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RESEARCH ARTICLE

Molluscan Community Recovery in a New England Back-Barrier Salt Marsh Lagoon 10 Years after Partial Restoration

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Abstract

Like many Eastern U.S. salt marshes, East Harbor salt marsh lagoon on Cape Cod was isolated from tidal flow in the 1800s, resulting in near-freshwater conditions and loss of native salt marsh species. After its partial restoration in 2002, a variety of marine and estuarine fauna recolonized East Harbor, and soft shell clam (*Mya arenaria*) recolonization was particularly prolific. The goal of our study was to evaluate molluscan community composition, density, and distribution at regular intervals for 10 years following restoration, and to relate molluscan community recovery to various physical properties at the site. In 2007, 2008, and 2011, we sampled mollusks at several points across East Harbor, and we also recorded water salinity and temperature, particle size distribution, and submerged aquatic vegetation density. In 2007 and 2008, we encountered 12 and 11 mollusk species, respectively; *M. arenaria* was the most abundant species in 2007 and the second most abundant species in 2008. In 2011, we encountered eight mollusk species and *M. arenaria* was the most abundant species. Mollusk species richness declined from 12 to 8 species between 2008 and 2011. Our results show that mollusk species richness and density have declined significantly since the first few years following restoration; related studies attribute this to high summer water temperatures in the Main Lagoon and severe macroalgal blooms during 2005–2006. This suggests that East Harbor is still equilibrating to baseline conditions and that full tidal restoration may be necessary to sustain a diverse mollusk community at East Harbor.

Key words: benthic invertebrates, bivalves, salt marsh restoration, soft shell clams, tidal restriction.

Introduction

Atlantic coastal salt marshes function as floodwater controls, repositories and filters for pollutants, and buffers against sea level rise, and they play an integral role in the lifecycles of many marine organisms (Odum 1981; Warren et al. 2002). Despite the many ecosystem services they provide, historical land use involving tidal restriction often transformed the function of these ecosystems completely (Portnoy et al. 2005), resulting in rapid declines in native estuarine/marine species (Warren et al. 2002; Portnoy et al. 2006; Thelen & Thiet 2009; Smith et al. 2011). In the past two decades, widespread restoration efforts by ecologists and managers have sought to reinstate tidal flow and reestablish biological integrity and ecological functioning to these systems (Dauer 1993; Portnoy et al. 2005; Roman & Burdick 2012).

Bivalve mollusks, often the most abundant suspension feeders in an estuary, are integral to ecosystem functioning (Prins et al. 1998; Peterson & Heck 1999). By filtering phytoplankton and suspended detritus from the water column, bivalves reintroduce nutrients to the sediment as fecal matter, which then provide food for other species (Prins et al. 1998). This relocation of nutrients supports seagrass populations (Peterson & Heck 1999; Peterson & Heck 2001) that provide critical habitat for several threatened and endangered species. In addition, bivalve mollusks remove bacteria, heavy metals, and toxins from the water column (Decho & Luoma 1996), and are considered indicator species of good water quality (Dauer 1993). Despite their important functions in global estuaries, few studies have documented long-term trends in mollusk recovery in previously degraded, restored tidal ecosystems (Borja et al. 2010).

The molluscan community in East Harbor, a back-barrier salt marsh lagoon on Cape Cod National Seashore (CCNS), MA, U.S.A. (Fig. 1), was extirpated after artificial isolation from Cape Cod Bay in 1868. In 2002, prompted by decades of water quality problems that led to outbreaks of nuisance midges and fish kills, CCNS and the Town of Truro, MA, partially restored tidal flow to the marsh by opening clapper

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Figure 1. East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A. We sampled mollusks and measured water salinity and water temperature in 2007, 2008, and 2011, submerged aquatic vegetation density in 2007 and 2008, and particle size distribution in 2008 in Moon Pond, the Main Lagoon, and the Northwest Cove.

valves that previously restricted water movement between the two water bodies. Mollusks are among the first species to recolonize restored salt marshes (Warren et al. 2002; Portnoy et al. 2006; Thelen & Thiet 2009), and several mollusk species recolonized East Harbor within 2 years of restoration. By 2005, soft shell clams (*Mya arenaria*) had established in very high densities, and the commercially valuable quahog (*Mercenaria mercenaria*) also established in moderate densities (Thelen & Thiet 2009). By 2009, water chemistry and nekton diversity were close to ranges that would occur naturally in the system (Smith et al. 2009). Nonetheless, mollusk species richness and density have declined since the first mollusk survey in 2005 (Portnoy et al. 2006; Smith et al. 2008; Thelen & Thiet 2009); this has been attributed to high water temperatures and low dissolved oxygen levels associated with macroalgal blooms (Portnoy et al. 2006; Thelen & Thiet 2009; Thiet et al. 2014). Clearly, despite several positive restoration outcomes at this site, optimal functioning has not yet been achieved and long-term monitoring is necessary to understand restoration outcomes.

