Geographic distribution, habitat characterization, and conservation status of *Bolboschoenus* bulrushes (Cyperaceae) in the Hudson River Estuary, USA

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Abstract. Bulrushes of the genus *Bolboschoenus* are robust, ecologically important sedges occurring in wetlands, including intertidal marshes and mudflats. Despite their importance and multiple serious threats to their habitats, estuarine *Bolboschoenus* species remain poorly known. We conducted herbarium and field research in order to document historic and current geographic distributions, characterize the habitats, and assess the conservation status of *Bolboschoenus* species in the Hudson River Estuary, New York, U.S.A. Three species of *Bolboschoenus* grow in intertidal zones in the Hudson Estuary. *Bolboschoenus fluviatilis* occurs in the northern, upstream, and freshwater portion of the estuary with multi-year mean surface salinities of 0.078–2.0 ppt. *Bolboschoenus robustus* occupies the southernmost, downstream, and brackish to saline portion of the estuary with salinities of 4.9–16 ppt. *Bolboschoenus novae-angliae* occurs in the slightly to strongly brackish region between the other two species with salinities of 1.8–8.0 ppt. The geographic ranges of *B. fluviatilis* and *B. robustus* do not overlap, but *B. novae-angliae* has short zones of sympatry with each of the other two species. Syntopy of *B. novae-angliae* with each of the other two species is rare. In the Hudson Estuary, *B. fluviatilis* is secure, but *B. novae-angliae* and *B. robustus* are critically imperiled. Threats to future survival of *Bolboschoenus* species in the Hudson Estuary include competition from invasive plant species (especially *Phragmites australis*), eutrophication resulting from excess nutrient pollution, and habitat destruction. Our data and analyses provide critical new information for management of existing environmental problems and planned habitat restoration efforts in the Hudson River Estuary.

Keywords: *Bolboschoenus fluviatilis*, *Bolboschoenus novae-angliae*, *Bolboschoenus robustus*, habitat restoration, intertidal, salinity.

Bulrushes of the genus *Bolboschoenus* (Cyperaceae) are robust, perennial sedges occurring in wetlands in many regions of the world. *Bolboschoenus* contains about 15 species. Until relatively recently, these species had been treated as members of *Schoenoplectus* and *Scirpus*. Molecular and morphologic analyses support the monophyly of *Bolboschoenus* and its distinctions from *Schoenoplectus* and *Scirpus* (Strong, 1994; Goetghebeur, 1998; Smith, 2002; Muasya et al., 2009; Hinchliff & Roalson, 2013; Glon et al., 2017).

Bolboschoenus species provide important ecosystem services. *Bolboschoenus fluviatilis* (Torrey) Soják and *B. robustus* (Pursh) Soják are important food sources, especially their fruits, for ducks, geese, and swans (Fassett, 1957; Stewart & Manning, 1958; Fredrickson & Reid, 1988). *Bolboschoenus fluviatilis* provides cover and

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nesting sites for many species of birds and small mammals (Allen, 1914; Weller & Spachter, 1965; Jaeger, 1972). Birds that spend much time in stands of *B. fluviatilis* include American Bitterns (*Botaurus lentiginosus*; Allen, 1914) and Least Bitterns (*Ixobrychus exilis*; Naczi, unpubl. data), both of which are of conservation concern in large portions of their ranges (USFWS, 2008; NYSDEC, 2017). Marsh vegetation dominated by *B. robustus* supports large, dense, and diverse populations of invertebrates, including molluscs, oligochaetes, polychaetes, insects, and fiddler crabs (Kerwin, 1971; Wenner & Beatty, 1988). Underground, *B. fluviatilis*, *B. novae-angliae* (Britton) S.G. Smith, and *B. robustus* possess strong rhizomes, corms, and tubers that stabilize intertidal habitats and prevent erosion (Schuyler, 1975; Smith, 2002; Naczi, unpubl. data). Additional characteristics of *B. fluviatilis*, *B. novae-angliae*, and *B. robustus* populations indicating their ecologic importance are great stature (typically 1.5–2.5 m tall), dense cover, and usually great areal extent (Naczi, Sheaffer, Werier, and Zimmerman, unpubl. data).

Several rivers in the northeastern U.S.A. and adjacent Canada have major estuaries in their lower reaches, e.g. the St. Lawrence, Penobscot, Kennebec, Connecticut, Hudson, Delaware, Susquehanna, and Potomac. Within these estuaries, intertidal marshes and mudflats host diverse communities of vascular plants rich in rare species restricted to intertidal habitats (Fassett, 1928; Ferren & Schuyler, 1980; Strong & Kelloff, 1994; Brouillet et al., 2004). Previous authors documented a total of four species of *Bolboschoenus* in northeastern estuaries, *B. fluviatilis*, *B. maritimus* (L.) Palla [*Scirpus paludosus* A. Nelson], *B. novae-angliae* [*Scirpus cylindricus* (Torrey) Britton], and *B. robustus* (Schuyler, 1975; Ferren & Schuyler, 1980). Based on observations in the Delaware, Kennebec, Penobscot, and Potomac estuaries, previous authors suggested *Bolboschoenus* distributions occurred in relation to salinity levels, with *B. fluviatilis* occurring in upstream freshwater habitats, *B. novae-angliae* in transitional brackish habitats, and *B. maritimus* and *B. robustus* in downstream saline habitats (Schuyler, 1975; Ferren & Schuyler, 1980; Strong, 1994).

Intertidal habitats and their vegetation face multiple threats to their ecologic integrity and survival, especially in the Hudson Estuary (Block & Rhoads, 2011; Strayer, 2012; Miller, 2013). Human development, invasive plant species, and pollution eliminate and degrade habitat. Pollution with excess nutrients and resulting eutrophication are serious problems in the Hudson Estuary, with wastewater the single greatest cause of nutrient loading (Howarth et al., 2000; Committee on Environment and Natural Resources, 2003; Howarth et al., 2006). Dredging activities and wave action from commercial shipping disrupt natural hydrologic and sedimentation cycles. Sea-level rise is an increasingly serious problem, especially for rivers such as the Hudson on which dams block potential upstream dispersal routes. Because threats to the survival of intertidal plants are multiple and grave, it is reasonable to expect that species that are restricted or nearly restricted to intertidal habitats, such as some *Bolboschoenus* species, may be of conservation concern.

Bolboschoenus bulrushes of intertidal habitats in the Hudson River Estuary have never been the focus of extensive study, and their distributions, habitats, and conservation status are poorly known. The dearth of knowledge about *Bolboschoenus* species in the Hudson Estuary hampers understanding of the most basic aspects of their biology and estuary restoration efforts that depend on such understanding (Miller, 2013). To remedy this lack of knowledge about intertidal bulrushes, we conducted extensive herbarium and field research to investigate *Bolboschoenus* in the Hudson Estuary. Our goals are first to construct a baseline of historic occurrences of *Bolboschoenus* species, report current distributions, and compare current with historic distributions. Second, we aim to elucidate habitats of *Bolboschoenus* species in the Hudson Estuary, including testing the hypothesis that occurrences of the species correlate with salinity levels. Finally, we assess the conservation status of *Bolboschoenus* bulrushes in the Hudson Estuary.

Materials and methods

Study site

The Hudson River Estuary of southern New York, U.S.A. extends 245 km (152 mi) in a mostly south to north direction from the mouth of the river at Battery Park in New York City north to the Troy Lock and Dam in the city of Troy (Miller, 2013). Lands bordering the Hudson are a composite of intensive urban development, moderate urban and suburban development, agricultural development, and undeveloped lands dominated by broad-leaved temperate deciduous forest (Fig. 1). Though the Hudson has several tributaries, tidal reaches of tributaries are quite short because tributaries usually descend from uplands immediately adjacent to the Hudson. Thus tidal habitat in the Hudson Estuary is nearly restricted to the stem of the Hudson. Within the estuary, saline, brackish, and freshwater habitats occur, with freshwater predominating. Intertidal habitats are quite patchy because many regions have uplands or human development bordering the Hudson. Intertidal habitats inhabited by vascular plants are mudflats and marshes.

Occurrence data sources

Herbarium specimens furnished all occurrence data for this study. We assembled historic occurrences (Appendix 1) by locating and identifying all *Bolboschoenus* specimens from the Hudson Estuary in these herbaria: BH, BKL, DOV, GH, NY, NYS, PENN, PH, US, and Bard College Field Station Herbarium (abbreviations of herbaria from Thiers, 2017). Collectors gathered historic specimens during the period 1869–2005 and did so opportunistically; no comprehensive surveys for *Bolboschoenus* occurred prior to our study.

