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RESEARCH ARTICLE

Shoreline infrastructure degradation and increasing littoral naturalization accommodates juvenile fish and crab assemblages in heavily urbanized Upper New York Harbor

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Many estuarine shorelines are influenced by urbanization. Extensive shoreline modification in Upper New York Harbor (UNYH) included port development, landfilling marshes, and armoring. Recent sedimentation in constructed shipping terminal embayments, abandonment of shoreline structure maintenance, subsequent recruitment of upland and intertidal vegetation, and restoration projects have naturalized some shorelines in this urban setting. We determined the species composition and relative abundance of fishes and crabs in shallow shoreline habitats in constructed embayments of UNYH with seine sampling to determine the potential for restoring similar isolated shallow water sites as functional habitats. Twenty-seven identified species of fishes and crabs, including seasonally transient and resident marsh species, were represented in samples dominated by *Menidia menidia*, but marsh resident and coastal ocean species were also periodically abundant. Differences in assemblage structure among the sampled embayments as measured by principal components analysis were weak despite some differences in the slope and colonization of vegetation along shorelines. The mere presence of shallow shorelines was sufficient to recruit numerous species. Assemblage differences relative to a nearby relatively unaltered estuary revealed a lack of southern, warm affiliated species reflecting a natural clinal gradient. Marsh resident species dominated in UNYH, but not as strongly as at the reference estuary. Together with a previously published evaluation of life cycle connectivity for several sentinel species, this study shows that even small, isolated projects seeking to restore shallow shorelines add value to the estuarine landscape and are worth pursuing.

Key words: crabs, fishes, nursery habitat, restoration, shallow, shoreline

Implications for Practice

- Despite small size, discontinuity, and a history of industrial use, naturalized shallow estuarine shorelines at the heads of commercial port embayments hosted rich and diverse juvenile fish and crab assemblages.
- Because recruitment for some species is through a planktonic larval dispersal phase, the total amount of shallow shoreline habitat, more than its continuity, may be important in restoring an estuary to its historical nursery function for those species.
- Natural processes can restore estuarine nursery function to constructed embayments when natural coves have been removed.

Introduction

Estuaries are critically important habitats for many fish and invertebrate species (Elliot & Hemingway 2002; Day et al. 2013), including in the northeastern United States (Able & Fahay 2010). The shallow waters of estuarine shorelines are especially important as transitions between terrestrial and aquatic habitats and, as such, integrate functions related to land and water quality (Abood & Metzger 1996; Bilkovic & Roggero 2008). Therefore, assessment of shallow shoreline waters is central to evaluating the effects of urbanization (Airoldi & Beck 2007; Wen et al. 2010; Vincent 2011; Gittman et al. 2015, 2016) and to developing plans for ecological engineering relevant to restoration. "Ecological engineering" follows Chapman and Blockley (2009) in referring to the placement or amendment of physical features, usually as mimics of natural features, with an intent to support indigenous biota. A focus on shallow shoreline restoration is evident in urbanized shorelines around the world, including Europe (Cattrijsse et al. 2002; Airoldi & Beck 2007; Verdiell-Cubedo et al. 2012), the United States (Lotze

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2010), and the tropics (Blaber 2000). This arises, in part, over concern for the continued structure and function of estuaries as habitat for fish, shrimp, and crabs (Whitfield & Elliot 2002; Peterson & Lowe 2009; Morley et al. 2012; Seitz et al. 2014).

Hardened shoreline borders are especially prevalent in the Hudson River estuary (Abood & Metzger 1996; Yozzo et al. 2004). The interface between water and land has been extensively altered along and near New York City since colonial times (Abood & Metzger 1996; Sanderson 2009). Alteration is evident in the geometry of shorelines along the New Jersey portion of Upper New York Harbor (UNYH), an area originally known as Oyster Bay (Cohen & Augustyn 1997) and later as the Jersey Flats (Figs. 1 & 2). Some of the greatest modifications there occurred as port and port-related development (Squires 1992). During World War II, earthen "piers" (e.g. Military Ocean Terminal at Bayonne, MOTBY) were built over the

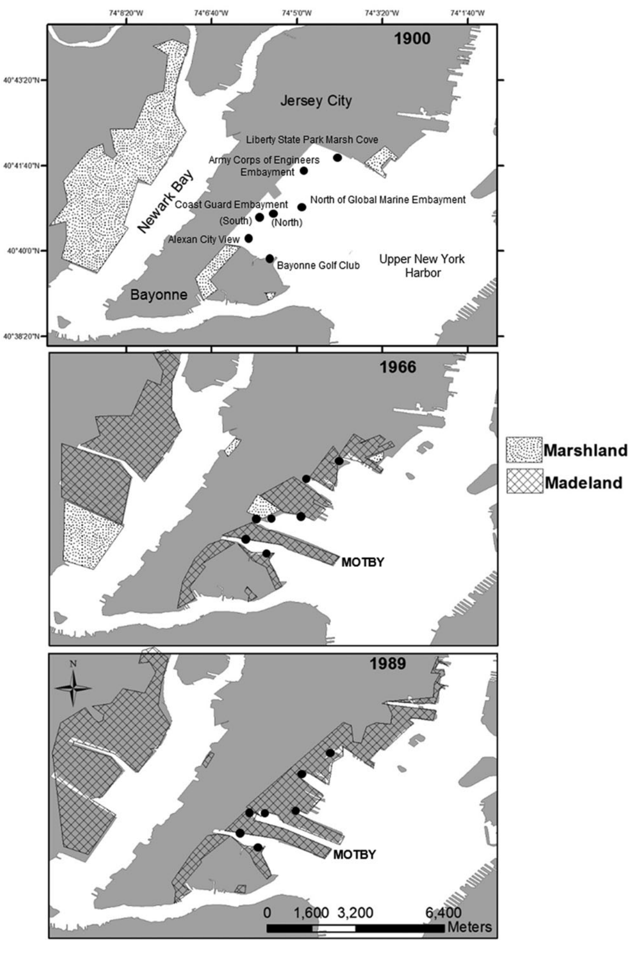

Figure 1. Diagrammatic representation of two major habitat types over time (1900–1989) in Upper New York Harbor shorelines (after Squires 1992). "Marshland" indicates areas of emergent aquatic vegetation. "Madeland" indicates areas where marshlands and shallow shorelines were filled with soil disposal, railroad construction, industrial development, and other sources as the result of human activity. Filled circles show the location of present day sample sites in historical context (see Fig. 2). "MOTBY" indicates the Military Ocean Terminal at Bayonne.

