



Caribbean Creep meets Chesapeake Creep: marine bioinvasions and community shifts along the Mid-Atlantic Coast, USA

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Abstract The Mid-Atlantic waters of North America are warming faster than > 90% of other global oceans, leading to significant increases in bottom water temperatures and influencing shifts in marine community structure. Given this modern-day scenario of significant community shifts over space and time, baseline surveys of species diversity are increasingly valuable. Therefore, we performed the first-ever marine bioinvasions Rapid Assessment Survey (RAS) along the Mid-Atlantic waters of the United States in

June 2023, focused on marina floating pontoons in Virginia, Maryland, Delaware, and New Jersey. We recorded 29 non-indigenous, 16 cryptogenic, and 10 species that have expanded their ranges in the mid-Atlantic. Seven of these 10 species have expanded northwards from southern locations in the Caribbean (“Caribbean Creep”) or the western Atlantic (“Chesapeake Creep”), and three have expanded southwards. Five non-indigenous species (NIS) were found at more than 60% of the 10 sampled sites: the bryozoans *Bugula neritina*, *Schizoporella pungens*, *Tricellaria inopinata*, macroalgae *Codium fragile* subsp. *fragile*, and the sea anemone *Aiptasiogeton eruptaurantia*.

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We did not document any new nonindigenous species not already recorded on the Western Atlantic coast. All 10 communities were distinctly different, and species dominance varied by latitude and by site. This first-ever RAS of the Mid-Atlantic waters of the United States provides critical insight into how marine communities have been and are changing as a result of colonization by NIS, including those that have expanded their ranges as a result of human-induced climate change.

Keywords Introduced species · Non-indigenous species · Range expansions · Virginia · Maryland · Delaware · New Jersey

Introduction

The tableau of community biodiversity, and thus community structure and function, are rapidly changing along all monitored coasts of the world, due in large part to the synergy of a continuous stream of biological invasions, the extirpation (if not extinction) of vast numbers of animal and plant populations, and human-induced climate change (Occhipinti-Ambrogi 2007; Poloczanska et al. 2013; Pinsky et al. 2020; Gervais et al. 2021). Over the past few decades, the Western North Atlantic Ocean has experienced an increased warming trend, warming faster than >90% of other oceans (Pershing et al. 2015; Saba et al. 2016; Lentz 2017), likely due to the northward shift of the Gulf Stream (Sachs 2007; Neto et al. 2021). Recently, average warming rates of the Northeast American Continental Shelf have been ~0.95 °C per decade and 1.1–2.4 °C per decade in the Mid-Atlantic Bight (Friedland et al. 2020), and sea surface temperature isotherms are predicted to shift up to 600 km

northwards by the end of the twenty-first century (Lee et al. 2011).

Ocean warming has led to significant increases in the bottom water temperatures along the Mid-Atlantic (Forsyth et al. 2015), influencing shifts in marine community structure (Nye et al. 2009; Poloczanska et al. 2013; Hiddink et al. 2015; Hale et al. 2017). These community-level changes largely center around population fluctuations, species additions, and species deletions. Along temperate climate coasts, for example, relative species proportions are changing, as cold-affinity species decline, at times to the point of disappearance, while warm-affinity species are increasing (Gervais et al. 2021). In turn, warming coastlines have become increasingly susceptible to invasions by warm-affinity non-indigenous species, both as introductions (for example, by shipping) from overseas, and as range expansions (by coastal currents and/or by shipping) from lower latitudes along the same continental margins (Ling 2008; Bates et al. 2014). In both cases, it is likely that species have been arriving to higher latitudes for centuries, but previous conditions were too cold for successful reproduction and establishment (Carlton and Schwindt 2024).

Given this modern-day scenario of significant community shifts over space and time, repeated, regular, baseline surveys of species diversity are increasingly crucial. Examples of such surveys include long-term monitoring at one or more study sites (e.g., deployment of colonization plates, permanent transects, eDNA metabarcoding surveys and qPCR assays), by bioblitzes (intensive collecting at one site over multiple days), or by Rapid Assessment Surveys (RASs) (intensive time-limited sampling at multiple sites, usually along a latitudinal gradient, over multiple days).

