



Historical insights, current challenges: tracking marine biodiversity in an urban harbor ecosystem in the face of climate change

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Abstract

The Boston Harbor Islands is the only coastal drumlin archipelago in the USA, featuring a distinctive and uncommon geological intertidal habitat known as mixed coarse substrate, which supports a range of coastal species and ecological processes. Recently designated as one of America's 11 most endangered historic places due to climate change impacts, coastal adaptation and restoration efforts are crucial to their preservation. Such efforts can benefit from historic and current knowledge of endemic and emergent biodiversity. To investigate broad trends in coastal biodiversity, we compiled an inventory of marine coastal macroalgae, macroinvertebrates, fish, mammals, and shorebirds observed in the harbor since 1861. Records span 159 years, consisting of 451 unique taxa from 19 phyla. Analysis of average taxonomic distinctness (AvTD) revealed increases in diversity towards the end of the twentieth and early twenty-first century, likely associated with improved water quality (dissolved oxygen; $AvTD > 85$, $p = 0.01$) due to harbor restoration in the 1980s. Macroinvertebrates comprised 50% of the records, making this the most diverse taxonomic group in the time series. A significant increase of non-indigenous species, primarily macroinvertebrates and macroalgae, was observed over the last 20 years near human infrastructure and across multiple islands, a consequence of global change and characteristic of most urban harbors. The mixed coarse intertidal habitat, which makes up > 70% of Boston Harbor's inner islands and supports high macroinvertebrate and macroalgal diversity (47% of species records), is not routinely monitored; our findings serve as a foundational resource for climate adaptation projects and decision-making.

Keywords Average taxonomic distinctness · Intertidal invertebrates · Intertidal macroalgae · Restoration · Mixed coarse substrate

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Introduction

In a time of rapid global change, marine ecosystems are increasingly vulnerable to human disturbance and climate change (Halpern et al. 2007, 2019). Urban marine harbors, compared to other marine systems, distinctly experience the effects of human-mediated global change through intense coastal development, increased human density, and regional and global maritime activity, with consequences such as pollution, habitat degradation, and biological invasion (Carlton 2010; Mayer-Pinto et al. 2015; Lyons et al. 2020; Alter et al. 2021). Despite these challenges, urban harbors, marinas, and ports across the globe can sustain high levels of biodiversity (Bang et al. 2012; Chou et al. 2023; Madon et al. 2023). For example, Australia's Sydney Harbor was found to support relatively high fish species diversity, compared to other related estuaries (Johnston et al. 2015). Similarly, in Singapore, one of the world's busiest ports, species diversity is high, with relatively high diversity of coral species and other reef associated species such as macroalgae, crustaceans, and molluscs (Tan et al. 2016). These findings underscore the complexity and sometimes unexpected biodiversity of urban marine harbors.

Boston Harbor is an essential port in North America and host to a variety of coastal and marine habitats including those on the Boston Harbor Islands, which are the only coastal drumlin archipelago in the United States. Boston Harbor has a long and complex history, first inhabited for millennia by indigenous peoples (pre-1600 s), then colonized by British settlers (1630), then as an important hub during the Revolutionary War (1776), and now maintains tourism, recreation, industry, and shipping supporting the Boston metropolis (Richburg and Patterson III 2005; Bowen et al. 2019; National Park Service 2021). In modern times (circa 1970–1980s), Boston Harbor was considered one of the most polluted water bodies in America, being known as the “harbor of shame” (Richburg and Patterson III 2005; Bowen et al. 2019) with extremely high concentrations of compounds such as polycyclic aromatic hydrocarbons (PAHs), heavy metals, and polychlorinated biphenyls (PCBs) (Donlin 2004; Hunt and Sloan 2010). Extremely high nitrogen and phosphorus pollution was derived from untreated sewage and wastewater entering the harbor (Dettmann 2001; Taylor 2010). Run-off and pollutants had major impacts on water quality and marine life including high rates of fin rot, liver tumors, and cancer in commercially and recreationally important fishes such as winter flounder (*Pseudopleuronectes americanus*) (Wallace 1986). In addition, Boston Harbor has experienced major disturbance across multiple habitat types, with over 50% of the original salt marsh and wetlands lost, declines in eelgrass beds, and negative impacts to

benthic communities due to urban development and dredging (Wallace 1986; Bowen et al. 2019). After decades of restoration and management efforts (e.g., Clean Water Act, 1972 and the federal court-ordered clean-up of 1985), water quality improved dramatically, and since the 1990s, Boston Harbor has been considered a model of successful harbor clean-up and restoration as evidenced by documented recovery of important indicator species such as eelgrass (Bowen et al. 2019) and the levels of toxic contaminant concentration (i.e. chlordanes, dieldrin, dichlorodiphenyltrichloroethane (DDT), PAHs, PCBs) in the tissues of winter flounder and American lobster (*Homarus americanus*) steadily decreasing over time (Hunt et al. 2006). Although Boston Harbor has experienced an impressive turnaround in water quality, it now faces new threats from the rising impacts of climate change. The surrounding areas of the Gulf of Maine and broader western Atlantic region are warming at a significantly higher rate compared to the rest of the world's oceans; this has manifested as record marine heat waves in the last 10 years in addition to increased frequency and intensity of coastal storms (Wuebbles et al. 2017; Salisbury and Jönsson 2018; Sims et al. 2022). Outer areas of Boston Harbor have shown a steady increase in both surface and bottom water temperatures since the 1990s and, in most recent years, have experienced the highest harbor-wide average temperatures on record (Taylor 2018).

In 2021, the National Trust for Historic Preservation (National Trust for Historic Preservation 2022) listed the Boston Harbor Islands National Recreation Area as one of America's 11 most endangered historic places due to climate change; specifically, sea level rise and increasingly intense storms are putting the cultural and biodiversity resources of the area under threat. Current observed and predicted rates of sea level change in the region (2.81 ± 0.17 mm/year over the last century) are 3–4 times higher than the global average and are significantly associated with risk of storm surge, flooding, and erosion (USGCRP 2018). Consequently, climate adaptation planning efforts are underway to implement shoreline stabilization projects across Boston Harbor, including nature-based solutions that support local biodiversity (Castango et al. 2021). In addition, as a major transportation and shipping hub, Boston Harbor, like other marinas and ports, is considered a hot spot for non-indigenous species (NIS) due to the high level of local and international movement of shipping vessels (Ojaveer et al. 2018). Indeed, since harbor-wide monitoring assessments of NIS began in 2001, approximately 39 species have been identified across Boston Harbor and more are expected as warming continues (McIntyre et al. 2013; Wells et al. 2014; Kennedy et al. 2020). Collectively, these direct and indirect climate impacts are anticipated to result in significant degradation and losses

of Boston Harbor's native biodiversity, natural habitats, human infrastructure, and historic cultural sites as protective and regulatory ecosystem services are compromised (Suarez et al. 2005; Kirshen et al. 2008; Maio et al. 2012).

Marine coastal biodiversity of the Boston Harbor Islands

Marine coastal biodiversity has been assessed at a number of islands in Boston Harbor through a limited number of one-time, short-term studies (Bell et al. 2002; Eddy and Roman 2016; Matassa and Hitchcock 2021). Regular monitoring is conducted by the National Park Service and partners at a subset of selected sites for rocky intertidal communities in permanent bedrock habitats (Northeast Temperate Network Monitoring program; Long and Mitchell 2015) and for taxonomic groups of high conservation concern such as shore and sea birds (Trocki et al. 2021).

A widespread but understudied habitat across the Boston Harbor Islands is mixed coarse substrate, which consists of varying amounts (≥ 50 and $\leq 75\%$ composition) of rocks, boulders, cobbles, gravel, shell, and sand (Bell et al. 2005; Thornbery-Ehrlich 2017). With the accelerating impacts of climate change in the region, monitoring biological communities in mixed coarse substrate and other habitats is important to establish and track baselines as environmental conditions change and as adaptive actions are undertaken by park managers. The historical context of species occurrence is needed to provide a relative perspective for retrospective and future projections of losses and gains (Armonies et al. 2018). Historical records can be useful to build inventories to provide such context and enhance our understanding of past dynamics and changes over time within a system of interest (Thurstan et al. 2015). For example, a synthesis and analysis of records of benthic invertebrates in Narragansett Bay revealed changes in community composition and a decline in biodiversity across a 182-year period associated with pollution and demonstrated a partial recovery due to management efforts and policy implementation (Hale et al. 2018). Historic inventories can also help identify and prioritize research, management, and monitoring targets for an area based on population changes and data gaps (Treibitz et al. 2019).

