta in the vicinity of Little Egg Inlet in Great Bay (Seven Islands) and Little Egg Harbor (Story Islands area). Throughout the lower estuary the marshes, which are dominated by *S. alterniflora*, sit on top of deep sediments (approximately 9 m) based on surveys of the length of the support pilings for the Rutgers University Marine Field Station [31], and multibeam imagery of the Sheepshead Meadows peninsula [26].

3. Methods

3.1. Peat reef mapping

Fifteen locations of varying depths (**Table 1**, **Figure 1**) were sampled during the summer and fall of 2017. Some of the representative sites include Little Thorofare, Big Thorofare, Little Sheepshead, Big Sheepshead and Jimmies Creek in the Sheepshead Meadows. The mouths of these waterways are between 2 and 6 km from the Little Egg Inlet, so they experience a 1 m range in tidal influence and a salinity range of 23.6–34.5 ppt [27]. The average depth in each creek ranges from 0.7 m to 4.2 m (**Table 1**). All of these creeks, thoroughfares, and channels are stable features, as they are evident on aerial photographs from the 1930s (historicaerials.com).

Bottom images of the study sites were mapped using a Helix 10 Humminbird side imaging sonar in the summer and fall of 2017. Data was collected at high tide to reflect the maximum possible number of submerged peat reefs, and because the shallower creeks cannot be accessed by boat at low tide. Both banks of the creek were scanned in narrower creeks (Teal Creek, Fence Creek, Jerry Creek, Bass River, Mathis Thorofare, Motts Creek, Little Thorofare, Jimmies Creek), while only one bank of the wider creeks and rivers were scanned (Wading River, Ballanger Creek, Nacote Creek, Big Thorofare, Big Sheepshead Creek, Little Sheepshead Creek).The recordings were downloaded to the program HumViewer and the locations of individual peat reefs were manually plotted using the Waypoints feature of Humviewer. Peat reef length was measured using the HumViewer program. GPS coordinates and depth of the peat reefs were downloaded to Google Earth and ArcGIS to create a map that showed distribution patterns of the peat reefs throughout the study area (**Figure 1**). Abundance in creeks was categorized as number of reefs per 100 m of marsh bank scanned (**Table 1**).

3.2. Faunal sampling

Field sampling was done in the summer and fall of 2017 to see which organisms utilize peat reefs as habitat relative to adjacent areas without peat reefs. The peat reefs and accompanying organisms were collected in large, enclosable mesh (4.8 mm) bags that surrounded the reef. These were returned to the laboratory for additional analysis. This technique was limited to peat reefs that were small enough and in water less than 2 m deep so that they could easily be collected. An additional seine haul with a 7.6 m, (4.8 mm) mesh seine net was performed adjacent to peat reefs in an area where no reefs were present. The collected reefs were measured (length, width, height) and volume was determined by water displacement. All fish, shrimp, crabs, and bivalves in each collection were removed, identified, measured, and expressed as catch-per-unit-effort, or CPUE (**Table 2**). Most fish and shrimp were measured as total length, fish with forked tails were measured as fork length, and crabs were measured as carapace width. Some components of the fauna at each study site/habitat type (e.g. fish, macroinvertebrates) were identified, measured, and released in the field. Others were removed from the peat reefs in the laboratory and then released.

Species/taxa	Abundance at peat reef (CPUE)	Length – range at peat reef (mm)	Abundance adjacent to peat reef (CPUE)	Length – range adjacent to peat reef (mm)
Fish	44.9	—	120.6	—
Apeltes quadracus	0.1	37–38	0.0	—
Bairdiella chrysoura	3.9	36–94	0.0	—
Chaetodon ocellatus	0.1	28	0.0	—
Cyprinodon variegatus	0.0	—	0.3	26–40
Etropus microstomus	0.0	—	0.1	48
Fundulus heteroclitus	15.1	26–112	64.2	26–95
Fundulus majalis	0.0	—	1.1	52–100
Gerreidae sp.	0.1	33–34	0.0	—
Gobiesox strumosus	0.1	49	0.0	—
Gobiosoma bosc	3.1	23–51	0.3	31–43
Menidia menidia	22.2	27–81	54.6	22–107
Menidia sp.	0.0	—	0.1	27
Opsanus tau	0.1	187	0.0	—
Tautoga onitis	0.1	57	0.0	—
Crabs	18.7	—	4.7	—
Callinectes sapidus	2.8	7–107	4.5	8–125
Carcinus maenas	0.1	15	0.0	—
Dyspanopeus sayi	3.7	5.2–21.5	0.2	8.4–12.5
Eurypanopeus depressus	0.1	9.2–10.7	0.0	—
Hemigrapsus sangueineas	0.1	21.8	0.0	—