RASs have been conducted worldwide, serving as useful tools for establishing baselines of diversity and distribution in communities, and can provide a key mechanism for quickly detecting and monitoring new species records (Lambert and Lambert 2003; Arenas et al. 2006; Ashton et al. 2006; Minchin 2007; Mathieson et al. 2008; Marques et al. 2013; Bishop et al. 2015; Collin et al. 2015; Nall et al. 2015; Park et al. 2017). In North America, RASs have previously been conducted on the Pacific coast from Washington to California (e.g., Cohen et al. 2001, 2005), and on the Atlantic coast from Maine to New York (e.g., Pederson et al. 2005, 2021; Mathieson et al. 2008;

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McIntyre et al. 2013; Wells et al. 2014; David and Krick 2019; Kennedy et al. 2020). However, no RAS had been conducted south of New York state along the Atlantic seaboard. The Mid-Atlantic portion of the United States is a key location to perform an RAS because of major shipping ports in the region (e.g., Norfolk, Virginia, Baltimore, Maryland and Philadelphia, Pennsylvania), as well as many smaller harbors where recreational boating and fishing are prominent. The Mid-Atlantic coast may thus represent a key hot-spot for the introduction and spread of non-indigenous species (NIS) into and out of the region.

NIS are frequently detected on artificial substrates in coastal environments (e.g., floating docks, pilings, and pontoons) (Glasby and Connell 2001; Paulay et al. 2002). RASs that focus on sampling communities on floating docks in marinas can therefore provide a means of early detection of new introductions or of range expansions of previously detected invasions (e.g., Pederson et al. 2021). In addition, marinas are often locations with high environmental stressors (i.e., fluctuating salinity and water quality) that may cause periodic mortality events, allowing bare surfaces to be colonized by newly arriving propagules (Bax et al. 2003). Thus, marinas can serve as key recipient locations for organisms brought in via ballast water, hull fouling, or aquaculture (reviewed in Wonham and Carlton 2005). As a result, artificial substrates in marinas can further serve as source pools for the additional spread of species (i.e., secondary spread) from their initial point of introduction due to movements with recreational vessels or via coastal currents (Bulleri and Airoidi 2005; Ros et al. 2016).

Progressively warming temperatures over the last few decades have resulted in additional northward introductions of species along the Atlantic coast (Foster et al. 2004; Canning-Clode et al. 2011; Canning-Clode and Carlton 2017; Mack et al. 2019). Coined “Caribbean Creep” by J.T. Carlton (Carlton 2010), species are expanding their ranges poleward due to human-induced climate change from the Caribbean Sea into temperate regions of the U.S. Atlantic coast (Canning-Clode et al. 2011). In a concurrent, analogous process, species formerly restricted to the greater Chesapeake Bay region of the Mid-Atlantic United States coast are expanding poleward toward New York, southern New England, and further north.