Due to the growing risks imposed by climate impacts and the prospective for adaptation projects to be implemented along the coastlines of Boston Harbor, the National Park Service and regional management partners identified mixed coarse substrate as a habitat of concern. This heightened focus was primarily due to a lack of data on the distribution and abundance of biodiversity associated with mixed coarse substrates in the intertidal zone. To address this need, this study synthesized historical records of coastal biodiversity for Boston Harbor from 1861 to 2020. We used this

historical inventory to describe broad trends in occurrence of marine macroalgae, birds, fish, macroinvertebrates, and marine mammals detected in the harbor across time. Results characterize native biodiversity relative to NIS, identify spatial and temporal gaps in information, and identify opportunities for future research and monitoring across the islands' at-risk intertidal habitats.

Materials and methods

Study area

Boston Harbor (Fig. 1) is a 130-km² temperate urban embayment located in Massachusetts (2°20'18.00" N, -70°57'34.79" W) with a mean depth of 6 m, a maximum depth of up to 14 m, and a mean salinity of 30.6 ppt (Taylor 2018). The harbor floor consists of glacial till, outwash, and clay, while the islands are mostly post-glacial drumlins (Thornbery-Ehrlich 2017). The 34 islands and peninsulas within Boston Harbor (Fig. 1) represent a rare geological history unique in North America (Himmelstoss et al. 2006; Bowen et al. 2019). Habitats across the islands include estuarine, marsh, and mudflat systems; rocky intertidal including rock bench, cobble, gravel, and mixed coarse; and sandy beaches. However, rocky mixed coarse is the dominant substrate for intertidal habitat across the Boston Harbor Islands (Bell et al. 2005).

Data sources and management

We constructed a biodiversity inventory for Boston Harbor by collecting and merging occurrence records, validating data sources, and compiling species-specific information (Treibitz et al. 2019) to summarize and describe patterns in occurrence and distribution across Boston Harbor (Putnam et al. 2024). Our species inventory for Boston Harbor was derived from 14 sources of which include datasets from state and federal agencies (e.g. Massachusetts Division of Marine Fisheries, Massachusetts Coastal Zone Management (MA CZM), National Park Service, etc.), peer-reviewed and gray literature, and scientific grade research observations from public biodiversity databases (e.g. Global Biodiversity Information Facility (GBIF) which includes observations from eBird, iNaturalist, Harvard University Museum of Comparative Zoology, Smithsonian Institution National Museum of Natural History, etc.) (Table 1). Sources included in this inventory were selected based on their inclusion of species-level data and corresponding information.

Species included in this inventory were associated with intertidal, subtidal, and open water habitats and include macroinvertebrates, macroalgae, fish, and marine mammals. Except for sea and shorebirds, which use coastal habitats

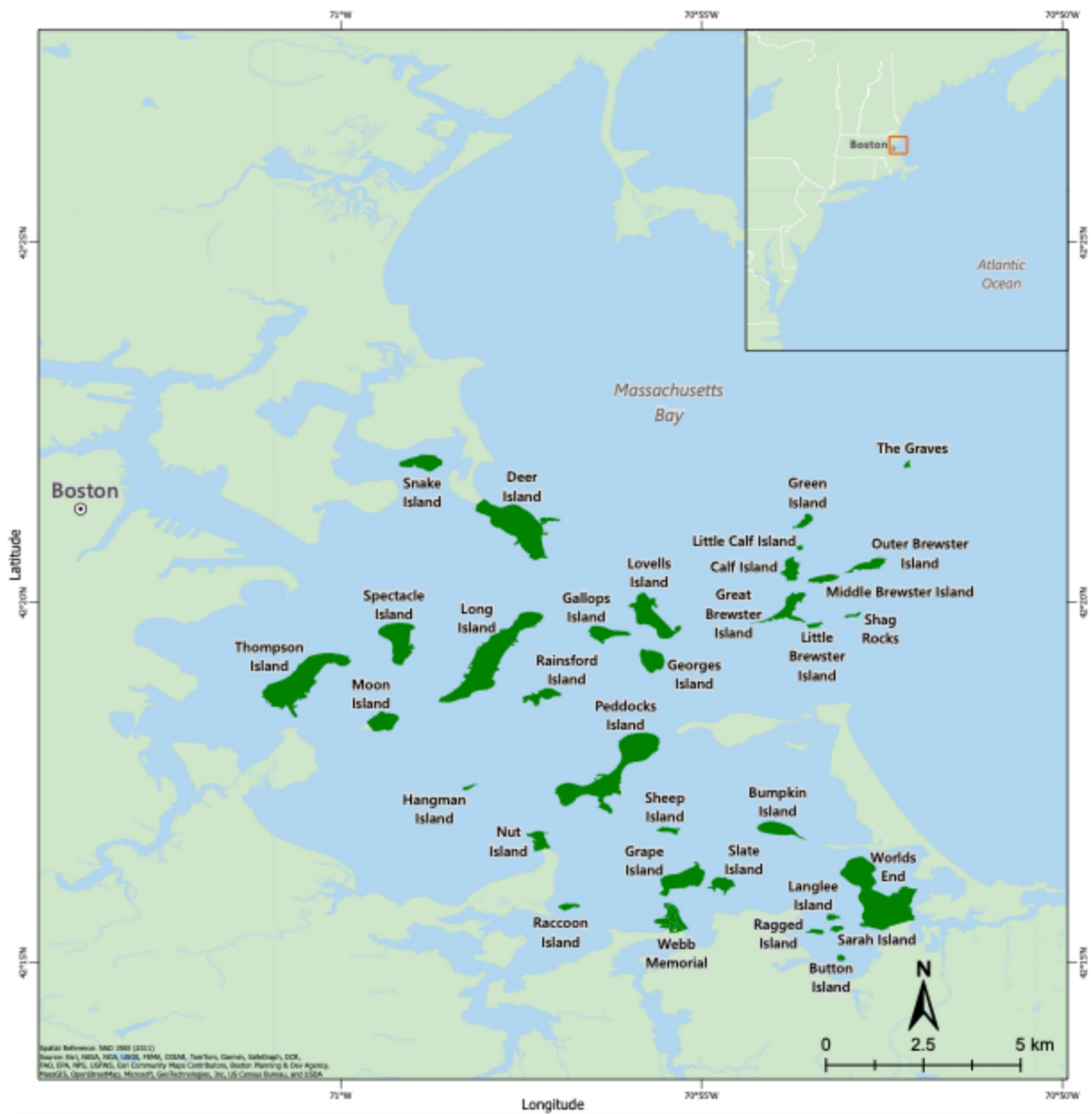


Fig. 1 The Boston Harbor Islands National and State Park depicted in dark green

for foraging and other activities, we excluded all terrestrial species from this dataset. In addition, we did not include microscopic coastal organisms such as zooplankton and phytoplankton. To validate and align species records, all taxonomic names were reviewed against the World Register of Marine Species (WoRMS Editorial Board 2023) and brought up to date or replaced with the current synonym, and full taxonomic information (phylum through species) was recorded for each species in the inventory. To make

this inventory accessible to diverse audiences, species common names were assigned alongside scientific names. Species were assigned into coarse-scale taxonomic categories of “algae,” “bird,” “invertebrate,” “fish,” and “mammal” and into functional ecological categories corresponding to their status as native, NIS, or cryptogenic (unknown origin) species. Species data records were assigned to the nearest island or peninsula when spatial reference points were available. Spatial points that occurred between islands or

Table 1 Descriptions of data sources used to develop the Boston Harbor species inventory (1861–2020)