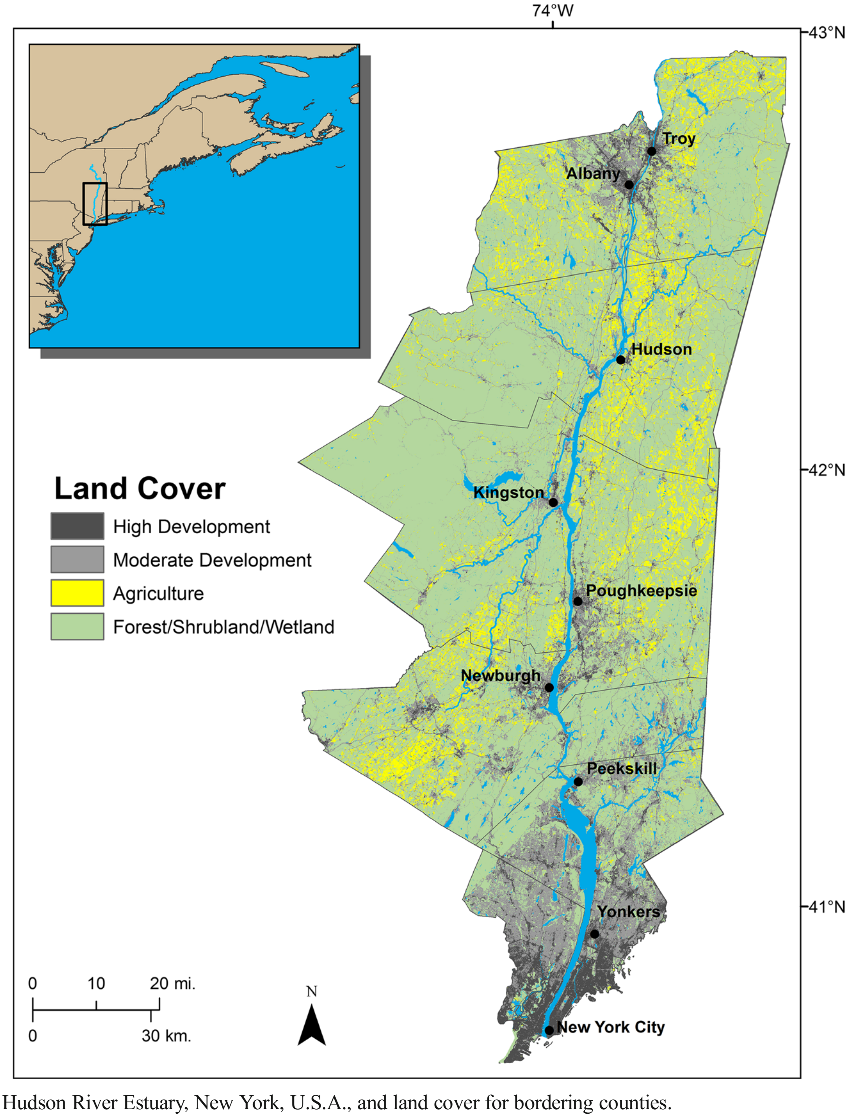

Fig. 1. Hudson River Estuary, New York, U.S.A., and land cover for bordering counties.

Current occurrence data are from our fieldwork of 2011–2017. During this time period, we explored precisely 120 sites throughout the Hudson Estuary in search of *Bolboschoenus* and other intertidal vascular plant species. We visited almost all historic sites as well as many previously unexplored ones to study first-hand most of the sites that support or have supported intertidal vascular plants in the Hudson Estuary. We documented all *Bolboschoenus* populations we encountered by preparing voucher specimens that we deposited in herbaria (Appendix 1).

Mapping

We georeferenced historic specimens using Google Earth Pro (Google, 2017), and georeferenced our field collections with handheld GPS units. For all mapping, we used ArcMap 10.5.1 (ESRI, 2017). We mapped recent land cover of areas adjacent to the Hudson Estuary (Fig. 1) by modifying the 2010 New York Cropland Data Layer (USDA, 2011), including clipping to counties bordering the Hudson Estuary. We plotted *Bolboschoenus* population occurrences by saving occurrence data as a layer in ArcMap projected to Lambert Conformal Conic. We consider populations distinct if at least 0.6 km (0.4 mi) apart, straight distance (not river miles), and the intervening habitat is different than that supporting neighboring populations.

Salinity

To augment direct field observations of habitat, we characterized salinity for each *Bolboschoenus* species we observed. To quantify salinity, we considered multi-year mean surface salinity values for Hudson River water adjacent to *Bolboschoenus* populations. To determine the range of values, we calculated means from the northernmost and southernmost known populations of each species.

Calculation of multi-year surface salinity means within the Hudson Estuary required the assembly of data sets from multiple institutions. We obtained data on salinity or specific conductance from 37 monitoring stations administered by United States Geological Survey, Hudson River Environmental Conditions Observing System, Riverkeeper, New York City Department of Environmental Protection, and the National Oceanic and Atmospheric Administration (see Suppl. Material 1 for sources and associated information). The data collection period ranged from 1970 to 2017, with an average of 6 years per multi-year mean. We converted specific conductance in microsiemens (μS) to parts per thousand (ppt) using the formula $[(x\ \mu S/cm)/1000]^{1.0878} * 0.4665 = y$ ppt (Williams, 1986).

We used monitoring station locations to create a shapefile that we converted to a raster, using the Point to Raster tool of ArcMap. We used surface salinity values from monitoring stations, and interpolated surface salinity for remaining portions of the estuary by using ordinary, spherical semivariogram kriging. Then, we clipped the raster to the feature class of the Hudson River Estuary.

We created polygons for each species' Hudson Estuary distribution by using the convex hull option of the Minimum Bounding Geometry tool in ArcMap. We calculated centroids for each polygon, using the Calculate Geometry tool in ArcMap. For each centroid, we calculated the multi-year mean salinity for the nearest monitoring station, and used these values to estimate salinity for the center of distribution of each *Bolboschoenus* species. All centroids are within 6 km (4 mi) of a monitoring station. We also report salinities for the northernmost and southernmost known populations of each species of *Bolboschoenus* in order to provide the low and high values of mean salinity for each species.

Results

Geographic distribution

Historic specimens document three species of *Bolboschoenus* in the Hudson River Estuary: *B. fluviatilis*, *B. novae-angliae*, and *B. robustus* (Appendix 1). The earliest known collection of *B. fluviatilis* is from Greene County in 1869 (*Howe s.n.*, NY), of *B. novae-angliae* from Bronx County in 1891 (*Bicknell s.n.*, NY), and of *B. robustus* from Bronx County in 1876 (*Howe s.n.*, NY). Current collections document the same three species in the Hudson Estuary (Appendix 1).

Bolboschoenus fluviatilis inhabits the northern portion of the estuary (Fig. 2). The northernmost known population is from Green Island, Albany County, documented in 1924 (*House 10,372*, NYS). The southernmost known population of