The goal of this study is to document molluscan community recovery in East Harbor at various intervals following partial tidal restoration in 2002. Our specific objectives are to (1) quantify molluscan species richness, density, and distribution throughout East Harbor 5, 6, and 9 years after restoration, (2) evaluate the relationships between molluscan species richness and density, water salinity and temperature, sediment particle size, and submerged aquatic vegetation (SAV) density, and (3) compare results from our 2007, 2008, and 2011 mollusk surveys to the first post-restoration mollusk survey of the site in 2005 (Thelen & Thiet 2009).

Methods

Site Description

East Harbor (42.10°N, 70.08°W) is a 291-ha back-barrier salt marsh lagoon within CCNS in Truro, MA, U.S.A. (Fig. 1). A culvert (1.2 m d × 213 m l) that connects East Harbor to Cape Cod Bay at the southeastern corner of the marsh has been kept open continually since partial restoration in 2002. The system is separated into three distinct areas based on salinity and distance from the culvert. From highest to lowest salinity, these areas are Moon Pond, the Main Lagoon, and the Northwest Cove (Fig. 1). An additional culvert (0.88 m high × 2.2 m wide × 9.5 m long) under High Head Road connects Moon Pond to the Main Lagoon and results in reduced tidal flow to the Lagoon and Northwest Cove; daily tide ranges in Moon Pond are ~46 cm but only 2–3 cm in the lagoon (Portnoy et al. 2007). The perimeter of the lagoon (average depth = 3 m) is characterized by a mix of sand dune vegetation and, in lower-lying areas, giant reed grass (*Phragmites australis*), while Moon Pond is a vegetated salt marsh with a patchy matrix of *P. australis* and halophytes such as salt marsh cordgrass (*Spartina alterniflora*) and slender glasswort (*Salicornia maritima*).

When CCNS was established in 1959, it was charged with preserving and restoring natural, cultural, and historical coastal resources. As such, its long-term goal for the restoration of East Harbor was to restore natural ecosystem functioning as measured by the reestablishment of native salt marsh plants and fauna and, if possible, its historical function as a recreational shellfishery. The Town of Truro supported the restoration because the project had the potential to mitigate nuisance fish kills and prevent biting midge population explosions, and to provide habitat for recreational shellfishing.

Since partial tidal restoration in 2002, Moon Pond Creek, which receives seawater directly from Cape Cod Bay because of its close proximity to the culvert, regularly encounters salinities of 30 ppt, while salinity in the Main Lagoon has increased to approximately 25 ppt. Salinity in the Northwest Cove only ranges from 15 to 20 ppt, because it receives substantial freshwater input from the Province Lands groundwater lens and is furthest from the culvert connecting the system to Cape Cod Bay (Portnoy et al. 2006; Thelen & Thiet 2009). The average summer water temperature of East Harbor is 22°C, but late-summer water temperatures may reach 28–30°C in the Main Lagoon (Smith et al. 2011).

Since 2002, benthic invertebrate diversity and density in East Harbor have increased substantially (Portnoy et al. 2005; Thelen & Thiet 2009). Mollusks were encountered in 2003 and 2004 (Portnoy et al. 2005) and by 2005, healthy molluscan communities had reestablished, especially in areas of highest salinity; in that year densities of *M. arenaria* reached 3,178 individuals m^{-2} in Moon Pond (Thelen & Thiet 2009). Submerged aquatic vegetation (widgeongrass, *Ruppia maritima* and eelgrass, *Zostera marina*) also established throughout the marsh (Portnoy et al. 2005). Macroalgal blooms occurred in East Harbor in 2005 and 2006, leading to oxygen depletion and extensive mollusk die-off (Portnoy et al. 2007), and although blooms have not been as prolific since then, macroalgae still dominate primary productivity at the site (Smith et al. 2011). Shellfishing is currently not permitted at East Harbor because mollusk populations are not sufficiently stable to support it.

Experimental Design

We characterized molluscan species richness, density (individuals m^{-2}), and distribution in East Harbor in 2007, 2008, and 2011. In the years 2007 and 2008, we established 65 stratified random sampling points using ArcGIS 9.2 software (Esri, Redlands, CA, U.S.A.): 20 in Moon Pond, 15 in the Northwest Cove, and 30 in the Main Lagoon; the number of sample points in each area was chosen to reflect their respective geographic extent (e.g. the Main Lagoon is much larger than the other two areas, so we sampled more points there). We chose stratified random sampling to capture a representative sample of mollusk communities in the three areas of East Harbor that differ significantly in salinity, temperature, dissolved oxygen, and distance from the culvert that connects East Harbor to Cape Cod Bay (Portnoy et al. 2005; Smith et al. 2008; Thelen & Thiet 2009). In 2011, we sampled 48 points: 20 in Moon Pond, 24 along the perimeter of the Main Lagoon, and 4 in the Northwest Cove.