Source name	Target species	Date range	Sampling methods	Spatial extent	Citation
Inventory of intertidal marine habitats, Boston Harbor Islands National Park Area	Macroalgae Macroinvertebrates	04/2001–10/2001	Opportunistic sampling (presence of macroinvertebrates and algae) as well as spatial cover of macroalgae	Outer Brewster, Calif, Great Brewster, Little Brewster, Lovells, Georges, Gallops, Peddocks, Hangman, Rainsford, Long, Spectacle, Thompson, Grape, Slate, Langlee, World's End, Sheep, Raccoon, Bumpkin	Bell et al. (2002), (2005)
Boston Harbor Habitat Atlas (BHHA)	Fish Macroalgae Macroinvertebrates	2018	List of species compiled by regional partners with local knowledge of the Boston Harbor system	No spatial data, Harbor-wide	https://cos.northeastern.edu/marine-science/outreach/bhen/
Boston Harbor Cruises	Cetaceans	2013–2019	Record of high and low estimates of the number of unique individuals obtained through visual sightings from boats	No spatial data, Harbor-wide	https://www.boston-discovery-guide.com/boston-harbor-cruises.html
MA Division of Marine Fisheries suction sampling	Fish Macroinvertebrates	1997–2019	Suction sampling related bycatch reports documenting counts of all crabs, shrimp, fish, and urchins encountered. Sampling effort varied over time	No spatial data, Harbor-wide	https://www.mass.gov/info-details/american-lobster-research-and-monitoring
Global Biodiversity Information Facility	Birds Fish Macroalgae Macroinvertebrates	1861–2020	Opportunistic observations—compilation of multiple sources including citizen science networks and experts that contribute data to platform	No spatial data, Harbor-wide	https://www.gbif.org
Massachusetts Water Resources Authority (MWRA)	Fish	1991 1992	Otter trawl	No spatial data, Harbor-wide	Moore et al. (1992), Moore and Stegman (1993)
MA Office of Coastal Zone Management—Marine Invader Monitoring and Information Collaborative (MIMIC)	Macroalgae Macroinvertebrates	2008–2019	Citizen scientists surveying for established marine invasive species and potential invaders during the growing season (June–October). Volunteers spend an hour searching for species	No spatial data, Harbor-wide	https://www.mass.gov/info-details/marine-invader-monitoring-and-information-collaborative-mimic
MA Office of Coastal Zone Management—Rapid Assessment Survey (CZM RAS)	Macroalgae Macroinvertebrates	2007 2010 2013 2018	Scientists sampled for up to 1 h by hand with paint scrapers or dip nets to capture motile animals. Undersides of floats and structures were sampled by a dive team	Rowes Wharf	McIntyre et al. (2013) Wells et al. (2014) Kennedy et al. (2020)
North Atlantic Right Whale Consortium	Fish Marine mammals	1976–2019	Sighting data, line-transect surveys, platforms-of-opportunity surveys, and immediate-format aerial surveys	No spatial data, Harbor-wide	https://www.narwc.org/

Table 1 (continued)

Source name	Target species	Date range	Sampling methods	Spatial extent	Citation
Northeastern Naturalist	Macroinvertebrates	07/2012–08/2012	Performed Generalized Random Tessellation Stratified sampling using 0.5 × 0.5-m quadrats for species > 1 mm	Bumpkin, Grape, Lovells, Peddocks, Spectacle, Thompson	Eddy and Roman (2016)
Northeastern Naturalist	Macroalgae Macroinvertebrates	10/18/2008	Sampled for one, 3–4-h period using 0.5 × 0.5-m quadrats and exploratory sampling	Outer Brewster, Calf, Little Brewster, Peddocks, Grape, Langlee	Matassa and Hitchcock (2021)
National Park Service (NPS)	Macroalgae Macroinvertebrates	09/2018	Measured percent cover using 0.5 × 0.5 m quadrats	Gallops, Georges, Lovells	Buchbinder (2018)
NPS Northeast Temperate Network (NETN)	Macroalgae Macroinvertebrates	2013–2019	Sampled for 9 full days twice/year – once in the winter (Feb/Mar) and once in the summer (June–Aug) using fixed plots (50 × 75 cm) with replicates. Sampling focused on small, sessile target species, motile macroinvertebrates, and barnacle recruitment	Calf, Green, Outer Brewster	https://www.nps.gov/im/netn/index.htm , Long and Mitchell (2015)
NPSpecies biodiversity database *	Macroalgae Macroinvertebrates	NA	Opportunistic presence/absence count of species	No spatial data, Harbor-wide	https://irma.nps.gov/npspecies

peninsulas were usually subtidal species and categorized as “mid-harbor.” However, 919 of 8492 occurrence records did not have geographical coordinates of latitude and longitude and were either linked to an island based on the original data source’s metadata description or the overall harbor. All records within the data set are occurrence points (presence) of a species documented in the harbor.

We compiled environmental data (e.g., dissolved oxygen, salinity, sea surface temperature (SST), sea level, and turbidity) for Boston Harbor to determine associations between environmental stressors and biodiversity over time. Dissolved oxygen, salinity, turbidity, and SST were obtained from the Massachusetts Water Resources Authority’s Environmental Monitoring and Mapping System (Data courtesy of Massachusetts Water Resources Authority (MWRA) (Moore et al. 1992; Moore & Stegman 1993). Sea level data, which is represented as monthly mean sea levels with the average seasonal cycle removed, was obtained from the National Oceanic and Atmospheric Administration (NOAA) relative sea level trends for Boston Harbor.

Biodiversity analysis

Cumulative trends

We computed species discovery and accumulation curves for all species detected in Boston Harbor across the time period of 1861–2020. A subset of species that are considered non-indigenous or cryptogenic and defined as NIS were analyzed separately from native species. We used the chao2 and jackknife models from the “vegan” package (Oksanen et al. 2022) to extrapolate the estimated number of species that still could be found in Boston Harbor with additional sampling.

Average taxonomic distinctness

Because a range of disparate resources were assembled to build our biodiversity inventory, we were faced with the problem of uneven and sometimes unknown sampling efforts across our dataset. Therefore, traditional biodiversity metrics such as the Shannon–Wiener and Simpson diversity indices, which require consistent sampling and abundance estimates, could not be reliably applied. Instead, we evaluated changes in Boston Harbor biodiversity over time using average taxonomic distinctness ($\Delta+$, AvTD; Clarke and Warwick 1998), a metric which has been applied in a range of previous studies assessing marine biodiversity, where sampling efforts are dissimilar, uneven, or unknown (Clarke and Warwick 1998, 2001; Brown et al. 2002; Leonard et al. 2006; Louzao et al. 2010; Trott 2016; Hale et al. 2018; Jiang et al. 2020). AvTD measures the degree to which species in a sample are taxonomically related to each other by calculating the

average length between species and a common ancestor on the taxonomic tree. AvTD is calculated independent of sampling effort and methodology and can be reliably applied to presence/absence data (Clark and Warwick 1998). Metric values range between 0 and 100, where lower values represent a sample where species are more closely related, or less diverse; in contrast, higher values represent a sample where species are less taxonomically related or are more diverse. In addition, AvTD also provides information on the differences in the calculated value and expected value (i.e., a baseline value of average taxonomic distinctness that would be anticipated in a theoretical randomly-assembled community based on the given sample), which is useful to determine if there has been a loss in biodiversity over time. This metric is also useful as it allows for diversity to be calculated and associated with other variables such as environmental stressors. For example, studies such as Hale et al. (2018) and Jiang et al. (2020) have used AvTD to assess changes in species diversity over time associated to environmental conditions such as water quality (i.e., eutrophication) and increasing water and air temperature. Using the full species inventory, we computed AvTD across our time series at the decade scale, incorporating all species independent of taxon to evaluate trends across time. We then used a one-way ANOVA to test for significant differences in AvTD by decade. We used a subset of our species inventory, focusing on the most diverse taxonomic groups found in the intertidal zone, macroinvertebrates and macroalgal species, to compute AvTD values by year and by island.

To ascertain whether patterns in AvTD were associated with changes in environmental conditions, we used linear regression models to relate annual and decadal AvTD scores for the full species inventory and the subset of intertidal macroinvertebrate and macroalgal species with harbor-wide metrics of sea level, SST, salinity, dissolved oxygen, and turbidity.