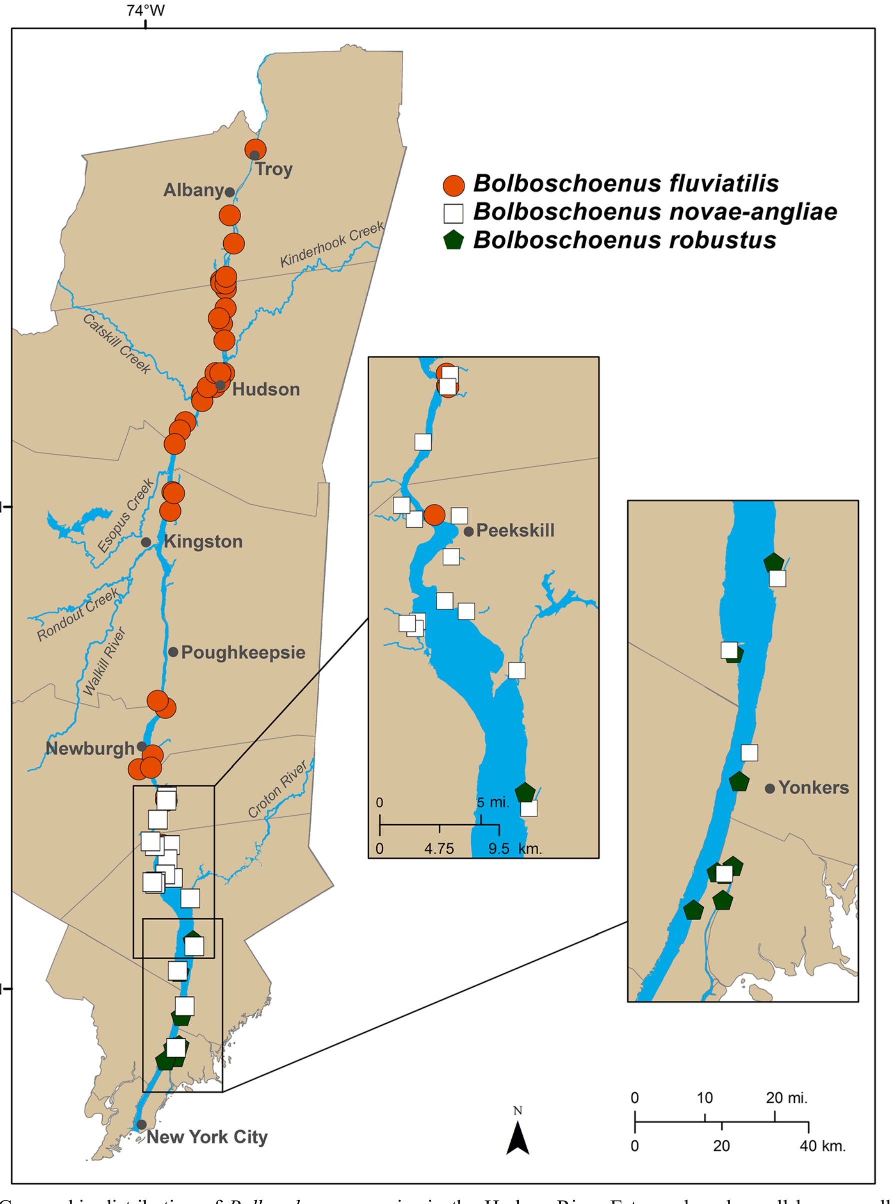

Fig. 2. Geographic distribution of *Bolboschoenus* species in the Hudson River Estuary, based on all known collections (historic and current). The inset distance scale applies to both insets.

B. fluviatilis is from NW of Annsville Creek, Westchester County, documented in 2013 (*Werier 5359*, NY). The geographic range of *B. fluviatilis* in the Hudson Estuary extends for 172 km (107 mi, river miles 45–152).

Bolboschoenus novae-angliae inhabits a southern portion of the Hudson Estuary, but not the southernmost (Fig. 2). It occurs south of most of the range of *B. fluviatilis*, and much of the range of *B. novae-angliae* is north of where *B. robustus* occurs. The northernmost known population of *B. novae-angliae* is from Indian Brook, Putnam County, documented in 2013 (*Werier 5328*, NY). The southernmost known population is from Spuyten Duyvil, Bronx County, documented in 1891 (*Bicknell s.n.*, NY). The geographic range of

B. novae-angliae in the Hudson Estuary extends for 63 km (39 mi, river miles 15–54).

Bolboschoenus robustus inhabits the southernmost portion of the Hudson Estuary (Fig. 2). The northernmost known population is from NW of Philipse Manor, Westchester County, documented in 2013 (*Naczi 15,122 & Dorey*, NY). The southernmost known population is from Fort Washington Point, New York County, documented in 1900 (*Bicknell 1086*, NY). The geographic range of *B. robustus* in the Hudson Estuary extends for 24 km (15 mi, river miles 13–28).

The geographic ranges of *Bolboschoenus fluviatilis* and *B. novae-angliae* overlap slightly (Fig. 2). In this area, both species occur in habitats along the Hudson River and at the mouths of tributaries. The zone of sympatry is 14 km long (9 mi, river miles 45–54) from Indian Brook, Putnam County to NW of Annsville Creek, Westchester County. Despite overlap, we encountered syntopy at only one site, Philipse Brook, Putnam Co. (*Werier 1794* and *5325* for *B. fluviatilis* and *Werier 1794* and *5324* for *B. novae-angliae*). In fact, one of the collections is mixed (*Werier 1794* at NYS is *B. fluviatilis*, and *Werier 1794* at NY is *B. novae-angliae*).

Another case of range overlap occurred with *Bolboschoenus novae-angliae* and *B. robustus* (Fig. 2). Both species occurred in a stretch of the Hudson River and mouths of tributaries from NW of Philipse Manor, Westchester County to Spuyten Duyvil, Bronx Co. The overlap between these species is historic; currently, populations of *B. novae-angliae* occur only north of the range of *B. robustus*. The historic zone of sympatry between *B. novae-angliae* and *B. robustus* extended for a distance of 21 km (13 mi, river miles 15–28). Syntopy or near syntopy was known at two sites, Piermont Marsh and Spuyten Duyvil (Piermont Marsh: *Muenscher 5678 & Curtis* and later collections for *B. novae-angliae*, and *Muenscher 21,564* et al. and later collections for *B. robustus*; Spuyten Duyvil: *Bicknell s.n.* for *B. novae-angliae*, and *Bicknell s.n.* and later collections for *B. robustus*).

The current and historic ranges of *B. fluviatilis* and *B. robustus* do not overlap. The nearest known populations of the two species are 27 km (17 river miles) apart.

Three of the populations we documented are unidentifiable (Appendix 1). Mature achenes are necessary for identification of *Bolboschoenus* species, but achenes were absent from these populations because they produced no infructescences. All three of these populations occur in regions of sympatry of pairs of species.

Habitat characterization

In the Hudson Estuary, all *Bolboschoenus* species grow in the upper 20–35% of the intertidal zone. *Bolboschoenus* species occur both in marshes and on mudflats.

Bolboschoenus fluviatilis occurs in the freshwater portion of the Hudson Estuary (Fig. 3). Salinity at the centroid of the estuarine geographic distribution is 0.10 ppt, and the range of multi-year mean salinities from the northernmost to the southernmost known populations is 0.078–2.0 ppt (Table I). Vascular plant species that frequently grow with *B. fluviatilis* are *Acorus calamus* L., *Amaranthus cannabinus* (L.) Sauer, *Bidens bidentoides* (Nutt.) Britton, *B. cernua* L., *Heteranthera reniformis* Ruiz & Pav., *Lythrum salicaria* L., *Persicaria punctata* (Elliott) Small, *Phragmites australis* (Cav.) Steud., *Pontederia cordata* L., *Sagittaria latifolia* Willd., *Sagittaria subulata* Buchenau, *Schoenoplectus pungens* (Vahl) Palla, *Typha angustifolia* L., and *Zizania aquatica* L.

Bolboschoenus novae-angliae occurs in slightly to strongly brackish portions of the Hudson Estuary (Fig. 3). Salinity at the centroid of the Hudson geographic distribution is 3.3 ppt, and the range of multi-year mean salinities from the northernmost to the southernmost known populations is 1.8–8.0 ppt (Table I). Closely associated vascular plant species are *Acorus calamus*, *Amaranthus cannabinus*, *Cyperus bipartitus* Torr., *Hibiscus moscheutos* L., *Limosella australis* R. Br., *Lythrum salicaria*, *Pontederia cordata*, *Persicaria punctata*, *Phragmites australis*, *Pluchea odorata* (L.) Cass., *Sagittaria spathulata* Buchenau, *Schoenoplectus americanus* (Pers.) Schinz & R. Keller, *Sporobolus cynosuroides* (L.) P.M. Peterson & Saarela (*Spartina cynosuroides* (L.) Roth), *Symphyotrichum subulatum* (Michx.) G.L. Nesom, and *Typha angustifolia*.