Each sample year during June–July, we collected five benthic core samples (10 cm diameter × 20 cm depth) at each 1-m^2 sample point, sieved them through 1 mm mesh to collect large mollusks, then searched the remaining material for 2 minutes to ensure unbiased detection of individual mollusks (Thelen & Thiet 2009). All live mollusks were identified to species and measured (cm) using a caliper.

Each year at each sampling point when benthic samples were collected, we also measured water temperature (°C) and salinity (ppt) (Table 1). In 2007 and 2008, we quantified SAV density by counting the number of shoots of *R. maritima* and *Z. marina* within a 0.25-m^2 quadrat placed on the substrate at each of sampling point (Table 1). We did not measure SAV density in 2011. In 2008 only, a sediment sample (5 cm depth) was also taken at each point using a 3 cm-diameter benthic corer and used for particle size analysis to evaluate the effects of sediment composition on mollusk species richness and density (Hyland et al. 2004; Kennish et al. 2004; Poulton et al. 2004). Each sediment sample was dried in a drying oven for 24 hours, and graduated sieves (2, 1, 0.5, 0.25, 0.10, and 0.053 mm) were used to separate particle size classes according to the Wentworth scale (Elefteriou & McIntyre 2005; Laswell et al. 2010).

Data Analysis

Mollusk species richness and density data (2007, 2008, and 2011) were nonnormally distributed and data transformation did not improve normality; thus, we used nonparametric Spearman's rank (R_s) correlations to evaluate relationships between mollusk species richness and density and salinity,

Table 1. Mean (± SE) salinity (ppt), temperature (°C), submerged aquatic vegetation (SAV) density (number of stems m^{-2}), and sediment particle size distribution (g) in East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Moon Pond			*Main Lagoon*			*Northwest Cove*		
	2007	*2008*	*2011*	*2007*	*2008*	*2011*	*2007*	*2008*	*2011*
Salinity	25.2 ± 0.1	23.7 ± 0.1	19.3 ± 0.3	25.1 ± 0.1	21.9 ± 0.1	17.8 ± 0.5	23.9 ± 2.5	19.5 ± 0.1	19.8 ± 0.3
Temp	24.3 ± 0.1	25.5 ± 0.1	21.7 ± 0.6	23.4 ± 0.1	22.8 ± 0.1	28.5 ± 0.3	21.6 ± 0.1	20.8 ± 0.0	28.0 ± 0.4
SAV density	0.2 ± 0.0	0.2 ± 0.0	—	0.1 ± 0.0	0.0 ± 0.0	—	0.2 ± 0.0	0.3 ± 0.0	—

	Moon Pond				*Main Lagoon*				*Northwest Cove*			
Sediment particle size (2008)	*Gravel + very coarse sand*	*Coarse + medium sand*	*Fine + very fine sand*	*Silt + clay*	*Gravel + very coarse sand*	*Coarse + medium sand*	*Fine + very fine sand*	*Silt + clay*	*Gravel + very coarse sand*	*Coarse + medium sand*	*Fine + very fine sand*	*Silt + clay*
	6.8 ± 0.7	12.9 ± 0.7	0.3 ± 0.2	0.0 ± 0.0	5.1 ± 0.7	14.1 ± 0.6	0.5 ± 0.2	0.0 ± 0.0	5.2 ± 0.6	14.5 ± 0.5	0.2 ± 0.1	0.0 ± 0.0

SAV density was measured in 2007 and 2008 only, and sediment particle size was measured in 2008 only.

Table 2. Mollusk species richness by region and study year in East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Moon Pond				*Main Lagoon*				*Northwest Cove*				*East Harbor Overall*			
Species	*2005*	*2007*	*2008*	*2011*	*2005*	*2007*	*2008*	*2011*	*2005*	*2007*	*2008*	*2011*	*2005*	*2007*	*2008*	*2011*
Anomia spp.	X												X			
Ensis directus	X			X									X			X
Euspira heros	X	X	X										X	X	X	
Gemma gemma	X	X	X				X						X	X	X	
Geukensia demissa					X	X			X				X			
Ilyanassa obsoleta		X	X	X				X						X	X	X
Littorina spp.	X	X			X								X	X		
Macoma balthica	X					X	X	X		X			X	X	X	X
Mercenaria mercenaria	X	X	X	X	X			X					X	X	X	X
Mulinia lateralis			X		X	X	X			X			X	X	X	
Mya arenaria	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Mytilus edulis	X	X			X		X						X	X	X	
Nucella lapillus	X	X											X	X		
Order Cephalaspidea	X		X		X	X	X	X			X	X	X	X	X	X
Petricola pholadiformis	X	X	X		X			X					X	X	X	X
Spisula solidissima	X			X	X			X				X	X			X
Tagelus plebeius	X												X			
Tellina agilis			X				X								X	
Total	14	9	9	5	9	5	7	7	2	3	2	3	16	12	11	8

Data from 2005 are taken from Thelen and Thiet (2009).

temperature, SAV density (2007 and 2008 only), and particle size distribution (2008 only) using the data collected at each sample point as replicates (i.e. $n = 65$ in 2007 and 2008, $n = 48$ in 2011). To determine if mollusk species richness and density differed among the three regions of East Harbor, we used nonparametric Wilcoxon/Kruskal-Wallis tests on 2007 and 2008 mollusk species richness and density data and on 2011 species richness data. Tukey's HSD post hoc tests were used for means comparisons.