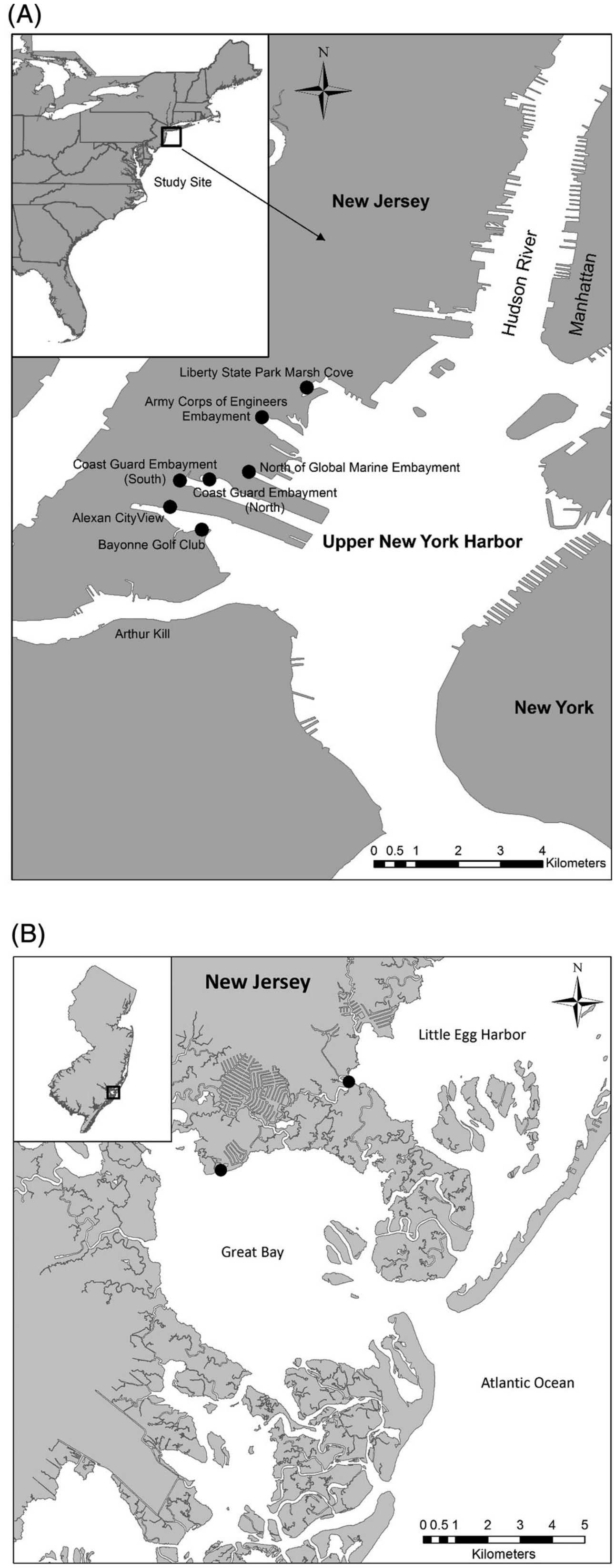

Figure 2. Study sites (filled circles) in New Jersey along the (A) Upper New York Harbor and the (B) Great Bay-Little Egg Harbor estuary.

Jersey Flats to extend into UNYH, reducing marsh land from 15.4×10^6 m^3 in 1900 to 4.3×10^6 m^3 in 1966 and none by 1989. At this time, steepening of the land/water interface and dredging of navigation channels dramatically reduced the extent and ecological integrity of shallows (Squires 1992). Shading by large piers along shorelines further reduced shallow shoreline habitat quality as reflected in reduced fish diversity and decreased abundance, feeding, and growth (Able & Duffy-Anderson 2006; Able et al. 2013).

Recently, emphasis has increased on fishes as indicators of ecosystem health within estuaries worldwide (Whitfield & Elliot 2002) including in UNYH. Water quality and shoreline structure in UNYH have changed in response to regulation, social values, and market forces (Strayer et al. 2012; Boicourt et al. 2016; Stinnette et al. 2018). Trawl and gillnet studies in channels and along bulkheaded, deepened shores of the harbor revealed use of the harbor by numerous fish, but the assemblage was more typical of a coastal assemblage than was to be expected of an estuary (Bain 2011). This was attributed especially to bulkheading and deepening (Bain 2011); however, the methods were unable to address shallow shoreline habitat. Thus, a comprehensive understanding of fish occurrence in shallow waters of UNYH is lacking, with the exception of a treatment of life history and habitat use for four sentinel species (*Fundulus heteroclitus* mummichog, *Fundulus majalis* striped killifish, *Menidia menidia* Atlantic silverside, and *Callinectes sapidus* blue crab) in the same area (Able & Grothues 2018). We advance an understanding of naturalized shoreline habitat here by quantifying the species composition and abundance of the entire fish and crab assemblage in shallow shoreline habitats of UNYH and comparing these to a nearby reference estuary. The overarching question is: given the duration and physical extent of modification to the estuary as a whole, can naturalization of small and fragmented shoreline patches support shallow shoreline assemblages?

Methods

Study Sites

Water in the UNYH fluctuates annually in daily mean temperature by ~27°C (Ashizawa & Cole 1994). A single 6-hour tide phase swing can bring a change of up to 3°C to a stretch of shoreline and salinity can swing at least 5 psu on a tide due to a prism that can move an isopleth many tens of kilometers despite a salinity gradient maximizing at only 0.6 psu/km (Ralston et al. 2008). The partial tidal draining and refilling of adjacent study embayments on a 12-hour basis from the adjoining heavy river flow (12,040 m^3/s in UNYH, Cooper et al. 1988) largely homogenize their physical and chemical water quality. Selection of seven sites in UNYH (Liberty State Park Marsh Cove, Army Corps of Engineers Embayment, Global Terminal Embayment—an active shipping terminal; Coast Guard Embayment [North], Coast Guard Embayment [South], Alexan CityView, Bayonne Golf Club, Table 1; Figs. 1 & 2) was based on the limited availability of shallow sloping shorelines between Liberty Island State Park and the Arthur Kill. The degree of alteration varied among sites as a function of their differing history of use, maintenance or neglect, intentional restoration efforts, and exposure. These histories resulted in different shapes and bathymetry. All embayments, however, were in close proximity to each other, ranging from 670 to 3,800 m in straight line distance among embayment mouths, the most relevant distance measure in terms of water and larval supply. The Coast Guard North and South beaches shared an embayment mouth but the southern beach was further west in the embayment (Fig. 2A). Minimum convex path distance following the shoreline ranged from 260 m (Coast Guard Embayment sites) to 6,300 m for adjacent embayments because of the extent of the protrusion of shipping terminals (Fig. 2A). Embayments for all beaches opened southeast into UNYH and shared a common water exchange through a semidiurnal tide of 1–2 m and flow of the Hudson River. All sites are historically armored. Naturalization processes that introduced shallow shorelines (beaches or fringing marsh) included intended mitigation over at least part of the embayment extent (Liberty State Park, Alexan CityView, Bayonne Golf Club). At other sites, collapse of neglected bulkheads, sediment trapping, and the subsequent recruitment of intertidal and upland vegetation behind fenced areas returned or created shallow slopes (Army Corps of Engineers basin, Coast Guard North, Global Terminal Embayment; Table 1; Fig. 3).