All statistical analyses were computed using RStudio (v. 2023.12.1 + 402; R Core Team 2022) of the R statistical software (v. 4.2.2) using the “tidyverse” and “vegan” packages (Wickham et al. 2019; Oksanen et al. 2022).

Results

The analysis of the full species inventory encompassed a total of 451 observed marine coastal macroalgae, birds, fish, macroinvertebrates, and marine mammal species in Boston Harbor between 1861 and 2020 (Table 2). The most diverse taxonomic group, which comprised 50% of the total species, were the macroinvertebrates with 226 species within 12 phyla. Seventy-two percent of the macroinvertebrate species were from three phylum: arthropoda ($n = 63$ species), mollusca ($n = 53$ species), and annelida ($n = 49$ species)

(Fig. 2a). The earliest observation of macroinvertebrate taxa from the data sources was made in 1861 (GBIF 2020). Macroalgae comprised the second largest taxonomic group with 98 species within 4 phyla, with the dominant phyla being red macroalgae Rhodophyta ($n = 38$ species) followed by brown macroalgae Ochrophyta ($n = 34$) (Fig. 2b). Data records for macroalgae spanned from 1887 to 2020. Coastal bird observations also date back as far as the 1870s. All 76 coastal bird species fall into one phylum and one class but are distributed across 10 orders and 20 families (Fig. 2c). Shorebirds are the largest order, which comprised 53% of the total bird species. Observations of fish were sparse and began in the late 1970s. Forty observed fish species from one phylum were documented (Fig. 2d). The smallest taxonomic group represented in the full species inventory was the marine mammals, which had 11 species from one phylum (Fig. 2e) documented across the years 1976–1989, 1992, and 1996–2019 (North Atlantic Right Whale Consortium 2020).

Diversity across the Boston Harbor Islands

Species records were documented on 19 islands, 6 peninsulas, and 5 mid-harbor benthic sampling sites (Fig. 1). Lovells and Peddocks islands had the highest number of unique species records across the time series ($n = 114$ and $n = 113$, respectively), with avian species making up the majority of observations ($n = 67$ and $n = 42$, respectively). Sites with the lowest number of species recorded were Ragged, Nut, and Hangman Islands, each having only one recorded species: beach hopper amphipod, (*Orchestia grillus*), red alga (*Grinnellia americana*), and a polychaete worm (*Eumida sanguinea*), respectively.

Species discovery and accumulation curves for all species

The species inventory discovery curve (Fig. 3a) showed that the total number of unique taxa detected and identified in Boston Harbor did not increase significantly until the 1970s when efforts of species monitoring, such as whales and sea and shorebirds, began. A second surge of new species observed in the 1990s that continued through 2020 coincided with the introduction of monitoring of the American lobster through a Settlement Collaborative suction sampling and bycatch survey conducted by the MA Division of Marine Fisheries, and monitoring by the MWRA. The more recent 15 years of the dataset showed an increase in species detections due to the added efforts of inventories facilitated by park managers, including bioblitzes (e.g. Matassa and Hitchcock 2021) and data collected by community scientists reporting sightings into platforms such as eBird (Sullivan et al. 2009) and iNaturalist (iNaturalist 2020), along with new monitoring of NIS, which started in 2000 led by the MA

Table 2 Total number of all taxonomic groups included in the full species inventory of Boston Harbor between 1861 and 2020

Taxon level	Macroinvertebrates	Macroalgae	Birds	Fish	Marine mammals
Phyla	12	4	1	1	1
Classes	24	9	1	3	1
Orders	62	29	10	14	2
Families	133	52	20	26	6
Genera	187	77	49	34	10
Total unique species	226	98	76	40	11

CZM. The species inventory accumulation curve (Fig. 3b) showed that although over 400 species have been recorded as of 2020, the curve does not reach a plateau, and the species extrapolation permuted model (jackknife and chao2) estimates there are between 175 and 300 additional species that potentially exist and could be found in Boston Harbor.

Species inventory sub-analysis of intertidal macroinvertebrates and macroalgae

Across the intertidal zone of the Boston Harbor Islands, 213 unique species of intertidal macroinvertebrates and macroalgae were recorded over the time series (Fig. 3c, Table 3); phyla with the highest species representation included Arthropoda ($n=38$), Rhodophyta ($n=32$), Ochrophyta ($n=28$), and Mollusca ($n=27$). The functional group with the most records of occurrence ($n=100$ –248) were NIS. Nearly half of the observed intertidal macroinvertebrates and macroalgae were considered rare with $n=68$ singletons (species only detected once across the time series), and $n=29$ species with only 2 detections across the time series. The islands with the highest number of unique macroinvertebrate and macroalgal species were Calf ($n=92$), Peddocks ($n=77$), and Thompson ($n=58$) islands. Islands with the lowest number of unique species were Gallops ($n=5$), Hangman, Nut, and Ragged islands ($n=1$).

Non-indigenous species

Within the Boston Harbor species inventory and 159-year period of the data series, 54 species were considered NIS ($n=35$) or cryptogenic ($n=19$) (Table 4). The earliest recorded NIS was for the Common periwinkle (*Littorina littorea*) in 1894. Arthropods (crabs, shrimp, and amphipods) had the highest representation of NIS in the dataset, followed by chordates (solitary and colonial tunicates). NIS with the greatest number of detection records across the data set included the European green crab (*Carcinus maenas*, $n=276$), the colonial chain tunicate (*Botrylloides violaceus*, $n=250$), the solitary club tunicate (*Styela clava*, $n=197$),

and the Asian shore crab (*Hemigrapsus sanguineus*, $n=156$). The species discovery curve (Fig. 3d) shows that the number of unique NIS taxa identified in Boston Harbor was relatively low until the early 2000s. Between 2000 and 2020, there was a significant and exponential increase in identified NIS ($R^2=0.77$, $p<0.001$). The jackknife and chao2 species extrapolation permuted models estimated there were between 6 and 13 more species that potentially exist and potentially could be found in Boston Harbor with additional sampling.

Average taxonomic distinctness of biodiversity

Decadal AvTD scores for the full species inventory was not significantly correlated with sample size (number of species; $t=1.86$, $p=0.09$). Significant differences were found among decadal AvTD scores for total species diversity in Boston Harbor ($F=3.67$, $p=0.003$) (Fig. 4). On average, decades in the second half of the twentieth century and the twenty-first century (1990s–2020s) had relatively higher values of AvTD than earlier decades, suggesting higher observed biodiversity in recent times. There is one exception: the 1890s AvTD values were extremely high; however, the sample size was very low (<10 species recorded during that decade) and thus may be an outlier when compared to more recent decades that have higher numbers of species recorded.

We found significant associations between annual values of AvTD and three out of the five environmental variables tested (Fig. 5a-c). Higher values of AvTD were significantly associated with higher values of dissolved oxygen ($R^2=0.23$ $p=0.01$) and sea level rise ($R^2=0.27$ $p<0.001$), while low values of AvTD were significantly associated with high SST ($R^2=0.17$ $p=0.03$). No relationships were found between AvTD and turbidity and salinity (p -values ≥ 0.05).

AvTD scores for the sub-analysis of intertidal macroinvertebrates and macroalgal species showed no detectable pattern across years or islands. Most years and islands did not meet the baseline expected value ($\Delta+94.63$ and 96.73 , respectively); however, most were greater than $\Delta+80$, suggesting a fairly diverse taxonomic spread. Exceptions include AvTD at Gallops Islands ($\Delta+76.26$) and years with no AvTD values signify years with less than two species recorded (e.g., 1861–1996, 1976, 1996, and 2003). Significant relationships between AvTD and environmental variables were not detected at the island or time scale for the macroinvertebrates and macroalgae sub-analysis ($p>0.05$).