Bolboschoenus robustus occurs in brackish and saline intertidal zones in the Hudson Estuary (Fig. 3). Salinity at the centroid of the Hudson geographic distribution is 8.0 ppt, and the range of multi-year mean salinities from the northernmost to the southernmost populations is 4.9–16

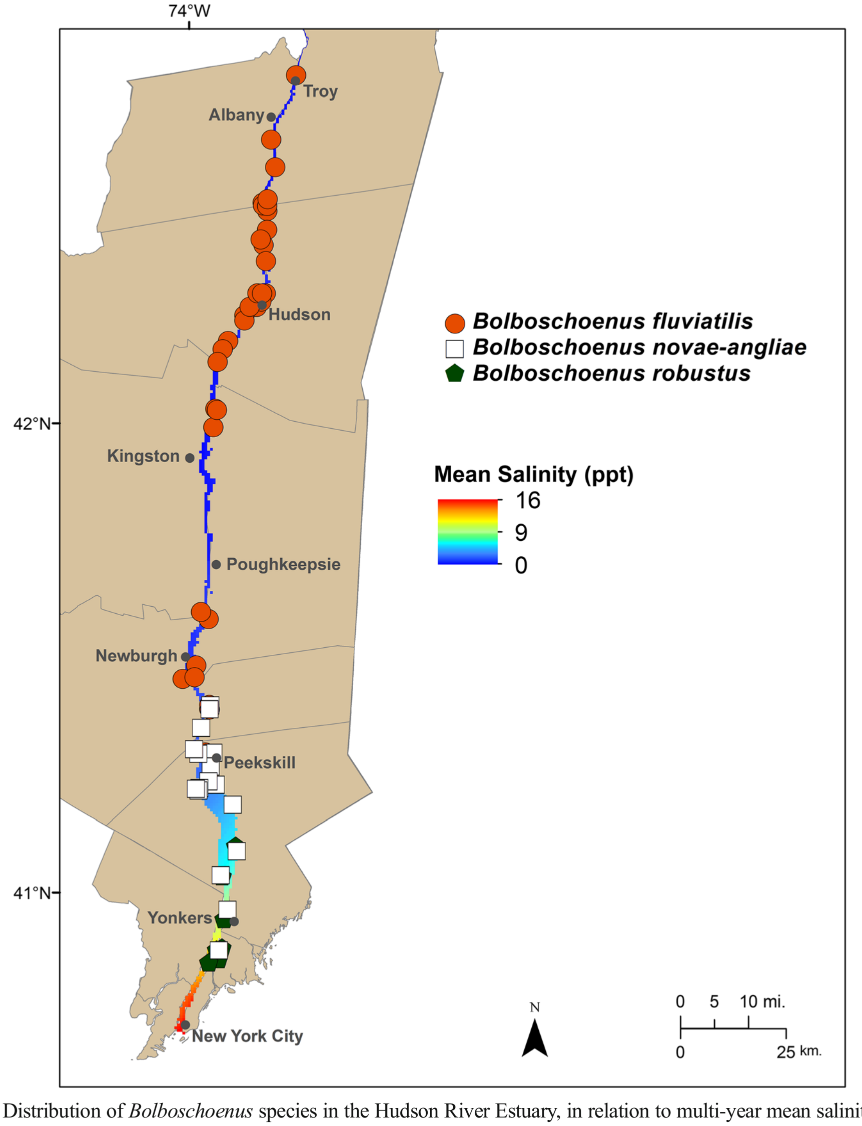

Fig. 3. Distribution of *Bolboschoenus* species in the Hudson River Estuary, in relation to multi-year mean salinity values of river water.

Table 1. Hudson River multi-year mean surface salinity values for intertidal populations of *Bolboschoenus* species, expressed as centroids and ranges.

Species	Salinity (ppt)
B. fluviatilis	0.10 (0.078–2.0)
B. novae-angliae	3.3 (1.8–8.0)
B. robustus	8.0 (4.9–16)

Low value in each range is salinity for northernmost known population in Hudson Estuary, and high value is salinity for southernmost known population

ppt (Table 1). The upper value of 16 ppt is the multi-year mean salinity at the Hudson River's mouth. We infer this value as the maximum mean salinity from the likely historic presence of *B. robustus* as far south as the Hudson's mouth. The actual salinity value for the southernmost known *B. robustus* population is 11 ppt. Vascular plant species closely associated with *B. robustus* are *Amaranthus cannabinus*; *Cyperus filicinus* Vahl; *Eleocharis parvula* (Roem. & Schult.) Bluff, Nees, & Schauer; *Lilaeopsis chinensis* (L.) Kuntze; *Phragmites australis*; *Schoenoplectus americanus*;

Sporobolus alterniflorus (Loisel.) P.M. Peterson & Saarela (*Spartina alterniflora* Loisel.); and *Symphyotrichum subulatum*.

Conservation status

Comparison of historic with current sets of collections permit a first consideration of conservation status of *Bolboschoenus* species in the Hudson Estuary. Historic and current collections of *B. fluviatilis* are nearly co-extensive (Fig. 4). In addition, current collections are known from all of the historic counties for *B. fluviatilis*, except Orange. We extensively explored the historic Orange County location, Moodna Creek, in 2013 but did not find *B. fluviatilis* there. We did document *B. fluviatilis* from a site opposite the mouth of Moodna Creek, across the Hudson River in Dutchess County.

Currently, *Bolboschoenus novae-angliae* occupies significantly less of its range than in the past (Fig. 5). Historic collections spanned 61 km (38 mi, river miles 15–53), whereas current collections span 32 km (20 mi, river miles 34–54). We explored all four historic sites in the southern

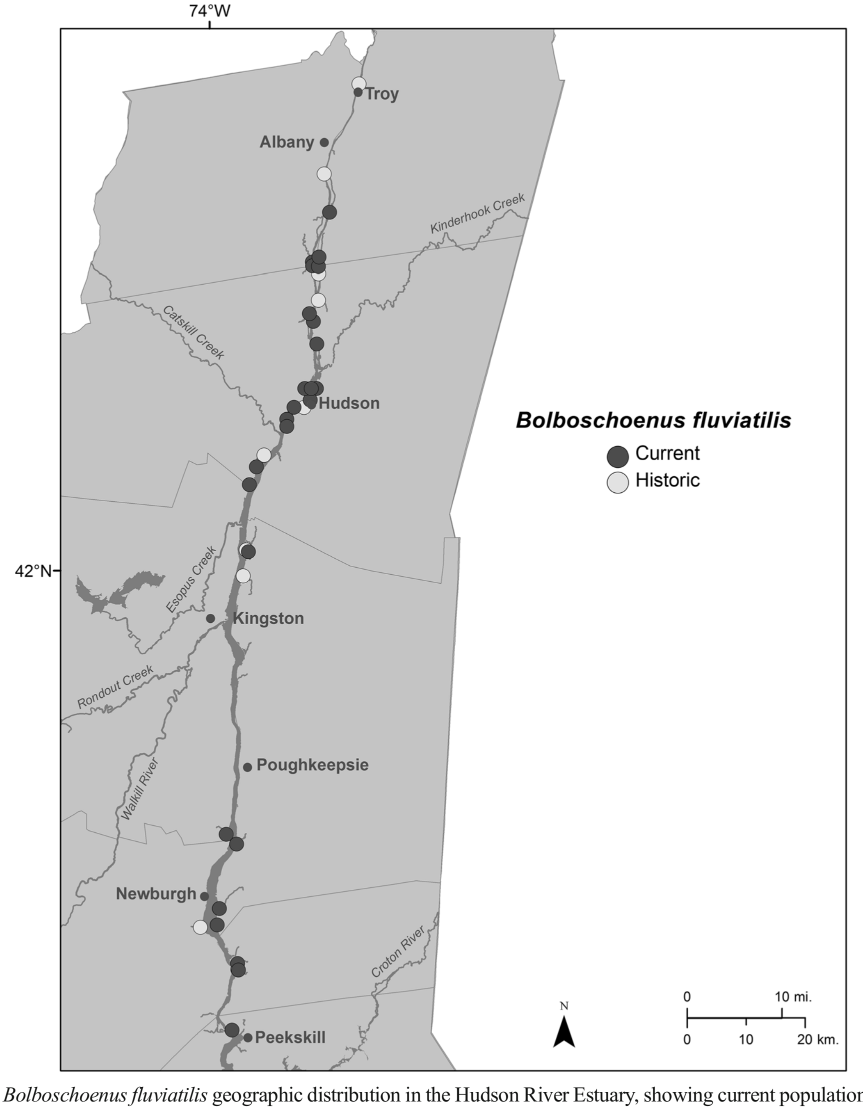

Fig. 4. *Bolboschoenus fluviatilis* geographic distribution in the Hudson River Estuary, showing current populations as well as those known only historically. A population known from a site both historically and currently maps as current.