In 2011, only three species were encountered with enough regularity to warrant detailed analyses: *M. arenaria*, *M. mercenaria*, and *Spisula solidissma* (Atlantic surf clam). We used Spearman's rank (R_s) correlation analyses to determine if relationships existed between density of these three species and water salinity and water temperature, again using sample points as replicates.

JMP statistical software (v. 9.0, Cary, NC, U.S.A.) was used for all analyses, and statistical significance was determined at $\alpha \leq 0.05$ unless otherwise noted.

Results

Species Richness

Sixteen mollusk species have been documented at East Harbor since 2005, only five of which have been encountered every sampling year (2005, 2007, 2008, and 2011): *Macoma balthica* (Baltic macoma), *M. mercenaria*, *M. arenaria*, Cephalaspidea, and *Petricola pholadiformis* (false angel wing) (Table 2). Species richness decreased in Moon Pond from 14 species to 5 species between 2005 and 2011, but richness did not change substantially in the Main Lagoon and the Northwest Cove during those years (Table 2).

We detected 12 mollusk species in East Harbor in 2007 (Table 2), 5 of which were found only in Moon Pond: *Euspira heros* (Northern moon snail), *Ilyanassa obsoleta* (eastern mudsnail), *M. mercenaria*, *Mytilus edulis* (blue mussel), and *P. pholadiformis*. We also observed *Crassostrea virginica* (Atlantic oyster) in Moon Pond but it did not occur in our benthic cores. Four species encountered in 2005 were not detected in 2007: *Anomia* spp. (jingle shell), *Ensis directus* (razor clam), *Spisula solidissima* (Atlantic surf clam), and *Tagelus plebeius* (stout razor clam) (Table 2).

We found 11 mollusk species in East Harbor in 2008 (Table 2), and 4 of these were found only in Moon Pond: *E. heros*, *I. obsoleta*, *M. mercenaria*, and *P. pholadiformis*. As in 2007, *Anomia* spp., *E. directus*, *Nucella lapillus* (dog-whelk), *S. solidissima*, and *T. plebeius*, all present in 2005, were absent in 2008. Two species found in 2007, *Geukensia demissa* (ribbed mussel) and *Littorina littorea* (common periwinkle), were not detected in 2008 (Table 2). Mollusk species richness was significantly positively correlated with water salinity and temperature in 2008 but not in 2007 or 2011 (Table 3), and richness and density were significantly positively correlated with very coarse sand content and negatively correlated with smaller sediment particle sizes (Table 4).

We found eight molluscan species in East Harbor in 2011 (Table 2). Four species were detected in the Main Lagoon in 2011 that were not detected there in 2008: *M. mercenaria*, *I. obsoleta*, *P. pholadiformis*, and *S. solidissima*. Five species seen in 2008 were not detected in 2011: *E. heros*, *Gemma gemma* (amethyst gem clam), *Mulinia lateralis* (dwarf surf clam), *M. edulis*, and *Tellina agilis* (Northern dwarf tellin) (Table 2). We did not encounter *L. littorea* in core samples or by observation in 2011, but the species was observed in