Discussion

Our synthesis of 14 historical datasets and resources cover over a century of observations (1861–2020) and revealed a total of 451 species reported across the various coastal

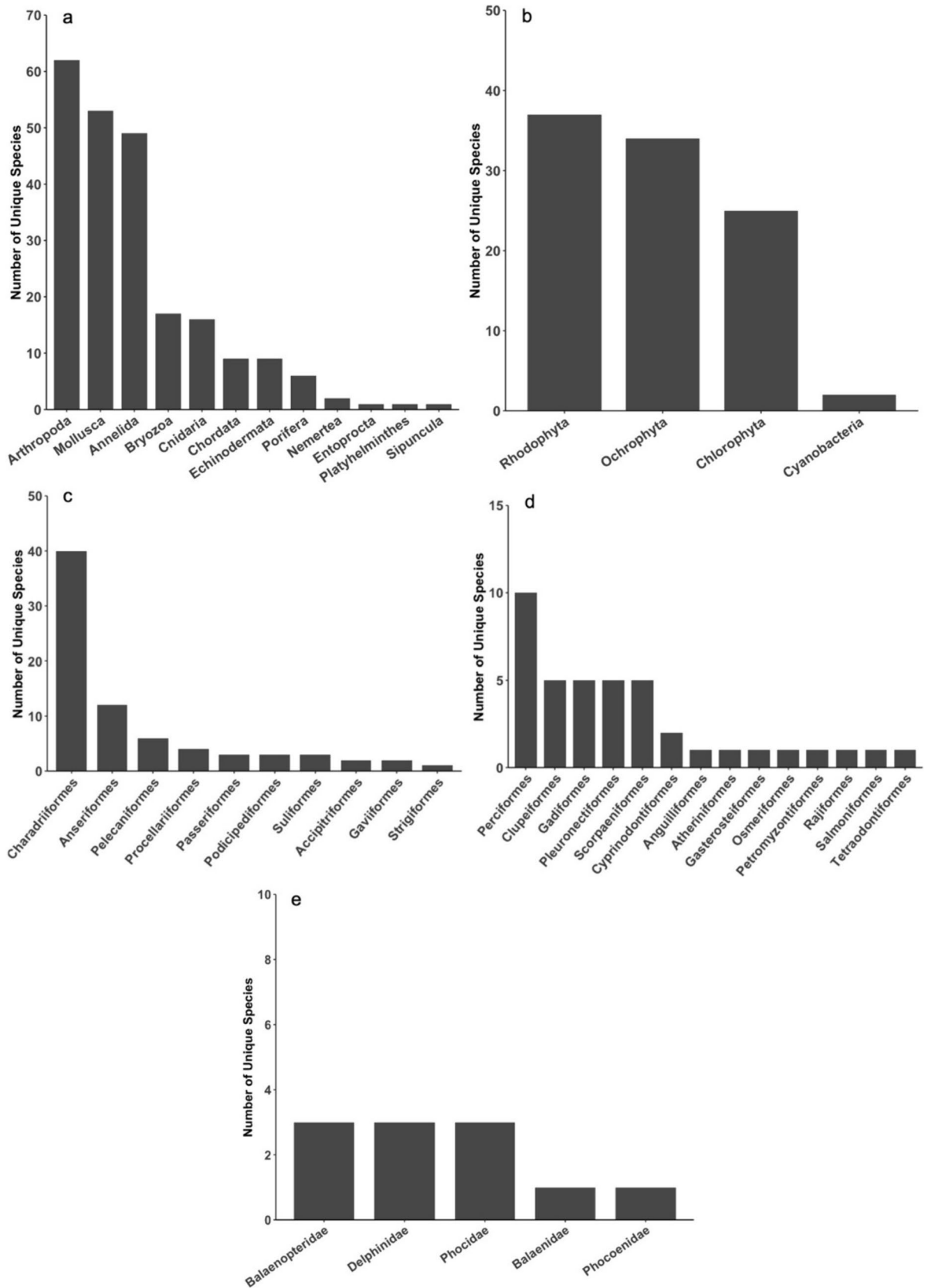


Fig. 2 Number of unique species observed in Boston Harbor between 1861 and 2020 organized by major taxonomic groups: **a** Intertidal macroinvertebrates per phylum; **b** macroalgae per phylum; **c** avian per order; **d** fish per order; **e** marine mammals per family

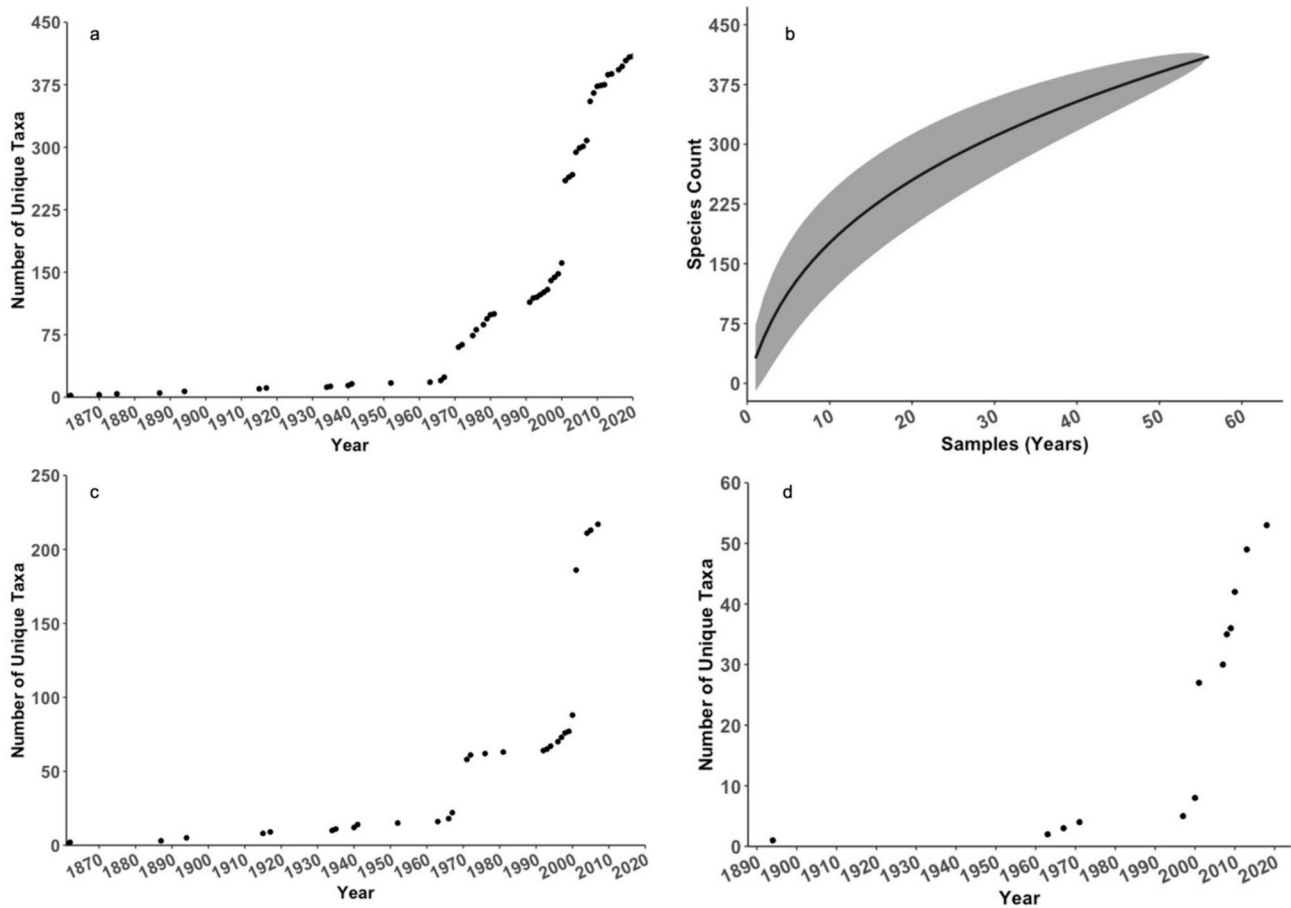


Fig. 3 Patterns in unique taxa found in Boston Harbor Islands between 1861 and 2020 for **a** all taxa species discovery curve; **b** species accumulation curve and sub-analyses discovery curves of: **c** intertidal macroinvertebrates and macroalgae; **d** non-indigenous species