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Species/taxa	Abundance at peat reef (CPUE)	Length – range at peat reef (mm)	Abundance adjacent to peat reef (CPUE)	Length – range adjacent to peat reef (mm)
Panopeidae sp.	2.4	5.3–23.3	0.0	—
Panopeus herbstii	8.7	4.4–39.4	0.0	—
Uca pugnax	0.4	9.5–14.2	0.0	—
Uca sp.	0.5	3.6–11.0	0.1	15.6
Shrimp	46.1	—	24.2	—
Crangon septemspinosa	0.3	25.4–30.4	0.8	19.8–29.0
Palaemonetes intermedius	0.5	18.2–32.7	0.0	—
Palaemonetes pugio	15.1	16.8–41.6	11.2	19.6–41.8
Palaemonetes vulgaris	28.6	23.3–32.9	11.8	24.5–36.0
Palaemonidae sp.	2.0	24.1–33.2	0.3	26.9
Bivalves	230.5	—	0.0	—
Crassostrea virginica	1.4	24–145	0.0	—
Geukensia demissa	228.6	5–113	0.0	—
Mytilus edulis	0.2	16–25	0.0	—
Petricolaria pholadiformis	0.1	19	0.0	—
Tellina agilis	0.1	10	0.0	—

See **Figure 1** for location of samples. Fish and shrimp measured as total length, crabs as carapace width, and bivalves as valve length

Table 2. Faunal species composition of peat reefs and adjacent sites lacking peat reefs based on in situ sampling in a variety of marsh seascapes.

4. Results

4.1. Peat reef formation

The formation of peat reefs in the study watershed occurs at the marsh edge when marsh peat and the associated marsh vegetation, fauna, and sediments calve off or split off from the marsh platform (**Figure 2**). Most are then either deposited in the low intertidal or subtidal portions of the adjacent waterway. These are evident and can be mapped because they are clearly visible on sidescan sonar images (**Figure 3**). Based on this approach, the in situ estimates ranged from 0.1 to 15.0 m in length (n = 1916), with most from 0.7 to 4.0 m (**Figure 4**).

Intertidal and shallow subtidal peat reefs that could be observed from the surface often still contained the *Spartina alterniflora* vegetation of the same apparent density, length, and orientation of the stems as they were on the marsh surface, thus identifying those that had recently split off from the marsh platform. These were often dominated by individuals or large clumps

Figure 2. Peat reef formation at deeper side of channel, in Little Sheepshead Creek – note scalloped marsh edge (top), in initial stage as pieces of marsh surface separate from the rest of the marsh platform (middle), and intertidal peat reef at edge of marsh thoroughfare (bottom).

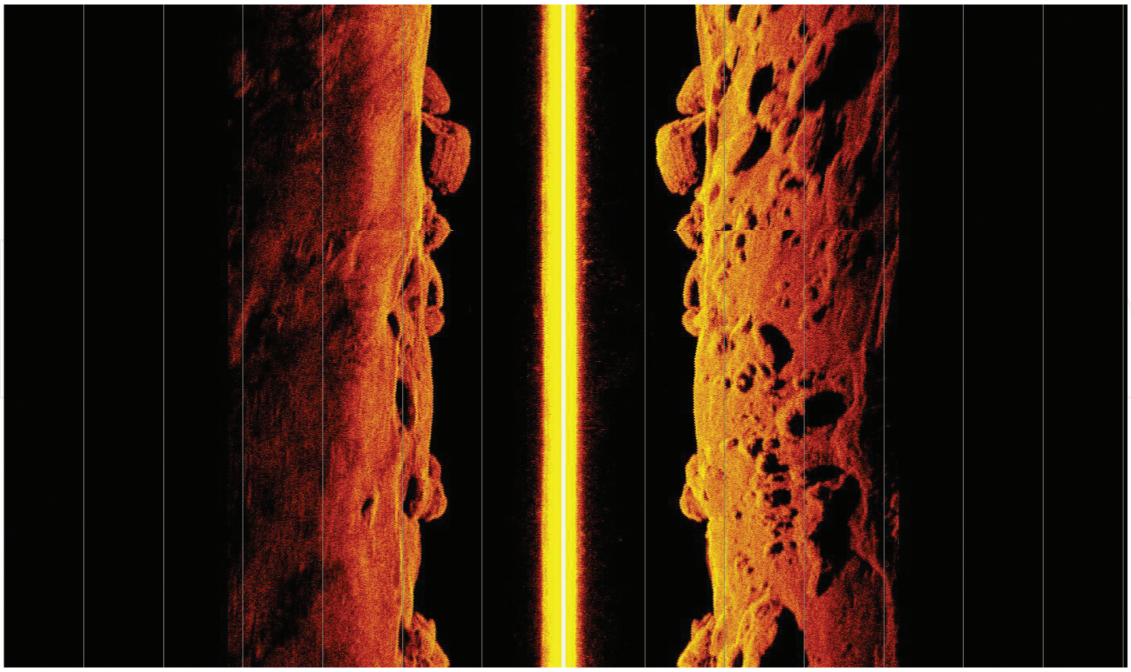

Figure 3. Sidescan sonar images of representative subtidal peat reefs within the Seven Islands study area. The sidescan image indicates that the boat passed directly over the largest pieces of peat thus they are reflected on each side. On the right side of the image smaller pieces of peat are evident.