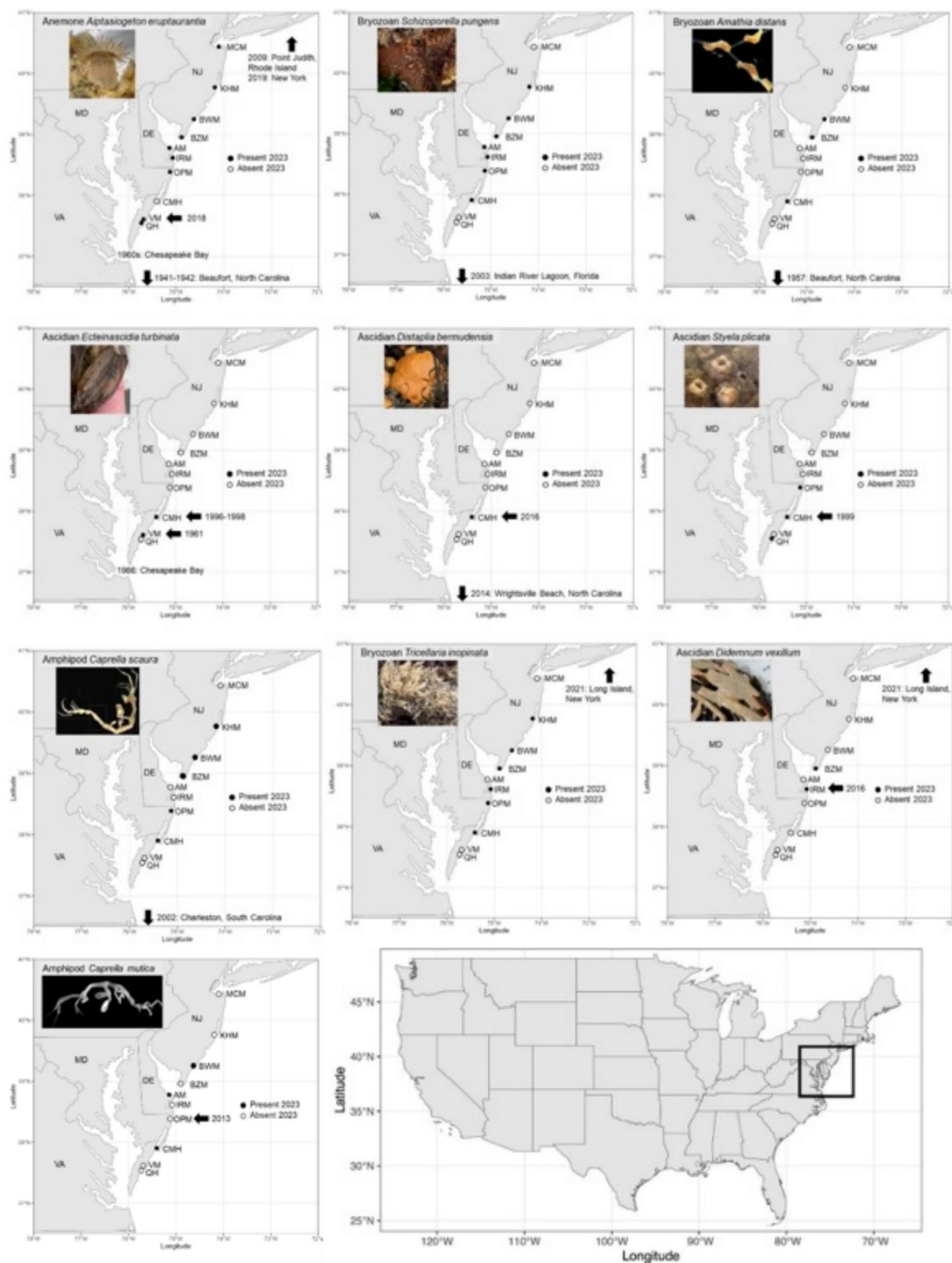
We here refer to this phenomenon as “Chesapeake Creep,” as we detail below.

We present here the results of a RAS conducted in June 2023 of fouling communities sampled at marinas and boat launches along the Mid-Atlantic coast of the United States from central Virginia, north of the entrance to Chesapeake Bay, to northern New Jersey near the New York border. We focus on the community composition and diversity of NIS, as well as their relative taxonomic proportions, community dominance, community similarities/dissimilarities, and patterns of distribution. Our dataset includes previously documented NIS, as well as newly-documented southern taxa (Caribbean and Chesapeake creepers) that have expanded north, and northern taxa that have expanded south, into our study region. The latter represent the post-introduction extensions of NIS that are expanding to their physiological temperature limits, regardless of direction. We also compare our results to previous, regional investigations of fouling communities in Delaware and New Jersey. This first-ever RAS of the Mid-Atlantic waters of the United States provides critical insight into how marine communities have been and are changing as a result of colonization by NIS, including those that have expanded their ranges as a result of human-induced climate change.