There are no natural habitats left in the entirety of the study region that can serve as reference sites. Given this, we follow the recommendations of Beninger et al. (2012) to adopt an observational approach relying on statistics of dispersion rather than forcing hypothesis testing as a matter of publishing culture. Instead of testing assemblage differences against each other in an analysis of variance design, we fit data to trends using ordination analysis for quantification of expectation (analogous to $\hat{y}$ and r^2 in linear regression) in the response of fishes to naturalization. We follow Rhoads et al. (1999) in using "naturalization" to refer to engineered or unintended recovery to a more natural state, where natural is judged in geoform and ecological function that are compatible with prevailing environmental conditions. We develop the concept of what natural could be for shallow shorelines of UNYH by comparing the fish assemblage there with that of a relatively unaltered estuary in southern New Jersey. Given the extreme annual temperature cycle of the Mid-Atlantic Bight and a very strong zonal cline, the assemblages are expected to differ some on the basis of temperature and its seasonal driver.

Samples from the reference estuaries were collected using the UNYH seine net in the Great Bay and Little Egg Harbor estuaries (collectively GBLEH, Fig. 2B) in June, July, September, and October 2014 and July 2015 as an indication of what a natural shoreline assemblage might hold in the same sampling period. Great Bay is the downstream portion of the estuary of the Mullica River that drains the National Pinelands Reserve in southern New Jersey (Good & Good 1984; Kennish 2004). This system is a shallow drowned river valley with an average depth of about 2 m and a surface area of 41.6 km^2 (Kennish 2004). It shares a common inlet (Little Egg Inlet) with the barrier spit-formed lagoonal Little Egg Harbor estuary. Salt marshes fringe most of the shoreline. The surrounding watershed is sparsely

Table 1. Characteristics of sampling sites in Upper New York Harbor in New Jersey during 2014 to 2015.

Site	*Width at head (m)*	*Differentiating intertidal sediment*	*Differentiating subtidal sediment*	*Shoreline Type*		*Mean and standard deviation of slope*	*Mean and standard deviation no. of stems (No./m^2)*	*Mean and standard deviation* Spartina *biomass (g/m^2)*	*Mean and standard deviation stem height (mm)*
				Intertidal	*Upland*				
Liberty State Park Marsh Cove	80	Slightly gravelly sand	Sandy-mud	Narrow rip-rap and fringing *Spartina alterniflora*	*Iva frutescens*, *Baccharis halimifolia*	0.03 ± 0.003	54 ± 43	188 ± 400	849 ± 307
Army Corps of Engineers Embayment	360	Sand, slightly gravelly sand, gravelly sand	Sandy-mud to mud	Broad with *Spartina alterniflora*, *Phragmites, Iva frutescens* and pools in marsh peat	*Iva frutescens, Baccharis halimifolia*, *Phragmites australis*	0.06 ± 0.036	48 ± 0	196 ± 201	1,187 ± 279
Global Terminal Embayment	118	Slightly gravelly sand, sand	Sandy, mud	Broad, sandy beach with some *Spartina alterniflora*, pool, some rip-rap	Bulkhead	0.06 ± 0.028	55 ± 96	137 ± 206	856 ± 386
Coast Guard Embayment (North)	400	Slightly gravelly sand	Sandy	Broad, sandy beach with some *S. alterniflora*	*Phragmites australis*, *Iva frutescens*, *Baccharis halimifolia*	0.05 ± 0.019	33 ± 8	158 ± 50	777 ± 293
Coast Guard Embayment (South)	400	Slightly gravelly sand	Sandy	Steep beach with rubble, small patches of *S. alterniflora*	*Phragmites australis*, *Iva frutescens*, *Baccharis halimifolia*	0.06 ± 0.028	45 ± 38	132 ± 8.5	1,057 ± 260
Alexan CityView	240	Slightly gravelly sand	Shallow sand, mud	Broad, beach with rip-rap and *S. alterniflora, Iva frutescens*	Bulkhead	0.08 ± 0.026	144 ± 0	604 ± 212	1,182 ± 230
Bayonne Golf Club	240	Sand, slightly gravelly sand	Shallow, sandy mud	Rubble with *S. alterniflora*	Golf course	0.16 ± 0.018	0.0	0.0	0.00

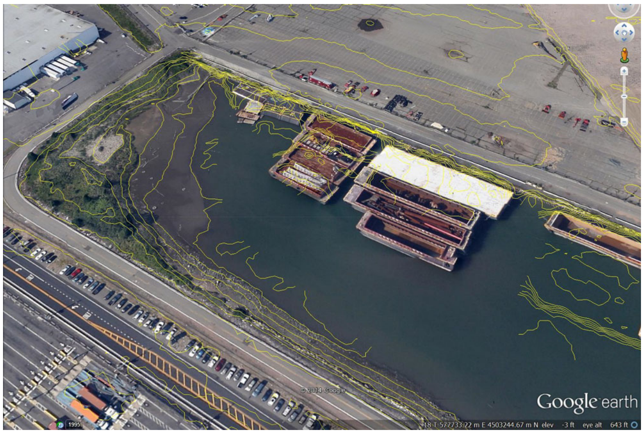

Figure 3. Aerial image of Global Terminal Embayment overlain by 0.5 ft. (0.1524 m) contour lines from LIDAR mapping conducted in 2012 by the U.S. Army Corps of Engineers Joint Airborne Lidar Bathymetry Technical Center of Expertise as the "Topobathy LIDAR: Post Super Storm Sandy—Coastal New Jersey and New York" product and graphed as a service of the Jacques Cousteau National Estuarine Research Reserve. Sediment accumulation and vegetation is evident especially in the southwest corner. A culvert empties into the embayment at the northwest corner. The embayment remains in service as a commercial port and barge laagering facility.

developed through the combined protections of the Pinelands National Reserve, Forsythe Wildlife Sanctuary, and Jacques Cousteau National Estuarine Research Reserve (Kennish 2004; Valenti et al. 2017). Like the UNYH, this reference estuarine complex is polyhaline with semidiurnal tide and broad seasonal temperature (Able et al. 1996; Jivoff & Able 2001).