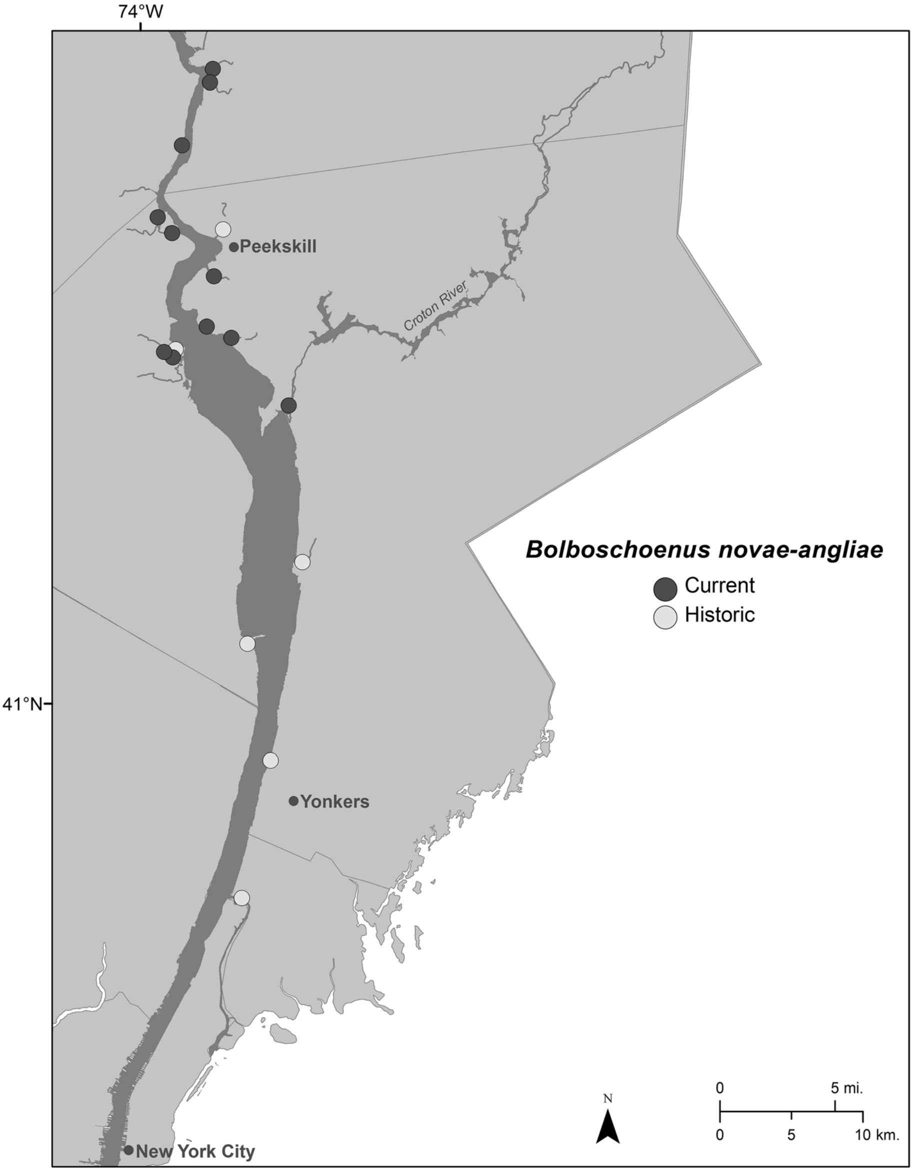

FIG. 5. *Bolboschoenus novae-angliae* geographic distribution in the Hudson River Estuary, showing current populations as well as those known only historically. A population known from a site both historically and currently maps as current.

portion of the known range of *B. novae-angliae* (Spuyten Duyvil, Bronx County; Piermont, Rockland County; North Tarrytown, Westchester County; and between Glenwood and Hastings, Westchester County), but did not observe *B. novae-angliae* at these sites.

Historic and current populations of *Bolboschoenus robustus* are nearly coextensive (Fig. 6). Historically, *B. robustus* occurred in the Hudson Estuary for a stretch of 21 km (13 mi, river miles 13–26). Currently known populations also span a stretch of 21 km (13 mi, river miles 15–28).

Another way of assessing conservation status of Hudson *Bolboschoenus* species is to consider the number and size of current populations per species. We documented 25 current populations for *B. fluviatilis*, 12 for *B. novae-*

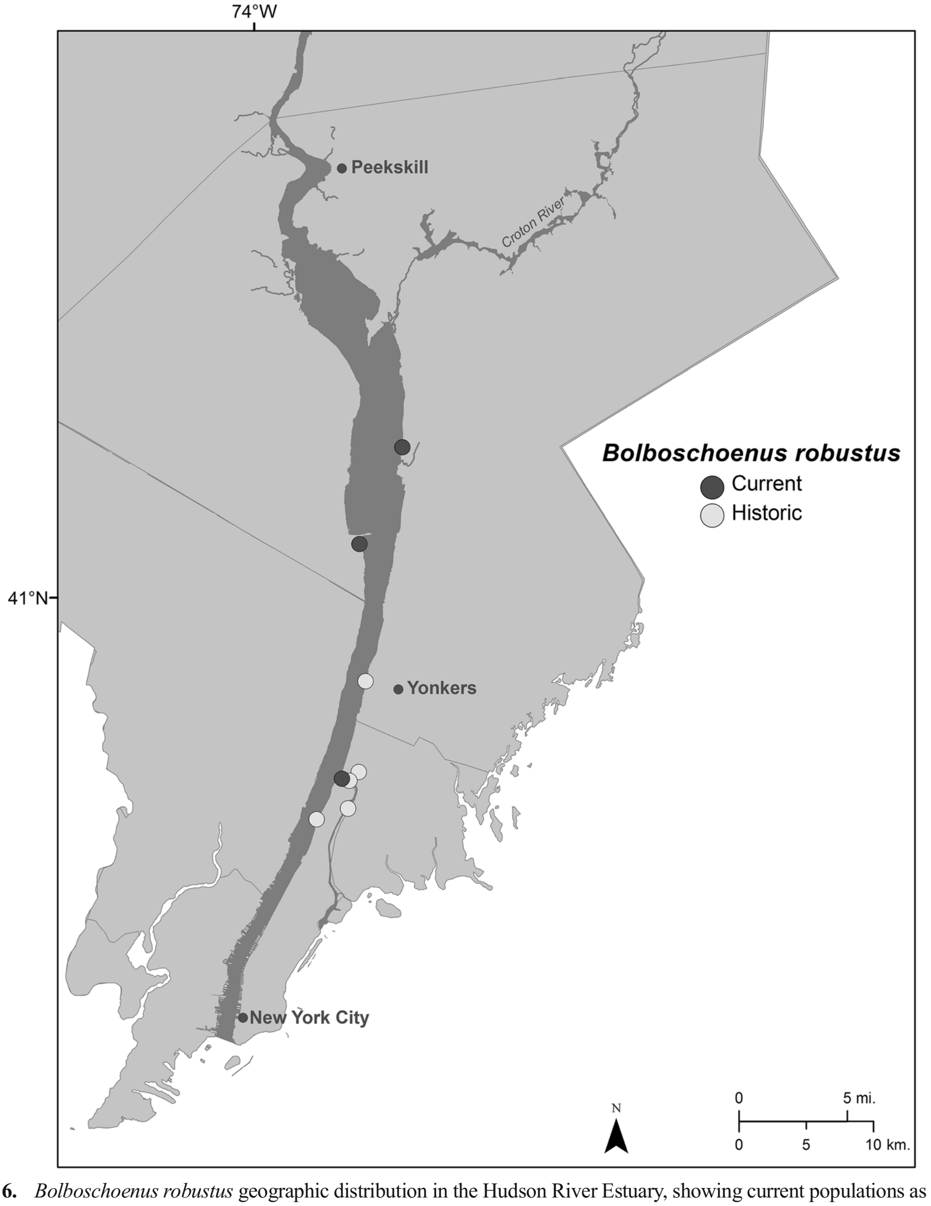

Fig. 6. *Bolboschoenus robustus* geographic distribution in the Hudson River Estuary, showing current populations as well as those known only historically. A population known from a site both historically and currently maps as current, including the northernmost population on the west side of the Hudson (Piermont).

angliae, and 3 for *B. robustus*. Several *B. fluviatilis* populations are large, each covering >200 m^2. Only one population of *B. novae-angliae* (Con Hook Marsh) is >200 m^2, with most very small (2–4 m^2). Only one population of *B. robustus* (Piermont Marsh) is >200 m^2, with the other two very small (2–4 m^2).