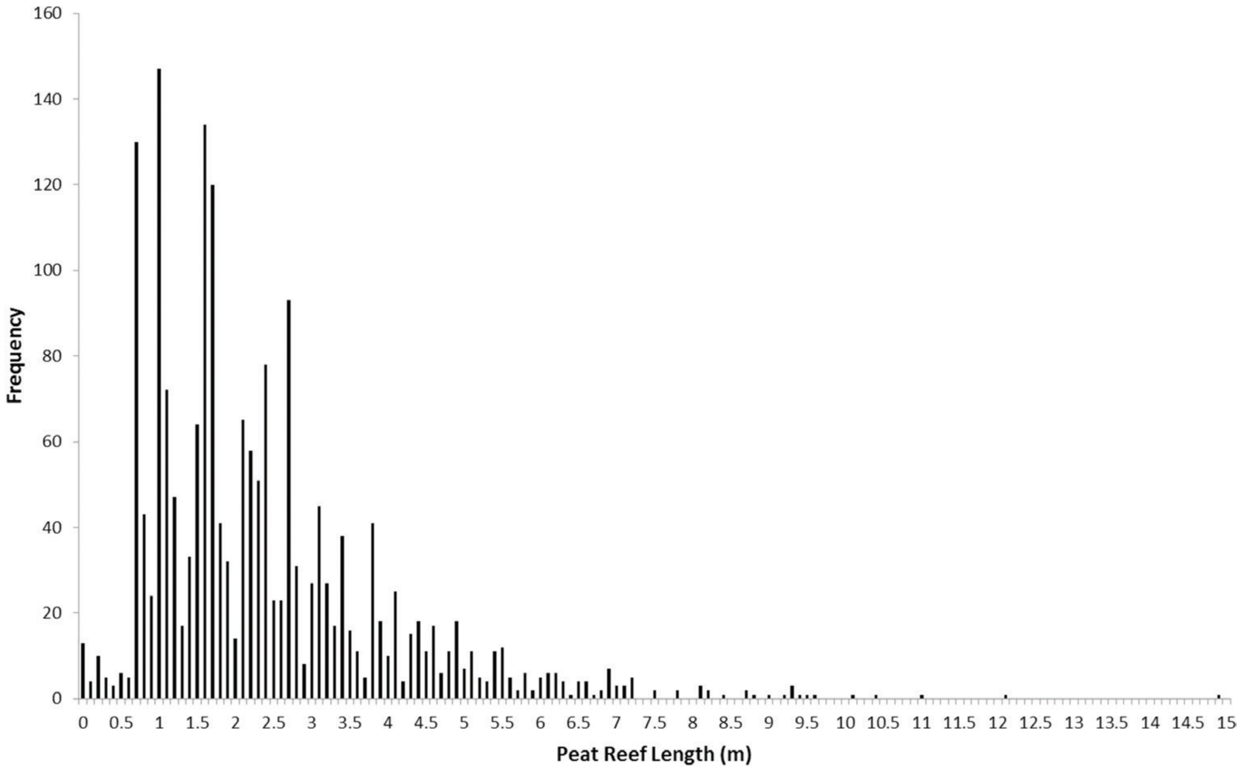

Figure 4. Frequency distribution of intertidal and subtidal peat reef length based on sidescan sonar estimates in the study area.

of *Geukensia demissa*. On some occasions, it was apparent that an individual peat reef had been deposited for at least two vegetation-growing seasons because the original vegetation, now decomposing due to near-constant immersion, was oriented at an angle toward the center of the channel. This was accompanied by new vegetation, from the current growing season, that was typically closer to the water surface and oriented vertically on the peat reef. At longer durations, or perhaps slightly deeper as well, the peat reefs lacked the original *S. alterniflora* vegetation. These often had *Ulva lactuca* and other macroalgae growing or accumulating on the reefs.

In other instances, during cold winters, individual peat reefs were ice rafted on to the marsh surface (**Figure 5**). In the following spring, *S. alterniflora* was still growing from them. Over time, the associated vegetation was less robust, the *G. demissa* died with the shells deposited on the marsh surface, and the mass of the peat reef, including sediments, was reduced. After approximately 1 year, only some sediment and shells remained.

4.2. Distribution of peat reefs

Based on sidescan sonar surveys throughout the salinity gradient in the Mullica River — Great Bay estuary, the highest densities occurred in the lower, saltier portions of the estuary (**Figure 1**, **Table 1**). Transect length, number of banks scanned, and water depth may have influenced the estimates of peat reef distribution and density. Transect lengths ranged from short creeks at the upper end of the estuary (Fence = 630 m, Jerry = 1290 m, Teal Creek = 1190 m) to much longer for several rivers (Bass River = 5210 m, Wading River = 4740 m, Nacote Creek = 7040 m) and thoroughfares (Motts Creek = 5940 m, Mathis Thorofare = 5330 m) (**Table 1**, **Figure 1**). The depth varied between and within transects (**Table 1**). Some of the deepest depths (>6 m) occurred in thoroughfares, some creeks, and rivers and ranged to 7.2 m. All of these types of marsh seascape had variable depths and the deeper holes were irregular in occurrence (**Figures 6**, **7**, **8**). Many of the deepest holes occurred in bends in thoroughfares and creeks (personal observation).