Environmental Characterization

Water temperature, salinity, dissolved oxygen, and pH were measured with a YSI logger (Yellow Springs Instruments, Yellow Springs, OH, U.S.A.) during fish and crab sampling in June, July, September, and October 2014 and July 2015 only to characterize the overall environment during sampling. Site differentiation focused on permanent or seasonally static features. Elevation data was measured at each site along intertidal shoreface transects using a Leica Viva CS15 unit (Able & Grothues 2018). Two transects were taken at Coast Guard North, Coast Guard South, and Liberty State Park while four transects were completed at longer Bayonne Golf Course, Alexan CityView, and Army Corps Embayment, and three at Global Terminal Embayment shorelines. Elevation was recorded whenever a change in slope was present along transects perpendicular to the shoreline. Elevation sample points varied from four total points at Coast Guard South to 81 total at Alexan CityView. The mean slope and variance (rugosity) for each transect were determined by ordinary least squares regression.

We sampled aboveground salt marsh vegetation in September 2014 at the peak of the growing season. At each sample position at each site, we clipped all vegetation within two replicate 0.0625 m^2 quadrats (0.25×0.25 m PVC frame randomly tossed along the elevation transect), counted the live and dead plant stems, measured the length of live stems, and dried all stems to a constant weight at 60°C prior to recording their biomass (g).

Sediment samples were cored (6.3 cm diameter $\times$ 4 cm deep) at each site with a PVC hand-held coring pipe along the established elevation sampling transect. Samples were stirred with a spoon to homogenize and then a 100 g oven-dried (at 53°C) portion of each was sorted by stacked sieve shaker following Folk (1954) and analyzed for percent sediment grain sizes in the Wentworth (1922) scale using the script SANDY_C v 1.75 (Ruiz-Martinez et al. 2016) in MATLAB (The Mathworks, Natik, CT, U.S.A.; see Able & Grothues 2018).

Assemblage Characterization

Fishes and crabs were collected by beach seine (15.2 m long, 1.8 m high, 4.8-mm mesh) at each site in June, July, September, and October 2014 and July 2015, except that Bayonne Golf Club was sampled only in June 2014 and July 2015 (Tables 2 & 3). Sample seines (at least three per site visit) were hauled as "pivot" sweeps with one seine staff planted at the water line, the net deployed perpendicular to the shore to either the maximum length of the net or to a maximum depth allowing footing for haulback (~1.5 m). Then the deep end of the net was hauled to shore in an arc. Catch was kept until all hauls at a site were complete. Most fish and crabs were identified in the field;

Table 2. Seine sampling effort for fishes and crabs at shallow shoreline sites in Upper New York Harbor during 2014 (June, July, September, October), and 2015 (July). See Figure 2 for locations of sites.

	Number of Seine Hauls		*Number Captured*			
			2014		*2015*	
Site	*2014*	*2015*	*Fish*	*Crabs*	*Fish*	*Crabs*
Liberty State Park Marsh Cove	10	3	3,989	58	9,381	3
Army Corps of Engineers	19	3	2,975	116	891	8
Coast Guard (North)	12	3	2,654	83	1,701	52
Coast Guard (South)	11	3	1,155	145	555	10
Alexan CityView	14	3	8,731	212	3,454	10
Bayonne Golf Club	3	3	945	0	92	2
Global Terminal Embayment	9	3	2039	144	1941	14

Table 3. Richness and Shannon's diversity (H') for seven sampled sites in the Upper New York Harbor in 2014 and 2015 and in Great Bay-Little Egg Harbor in 2014. Note that sampling at Bayonne Golf Club was incomplete relative to other UNYH sites (see Table 1). Combined richness of UNYH sites was 27.

Site	*Liberty State Park*	*Army Corps of Engineers*	*Global Marine Terminal*	*Coast Guard North*	*Coast Guard South*	*Alexan City View*	*Bayonne Golf Club*	*GBLEH*
Richness	11	16	16	14	20	16	13	30
H'	1.48	1.24	1.58	1.58	1.82	1.17	0.46	0.81

ambiguous cases were preserved in 90% ethanol and identified in the laboratory with the aid of a microscope and a key to the juvenile fishes of mid-Atlantic estuaries (Able & Fahay 1998). Successive hauls at a site were staggered along the shoreline by an intervening (un-sampled) space of the net length to minimize dependence although independence is not a requirement of gradient analysis. Seine hauls were combined within a sampling event at a site as single catch-per-unit-effort (CPUE, where effort is the number of hauls) value to make a single seasonal, larger, more spatially representative sample. Thus, a sample unit for analysis is defined here as the effort-standardized collection resulting from a visit to a particular site on a particular date. This resulted in effort differences among sites in 2014 due to shoreline length. Hauls were limited to three per site in July 2015 for more even sample distribution. The first 20 of any given nominal taxa in a haul were measured (total length for fishes and carapace width for crabs). In the case where more than 20 individuals of taxa were captured in a haul, the length frequency distribution was taken to be indicative of that taxa in that haul. Sampling at the reference GBLEH sites followed the same protocol as for UNYH.

Data Analysis

Assemblages were compared among sites. Assemblage data were reduced to the most important dimensions using principal components analysis (PCA). Data (CPUE) for PCA were log (y + 1) transformed to mitigate for heteroscedastic distribution owing especially to schooling behavior. Log-transformed CPUE were centered and standardized to units of standard deviation to keep abundant species from unduly driving sample ordination, as species that are naturally less abundant may be just as sensitive and potentially as indicative of underlying environmental gradients as others. Rare species, those with less than three occurrences in all site visits, were excluded from ordination due to a lack of confidence in their true distribution. Untransformed CPUE for included taxa was inspected as an indicator of the dispersion of abundance among sites.

Since PCA eigenvalues are determined by the latent trends in data (rather than against an external independent variable), samples were graphically classified by site and date post-analysis to examine the strength of differences among them. Analyses were performed in MATLAB (The MathWorks, Inc., Natick, MA, U.S.A.) and CANOCO 4.5 (Microcomputer Power, Ithaca, NY, U.S.A.). Richness (R) and Shannon's diversity index (H') were calculated for each UNYH sample station based on the cumulative (all dates) catch and for the reference estuary assemblage as a whole. The composition of species among UNYH and GBLEH sites was compared with a focus on shared versus unique species interpreted on the basis of life history traits.