Table 3 Total number of intertidal macroinvertebrates and macroalgae taxonomic groups included in the sub-analysis of Boston Harbor between 1861 and 2020

Taxon level	Macroinvertebrates	Macroalgae
Phyla	10	4
Classes	19	8
Orders	43	26
Families	85	45
Genera	111	65
Total unique species	130	83

habitats of Boston Harbor. The most diverse taxonomic groups were the macroinvertebrates and macroalgae with over half (72%) of all unique species observed across the islands, peninsulas, and benthic habitats of Boston Harbor. Macroinvertebrates and birds were the taxonomic groups with the highest number of observations (40 and 34%, respectively). Our findings show that community scientist platforms such as iNaturalist and eBird are an important

Table 4 Number of non-indigenous and cryptogenic taxonomic groups observed in Boston Harbor between 1861 and 2020

Taxon level	Macroinvertebrates	Macroalgae
Phyla	7	3
Classes	10	3
Orders	19	8
Families	34	8
Genera	43	8
Total unique species	46	8

source of data for commonly observed and novel species. Data from these types of networks have aided researchers in monitoring biodiversity generally (Di Cecco et al. 2021), assessing changes in species phenology (Primack et al. 2023), development of species distribution models (Heberling et al. 2021), and documenting emerging species (Moulin 2020). Observations submitted to iNaturalist and eBird for Boston Harbor were composed of various user types of known and unknown expertise, such as individuals

from the public to National Park Service staff and project leads from academic and agency partner organizations. For example, included in the iNaturalist data set are observations made by students attending the University of Massachusetts Boston, which has periodically held a 2-day annual retreat on Thompson Island for Honors students. One activity involves a 3-h biodiversity survey where all observations are entered into the iNaturalist platform. Participants in the University of Massachusetts Boston program have collected and entered > 5600 images in iNaturalist, resulting in the identification of > 200 terrestrial and marine species (Stevenson et al. 2021). Approximately half of these observations in the iNaturalist platform were of high enough quality (i.e., research grade) that they were integrated into our species inventory.

It should be noted that the varying level of effort in how data were collected limits our ability to estimate trends in species abundance over time and across spatial areas within Boston Harbor. In addition, patterns in species detections across Boston Harbor likely reflect the accessibility of different islands to the public and infrastructure; for example, islands reported with only one detection (e.g. Hangman and Ragged islands) do not have public transportation and the limited number of detections on Gallops Island is due to the island being closed to the public as of 2000 because of the presence of asbestos (National Park Service 2023). In contrast, there are likely numerous species records on Peddocks

Island due to the availability of public transportation to the island which facilitates community science observations collected and archived in online platforms such as eBird. Further, islands and years targeted by sporadic scientific research projects such as the Boston Harbor Islands Bioblitz (Mattassa and Hitchcock 2021) resulted in disproportionately greater records of intertidal biodiversity at sites targeted by those studies. Similarly, there were several species in our data that were considered rare (1–2 occurrences); however, many of these rare species such as *Amphibalanus improvisus*, *Leathesia marina*, *Minuca pugnax*, and *Ulva prolifera* are generally considered more common in regional intertidal habitats and were likely only observed less frequently due to the limited sampling that has occurred across the many islands of Boston Harbor. Finally, it is important to highlight that while there are details on species presence pre-1861, this information is stored in early museum records not fully digitized (e.g. Muséum National d'Histoire Naturelle, Paris), in early colonial writings (e.g. William Wood's 1634 "New England Prospect"), and other early period scientific writings where species names are no longer synonymous (Gould 1841), all of which are outside the scope of this project to acquire.

Species of concern

Several ecological and economically important species have been documented in Boston Harbor over the 159-year period of our data series. For example, the foundational algal species *Ascophyllum nodosum* was documented at eight islands. *A. nodosum* plays an important functional role forming extensive canopies that support > 100 species of invertebrates and sub-canopy algal species (Kay et al. 2016), as well as providing habitat to juvenile economically important fisheries species such as Atlantic cod (*Gadus morhua*), Atlantic herring (*Clupea harengus*), American pollock (*Polachius virens*), and American lobster (Lotze et al. 2019). In addition, *A. nodosum* and other related macroalgae are highly productive and play an important role in the transfer of carbon as a blue carbon system (Lewis 2020; Lauzon-Guay et al. 2022). Unfortunately, the edge of the southern distribution of *A. nodosum* is contracting northward which is believed to be associated with climate change (Pereira et al. 2020; Hernández et al. 2023). Given its ecological and climate regulatory service roles (i.e., carbon sequestration), it may be a candidate for new protections and increasingly valued for its mitigation potential whereas in the past, it has been overlooked in conservation prioritization decision-making (Chung et al. 2011).

The number of marine mammal species observed in Boston Harbor and included in our inventory were low compared to other taxonomic groups in part because they are a less biodiverse group overall; however, their increased

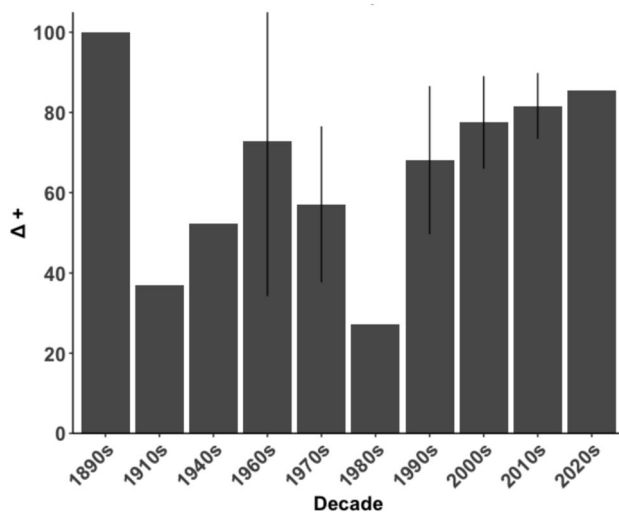


Fig. 4 Average taxonomic distinctness ($\Delta+$, \pm sd) by decade of all species found in Boston Harbor 1861–2020. Higher $\Delta+$ values indicate species are less taxonomically related or are more diverse within the sampling unit, while lower $\Delta+$ values indicate higher associations and less diversity within the sampling unit. Bars without standard deviation lines represent decades with 2 or fewer years of species observations (however, each year had documented greater than 2 species)