Table 3. Results from Spearman's rank (R_s) correlation analyses between mollusk species richness, density, and size versus water salinity, water temperature, and submerged aquatic vegetation (SAV) (2007 and 2008 only) at East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Salinity			*Temperature*			*SAV*		
	2007	*2008*	*2011*	*2007*	*2008*	*2011*	*2007*	*2008*	*2011*
Richness	$R_s = 0.17$ $p < 0.19$	**$R_s = 0.45$** **$p < 0.00$**	$R_s = 0.18$ $p = 0.23$	$R_s = 0.03$ $p = 0.81$	**$R_s = 0.52$** **$p < 0.00$**	$R_s = 0.05$ $p = 0.74$	$R_s = 0.12$ $p < 0.35$	$R_s = 0.01$ $p < 0.96$	—
Density	$R_s = 0.18$ $p < 0.16$	**$R_s = 0.34$** **$p < 0.01$**	*Ma*: $R_s = 0.07$ $p = 0.58$ *Mm*: $R_s = 0.26$ $p = 0.08$ *Ss*: $R_s = -0.03$ $p = 0.85$	$R_s = 0.125$ $p = 0.36$	**$R_s = 0.50$** **$p < 0.00$**	***Ma*: $R_s = -0.31$** **$p = 0.04$** *Mm*: $R_s = -0.03$ $p = 0.84$ ***Ss*: $R_s = 0.37$** **$p = 0.01$**	$R_s = 0.09$ $p < 0.46$	$R_s = 0.04$ $p < 0.74$	—
Size	**$R_s = -0.31$** **$p < 0.00$**	**$R_s = 0.14$** **$p < 0.00$**	*Ma*: $R_s = 0.06$ $p < 0.71$ *Mm*: $R_s = 0.08$ $p = 0.60$ *Ss*: $R_s = 0.02$ $p = 0.9$	**$R_s = 0.11$** **$p < 0.00$**	$R_s = 0.02$ $p = 0.47$	*Ma*: $R_s = 0.14$ $p = 0.37$ *Mm*: $R_s = -0.04$ $p = 0.79$ ***Ss*: $R_s = 0.43$** **$p = 0.00$**	**$R_s = -0.28$** **$p < 0.00$**	**$R_s = -0.29$** **$p < 0.00$**	—

Bolded values are significant correlations. For 2011 analyses, "*Ma*," *Mya arenaria*; "*Mm*," *Mercenaria mercenaria*; and "*Ss*," *Spisula solidissima*. That year, these were the only species with high enough densities to run correlation analyses.

Table 4. Results from Spearman's rank (R_s) correlation analyses between mollusk species richness and density and particle size class at East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Gravel	*Very Coarse Sand*	*Coarse Sand*	*Medium-Grain Sand*	*Fine Sand*	*Very Fine Sand*	*Silt and Clay*
Richness	$R_s = 0.18$ $p = 0.17$	**$R_s = 0.37$** **$p < 0.00$**	$R_s = -0.23$ $p = 0.07$	**$R_s = -0.34$** **$p < 0.01$**	$R_s = -0.01$ $p = 0.31$	$R_s = -0.24$ $p = 0.06$	**$R_s = -0.31$** **$p < 0.01$**
Density	$R_s = 0.09$ $p = 0.47$	**$R_s = 0.26$** **$p = 0.04$**	$R_s = -0.08$ $p = 0.51$	**$R_s = -0.27$** **$p = 0.04$**	$R_s = -0.06$ $p = 0.08$	$R_s = -0.22$ $p = 0.08$	$R_s = -0.23$ $p = 0.07$

Particle size distribution was measured in 2008 only. Bolded values are significant correlations.

East Harbor in 2005 and 2007. Molluscan species richness in 2011 was not significantly different among Moon Pond, the Main Lagoon, and the Northwest Cove (Wilcoxon $\chi^2 = 1.20$, $p = 0.55$).

Density

Mya arenaria was the species with the greatest density in East Harbor in 2005, 2007, and 2011; however, density of this species declined precipitously between 2005 and 2007 and remained low in 2011 (Table 5). In 2007, 7 of the 12 mollusk species detected occurred in the greatest densities in Moon Pond: *E. heros*, *G. gemma*, *I. obsoleta*, *M. mercenaria*, *M. arenaria*, *M. edulis*, and *P. pholadiformis* (Table 5). That year, *M. arenaria* density dropped precipitously in Moon Pond to 2.4 (±0.57) individuals m^{-2} (Table 5).

In 2008, 6 of the 11 mollusk species we encountered occurred in the greatest densities in Moon Pond: *E. heros*, *G. gemma*, *I. obsoleta*, *M. mercenaria*, *P. pholadiformis*, and *T. agilis*, and Cephalaspidea density increased, particularly in the Northwest Cove (Table 5).

Of the eight species we encountered in 2011, only *M. arenaria* and *S. solidissma* were detected in all three regions of East Harbor, and five of the eight mollusk species detected that year had the greatest densities in the Main Lagoon: *I. obsoleta*, *M. balthica*, *M. mercenaria*, *P. pholadiformis*, and *S. solidissima* (Table 5). Density of all species encountered in Moon Pond in 2005 decreased substantially by 2011, and *M. arenaria* density declined the most, from 3,178.33 (±1,809.94) individuals m^{-2} in 2005 to 8.4 (±1.57) individuals m^{-2} in 2011. *Mya arenaria* density in the Main Lagoon also declined from 2,971.09 (±726.64) m^{-2} in 2005 to 6.83 (±1.64) m^{-2} in 2011 (Table 5). In 2011, neither *M. arenaria* nor *M. mercenaria* densities were significantly different among the three regions of East Harbor (Wilcoxon $\chi^2 = 2.56$, $p = 0.28$ and Wilcoxon $\chi^2 = 2.24$, $p = 0.33$, respectively), but *S. solidisima* density was significantly greater in the Main Lagoon than in Moon Pond and the Northwest Cove, and significantly greater in Moon Pond than in the Northwest Cove (Wilcoxon $\chi^2 = 8.42$, $p = 0.02$).