Population health is another essential factor in assessment of conservation status. Most *Bolboschoenus* populations in the Hudson Estuary co-occur with invasive plant species. *Phragmites australis* is especially common, co-occurring with *Bolboschoenus* at most sites. *Phragmites* was actively invading and overwhelming nearly all of the populations of *B. novae-angliae* that we observed (Fig. 7A). Along the Croton River, Westchester County, we discovered the population in 2012 and revisited it

FIG. 7. *Bolboschoenus* species in the Hudson River Estuary. **A.** *Bolboschoenus novae-angliae* population (foreground, plants with green foliage held by Scottie Sheaffer) being invaded by *Phragmites australis* (background, taller plants with blue-green foliage), 27 September 2017, upper portion of intertidal mudflat near mouth of Croton River, Westchester County, New York, U.S.A. **B.** Habitat of *Bolboschoenus robustus*, 19 September 2013, along Spuyten Duyvil Creek, Bronx County, New York, U.S.A.

in 2017. In the intervening years, *Phragmites* had greatly expanded its coverage and *B. novae-angliae* had diminished relative to its former areal extent (28 m^2 in 2012, 15 m^2 in 2017). Fruiting had reduced, too; in 2012 we observed 11 fruiting stems, whereas in 2017 we observed 2 fruiting stems. In both years, we carefully searched the entire *B. novae-angliae* population for fruiting stems. Though Piermont Marsh, Rockland County hosted fruiting *B. novae-angliae* at least as recently as 1984 (*Schuyler 6201*, PH), we failed to observe the species there, despite 4 days' extensive explorations throughout the marsh during 2012 and 2015. We did observe a very few, widely spaced *Bolboschoenus* stems in dense *Phragmites* that may be *B. novae-angliae*, but none of them were fruiting (Appendix 1).

Another serious threat to the survival of *Bolboschoenus* is excess nutrient pollution. Especially noteworthy in this regard is the Moodna Creek site. Though Moodna Creek hosted fruiting *B. fluviatilis* as recently as 1988, our extensive explorations of the site in September 2013 failed to find *Bolboschoenus*. Intertidal zones were common and in good physical condition at Moodna Creek in 2013. However, serious eutrophication was obvious. Vascular plant diversity was reduced relative to most other intertidal sites in the Hudson Estuary; we observed only 11 native and 2 non-native species growing in intertidal habitats of Moodna Creek (native: *Amaranthus cannabinus*, *Bidens cernua*, *B. connata* Willd., *Mikania scandens* (L.) Willd., *Nuphar advena* (Aiton) W.T. Aiton, *Peltandra virginica* (L.) Schott, *Pilea pumila* (L.) A. Gray, *Persicaria punctata*, *Sagittaria subulata*, *Typha angustifolia*, and *Zizania aquatica*; non-native: *Persicaria hydropiper* (L.) Delarbre, *Phragmites australis*). Especially abundant was *Persicaria hydropiper*, a known nitrophile (Leuschner & Ellenberg, 2017). Only two of these species are intertidal-restricted, *A. cannabinus* and *S. subulata*, and both were quite rare. Dense growths of algae covered many of the intertidal zones. An outfall pipe for municipal sewage and other wastewater was evident in the intertidal zone. Apparently, discharges from the outfall pipe were the sources of eutrophication. We observed similar signs of eutrophication in many other portions of the Hudson Estuary in the course of our fieldwork.

In contrast, a site with a *Bolboschoenus fluviatilis* population (Hannacrois Creek, Albany

County, September 2012, Appendix 1) and only mild eutrophication hosted 22 native and 4 non-native vascular plant species in the intertidal zone (native: *Amaranthus cannabinus*, *Bidens bidentoides*, *B. cernua*, *B. tripartita* L., *Bolboschoenus fluviatilis*, *Cyperus bipartitus*, *Eleocharis acicularis* (L.) Roem. & Schult., *E. aestuum* A. Haines, *E. intermedia* Schult., *E. obtusa* (Willd.) Schult., *Heteranthera reniformis*, *Lindernia dubia* (L.) Pennell, *Ludwigia palustris* (L.) Elliott, *Najas canadensis* Michx., *Najas muenscheri* R.T. Clausen, *Persicaria punctata*, *Potamogeton* sp., *Sagittaria graminea* Michx., *Sagittaria subulata*, *Schoenoplectiella smithii* (A. Gray) Hayas. var. *smithii*, *Schoenoplectus pungens*, *Zizania aquatica*; non-native: *Cyperus fuscus* L., *Lythrum salicaria*, *Phragmites australis*, *Plantago lanceolata* L.). At this site, intertidal-restricted plants were frequent and diverse (7 species: *Amaranthus cannabinus*, *Bidens bidentoides*, *Eleocharis aestuum*, *Heteranthera reniformis*, *Najas muenscheri*, *Sagittaria subulata*, and *Schoenoplectiella smithii* var. *smithii*). This site is one example of several in the northern portion of the estuary we observed having mild eutrophication and relatively high vascular plant species diversity.

Discussion

We used the herbarium specimen record to construct a baseline of historic occurrences of *Bolboschoenus* bulrushes in the Hudson River Estuary. We also assembled a record of current occurrences using our fieldwork, which is the most extensive study of Hudson River intertidal plants to date. We used historic and current specimens to document fine-scale geographic distributions of *Bolboschoenus* species in the Hudson Estuary, habitat characteristics, and current conservation status.

Each of the three *Bolboschoenus* species occurs in a specific region of the Hudson River Estuary. *Bolboschoenus fluviatilis* occupies the upstream (northern) portion of the estuary, *B. robustus* occupies the southernmost portion of the estuary, and *B. novae-angliae* occupies a region between the ranges of the other two species. These results parallel intra-river distributions reported by Schuyler (1975) and Ferren and Schuyler (1980) for the Delaware, Kennebec, and Penobscot estuaries, and Strong (1994) for the Potomac estuary. This study is the first, however, to map in detail *Bolboschoenus* allopatry, sympatry, syntopy, and salinity values within an estuary.

In the Hudson Estuary, the ranges of *Bolboschoenus fluviatilis* and *B. robustus* are completely separate, occurring 27 km (17 mi) apart, a substantial separation (11% of the estuary's length). This allopatry is in contrast to Smith's report (2002: 43) of a "zone of sympatry" between the two species, though he does not specify locations of this zone. The range of *B. novae-angliae* does overlap the ranges of the other two species. Sympatry of *B. novae-angliae* with the other species occupies only a narrow zone northward (with *B. fluviatilis*) and southward (with *B. robustus*).

The known range of *Bolboschoenus robustus* is almost certainly only a portion of its original range in the Hudson Estuary. *Bolboschoenus robustus* is frequent in coastal marshes along the Atlantic Ocean (Beetle, 1942; Gleason & Cronquist, 1991; Smith, 2002), and occurs in estuaries near their mouths (Schuyler, 1975; Strong, 1994). Development of New York City occurred well before collecting of *Bolboschoenus* began along the Hudson in 1869. This early development almost certainly eliminated *B. robustus* populations, and the species probably occurred south from the known range to the mouth of the Hudson.

Of the three Hudson Estuary *Bolboschoenus* species, *B. fluviatilis* has the longest range (172 km/107 mi, 70% of the estuary's length, historic and current populations included). *Bolboschoenus novae-angliae* has a short range (63 km/39 mi, 26% of the estuary's length). The documented range of *B. robustus* is very short (24 km/15 mi, 9.9% of the estuary's length). If the inferred range of *B. robustus* (south to the Hudson's mouth) is considered, the range is 45 km (28 mi), 18% of the estuary's length.

Evidently, each *Bolboschoenus* species has a narrow niche. Despite occurring along the same river, each species has a distinct geographic range within the estuary. Furthermore, zones of sympatry are narrow (14 km/9 mi for sympatry of *B. fluviatilis* and *B. novae-angliae*, and 21 km/13 mi for *B. novae-angliae* and *B. robustus*). In addition, even though sympatry does occur, syntopy is quite rare (known for *B. fluviatilis* and *B. novae-angliae* at only one site, and no more than two sites for *B. novae-angliae* and *B. robustus*). Multi-year mean surface salinity values of Hudson River water adjacent to *Bolboschoenus* populations also provide evidence of narrow niches for the bulrushes. Each species grows within a narrow range of salinities, *B. fluviatilis* in freshwater (mean salinities 0.078–2.0 ppt), *B. novae-angliae* in slightly to strongly brackish water (mean salinities 1.8–8.0 ppt), and *B. robustus* in brackish to saline water (4.9–16 ppt, using inferred southern range limit at Hudson's mouth). The salinity values we report for *B. robustus* essentially agree with ranges reported by Anderson et al. (1968) for this species at two sites in the Patuxent River Estuary, Maryland (6.0–17 ppt, though they report an outlier of 0.85 ppt on one date). Salinity does correlate with distributions of *Bolboschoenus* species, as reported by Schuyler (1975) for other estuaries. From all this evidence, we conclude that each *Bolboschoenus* species requires relatively restricted habitat in the Hudson Estuary.