Materials and methods

Study sites and sample collection and processing

Ten stations were surveyed along the Mid-Atlantic coast of the United States for invertebrate and algal species in marine fouling communities from June 22 to June 26, 2023, between Quinby, Virginia and Port Monmouth, New Jersey over three degrees of latitude (37.55°–40.43° north), equivalent to a linear distance of 350 km (Fig. 1, Table S1). These stations ranged from near the southern end of the “Delmarva” Peninsula of Virginia, Maryland, and Delaware, including Chincoteague Bay, and proceeded up the New Jersey coast, including Barnegat Bay, to Sandy Hook Bay at the New York state border. Physical–chemical data collected included temperature, salinity and dissolved oxygen (obtained with a YSI SCT-DO meter), water transparency (using a Secchi disk), and maximum depth (Table S1).



◀**Fig. 1** Species distribution maps for Caribbean Creep (*S. pungens*, *A. distans*, *D. bermudensis*, *C. scaura*), Chesapeake Creep (*A. eruptaurantia*, *E. turbinata*, *S. plicata*) and north-to-south range expanding non-indigenous species (*T. inopinata*, *D. vexillum*, *C. mutica*), showing sampled locations during the June 2023 Mid-Atlantic RAS. Each panel depicts the presence (filled circles) or absence (open circles) per species and any previous record data

The survey protocol was as follows. Survey teams consisted of marine ecologists, invertebrate zoologists, phycologists, taxonomic specialists, and undergraduate and graduate students. Sites were visited for 60 min from the start to the end of sampling. Two sites were visited each day. Some team members were tasked with securing multi-species samples for laboratory analysis, whereas taxonomic specialists concentrated on collecting species within their specialty. A 1-L “community voucher” sample of all common species was retained for museum deposition at the North Carolina Museum of Natural Sciences. Taxonomic specialists retained polychaete, ascidian, and isopod specimens for DNA barcoding (see below). Morphological hydroid vouchers were deposited in the Invertebrate Zoology collections, Royal BC Museum, in Victoria, Canada (RBCM).

Only floating or suspended structures were formally sampled to ensure a standardized sampling protocol. These included the submerged portions of pontoons (floats), as well as ropes, tires, bumpers, and buoys up to 30 cm depth. The fouling community was sampled by hand as well as by scrapers and dip nets, with all organisms then placed alive into labeled plastic bags with seawater and stored in coolers (ice chests) for transportation to the laboratory. At each site, we also recorded aspect dominant species; i.e., those species that were visually estimated to have > 50% cover at a site. These field estimates were then checked against photo documentation (Fig. 2).

At the end of each afternoon and until late evening, all samples were then sorted, and further identifications were undertaken in the laboratory using light microscopy. There are currently no taxonomic keys or guides specific to most of the marine flora and fauna of the Mid-Atlantic coast. Instead, taxa were identified to species by expert systematists who participated in this survey and who are co-authors of this report. That said, we did consult broader regional or extra-regional taxonomic guides to assist with taxonomic identification, and these included, for algae, Fraser

1944; for polychaetes, Mathieson & Dawes 2017 for hydroids, Bakken et al. 2009; Bastida-Zavala et al. 2017; Blake 2006; Eklof et al. 2007; Lavesque et al. 2021; and Wilson et al. 2023; for mollusks, Abbott and Morris 1995; and Emerson and Jacobson 1976 for barnacles, Bousfield 1973; for isopods, Schultz 1969; for bryozoans, Williams 1984; for amphipods, Winston and Hayward 2012, and for ascidians, Zullo 1979; for decapods, Van Name 1945. Because many of these guides are older or do not cover the mid-Atlantic region, numerous newer or additional published papers and monographs, as appropriate, supplemented these works. Current names of species followed those accepted as valid in the World Register of Marine Species (WoRMS) (WoRMS Editorial Board 2025). Taxa resolved to only genus level may represent more than one species, and thus the total number of species we detected is likely underestimated (Table 1).

Identified taxa were categorized as native (N), non-indigenous (including both introduced (NIS) species and range expansions (NIS* for Caribbean Creep species and NIS+ for Chesapeake Creep species)), cryptogenic (C), or unassigned (U) (Carlton and Schwindt 2024). This last category (U) included species with insufficient resolution to assign a probable biogeographic status (e.g., to genus level, per above). We followed the current literature (for example, Fofonoff et al. 2018; Davinack et al. 2024) or the expert opinion of our RAS systematists to assign biogeographic status.