We did not observe any consistent correlations between mollusk density and salinity, temperature, or SAV in our sample years (Table 3); however, mollusk density was significantly positively correlated with coarse sand content and negatively correlated with smaller particle sizes (Table 4).

Size Class

In 2007 and 2008, *M. arenaria* were the largest mollusks in East Harbor, ranging from 2.71 (±0.06) cm in the Main

Table 5. Mollusk species density (individuals m^{-2}) by region and study year in East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Moon Pond				*Main Lagoon*				*Northwest Cove*			
	n = *10*	n = *20*		n = *20*	n = *30*	n = *50*		n = *24*	n = *10*	n = *15*		n = *4*
Species	*2005*	*2007*	*2008*	*2011*	*2005*	*2007*	*2008*	*2011*	*2005*	*2007*	*2008*	*2011*
Anomia spp.	3.2 ± 3.2	—	—	—	—	—	—	—	—	—	—	—
Ensis directus	1 ± 0.7	—	—	0.4 ± 0.3	—	—	—	—	—	—	—	—
Euspira heros	1.1 ± 1.1	0.1	0.1	—	—	—	—	—	—	—	—	—
Gemma gemma	178.3 ± 118.5	1.5 ± 0.6	1.1 ± 0.4	—	—	—	0.1	—	—	—	—	—
Geukensia demissa	—	—	—	—	0.8 ± 0.4	0.1	—	—	0.1 ± 0.1	—	—	—
Ilyanassa obsoleta	—	0.1	0.1 ± 0.0	0.2 ± 0.1	—	—	—	0.5 ± 0.3	—	—	—	—
Littorina littorea	42.5 ± 30.3	0.1	—	—	1.0 ± 0.4	—	—	—	—	—	—	—
Macoma balthica	0.1 ± 0.1	—	—	—	—	0.2 ± 0.0	0.1 ± 0.0	0.8 ± 0.6	—	1.3	—	—
Mercenaria mercenaria	18.1 ± 13.6	0.2 ± 0.0	0.2 ± 0.1	1.4 ± 0.8	4.4 ± 3.1	—	—	2.2 ± 0.9	—	—	—	—
Mulinia lateralis	—	—	0.1	—	6.4 ± 4.7	0.1 ± 0.0	0.1 ± 0.0	—	—	0.2 ± 0.0	—	—
Mya arenaria	3,178.3 ± 1,809.9	2.4 ± 0.6	0.7 ± 0.1	8.4 ± 1.6	2,971.1 ± 726.6	0.8 ± 0.2	0.7 ± 0.2	6.8 ± 1.6	0.2 ± 0.2	0.7 ± 0.1	0.6 ± 0.2	1 ± 0.6
Mytilus edulis	47.3 ± 32.9	0.2 ± 0.1	—	—	0.04 ± 0.04	—	0.1	—	—	—	—	—
Nucella lapillus	0.2 ± 0.2	0.1	—	—	—	—	—	—	—	—	—	—
Order Cephalaspidea	*	—	0.1	—	*	0.1 ± 0.0	1.0 ± 0.2	0.3 ± 0.3	*	—	2.2 ± 0.5	1 ± 1
Petricola pholadiformis	*	0.3 ± 0.1	0.1	—	*	—	—	0.1 ± 0.1	*	—	—	—
Spisula solidissima	*	—	—	1.5 ± 1.5	*	—	—	4.7 ± 2.0	*	—	—	1 ± 0.6
Tagelus plebeius	0.1 ± 0.1	—	—	—	—	—	—	—	—	—	—	—
Tellina agilis	—	—	0.4 ± 0.1	—	—	—	0.1 ± 0.0	—	—	—	—	—

Data are mean ± SE; where no SE is given, only one individual was found. Data from 2005 taken from Thelen and Thiet (2009). Asterisks indicate species for which low numbers of small (<2 cm) individuals were detected with the shovel method only; thus, that year those species were represented in species richness analyses but were not included in density calculations.

Lagoon to 5.51 (±0.09) cm in the Northwest Cove, but *M. arenaria* individuals were much smaller in 2011 (Table 6). We also encountered relatively large individuals of *E. heros* and *M. edulis* in 2007 (Table 6). We did not observe any consistent correlations between mollusk size and salinity, temperature, or SAV in any of our sample years (Table 3).