The density of peat reefs also varied independently of marsh seascape type (**Table 1**, **Figures 6–8**). Some of the highest and lowest densities occurred in thoroughfares, including those around islands. Peat reef densities in rivers and creeks were typically lower. The variability that occurred is evident when individual peat reefs are mapped along the transects of the Sheepshead Meadows (**Figure 9**). In some thoroughfares the peat reefs are quite sporadic or in distinct patches (Big Thorofare, Jimmies Creek, Little Sheepshead Creek). In others, they are more or less continuous, as in Little Thorofare.

The size of peat reefs, based on sidescan sonar images, ranged from 0.1 to 15.0 m in length (**Figure 4**). The reefs that were sampled in situ and brought back to the laboratory were smaller and collected primarily from the Sheepshead Meadows, Seven Islands, and Story Islands (**Figure 1**). These came from 0.5 to 1.4 m water depth and ranged from, 23 to 13 cm in length, 15 to 50 cm in width, 13 to 51 cm in height, 0.5 to 77 liters in volume, and 3.1 to 73.0 kg in weight.

4.3. Associated fauna

A variety of fishes (n = 14 species), crabs (n = 7 species), shrimps (n = 4 species) and bivalves (n = 5 species), were collected at peat reefs and on adjacent substrate without

Figure 5. Ice rafted peat reef after a storm (top left) and its remains, including *Geukensia demissa* shells (top right) and after one year (bottom).

peat, with some species having a distinct pattern based on occurrence and abundance (**Table 2**). All faunal groups had more species collected on peat reefs. Also individuals of a single species were typically more abundant on peat reefs. This was most obvious for bivalves and crabs but also occurred for fish and shrimp. The most striking example is for the bivalves (n = 3227 individuals), all of which occurred only on the peat reef.