We follow Carlton & Schwindt (2024) in our categorization of NIS status, as any species historically absent from a given area, regardless of their origin or vector. Thus, both human-vectored species introductions (e.g., shipping, hull fouling, etc.) and range expansions from human-induced climate change are treated as NIS in their newly invaded regions. To be clear, taxa indicated herein as NIS* or NIS+ in the mid-Atlantic region are considered—based on current evidence—to be either native or cryptogenic in their southern ranges.

DNA extraction, PCR and sequencing summary

In some cases, we used DNA barcoding techniques to assist in species identifications of some polychaete, crustacean, and ascidian samples that we wanted to confirm or were difficult to identify morphologically.

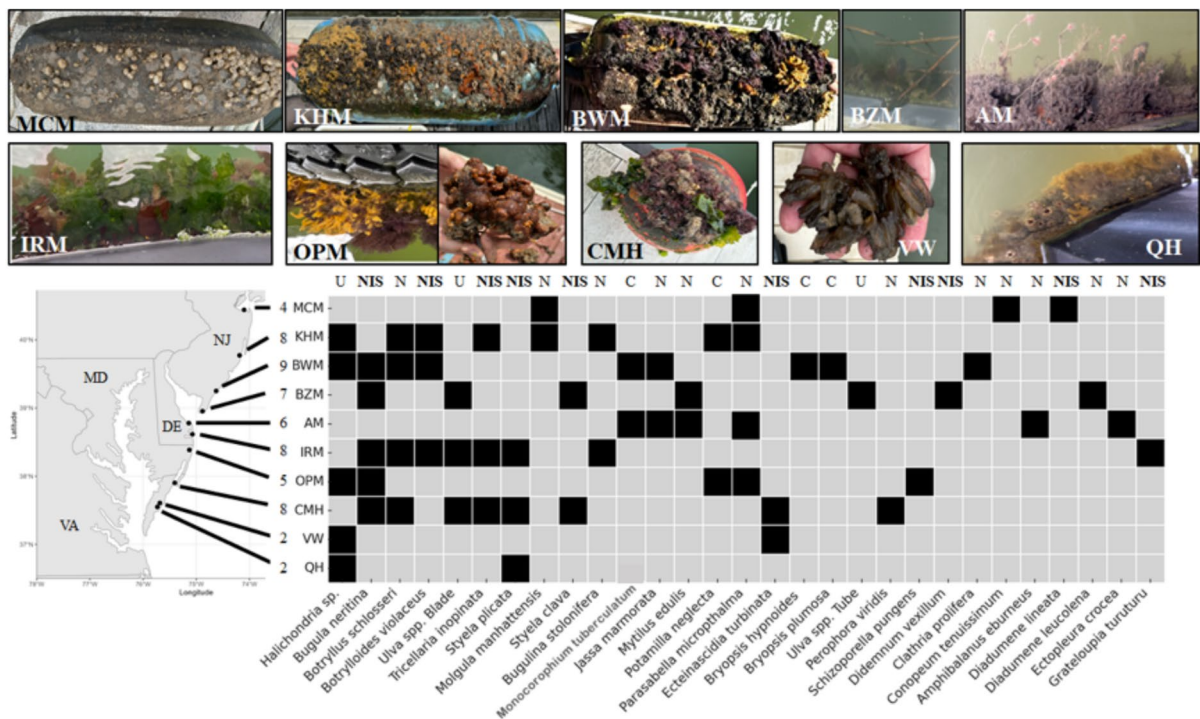


Fig. 2 Field community pictures and heatmaps of aspect dominant species (comprising >50% of the community, assessed visually) presence (black) or absence (grey) by site. Profile of species by site are arranged with most frequently encountered species to the left. Numbers to the left of the station code

indicate the total number of aspect dominant species per site. Letters above the heatmap indicate the status of the species in the Mid-Atlantic (N, Native; C, Cryptogenic; NIS, Non-indigenous; U, unassigned)