Discussion

Mollusks were among the first organisms to recolonize East Harbor following partial restoration in 2002, likely via larvae entering the system in tides (Portnoy et al. 2006; Portnoy et al. 2007; Smith et al. 2008); however, mollusk species richness and density declined significantly between 2005 and 2011, particularly in Moon Pond and the Main Lagoon. These declines have likely been caused by a combination of factors. High summer water temperatures in the Main Lagoon may directly kill mollusk adults, larvae, and eggs (Kennedy & Mihursky 1971; Cargnelli et al. 1999; Christian et al. 2010; Smith et al. 2011). Elevated water temperatures in the lagoon also contributed to macroalgal blooms during 2005–2006 (after our original sampling in 2005), which led to severe anoxia and, subsequently, high shellfish mortality (Portnoy et al. 2006; Portnoy et al. 2007; Smith et al. 2008; Smith et al. 2011). Bottom water and benthic oxygen levels are the primary factors influencing soft-bottom macroinvertebrate recolonization of previously degraded marine benthic communities (Borja et al. 2006).

Shellfish populations in other New England salt marshes recover rapidly after tidal restoration (Peck et al. 1994; Borja et al. 2010) but remain sensitive to fluctuations in salinity, temperature, oxygen, and SAV density (Dauer 1993; Hyland et al. 2004). Although their populations have fluctuated, the consistent presence of *M. arenaria*, *M. mercenaria*, and *M. balthica* at East Harbor may indicate that water quality and sediment chemistry are generally suitable to support these species over time (Warwick 1986; Dauer 1993). Despite the stochastic, r-selected recruitment strategy of *M. arenaria* (Lotze et al. 2006), Dauer (1993) considers *M. arenaria* and *M. mercenaria* to be "equilibrium species," which are defined as relatively long-lived species that achieve high biomass in undisturbed systems. Nonetheless, East Harbor still experiences significant episodes of stress (e.g. high water temperatures) that directly kill mollusks, and which contribute to algal blooms that lead to anoxia, resulting in SAV, fish, and shellfish mortality. Since macroalgae still account for the majority of primary productivity at the site (Smith et al. 2011), mollusk die offs may recur unless steps are taken to remedy conditions that promote algal growth.

A recent study at East Harbor (Thiet et al. 2014) suggests that rapid and prolific recolonization of East Harbor by mollusks following tidal restoration directly contributed to the algal blooms of 2005–2006, resulting in a negative feedback

Table 6. Mollusk size (cm) by region and study year in East Harbor back-barrier salt marsh lagoon, Cape Cod National Seashore, Truro, MA, U.S.A.

	Moon Pond			*Main Lagoon*			*Northwest Cove*		
	n = *20*		n = *20*	n = *50*		n = *24*	n = *15*		n = *4*
Species	*2007*	*2008*	*2011*	*2007*	*2008*	*2011*	*2007*	*2008*	*2011*
Anomia spp.	—	—	—	—	—	—	—	—	—
Ensis directus	—	—	7.4 ± 0.2	—	—	—	—	—	—
Euspira heros	2.10	4.2	—	—	—	—	—	—	—
Gemma gemma	0.2 ± 0.0	0.2 ± 0.0	—	—	0.1	—	—	—	—
Geukensia demissa	—	—	—	3.2	—	—	—	—	—
Ilyanassa obsoleta	1.5	2.5 ± 0.2	2.0 ± 0.2	—	—	1.8 ± 0.2	—	—	—
Littorina spp.	1.5	—	—	—	—				
Macoma balthica	—	—	—	1.6 ± 0.2	2.2 ± 0.3	0.25	24.0	—	—
Mercenaria mercenaria	1.4 ± 0.1	1.1 ± 0.2	2.4 ± 0.7	—	—	1.0 ± 0.4	—	—	—
Mulinia lateralis	—	0.6	—	1.3 ± 0.1	1.0 ± 0.1	—	19.9 ± 1.1	—	—
Mya arenaria	3.6 ± 0.1	3.0 ± 0.3	2.0 ± 0.5	2.7 ± 0.1	3.0 ± 0.1	3.9 ± 0.2	55.1 ± 0.9	51.7 ± 0.9	1.9 ± 1.6
Mytilus edulis	3.0 ± 1.6	—	—	—	0.1	—	—	—	—
Nucella lapillus	1.6	—	—	—	—	—	—	—	—
Order Cephalaspidea	—	0.9	—	1.3 ± 0.2	0.6 ± 0.1	0.6	—	5.3 ± 0.1	0.7
Petricola pholadiformis	1.2 ±0.1	0.6	—	—	—	4.0	—	—	—
Spisula solidissima	—	—	0.2 ± 0.0	—	—	1.2 ± 0.2	—	—	0.4 ± 0.2
Tagelus plebeius	—	—	—	—	—	—	—	—	—
Tellina agilis	—	0.8 ± 0.0	—	—	1.0 ± 0.1	—	—	—	—

Data are mean ± SE; where no SE is given, only one individual was found.

on molluscan richness and density. In that study, *M. arenaria* significantly increased macroalgal biomass by increasing benthic and water column N and P levels and clarifying the water column (Thiet et al. 2014). Similarly, zebra mussel invasion has increased macroalgal productivity in northern U.S. lakes via nutrient deposition and clarification of the water column (Lowe & Pillsbury 1995; Mayer et al. 2002). Further, two gastropod grazers that commonly regulate macroalgal growth in New England salt marshes, *Ilyannassa obsoleta* (mud snail) and *L. littorea*, have been largely absent from the East Harbor Main Lagoon (where algal blooms are most extensive) owing to high summer water temperatures (Smith et al. 2011). Thiet et al. (2014) also observed that the presence of *L. littorea* significantly reduced macroalgal growth in experimental mesocosms.