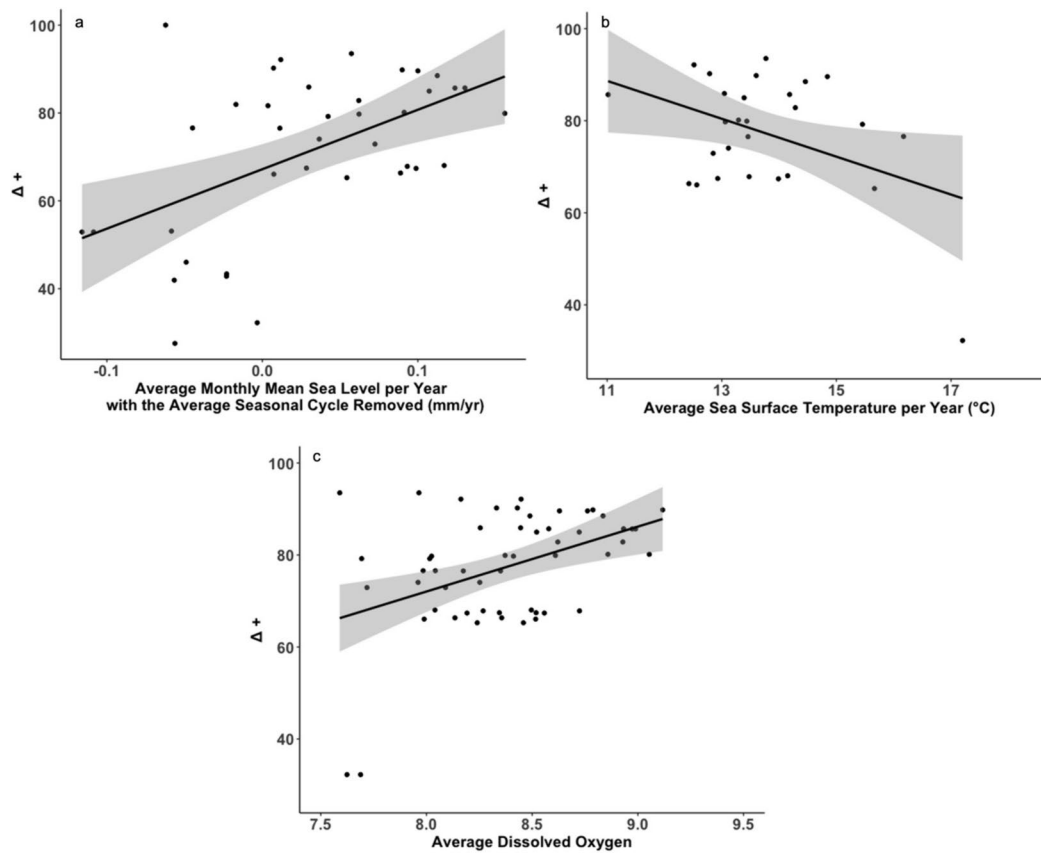


Fig. 5 Linear models showing the association between annual average taxonomic distinctness ($\Delta+$) and three environmental variables. Higher $\Delta+$ values indicate species are less taxonomically related or are more diverse within the sampling unit, while lower $\Delta+$ values

indicate higher associations and less diversity within the sampling unit. **a** average monthly mean sea level (with the average season cycle removed); **b** average annual sea surface temperature; **c** average dissolved oxygen in Boston Harbor between 1861 and 2020

presence in the region is a sign of population recovery and conservation success (Wood et al. 2020). Cetaceans and pinnipeds play important ecological roles in marine coastal ecosystems through foraging, predation, and other processes (i.e., bioturbation and nutrient cycling) (Katona and Whitehead 1988; Sette et al. 2020; Kiszka et al. 2022). Species detections were obtained from aerial transect surveys and opportunistic sighting surveys (North Atlantic Right Whale Consortium 2020). Recent work has shown that the use of topographic habitat can serve as a proxy for species distribution (Madon et al. 2022) and can enhance the number of sightings during specified sampling periods. Citizen science observations from whale watches in the harbor and by recreational anglers and boaters could also increase records for rare and endangered species that are only occasional visitors to the area, especially during gap periods between dedicated boat and aerial survey.

The blue mussel (*Mytilus edulis*) is another ecological and economically important species that is widespread within the Gulf of Maine and southern New England. Similarly to *A. nodosum*, *M. edulis* is an ecosystem engineer that

promotes and enhances biodiversity by creating a structural matrix through their attachment to substrate and formation of connected mats that provide habitat to a diverse range of other invertebrates and macroalgae (Suchanek 1985; Albrecht 1998; O'Connor and Crowe 2007; Arribas et al. 2013). Petraitis and Dudgeon (2020) attributed declines in this species in the Gulf of Maine region starting in the 1970s due to rising ocean temperatures associated with climate change. Within Boston Harbor, we documented *M. edulis* across 19 islands with its earliest record dating back to 1941. A recent monitoring survey identified large, healthy mussel beds at two islands (Gallops and Rainsford island), which were not previously recorded within our historic species inventory and synthesis (Byrnes et al. 2022). Petraitis and Dudgeon (2020) identified several other invertebrate species as indicators of biological declines in association with climate change. These species, *L. littorea*, *Nucella lapillus*, *Semibalanus balanoides*, and *Testudinalia testudinalis*, occupy a variety of important ecological roles within the intertidal community as food resources to higher trophic level species, and regulatory services through water filtration. Although records of

occurrence were documented within Boston Harbor since the early 2000s, these populations have not been assessed well enough to track population trends and or association with climate drivers. Many charismatic macrofauna (i.e., shorebirds, fishes, and marine mammals) have been evaluated in recent climate change vulnerability assessments to both understand the impacts of climate change on their populations and rank them relative to other species to prioritize conservation efforts; however, this information is significantly lacking for most intertidal invertebrates and macroalgae that are known to be important in terms of their ecosystem and socioeconomic services (Staudinger and Albert 2023). Understanding the impacts of climate change and other environmental stressors in Boston Harbor necessitates regular and systematic monitoring to obtain sufficient data on abundance, distribution, and population demographics. This vital information would support future climate vulnerability assessments and conservation efforts for these under-assessed species.

Non-indigenous species

Our data inventory revealed that the detection of NIS increased significantly in Boston Harbor at the end of the twentieth century. The number of documented NIS rapidly increased from 5 to 27 between 1997 and 2001 followed by 19 additional new NIS in 2001. This increase in detections can largely be attributed to the implementation of Rapid Assessment Surveys (RAS) for NIS species across the Northeast region beginning in 2000. This program was conducted by a group of taxonomic experts that survey biofouling communities on floating pontoons and docks in marinas and harbors every 3 to 5 years (Pederson et al. 2021). Although there was an initial surge in observations of NIS at the beginning of this effort, observations of new species have slowed to an average of four per year since 2001 and new species were only found during survey years between 2001 and 2018. While RAS has dramatically increased the number of records of NIS in the region, efforts are primarily limited to areas around anthropogenic infrastructure. Consequently, the broader true distribution of new and currently known NIS in natural habitats and ecological communities across Boston Harbor is not fully understood. Other records of NIS largely come from community-based projects such as the Marine Invader Monitoring and Information Collaborative (MIMIC), which started monitoring for a specific suite of NIS in 2008. MIMIC also primarily focuses survey efforts at docks and tracks specific fouling organisms such as the colonial chain tunicate, skeleton shrimp (*Caprella mutica*), and the solitary club tunicate; however, MIMIC has surveyed tidal pools at Thompson and Lovells islands where other specific species such as green crab, Asian shore crab, and the European rock shrimp (*Palaemon elegans*) were found.

Peddocks, Lovells, and Calf islands have the greatest number of unique NIS, while Thompson and Spectacle islands had the most detections overall of NIS, notably green crab, European oyster (*Ostrea edulis*), and the ubiquitous common periwinkle (*Littorina littorea*), likely due to public accessibility as most observations were documented through iNaturalist. *L. littorea* was the first observed NIS in Boston Harbor in 1894; however, this species was certainly present in Boston Harbor earlier than this as it had been documented across the Gulf of Maine south to Cape Cod throughout the early 1870s, including the Boston region (Ganong 1887). Indeed, it is one of the most abundant and widespread NIS in the Northeast (Carlton 1982) and was found on almost all islands and peninsulas across Boston Harbor throughout our time series. In regions in the North Atlantic, *L. littorea* is ubiquitous and can reach densities up to 2000 m⁻² (Buschbaum 2000) and is capable of regulating intertidal algal and invertebrate diversity through intense grazing (Petraitis 1983).

Similarly, green crab was found at almost all sites across Boston Harbor and is a well-established NIS. Although the earliest documented record for this species was 1997, it was introduced to southern New England in the early 1800s and first collected in Provincetown, MA, in 1872 (Carlton and Cohen 2003); thus, it was likely in Boston Harbor much earlier than the first documented record in this data set. Green crab has caused significant disturbance to marine coastal communities since its arrival, preying on important ecological and economically valuable species such as blue mussel, soft-shelled clams (*Mya arenaria*), and winter flounder (Pickering and Quijón 2011; Fulton et al. 2013; Tan and Beal 2015). It is also responsible for degrading salt marsh systems (Aman and Grimes 2016) and competing with other important species (e.g. American lobster) for resources (Williams et al. 2006). The European oyster was first introduced to Connecticut and midcoast Maine in 1949 by the US Bureau of Fisheries with the intention to support shellfish fisheries (Loosanoff 1955). Although not documented in Boston Harbor until 2001, it is likely this species spread southward earlier in time and was present in Boston Harbor long before this detection (Bell et al. 2002). Indeed, Boston Harbor is vulnerable to continued introductions given its role in shipping and transportation and the continued effects of climate change. To illustrate, during an opportunistic sampling trip to Calf Island, we made the first observation of a newly introduced nudibranch (*Doris pseudoargus*), which was found in the low intertidal zone during the winter of 2020 (Putnam 2020). A recent study suggested this species to have likely been in the New England region for years before then but to be expanding in population size and range (Harris et al. 2023).