Results

Environmental Characteristics

All of the sampled shorelines were naturalized as evidenced by sediment banking into the high intertidal. Along bulkheads and rip-rap this was an obvious slope reduction relative to historical dredging, where it would have been as steep as 90° at bulkheads. The least sloping shoreline in UNYH was at Liberty State Park (b = 0.03 ± 0.003), but slopes at Coast Guard North (b = 0.05 ± 0.019), Army Corps Embayment (b = 0.06 ± 0.036), Global Terminal Embayment (b = 0.06 ± 0.028), and Alexan City-View Embayment (b = 0.08 ± 0.026) were also less than 10% grade (Table 1). Bayonne Golf Course (b = 0.12 ± 0.057) and Coast Guard South (b = 0.16 ± 0.018) had the steepest grades. Coast Guard South also contained abundant rubble, including bricks and concrete fragments, in all transects that differentiated it from other shorelines. Transects at Global Terminal Embayment varied most within site. Sediments at all sites were dominated by medium sand and were very well sorted. Fine sand was similar in proportion (9.0–15.4%) at these sites and very fine sand and silt together made up less than 6% at any site and as little as 0.1% at Bayonne Golf Club. Although constituting less than 20% of the sediment at most sites, the proportion of coarse sands varied inversely to medium sand and best described the small differences among sites (Table 1, Able & Grothues 2018).

The dominant intertidal vegetation at all sites was *Spartina alterniflora* (Smooth cordgrass). Averaged by site, 67–100% of quadrats that had any vegetation contained *S. alterniflora* (Table 1). *S. alterniflora* was robust with the number of live stems ranging from 33 to 144, biomass ranging from 132 to 604 g dry weight per 0.0625 m^2 quadrat, and stem height ranging from 78 to 118 cm. In comparison, natural marsh in New Jersey had 205 live stems per 0.0625 m^2 with stem heights (for short form) ranging from 27 to 32 cm (converted from 1 m^2 quadrat, Strakosh 1992). Other, less abundant species included *Spartina patens* (Saltmeadow cordgrass), *Phragmites australis* (Common reed), and *Salicornia* spp. (Pickleweeds). Upland vegetation included *Baccharis halimifolia* (Eastern baccharis), *Iva frutescens* (Jesuit's bark), and *Schoenoplectus pungens* (Common threesquare).

The range of salinity (16–25 psu), daytime dissolved oxygen (4.4–17.8 mg/L and 60.8–222.4% saturation), and pH (7.1–8.6) were similar across all UNYH sites owing to large range and within-site/across-time variation. Temperatures were far more variable as a function of season than site, ranging from 14.2°C in October 2014 to 28.7°C in July 2014 (Able & Grothues 2018).

Fish and Crab Assemblages

A total of 32 nominal taxa, including 27 identifiable fish and crab taxa, were collected at the UNYH sites (Table S1). The size distribution, 6–422 mm, mean = 55 mm, median = 53 mm, SD = 24.9, reflected the dominance by young-of-the-year or small adult fish; only three exceptions exceeded 200 mm. Individuals that could not be identified were likely to have been already included in the identified species list as represented by larger individuals (Table S1). For example, *Morone* sp. were all very small and were episodically abundant. Later collections in the same year of many, slightly larger *Morone saxatilis* suggests that the small unidentified *Morone* sp. were *M. saxatilis*.

All sites were represented by at least 11 species and Coast Guard South was represented by 20 species (Table 3). Half of the species were represented by less than 20 individuals and 10 of the taxa were represented by one or two individuals. Cumulatively across dates, the faunal assemblage was dominated at most sites by *M. menidia* (Atlantic silversides), *F. heteroclitus* (Mummichog), *F. majalis* (Striped killifish), *M. saxatilis* (Striped bass), and *C. sapidus* (Blue crab). The CPUE of any of these species at a given site differed over time by up to two orders of magnitude (Table S1; Fig. 4). Shannon's diversity ranged from 0.46 (Bayonne Golf Club) to 1.82 at Coast Guard South with a mean of 1.47 (excluding Bayonne Golf Club, which was not regularly sampled) (Table 3). Shannon's diversity was inversely correlated to the abundance of *M. menidia* and *F. heteroclitus* ($\rho = -0.44$) and positively correlated with Richness ($\rho = 0.44$).

PCA included 228 occurrences of 20 species. The first and second principal component axes resolved only 18.8 and 14.8% of the total variation respectively, and the first four axes accounted for only 54.2% cumulatively (Tables S2, S3; Figs. 5 & 6). High variance of abundant species had a homogenizing effect among sites. Explained variation on the first two principal components aligned with seasonality but not sites. Four of the five most common species by rank, *M. menidia*, *F. heteroclitus*, *F. majalis*, and *C. sapidus*, could be found at any site at any time. June assemblages differentiated from those of all other sampled months (Fig. 6, upper) largely by numerous *Anchoa mitchilli* (Bay anchovy), *Leiostomus xanthurus* (Spot), and *Microgadus tomcod* (Atlantic tomcod) (Table S3; Fig. 5). Overall CPUE was low in June samples of either year despite a pulse of *L. xanthurus* and *A. mitchilli*, but by July in both years *F. heteroclitus* and *F. majalis*, and to some extent *M. menidia*, became highly abundant (Figs. 4 & 5). Assemblages from September and October 2014 were within the broad variation of July assemblages (Figs. 5 & 6). July samples differed in the relative contribution of *F. heteroclitus*, which dominated at Liberty State Park, whereas *F. majalis* was codominant with *F. heteroclitus* at Alexan CityView embayment. The three most abundant species were particularly abundant in July at Alexan CityView Embayment and Liberty State Park, the most naturalized of the sites and those with the most and densest *Spartina* (Figs. 5 & 6 lower). *Paralichthys dentatus* (Summer flounder), although uncommon, were strongly associated with a July sample at Coast Guard South, a sandy beach with only sparse *Spartina* growth, while *Syngnathus fuscus* (Northern pipefish) were strongly associated with a July sample at Bayonne Golf Club. Gradients in the relative abundance of *Mugil curema* (White mullet) and *Mugil cephalus* (Flathead grey mullet), *Brevoortia tyrannus* (Atlantic menhaden), *Menidia beryllina* (Inland silverside), and *Menticirrhus saxatilis* (Northern kingfish) were weak (Table S2; Fig. 5). The site with the most extensive *Spartina*, Liberty State Park, showed all the dominant species in the same approximate rank order of CPUE.