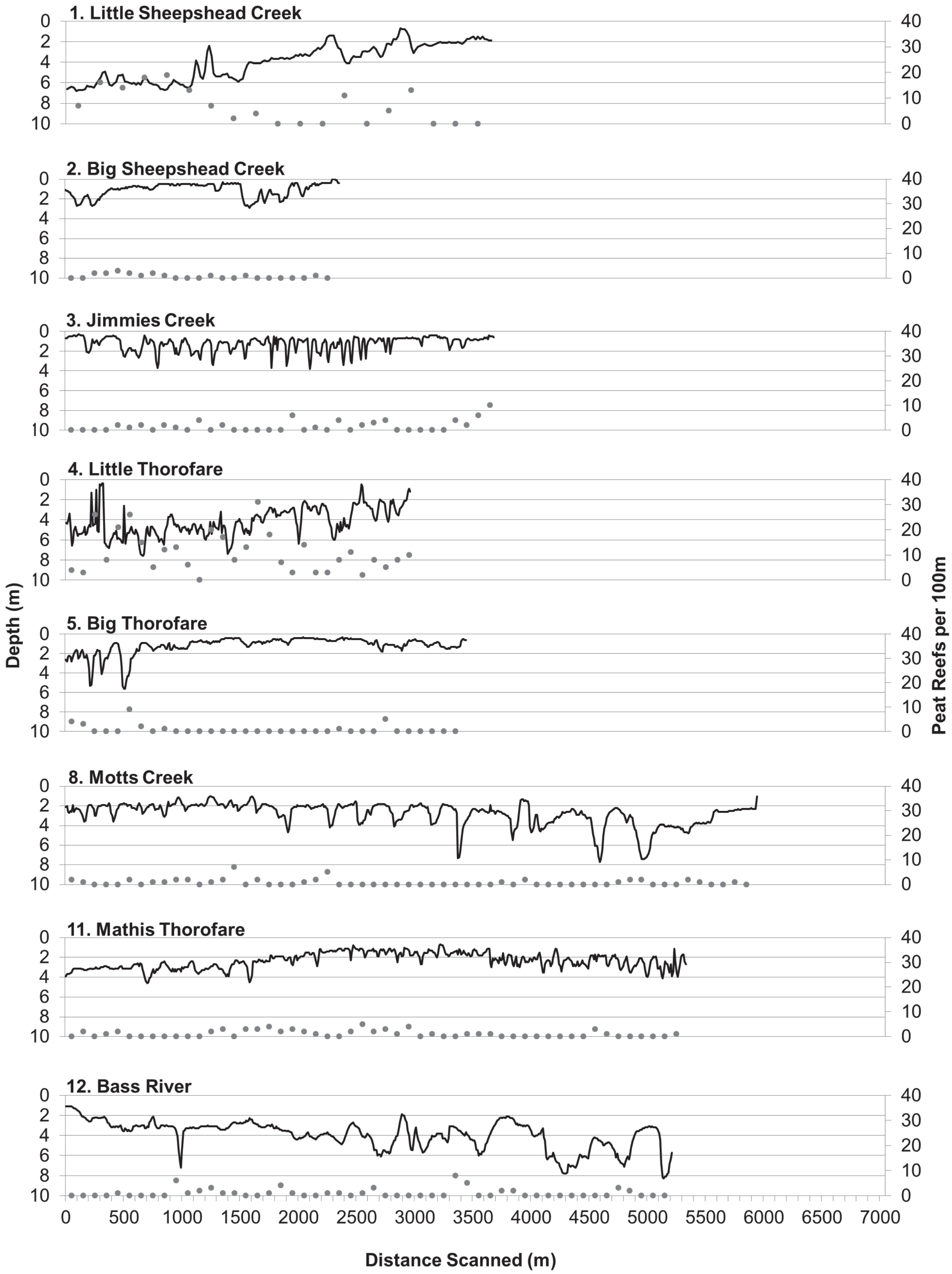

Figure 6. Depth profiles and distribution of peat reefs along sidescan sonar transects in various creeks and thoroughfares throughout the Mullica River – Great Bay estuary. See **Figure 1** for location of sites. Sites with very low peat reef densities or very short transects (see **Table 1**) are not included. Line indicates creek depth. Individual points depict number of peat reefs per 100 m. Scans of thoroughfares run west to east while creek scans run from upper creek to the mouth of the creek. Only one bank of Big Thorofare, Little Sheepshead Creek, Big Sheepshead Creek, Ballanger Creek, Motts Creek, and Wading River was scanned. All other locations were scanned on both banks.