Currently the tide range in Moon Pond is <0.5 m (tide range at a nearby unrestricted site is 2.5–3.5 m), and a culvert separating Moon Pond from the lagoon and Northwest Cove severely restricts tide ranges in those areas of East Harbor to only 3 cm (Portnoy et al. 2006). Consequently, aerated seawater entering East Harbor from Cape Cod Bay accounts for a mere fraction of the lagoon's total volume, and thus has no notable effect on the system's oxygen budget (Portnoy et al. 2005, 2006). Improved tidal flushing of East Harbor would have several positive effects on the system and would likely improve long-term restoration outcomes. First, better tidal flow would alleviate oxygen stress that directly kills mollusks, remove excess nutrients that facilitate algal productivity, and regulate summer water temperatures so that algal grazers may establish viable populations. Lower water temperatures would also stabilize mollusk populations that are sensitive to temperature and salinity (Kennish et al. 2004; Dethier & Schoch 2005). Second, increased tidal flow would likely increase salinity in areas of East Harbor such as the lagoon and Northwest Cove (Portnoy 1991; Burdick et al. 1997) to levels that support greater mollusk richness and diversity. Third, higher tides would deposit more coarse sediment throughout East Harbor, which would support better mollusk recruitment (Christiansen et al. 2000; Hyland et al. 2004; Kennish et al. 2004; Poulton et al. 2004). Fourth, increased tidal exchange would help buffer East Harbor against climate change, as large areas of the system are currently more influenced by climatic conditions than by the quality of seawater from Cape Cod Bay. Climate change on Cape Cod is predicted to include higher summer temperatures and increased precipitation (Frumhoff et al. 2007), which, respectively, would raise water temperatures and reduce salinity.

Studies are underway to understand that role of predators in mollusk species richness and density at this site. Predaceous fishes are notably absent from the East Harbor lagoon (Portnoy et al. 2007), likely because grates in the culvert that connects the system to Cape Cod Bay block their entry. We regularly observed American eels (*Anguilla rostrata*) and moonsnails (*E. heros*) in Moon Pond; both are voracious predators of bivalve mollusks, especially *M. arenaria* (Hunt & Mullineaux 2002). Horseshoe crabs (*Limulus polyphemus*), also a common predator of benthic mollusks, increased in the Main Lagoon in 2008, with a notable increase in density in 2009 (they were not captured in our benthic coring) (Smith et al. 2009). In addition, invasive green crabs (*Carcinus maenas*) have increased dramatically in Moon Pond since 2005 (Smith et al. 2008); *C. maenas* has severely reduced bivalve populations in other regions of the Gulf of Maine (Ropes 1968).

In addition to their ecological implications, our results have implications for recreational uses of East Harbor. Cape Cod has a deep cultural and economic history of shellfishing, and much of the economy of its coastal communities is dependent upon the shellfishing industry. Several valuable mollusk species are present at the site, with *M. arenaria* and *M. mercenaria* being particularly valuable species. *M. arenaria* of harvestable size (2.54 cm hinge width for commercial harvest, 5.08 cm anterior–posterior length for recreational harvest) were documented in both 2005 (Thelen & Thiet 2009) and 2007, and although no harvestable individuals of either *M. arenaria* or *M. mercenaria* were encountered in 2011, juveniles of both species were abundant. Other valuable species are present at the site as well; density of *M. edulis* has declined since 2005, when the species was abundant in Moon Pond (Thelen & Thiet 2009), and we observed eastern oyster (*Crassostrea virginica*) in 2007 and subsequent years (although they were not captured by our sampling efforts). These observations suggest that if conditions at East Harbor stabilize, then mollusk communities at the site may recover sufficiently to support recreational shellfishing in the future. This added function of East Harbor could increase public support for on-going restoration efforts at the site.

Implications for Practice

- Because coastal salt marsh lagoons with restored tidal flow may take years to reach equilibrium, long-term monitoring of physical and biological properties is necessary to understand restoration outcomes and evaluate restoration goals.
- Restorationists and managers should prioritize full tidal flushing of back-barrier salt marsh lagoons to mitigate high summer water temperatures that directly kill mollusks and facilitate algal blooms, and to ensure coarse sediment deposition that supports mollusk establishment.
- Macroalgal blooms that cause anoxia and mollusk mortality should be addressed by restoring for conditions that mitigate nutrient loading and ensure colonization by algal grazers.

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