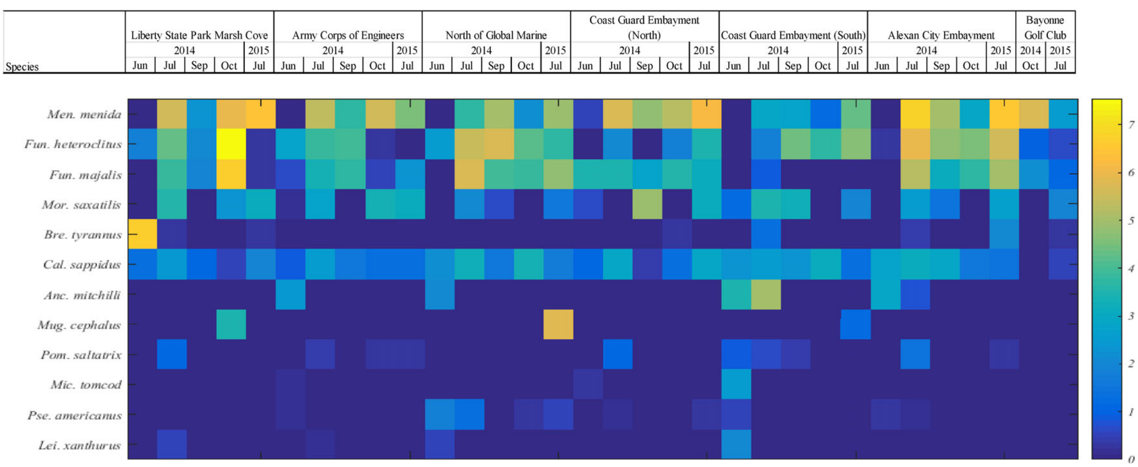

Figure 4. Seine-haul standardized catch-per-unit-effort (CPUE) for the 12 most abundant species by date at Upper New York Harbor sampling sites in 2014 and 2015. CPUE is log(y + 1) transformed in order to show structure of less abundant assemblage members. Maximum value corresponds to 857 individuals per standardized effort.

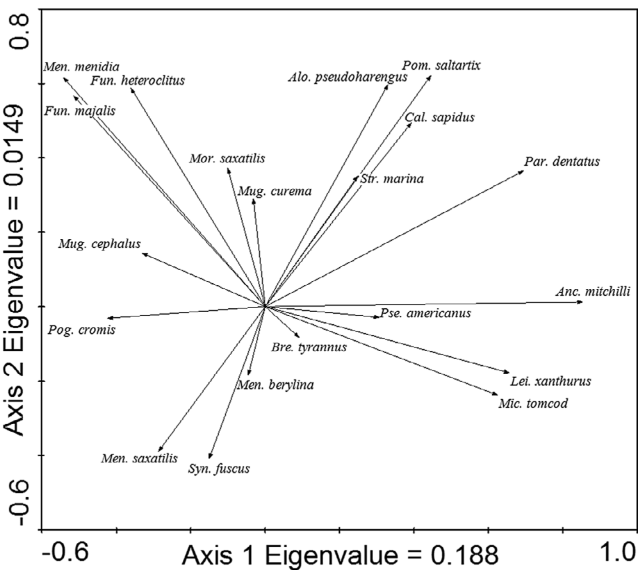

Figure 5. Vector plot of species gradients along the first and second principal components in PCA for species occurrence among Upper New York Harbor sampling sites in 2014 and 2015 (see Fig. 6, for corresponding spatial and seasonal sample distribution in the same coenospace). Generic names are abbreviated to fit (see Table S1 for complete name).

Comparison With Reference Site

Shoreline seine samples from UNYH naturalized embayments shared a number of species with those from the same months and within a similar salinity regime collected in the GBLEH, but both also had unique species. The most common species in UNYH in particular were the same as those from the GBLEH: *M. menidia*, *C. sapidus*, *F. heteroclitus*, and *F. majalis*. Other species were less common in both areas: *B. chrysoura* (Silver perch), *P. americanus* (Winter flounder), *M. beryllina*, *S. fuscus* (Northern pipefish), and *S. marina* (Atlantic needlefish). In contrast, *B. tyrannus*, *A. mitchilli*, and *Morone saxatilis* were abundant in UNYH but absent from GBLEH comparison samples. Altogether, there were 30 identifiable species, 17 of them unique, in GBLEH samples and 27 identifiable species with 15 unique species in the UNYH. Shannon's diversity ($H' = 0.81$) in GBLEH reference samples was lower than the mean and individual site values for all of the regularly sampled UNYH sites (Table S1).

Discussion

Habitat Value

Shoaling at the head of industrialized commercial embayments in UNYH, a form of naturalization, accommodated the recruitment of a relatively rich fish and crab assemblage. The assemblages included juveniles from diverse marine taxa that arrive as planktonic larvae as well as adults and juveniles of small marsh-resident species. Embayments that have gained shallow shorelines through natural sedimentation processes thus provide a shallow water habitat with an assemblage similar to that of reclaimed embayments in the same area. The assemblage composition and diversity and the overall abundance of its constituents to the extent quantifiable by beach seine, are consistent with what can be expected of estuarine shallow shoreline recruitment in this region (Able & Fahay 2010 and references therein), including that marsh-spawning/marsh-resident species are less dominant where less fringing marsh is accessible. In general, the strong temporal overlap in fish and crab species assemblages among our sample sites in UNYH suggests a lack of overall site distinction in terms of fish and crab assemblage among these shorelines. For example, all sites at least periodically hosted similar CPUE of *M. menidia*. However, the shallow, naturalized, marsh-bordered shorelines of Alexan CityView most consistently hosted abundant *F. heteroclitus*. This species feeds and incubates eggs in intertidal vegetation but will also use other structures with small apertures such as ribbed mussel shells that occur in *Spartina* marshes for egg deposition (Able & Fahay 2010). For other species, a pattern was much more difficult to discern because of temporal variation. This is consistent with findings in manipulative laboratory experiments that microhabitat diversity should lead to higher species diversity in shallow marine nurseries (Mercador et al. 2019).

The PCA provided a dimensional reduction to this view and pointed to a general spatial homogeneity with a seasonal dynamic. Some individual species trends were strong, but these were not the dominant species. Both stabile and temporary structural aspects may have influenced the fish and crab habitat use. The stabile presence of concrete and brick rubble may have attracted recruiting *L. xanthurus* or differentially allowed their survival at Coast Guard South while the lack of the same may have attracted or promoted subsequent survival of *P. americanus*, a burying flatfish, to the Global Terminal Embayment. Burial is important to juvenile flatfish and is differentially enabled by grain size (Tanda 1990; Gibson & Robb 2000).