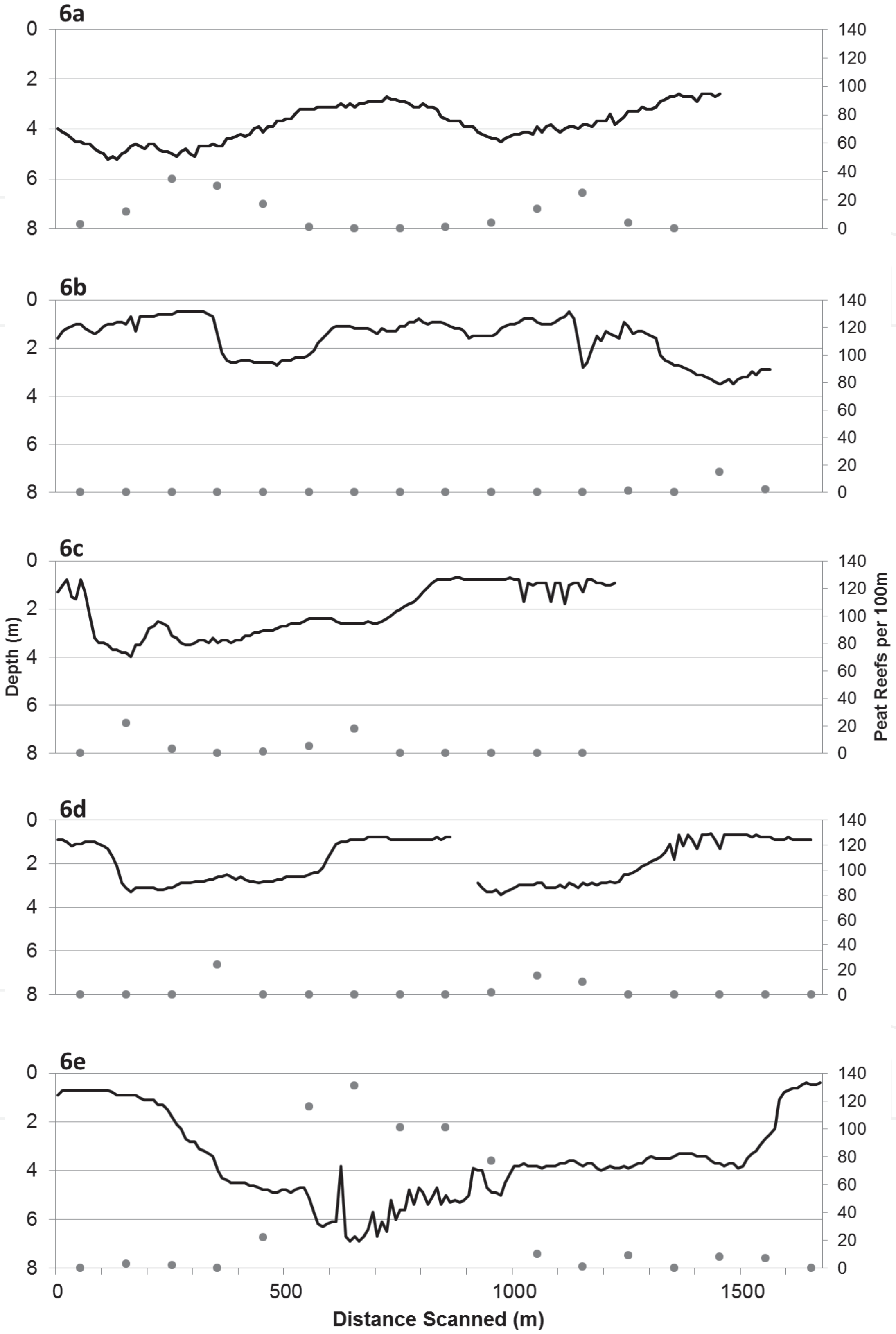

Figure 7. Small scale distribution and depth of peat reefs along sidescan sonar transects at Seven Islands. See **Figure 1** for location of sites. Line indicates creek depth. Individual points depict number of peat reefs per 100 m. One bank was scanned per transect. Scans of thoroughfares (6a, 6b, 6c) run northwest to southeast. The island scan 6d runs counter-clockwise starting at the northern point; there is a 50 m gap between two scans that circle the island. 6e runs clockwise starting at the northern side of the island.

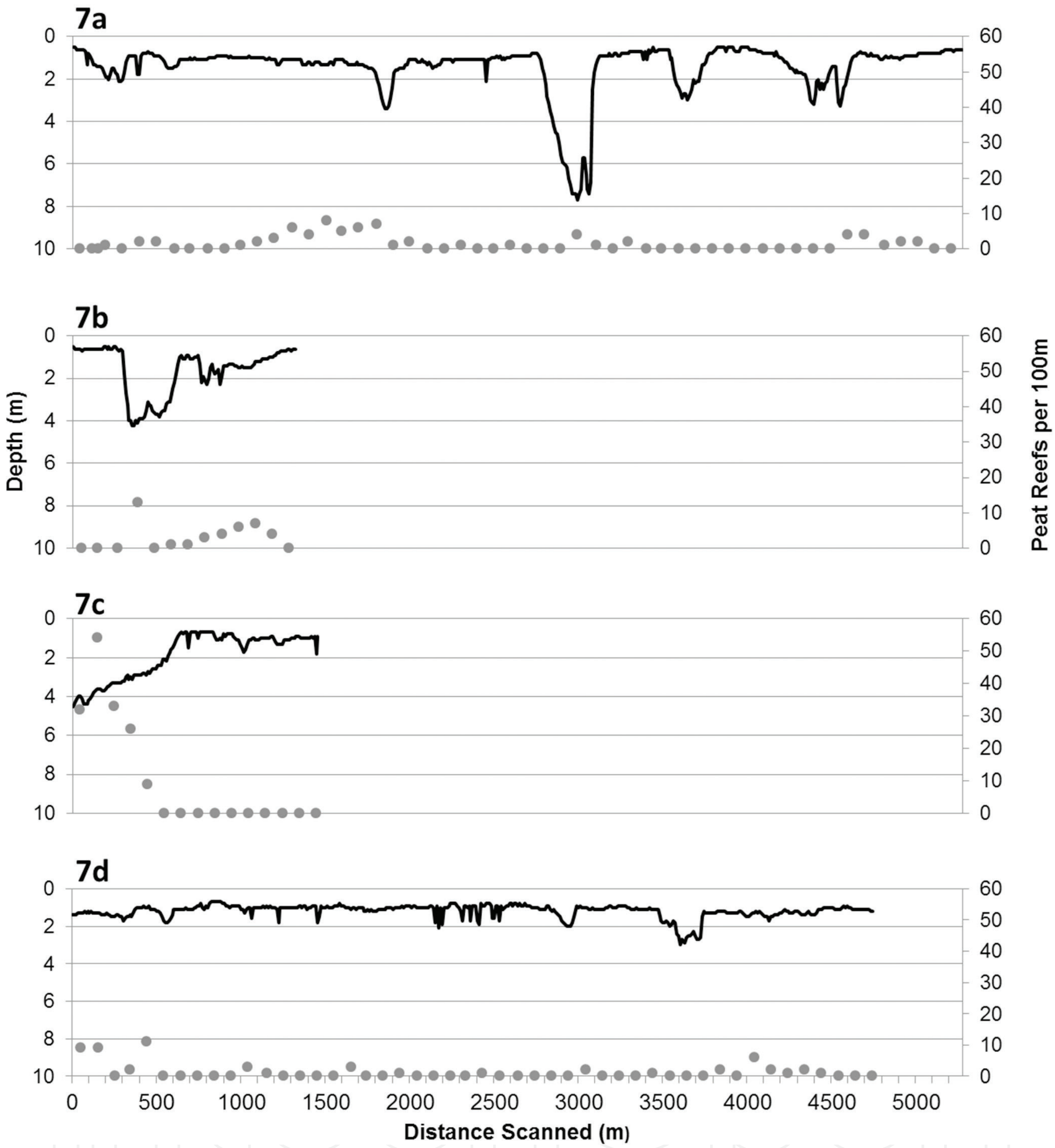

Figure 8. Depth profiles and distribution of peat reefs along sidescan sonar transects at Story Island area. See **Figure 1** for location of sites. Line Indicates creek depth. Individual points depict number of peat reefs per 100 m. One bank was scanned per transect. Scans of thoroughfares (7c) run northwest to southeast, the island scans (7a, 7d) run counter-clockwise starting at the northern point, 7b starts at the western side of the island.