Global geographic distributions and habitats also provide important data on niche breadth in *Bolboschoenus* species. Though *B. fluviatilis* is relatively frequent in freshwater tidal habitats, it also grows in nontidal marshes and river shores, and occurs transcontinentally (Gleason & Cronquist, 1991; Strong, 1994; Smith, 2002). *Bolboschoenus novae-angliae* grows only in intertidal marshes and mudflats along the Atlantic Coast from Maine to North Carolina and possibly Georgia (Schuyler, 1975; Strong, 1994; Smith, 2002). *Bolboschoenus robustus* is most frequent in tidal marshes along the Atlantic Coast from Maine south to Texas and South America, but also occurs in inland salt marshes (Smith, 2002). Thus, *B. novae-angliae* has the smallest global range and most restricted habitat (endemic to eastern North American brackish intertidal zones) of the three congeners occurring in the Hudson Estuary.

The historic baseline reveals that the historic extent of *Bolboschoenus fluviatilis* is nearly the same as the current extent (Fig. 4). Probably, the number of populations has remained relatively stable, too. Great differences in collection intensity and strategy between current (intensive and systematic) and past efforts (spotty and opportunistic), however, make it impossible to ascertain with certainty any trends in population numbers for *B. fluviatilis*. Despite uncertainty about trends, the substantive matters about conservation status of *B. fluviatilis* are 25 populations are currently known, several of the populations are large, and populations occur through an extensive portion of the estuary. These factors lead us to assess the conservation status of *B. fluviatilis* in the Hudson Estuary as secure. Most *B. fluviatilis* populations occur in portions of the estuary with little urban and suburban development, and probably that low level of development is a major factor in the healthy status of this species in the Hudson Estuary (Figs. 1 and 2).

Range contraction is evident for *Bolboschoenus novae-angliae*. The historic specimen record documents a portion of the range currently unoccupied by the species (Fig. 5). The contraction is northward, with currently known populations occurring almost entirely within the historically documented range. The currently known range is 53% of the length of the historic range (reduction from 61 to 32 km/38 to 20 mi). Chief reasons for decline of *B. novae-angliae* in the Hudson Estuary appear to be habitat destruction through urbanization, competition from invasive plant species, and excess nutrient pollution. Quite likely, urbanization, invasive plant species, and eutrophication have created unfavorable conditions for *B. novae-angliae* in the southern portion of its former range, and the species now grows only in sites where conditions are more favorable. Sea level rise with consequent increase in salinity may have contributed to or even caused range contraction, but it is impossible from available data to determine if sea level rise has influenced the distribution of *B. novae-angliae*.

Urbanization is intense to moderate in three of the four sites from which *Bolboschoenus novae-angliae* has disappeared (Figs. 1 and 5). Extirpations of the historic North Tarrytown and "between Glenwood and Hastings" localities are most likely due to development since our explorations of these areas disclosed extensive human destruction of intertidal habitats, with almost no suitable intertidal habitat remaining. The Spuyten Duyvil locality has similar challenges from urbanization for intertidal plants, though we did find a bit of intertidal habitat there (Fig. 7B) that supported a very small population of *B. robustus*, but not *B. novae-angliae*.

Invasive plant species are a substantial threat to *Bolboschoenus novae-angliae*. *Phragmites australis* appears to be the most serious of the invasive plant species impacting *B. novae-angliae*. The Eurasian *Phragmites australis* is a superior competitor that invades natural areas, including the upper portions of fresh, brackish, and saline intertidal zones (Vasquez et al., 2005; Rudrappa et al., 2009; Uddin & Robinson, 2017). In a short period of time, it forms stands in which it is the dominant and often the only vascular plant species growing. Thus, in areas it has invaded, it soon occupies space formerly inhabited by native plants. These problems are especially serious for native species that inhabit only the upper portions of intertidal zones, such as *B. novae-angliae*. We measured reductions in *B. novae-angliae* coverage and fruiting at the Croton River site, apparently caused by *Phragmites* expansion there. More widely, we have observed *Phragmites* to be ubiquitous in the Hudson Estuary, increasing in its geographic coverage, and invading most of the currently known populations of *B. novae-angliae*.

Eutrophication caused by excess nutrient pollution appears to make intertidal sites inhospitable for many native vascular plants, including *Bolboschoenus fluviatilis*. Our own observations at the same time of year (September) at sites in the freshwater portion of the estuary with contrasting levels of eutrophication reveal markedly different recent patterns of vascular plant diversity. The highly eutrophic site (Moodna Creek) hosted half the number of native vascular plants of the site with mild eutrophication (Hannacrois Creek). The negative effects of eutrophication appear especially grave for those plants restricted to intertidal habitats; the Moodna Creek site hosted only 2 intertidal-restricted plant species, whereas the Hannacrois Creek site hosted 7 such species. We observed several other low-eutrophication sites that hosted high intertidal plant diversity similar to Hannacrois Creek. Problems with eutrophication that we noticed at Moodna Creek are widespread and common in the estuary. It is reasonable to expect eutrophication is negatively impacting all three *Bolboschoenus* species in the Hudson Estuary.

We assess the conservation status of *Bolboschoenus novae-angliae* in the Hudson Estuary as critically imperiled. Currently known populations are few (12), most are very small, and the species currently occurs in only a short section of the estuary (32 km/20 mi). Threats to the survival of *B. novae-angliae* are grave, and the threat from invasive *Phragmites australis* is intensifying. We expect *Phragmites* will outcompete *B. novae-angliae* and eliminate it from most sites in the Hudson Estuary within the next decade, unless management practices halt the continuing spread of *Phragmites*.

Bolboschoenus novae-angliae is of conservation concern throughout most of its geographic range. Authorities have assigned the rank of S1/critically imperiled to the species in Delaware (McAvoy, 2016), Maine (Maine Natural Areas Program, 2015), and New York (Young, 2017); S2/imperiled in Maryland (Maryland Natural Heritage Program, 2016) and New Jersey (Snyder, 2016); and S3/concern, special concern, or watch list in Connecticut (Connecticut Department of Energy and Environmental Protection, 2015), Massachusetts (Massachusetts Natural Heritage and Endangered Species Program, 2017), Rhode Island (Rhode Island Natural History Survey, 2016), and Virginia (Townsend, 2016).

Bolboschoenus robustus currently occurs along a very short stretch of the Hudson River (21 km/13 mi). It occurs in only three populations in the estuary, two of which are quite small. Relative to the seven known historic populations, *B. robustus* has declined, though the current and historic geographic distributions are similar. Declines are likely due to habitat destruction through urbanization, competition from invasive plant species, and pollution with excess nutrients. Urbanization along the Hudson is especially intense in the geographic range of *B. robustus* (Fig. 1). Several of the historic populations of *B. robustus* have been destroyed through human development, including Kingsbridge Creek, Bronx County; Fort Washington Point, New York County; and between Yonkers and Hastings, Westchester County. *Phragmites australis* is invading *B. robustus* populations at two of its current sites, Piermont Marsh and NW of Philipse Manor. Pollution with excess nutrients, especially through sewage dumping, threatens *B. robustus* in the Hudson Estuary. We assess the conservation status of *B. robustus* in the Hudson Estuary as critically imperiled due to the serious threats facing the very few remaining populations.

Though critically imperiled in the Hudson Estuary like *B. novae-angliae*, *B. robustus* differs from that species in being frequent throughout most of its geographic range. Only one state in the northeastern U.S.A. considers *B. robustus* as of conservation concern, Maine (Maine Natural Areas Program, 2015). Maine is at the northern edge of the range of *B. robustus*, and few populations occur there.

For the Hudson Estuary, we have provided new and much-needed data and analyses on the current and historic distributions, habitats, and conservation status of *Bolboschoenus* bulrushes. These species are integral and ecologically important parts of intertidal habitats in the Hudson Estuary and elsewhere in the northeastern U.S.A. and adjacent Canada. Our data and analyses provide critical information for prioritization of responses to environmental threats, and for planned restoration efforts (Miller, 2013). With appropriate environmental management and restoration, *B. fluviatilis*, *B. novae-angliae*, and *B. robustus* bulrushes could flourish in the Hudson River Estuary.

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Appendix 1. Specimens examined. All collections are from New York, USA. Unless noted, all are from shores of the Hudson River. We cite the earliest known collection per population, for historic sites and also for current sites, but do not cite later collections that are population duplicates. Historic collections = those collected 1869–2005. Current collections = 2011–2017. Herbarium abbreviations are as in Thiers (2017), except "Bard" = Bard College Field Station Herbarium.