Overall, the richness of UNYH samples was similar to that of the nearby natural GBLEH marsh-lined estuary, but the mean Shannon's diversity was about 1.5 times greater in UNYH than in GBLEH. Diversity is not necessarily a hallmark of marsh-lined shallow shorelines because these may be dominated by marsh spawning fishes even when richness is high. As an example, in comparison to trawl samples of narrow marsh creek channels and submerged aquatic vegetation beds in nearby Barnegat Bay (including Little Egg Harbor), richness from UNYH was about half and Shannon's diversity was nearly double but overlapped the range of those trawl samples ($H' = 1.05–1.74$; Valenti et al. 2017). Those trawl samples only uncommonly collected *F. heteroclitus* despite abundant *Spartina* there; yet, that species was very abundant in trap sampling of the same creeks (Able et al. 2015). This difference likely owes to the very fine spatial scale partitioning of those creeks into shallow versus very shallow, untrawlable shoreline water. The lower diversity and richness in seined shoreline samples than in trawled creek samples illustrates the natural monopolization of the shallow shorelines, rather than a depauperate state stemming from habitat degradation. For the same reason, Shannon's diversity was lower while richness was higher in the GBLEH reference than in UNYH seine samples combined—there were more rare species in

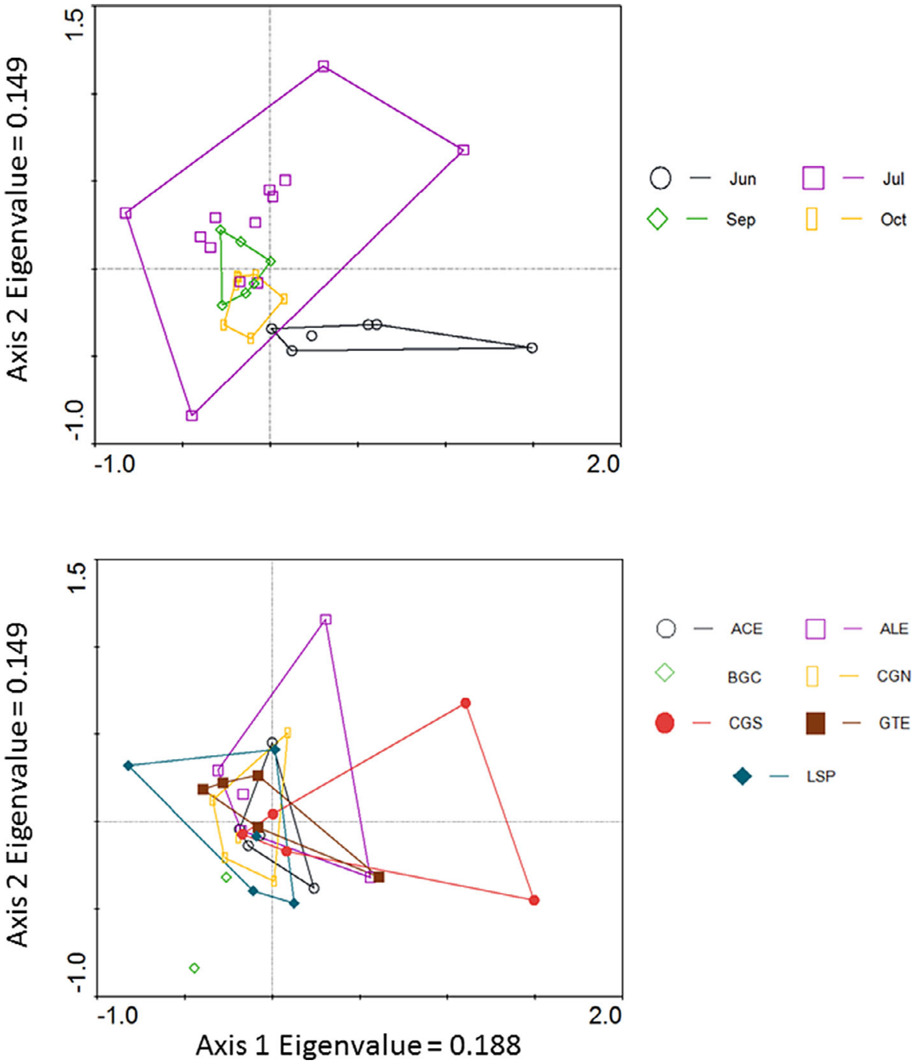

Figure 6. (Upper) Scatter plot of site scores along the first and second principal components in PCA for samples classified by the month of collection among Upper New York Harbor sampling sites in 2014 and 2015. (Lower) Scatter plot of the same site scores classified by location (see Fig. 5 for corresponding species distribution in the same coenospace for both upper and lower plots). Abbreviation of the site score key is as follows: ACE, Army Corps of Engineers; ALE, Alexan CityView; BGC, Bayonne Golf Club; CGN, Coast Guard North; CGS, Coast Guard South; GTE, Global Terminal Embayment; LSP, Liberty State Park.

GBLEH but highly abundant fundulids and *M. menidia* dominated there even more than they dominated in UNYH.

A species-by-species review of the life histories provides insight into these differences. Broadly classified, one group of species is resident and spawns, hatches, and grows in estuarine shallows and marshes (typified by the three fish sentinel species examined in Able & Grothues 2018), while a second group arrives there from diverse origins (Able & Fahay 2010; Nickerson et al. 2018). Species that were unique to the GBLEH samples, and especially those that were rare, were southern-affiliated species (*Symphurus plagusia* [Blackcheek tonguefish], *Chilomycterus schoepfi* [Spotted burrfish], *Spheroides maculatus* [Northern puffer], *Chasmodes bosquianus* [Striped blenny], *G. bosc* [Naked goby]) reaching the northern end of their range distribution in the Mid-Atlantic Bight. Although any of these could have reached the UNYH and have been previously documented north of there (Able & Fahay 2010), the probability of occurrence can be expected to decline northward of the reference estuary. Other unique species are closely associated with infrequently flooded marsh or upland pools (*Lucania parva* [Rainwater killifish] and *Cyprinodon variegatus* [Sheepshead minnow]). The rarer species unique to the UNYH samples are also known to occur and are even abundant in the GBLEH estuaries but include more widely distributed species such as *A. mitchilli*, *L. polyphemus* (Atlantic horseshoe crab), and *Anguilla rostrata* (American eel). One highly abundant species unique to UNYH, *Morone saxatilis*, is anadromous and spawns abundantly in fresh water of the Hudson River upstream of the sampled sites followed by movement of the juveniles into the estuary (Westin & Rogers 1978). This species only rarely spawns successfully in the Mullica River due to low natural pH in the fresh reaches (Grothues et al. 2009; Able & Fahay 2010; Able et al. 2011). Differences in life history for most of the species, in terms of relative abundances that constitute the differences in the UNYH and GBLEH assemblages, do not point to the UNYH shoreline as degraded in shoreline habitat function, except that the marsh grass associated *F. heteroclitus* and *M. menidia* were not as dominant at some sites. Differences include those promoted by larval transport into the estuary from complex coastal hydrodynamic delivery mechanisms (Grothues et al. 2002; Able & Fahay 2010; Able et al. 2011) and reflect the importance of context as a driver of assemblage differences for similar habitats (Bradley et al. 2019). Nevertheless, comparison with GBLEH provides a semblance of the extent to which diverse juvenile fishes populate shallow shorelines in this region.