Average taxonomic distinctness

Measurement of species diversity and species richness typically depend on even and standardized sampling efforts. Given the nature of our species inventory, which was developed from multiple data sources with uneven and sometimes unknown sampling effort, conventional metrics (e.g. Shannon Wiener Index) were not appropriate to evaluate patterns over time and across subareas of Boston Harbor. The use of AvTD provided an alternative method to overcome these limitations. Lower values of AvTD indicated species which were more closely related to each other (i.e., a less diverse sample) and can be a sign of ecological simplification (i.e., reduction in niche diversity), caused by anthropogenic influence (Peipoch et al. 2015). Hale et al. (2018) found negative associations between AvTD and environmental stressors (e.g., nitrogen input, human population in the bay, and copper discharge from a local wastewater treatment facility) suggesting negative impacts resulting in decreased diversity of benthic invertebrates in Narragansett Bay. Our analysis of AvTD values in Boston Harbor across decadal periods generally align with conservation efforts initiated in the 1980s that improved water quality. Since the early 1980s, dissolved oxygen levels in Boston Harbor have increased steadily (MWRA). This is largely due to the clean-up of waste discharge in Boston Harbor that previously caused eutrophic conditions. We found that AvTD was positively correlated with dissolved oxygen concentrations. Dissolved oxygen and oxygen saturation are important to the survival, growth, and behavior of many marine animals such as fish (Bejda et al. 1992; Thorarensen et al. 2017), crustaceans (Miller et al. 2002), and bivalves (Baker and Mann 1994). Oxygen concentration also plays a prominent role in supporting biodiversity (Deutsch et al. 2024). For example, eelgrass (*Zostera marina*), an important species for juvenile fish and carbon sequestration, increased in abundance in Boston Harbor as a result of increased bottom dissolved oxygen associated with clean-up efforts (Taylor et al. 2020).

The relationship between increased SST and concurrent decreases in native climate-vulnerable species abundance and diversity are well-known climate change responses (Chaudhary et al. 2021; Reddin et al. 2022). Our results provide additional evidence for this trend using AvTD as a metric for measuring system responses. Years with lower AvTD values were associated with years with high SST measurements. Interestingly, our results show a significantly positive relationship between sea level rise and taxonomic diversity. This is opposite to the majority of studies showing that increasing sea level is associated with decreasing biodiversity (Rilov et al. 2021). Biological responses to sea level rise vary across coastal habitat types and shoreline slopes and depend on the amount of sea level rise a location experiences; some species and functional groups have

benefited from rising waters when water quality remained high (Flowers et al. 2023) or transformations increased habitat availability (Powell et al. 2017). Metrics for intertidal macroinvertebrates and macroalgae showed no discernible trends across years or islands. The inability of our models to detect relationships between biodiversity and some environmental drivers may be due to limited data during the early years of our data series, particularly the 1860s–1970s, but also suggest stable diversity during years where species have been regularly recorded (2000–2020).

Mixed coarse intertidal

Although our records show nearly half (47%) of the unique species across our dataset were intertidal macroinvertebrates and macroalgae, the biodiversity associated with mixed coarse substrates in intertidal areas of Boston Harbor is still poorly known due to a lack of habitat-specific and regular survey methods; this analysis underscores the gap in monitoring and conservation efforts to detect and track changes for this habitat type. This is of high importance as coastal areas in the greater Boston Harbor region face rising threats from climate change, which has the potential to substantially alter environmental conditions and species survival (Halperin et al. 2019). Sporadic surveys and studies have been conducted in mixed coarse substrate habitats in recent decades (e.g. Bell et al. 2002; Eddy and Roman 2016; Matassa and Hitchcock 2021), yet a standard and repeatable biodiversity monitoring protocol equivalent to other coastal habitats does not currently exist. For example, three of the outer islands of Boston Harbor, which are made of solid bedrock, are surveyed and monitored annually by the Northeast Temperate Inventory and Monitoring Network (NETN). Methods used in the NETN program are specific to solid bedrock substrate and use fixed plots to document the abundance and percent cover of a targeted subset of intertidal invertebrates and macroalgae (Long and Mitchell 2015). The program has recorded over a decade of species abundance at these three islands (e.g., Calf, Green, and Outer Brewster Island) and has the ability to quantify long-term changes in bedrock intertidal communities in association with corresponding environmental conditions. Until a standard protocol is developed, similar capabilities remain unrealized for the majority of the Boston Harbor Islands, > 70% of which have intertidal zones composed of mixed coarse substrates. The NETN protocol is not fully transferable to mixed coarse substrate, as a pivotal component includes fixed transects and survey plots, which are intended for static substrate. Mixed coarse substrate is a dynamic habitat that undergoes erosion and other movement during regular tidal action and more extreme storm events; therefore, it is not suitable for bolt style fixed transects and plots. Our historic records show that many foundational species including macroalgae,

ecologically and economically pertinent shellfish, and migratory sea and shorebirds are present and use mixed coarse substrate habitats for a variety of activities; however, high-quality biodiversity metrics such as population size and fine scale biogeographical distribution of species is limited. Without this information, we are unable to determine any effects of climate change or other human disturbance.

Conclusion

Our species inventory and historic analysis across time in Boston Harbor provides the first consolidated and concentrated review on marine coastal biodiversity for this area. Lack of historical knowledge of a system can preclude conservation and restoration efforts (Thurstan et al. 2015), and this knowledge is especially crucial in systems that lack routine monitoring such as that of the mixed coarse intertidal of the Boston Harbor Islands. This review of historic biodiversity in combination with continuing and new monitoring and conservation efforts (i.e. habitat specific monitoring (Staudinger and Albert 2023), horizon scanning (O’Shaughnessy et al. 2023), and use of eDNA (Manel et al. 2024)) can support decision making in the face of climate adaptation actions that stakeholders such as NPS, the City of Boston, the Massachusetts Department of Conservation and Recreation, and others are considering on an ongoing basis. For example, across our dataset, 154 native species had final sightings during the same year as a new NIS was recorded. This does not necessarily indicate that NIS are displacing natives, but that their addition to the dataset as other species were absent may have contributed to the stable AvTD values across years. A review of all species that only occurred once in the data series indicated that most, if not all, are known to still be present in the region. This suggests that periodic and opportunistic (e.g., citizen science platforms) observations may inadvertently overlook some species that are either rare, cryptic, or not easily discerned from other closely related species. These data gaps and trends can inform coastal managers and developers to prioritize new surveys to track foundational, rare, or nuisance species to watch for, avoid, or track at sites that are slated for adaptation and restoration projects before and after implementation. Further, our species inventory provides a historical inventory for NPS to support their mission of engaging and educating the public on the value of public lands and waters in supporting and preserving biodiversity. Considering the most recent designation of being one of America’s 11 most endangered historic places due to climate change impacts, coastal adaptation, resilience, and restoration efforts will be crucial to the preservation of the Boston Harbor Islands. These efforts must consider the possible impacts to marine coastal ecosystems such as mixed coarse intertidal habitats,

but this can only be fully realized with baseline and up to date knowledge of biological communities achieved through inaugural and routine monitoring.

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Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed in this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability Data used to generate the species inventory and all statistical analyses are published and available: <https://doi.org/https://doi.org/10.5066/P1AUHDNM> (Putnam et al. 2024).

Author contribution All authors contributed to the study. Material preparation and data collection were performed by Alysha B. Putnam, Sarah C. Endyke, Justin Taylor, and Ally Jones. Data analysis was performed by Alysha B. Putnam. The first draft of the manuscript was written by Alysha B. Putnam, and writing—review and editing was performed by Alysha B. Putnam, Michelle D. Staudinger, Sarah C. Endyke, Lucy A.D. Lockwood, Marc Albert, and Ally Jones. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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