Of these the most abundant, by far, was *Geukensia demissa*, with a mean abundance of over 200 individuals. The shrimp, (n = 964 individuals) *Palaemonetes vulgaris* had higher abundance on peat reefs but also occurred at relatively high abundance on adjacent substrate (**Table 2**). The mud crabs (n = 211 individuals), *Dyspanopeus sayi, Panopeus herbstii, Eurypanopeus depressus,* and unidentified panopeids were all abundant on peat reefs, as were fiddler crabs (n = 14 individuals) *Uca pugnax* and unidentified *Uca sp.* (**Table 2**). A few fish species were slightly more abundant in the adjacent substrates away from peat

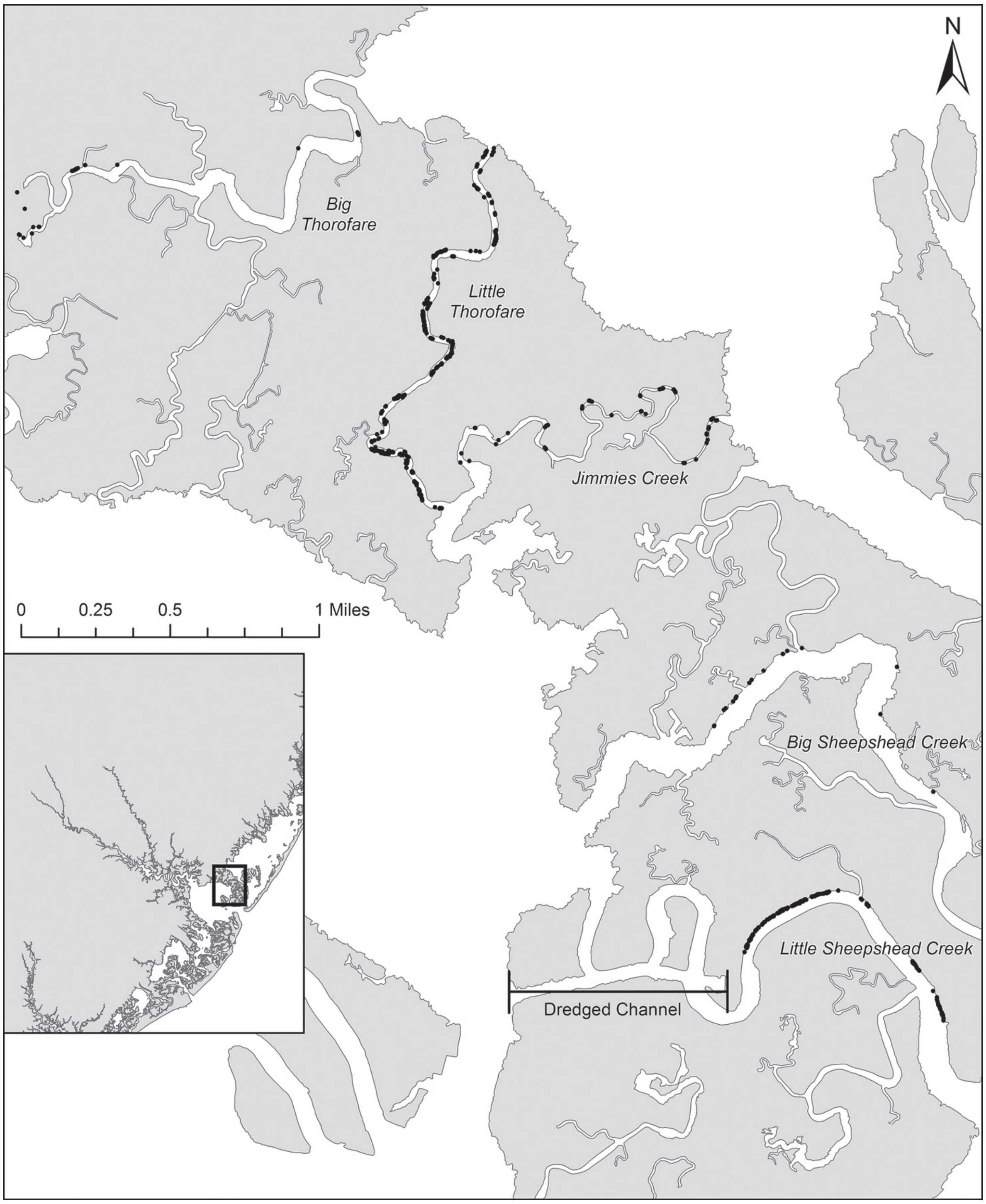

Figure 9. Distribution of individual peat reefs along marsh thoroughfares with some of the highest (Little Thorofare, Little Sheepshead Creek), moderate (Jimmies Creek), and lowest (Big Sheepshead Creek, Big Thorofare) densities. Note that altered portion (dredged channel) in Little Sheepshead Creek was not sampled. Only one bank of Big Thorofare, Little Sheepshead Creek, and Big Sheepshead Creek was scanned.

reefs (**Table 2**), including *Fundulus heteroclitus* and *Menidia menidia*, but in each case, the values were of the same order of magnitude. On most peat reefs, traces of *Spartina alterniflora*, *Ulva lactuca*, and other macroalgae were present. Where comparisons were possible, the lengths of individuals for all fauna were similar between peat reefs and the adjacent substrates (**Table 2**).