The sampled shallow shorelines in urbanized UNYH shared water masses from a highly dynamic estuary with a twice daily tidal exchange. Thus, static or seasonally stabile characters are of greatest interest as potential differentiating factors. For example, the static variable of the amount of rubble differentiated Coast Guard South and to a lesser extent Global Terminal Embayment and Alexan CityView from other sites. The shoreline with rubble was steepest, and rubble content and slope were probably functionally related. *Ulva lactuca* (Sea lettuce) was periodically abundant but can also be extremely ephemeral, meaning that its absence at a site on a particular day does not reflect its history there. That hidden history may be an important factor in early recruitment (as for *C. sapidus*; Wilson et al. 1990) that leaves an impression on the subsequent assemblage. Dissolved oxygen fluctuation undetected in our daytime measurements might similarly leave a site-specific legacy on the time scale of the seasonal recruitment period.

As in other temperate estuaries, assemblage seasonality is an important part of variation as a function of spawning season (Able & Fahay 2010) and interacts with the distance that larvae traveled from a spawning location (e.g. for *Pomatomus saltatrix* [Bluefish], Hare & Cowen 1996). However, the effect of sampling month is potentially influenced by the environment in the sense that recruits persist longer (and show up more in later samples and at larger sizes, i.e. survivors) at shorelines with more favorable habitat qualities for that life stage. An example is that the catch of *M. saxatilis* at Liberty State Park roughly halved between July and September of 2014 and nearly disappeared from Army Corps Embayment but increased over that same period at Coast Guard North. It is possible that this could result from an ontogenetic shift from shallower, less steeply sloped shoreline to more steeply sloped and deeper habitat for these rapidly growing juveniles, thus changing vulnerability to seine sampling within a site. Patchiness in seine samples due to schooling behavior is another possibility, as is increased among-site motility for this species. This might also apply to the less benthic-oriented, schooling planktivorous filter feeders such as *B. tyrannus* and *A. mitchilli*.

This study also provides insights into understanding resilience of assemblages relative to dispersal capability and habitat use. Three of the four dominant species have a highly mobile dispersal phase. Of these, adult *M. menidia* move between coastal ocean water and estuarine spawning habitats, while *C. sapidus* arrive as plankton from the coastal ocean (Able & Grothues 2018). Most of the other common species encountered (e.g. *L. xanthurus*, *M. curema, M. cephalus*, and *P. saltatrix*) also disperse from the ocean into estuaries as larvae, and once in the estuary would have similar access to all of the potential nursery habitats in UNYH. For that reason, naturalized embayment shorelines offer the possibility of nursery habitats to some species independent of the size, distance, or fate of similar nearby shorelines. Because the connection is made by a larval dispersal phase through the natal river or from the ocean, the total amount of shallow shoreline habitat, more than its alongshore continuity, may be the most important consideration in restoring an estuary to its historical nursery function for such species. Alternatively, the second and third most abundant species, *F. heteroclitus* and *F. majalis*, complete their entire life cycle at these naturalized shorelines. Their potential to re/colonize impacted or restored shorelines is not known because, although adjacent to each other, such embayments are isolated by up to kilometers-long sections of deep, bulkheaded portions of the embayments not considered to be *Fundulus* habitat (Crum et al. 2018) and instead are typified by assemblages of larger fish (Kornis et al. 2018). Coded-wire tagged adult *F. heteroclitus* do not move from their natal shorelines for much of the year (Able et al. 2012; Crum et al. 2018) including in some of these study sites (Able & Grothues 2018), but juveniles in marshes may move on the order of kilometers during large storm floods (Teo & Able 2003). Such events should allow periodic connection and access to new or restored shallows for those substrate spawning species. A remaining question is: is there a lower limit to the size of a restoration or naturally forming shallow shoreline habitat patch that would allow self-recruitment and population maintenance for those species?

Limitations of This Study

Several characteristics of the study area make effective evaluation difficult, but recognizing these paves the way for improved evaluation in the future. First, the extent of development compromises our ability to determine how fish and crab assemblages might differ from a true reference marsh simply because such marshes no longer exist in UNYH. Second, the varied geomorphology of the shoreline confounds quantitative sampling. Swept area or volume differs among shorelines because slope influences the distance-from-shore that a seine may reach. Steeper slopes have a narrower shallow stretch. However, higher net-standardized CPUE should reflect the integrated value of a site; that is the density multiplied by the shoreline width.

Relevance to Restoration

Despite an increase in restoration efforts, shallow shorelines remain rare as a percent of total waterfront in UNYH (Stinnette et al. 2018). Restoration possibilities exist as habitat fragments at the largely forgotten heads of engineered, commercially active and publicly inaccessible embayments. While most of each of these are dredged and steep-sided to receive large vessels, their elongate aspect acts naturally as a trap for suspended sediments. As a result, some have developed mudflats and beaches at their heads that are occasionally crossed by erosion channels from culvert drains or creeks and that allow marsh vegetation to develop. These are functional shoreline habitats and could be exploited for inexpensive restoration as foothold habitats for impacted estuarine species. This may be especially true for those that connect to upland or marsh habitats that provide subsidies to shallow water communities (Strayer et al. 2012; Wensink & Tiegs 2016) and estuaries (Kneib 2000). If engineered embayments are abandoned for use by deepwater vessels as commercial infrastructure projects move to new locations or are updated for tasks other than stevedoring, opportunity exists to include ecological equivalents or mitigations into their engineering designs at planning, rather than retroactively (Urbanski & Gleeson 2012). In this, they can act as ecological equivalents of natural coves that were eliminated during shoreline straightening. In New York and New Jersey sides of UNYH (jointly managed under the Port Authority of New York and New Jersey), funds derived from penalties or permitted environmental offsets were used to create small restorations with many of the characteristics of natural marshes and these now appear to be flourishing (Princeton Hydro 2007; Able & Grothues 2018). These practices are echoed on the west coast of the United States (Toft et al. 2013) and in other countries (Blaber 2000; Cattrijsse et al. 2002; Airoldi & Beck 2007). All of these considerations are compounded by a need for cities to contend with sea level rise, often by armoring "up" (Rosenzweig et al. 2011; Ezer & Atkinson 2014). Given time, natural sediment deposition can be exploited or encouraged to promote reclamation of shoreline nursery habitat at little cost compared to active beach nourishment due to the resiliency of a connected system. As a city that grew up around an estuary valued as a port, New York is typical of many other large cities worldwide. Insights from this study should be valuable to agencies considering, permitting, or requiring shoreline restorations in similar settings.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Species composition, abundance, and numerical rank of fishes and crabs.

Table S2 Cumulative fit per species as a fraction of variance for Principal Components 1 and 2.

Table S3 Squared residual length per sample for Principal Components 1 and 2.

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