***Bolboschoenus fluviatilis*, historic.** Albany Co.: Glenmont, 29 Jul 1919, *House 6572* (GH, NYS, US); Green Island, 22 Jul 1924, *House 10,372* (NYS). Columbia Co.: just S of city of Hudson, 18 Jul 1933, *House 20,490* (NYS); Stuyvesant, Mill Creek, 29 Jul 1933, *McVaugh 1817* (NYS); Hotaling Island, 25 Jun 1935, *McVaugh 3146* (NYS). Dutchess Co.: 2 mi S of Tivoli, E of Cruger's Island, 11 Aug 1934, *McVaugh 2898* (NYS); Tivoli Bays, North Bay, 31 Aug 1972, *Kiviat s.n.*

(Bard); Tivoli Bays, South Bay, 2 Jul 1973, *Kiviat s.n.* (Bard); Cruger Island Neck, 14 Jun 1985, *Westad s.n.* (Bard); Red Hook, Mudder Kill, 18 Aug 1987, *Zaremba 4713* (NYS). Greene Co.: on the island opposite New Baltimore, Aug 1869, *Howe s.n.* (NY); Catskill, Embough Road [Imbocht Bay], 15 Jun 1993, *Barbour s.n.* (BH). Orange Co.: New Windsor, Moodna Creek, 5 Aug 1988, *Zaremba 5670* (NYS). Putnam Co.: Philipstown, foot of Philipse Brook, 14 Aug 2003, *Werier 1794* (NYS).

***Bolboschoenus fluviatilis*, current.** Albany Co.: 0.7 mi SSE of Coeymans, Hannacrois Creek, 19 Sep 2012, *Naczi 14,536* (NY); 0.3 mi S of Coeymans, 7 Oct 2013, *Naczi 15,170* (NY). Columbia Co.: 3.4 mi SSW of city of Hudson, opposite S end of Rogers Island, 10 Sep 2011, *Naczi 13,937* (NY); 3.0 mi SW of city of Hudson, NW side of Rogers Island, 28 Aug 2013, *Naczi 15,034* (NY); 1.9 mi N of Poolsburg, Schodack Creek, 20 Sep 2012, *Naczi 14,558* (NY); Stuyvesant, small tributary of Hudson River, 6 Oct 2013, *Werier 5371* (NY); Stuyvesant, 8 Oct 2013, *Werier 5401* (NY); Hudson, South Bay, 9 Oct 2013, *Werier 5410* (NY); Greenport, N end of North Bay, 9 Oct 2013, *Werier 5411* (NY). Dutchess Co.: 2.1 mi SSW of Tivoli, channel to South Bay, 13 Sep 2013, *Naczi 15,098 & Zimmerman* (NY); Poughkeepsie, Wappinger Creek, 24 Sep 2013, *Werier 5281* (NY); Beacon, Fishkill Creek, 25 Sep 2013, *Werier 5303* (NY); Fishkill, NE of Pollepel Island, 25 Sep 2013, *Werier 5308* (NY). Greene Co.: 2.8 mi N of Coxsackie, Coxsackie Creek, 22 Sep 2011, *Naczi 14,050* et al. (NY); 2.0 mi NE of Cementon, Duck Cove, 29 Aug 2013, *Naczi 15,043* (NY); 0.4 mi SE of Cementon, 29 Aug 2013, *Naczi 15,056* (NY); Athens, NW side of Middle Ground Flats, 29 Aug 2013, *Werier 5136* (NY); SW of Athens, Brandow Point, 2 Oct 2012, *Werier 4825* (NY); Athens, Murderers Creek, 7 Oct 2013, *Werier 5392* (NY). Putnam Co.: Philipstown, Philipse Brook, 26 Sep 2013, *Werier 5325* (NY); Philipstown, Constitution Marsh, 26 Sep 2013, *Werier 5327* (NY). Rensselaer Co.: 0.2 mi W of community of Schodack Landing, Schodack Creek, 20 Sep 2012, *Naczi 14,550* (NY); Schodack, Papscanee Creek, 11 Sep 2013, *Werier 5196* (NY). Ulster Co.: Marlborough, tributary of Lattintown Creek, 24 Sep 2013, *Werier 5293* (NY). Westchester Co.: Cortlandt, ca. 900 m NW of mouth of Annsville Creek, 30 Sep 2013, *Werier 5359* (NY).

***Bolboschoenus novae-angliae*, historic.** Bronx Co.: Spuyten Duyvil Creek, 1 Jul 1891, *Bicknell s.n.* (NY). Orange Co.: Con Hook, 19 Aug 1987, *Zaremba 4302* (NYS). Putnam Co.: Philipstown, foot of Philipse Brook, 14 Aug 2003, *Werier 1794* (NY). Rockland Co.: Haverstraw, Grassy Point, 25 Aug 1936, *Muenscher 5679 & Curtis* (BH); Piermont, 26 Aug 1936, *Muenscher 5678 & Curtis* (BH, GH); Iona Island, S side of entrance road, 31 Aug 1954, *Lehr 575* (NY); N of Dunderberg, between Iona Island and route 9W, 25 Jun 1993, *Barbour 908* (NYS); Iona Island, S end near railroad tracks, 21 Sep 1993, *Tucker 9432* et al. (NYS). Westchester Co.: North Tarrytown, 18 Jun 1895, *Barnhart 999* (NY); between Glenwood and Hastings, 5 Sep 1898, *Bicknell s.n.* (NY); near mouth of Peekskill Creek, 22 Aug 1936, *Muenscher 5680 & Curtis* (BH).

***Bolboschoenus novae-angliae*, current.** Orange Co.: 1.2 mi S of community of Highland Falls, Con Hook Marsh, 8 Oct 2012, *Naczi 14,609* (NY). Putnam Co.: Philipstown, Philipse Brook, 26 Sep 2013, *Werier 5324* (NY); Philipstown, Indian Brook, 26 Sep 2013, *Werier 5328* (NY). Rockland Co.: 5.3 mi N of community of Stony Point, just W of northern end of Iona Island, 30 Aug 2012, *Naczi 14,411 & Werier* (NY); 4.9 mi N of community of Stony Point, just W of Iona Island, 30 Aug 2012, *Naczi 14,413 & Werier* (NY); 4.7 mi NNE of community of Stony Point, just S of Iona Island, 31 Aug 2012, *Naczi 14,414 & Werier* (NY); 1.0 mi SE of community of Stony Point, along tributary of Hudson River, 30 Aug 2013, *Naczi 15,057* (NY); 0.6 mi SE of community of Stony Point, along tributary of Hudson River, 30 Aug 2013, *Naczi 15,069* (NY). Westchester Co.: 0.3 mi W of Crotonville, Croton River, 2 Sep 2012, *Naczi 14,440* (NY); 1.7 mi SSW of center of Peekskill, Dickey Brook, 11 Sep 2012, *Naczi 14,502* (NY); 1.2 mi SW of Montrose, 18 Sep 2013, *Naczi 15,105* (NY); 0.2 mi SSW of Crugers, Furnace Brook, 18 Sep 2013, *Naczi 15,113* (NY).

***Bolboschoenus robustus*, historic.** Bronx Co.: New York 24th Ward, Aug 1876, *Howe s.n.* (NY); Harlem River, below Fordham Heights, 14 Oct 1890, *Bicknell s.n.* (BKL, NY); Spuyten Duyvil Creek, 19 Jul 1891, *Bicknell s.n.* (BKL); Kingsbridge Creek, 8 Sep 1898, *Bicknell s.n.* (NY, NYS, PH). New York Co.: Manhattan, Fort Washington Point, 25 Aug 1900, *Bicknell 1086* (NY). Rockland Co.: Piermont, 24–26 Aug 1944, *Muenscher 21,564* et al. (BH). Westchester Co.: between Yonkers and Hastings, 5 Sep 1898, *Bicknell 1100* (NY, NYS, PH).

***Bolboschoenus robustus*, current.** Bronx Co.: Spuyten Duyvil Creek, 19 Sep 2013, *Werier 5260* (NY). Rockland Co.: 0.8 mi SE of Piermont, Piermont Marsh, 16 Aug 2012, *Naczi 14,370* (NY). Westchester Co.: 0.4 mi NW of Philipse Manor, along small tributary of Hudson River, 19 Sep 2013, *Naczi 15,122 & Dorey* (NY).

***Bolboschoenus* unidentifiable, due to absence of infructescences and achenes from source populations.** Putnam Co.: 0.5 mi SW of Manitou, Manitou Marsh, 16 Oct 2017, *Naczi 17,078 & Sheaffer* (NY). Rockland Co.: 0.5 mi SE of Piermont, Piermont Marsh, 22 Sep 2015, *Naczi 16,031 & DeGasperis* (NY). Westchester Co.: 1.4 mi NW of center of Peekskill, mouth of first tributary of Hudson River W of Annsville Creek, 24 Sep 2012, *Naczi 14,573* (NY).