5. Discussion

5.1. Peat reefs in marsh seascapes

The wide distribution and abundance of forming and submerged peat reefs in the Mullica River — Great Bay estuary indicates that they may play significant roles in this relatively undisturbed ecosystem. This includes influences on the geomorphology and ecology based on our studies of peat reefs and the associated fauna, and the natural history of the system [32]. Also importantly, the findings from our study estuary probably reflect the importance of peat reefs in other estuaries. This is particularly likely in marshes in the northeastern United States, i.e. those stretching from Maine to southern New Jersey, that are characteristically composed of peat substrates [13, 33]. This general pattern is evident from other studies in Massachusetts marshes [14, 18, 19]. The frequency of occurrence of peat reefs may be less so in more southern marshes, from Delaware Bay and south to Florida, because marsh peat is less common [13, 33]. The difference may also be reflected in the more frequent occurrence of slump blocks in these southern marshes [13, 15].

Another source of geographical variation in marsh peat dispersal is ice rafting [9, 10]. It is much more likely that this will be a frequent occurrence in New England marshes because of the increasing frequency of ice formation at the colder temperatures in more northern marshes. In addition, the frequency of occurrences in the study estuary over time is likely to diminish because of increasing water temperatures and the decreasing frequency of cold winters in this estuary [34] and others [16] in the region. Variation in the occurrences of ice rafting could also occur because ice formation is more frequent in the upper portion of the estuary, which can be colder, as a result of the lower salinities there [34, 35] and distance from the moderating influence of the ocean [25].

The distribution of peat reefs in the study area, although quite variable, is influenced by marsh seascape type. The overall reduced number of peat reefs further up the estuary may be due to changes in vegetation along the salinity gradient. This appears most evident along the edges of low salinity creeks where the invasive form of *Phragmites australis* is common (personal observation), especially in late stages of the invasion [29]. It may be that the extensive and deep rhizome mat of this species prevents peat reef formation. The other component of marsh seascapes that may contribute to peat reef formation is the open and bi-directional flow of water, perhaps at higher speeds, that may occur in thoroughfares and around islands, where we report some of the highest densities of peat reefs. This is particularly evident at the end of the Sheepshead Meadows peninsula where high current speeds likely contributed to the accumulation of peat reefs in deep water [26]. Exceptions, such as in Big Sheepshead Creek, provide insights. A prominent sill is present at the easternmost end of this thoroughfare, which drastically reduces water flow and thus perhaps erosion at the marsh edge. This same process, but at much lower current speeds in dead end creeks, may account for the reduced number of peat reefs there.

An earlier study in the same system found that waves, from storms or boat traffic, may also influence erosion at the edge and thus peat reef formation [14]. This same pattern has been identified from commercial boat traffic in other systems [36]. Another potential contributor is eutrophication influenced reduction in the structural integrity of creek banks [18]. Once peat reefs are formed they may last relatively long periods of time. Peat reefs in Nauset Marsh on Cape Cod were estimated to last 7.5–15 years [14].

5.2. Ecological significance of peat reefs

Intertidal and subtidal peat reefs provide relatively unrecognized habitat for estuarine flora and fauna that do not occur on the marsh platform as indicated in this study. The abundant mud crabs (*D. sayi, P. herbstii,* and unidentified panopeids), and shrimps (*P. vulgaris,*), are good examples. Alternatively, the *G. demissa* is transported from the marsh platform to the deeper intertidal and subtidal channels, where they survive for a while on peat reefs but not on the, presumably older, deeper ones (personal observations). Once immersed, several common fishes (*Bairdiella chrysoura, Gobiosoma bosc*), including some rarer ones, can also occur.

The complex structure of peat reefs, such as living and decaying *S. alterniflora*, rugose surface of the peat, macroalgae, and crab burrows, may provide increased habitat complexity that is seldom available in most marsh creek channels [19]. Peat reefs may provide food and refuge, and thus nurseries for fishes and crabs. In fact, laboratory studies have shown reduced predation on juvenile lobsters while associated with peat reefs [37, 38]. Further studies of the structural and functional significance should place them in the broader context of the coastal seascapes [39, 40]. Included in this broader understanding should be how peat reef production influences salt marsh channel morphology and sediment and nutrient transport from the edge of the marsh platform to intertidal and subtidal environments [41], and if this is likely to be influenced by sea level rise, as is currently occurring in the study estuary [42] and coastal eutrophication in general [18, 43].

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