For polychaete samples, a 0.5 mm section of the pygidium from each polychaete was amputated and digested in a proteinase K/lysis buffer solution at 56 °C. Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. The total genomic DNA yield ranged between 40 and 60 ng/μl. A ~700 bp fragment of the cytochrome c oxidase I (COXI) gene was amplified using the forward and reverse primer pair polyLCO and polyHCO (Carr et al., 2011). PCR conditions for COXI were as follows: an initial denaturation at 94 °C for 1 min, followed by five cycles of 40 s at 94 °C and 1 min at 72 °C. This was followed by 35 cycles of 40 s at 94 °C, 40 s at 51 °C, and 1 min at 72 °C, with a final extension at 72 °C for 10 min. For the 16S ribosomal RNA marker, a ~470 bp fragment was amplified using the forward and reverse primers 16SarL and 16SbrH (Palumbi, 1996). PCR conditions followed those described by Álvarez-Campos et al.

(2017). Amplicons were visualized on a 2% agarose gel, excised, and purified using the QIAquick Gel Extraction Kit (Qiagen, Hilden, Germany). Purified PCR products were sequenced via Sanger sequencing at Azenta LLC (Plainfield, NJ) using the forward primers for both markers. Returned sequences were assessed for quality, and COXI sequences were translated using the ExPASy translation tool to verify gene functionality. Initial taxonomic identifications were performed using BLASTn against the NCBI database.

For isopods and ascidians, a small (~25 mm³) section of tissue was dissected from each individual, placed in a sterile 0.75 ml microcentrifuge tube containing 150 μl of TD-M2 extraction buffer (Autogen, Holliston, MA, USA) and frozen until DNA amplification and sequencing. DNA was extracted using the Autogen Prep 965 phenolchloroform automated extractor (Autogen, Holliston, MA, USA). We amplified a ~500 bp region of the mitochondrial 16S rRNA16S rRNA gene

Table 1 Non-indigenous and cryptogenic species detected in June 2023 Mid-Atlantic RAS: Biogeographic Status in the Mid-Atlantic, Origins, and Presence at Stations

Taxon	Species	Status in mid-atlantic	Stations south to north (Number and Stations)	Origin
Cnidaria: Hydrozoa (hydroids)	<i>Gonothyrea loveni</i>	C	1 (KHM)	Unknown
	<i>Obelia dichotoma</i>	C	3 (IRM, BZM, BWM)	Unknown
Cnidaria: Anthozoa (sea anemones)	<i>Aiptasiogeton eruptaurantia</i>	NIS*	7 (QH, VW, OPM, IRM, AM, BWM, KHM)	Caribbean-SE USA
	<i>Diadumene lineata</i>	NIS	5 (QH, OPM, AM, KHM, MCM)	NW Pacific
Annelida: Polychaeta (worms)	<i>Amphitrite cirrata</i>	C	3 (IRM, BZM, BWM)	Unknown
	<i>Ficopomatus enigmaticus</i>	NIS	1 (KHM)	Australia
	<i>Neoamphitrite figulus</i>	C	4 (CMH, OPM, IRM, BZM)	Unknown
	<i>Potamilla neglecta</i>	C	5 (CMH, OPM, AM, KHM, MCM)	Unknown
Crustacea: Cirripedia (barnacles)	<i>Loxothylacus panopaei</i>	NIS	1 (VW)	Gulf of Mexico
Crustacea: Amphipoda (amphipods)	<i>Apocorophium acutum</i>	C	3 (QH, VW, IRM)	Unknown
	<i>Caprella equilibra</i>	C	3 (OPM, IRM, AM)	Unknown
	<i>Caprella mutica</i>	NIS +	3 (CMH, AM, BWM)	NW Pacific
	<i>Caprella penantis</i>	C	2 (CMH, OPM)	Unknown
	<i>Caprella scaura</i>	NIS*	5 (CMH, OPM, BZM, BWM, KHM)	Unknown
	<i>Microdeutopus gryllotalpa</i>	NIS	2 (KHM, MCM)	NE Atlantic
Crustacea: Isopoda (isopods)	<i>Ianiropsis serricaudis</i>	NIS	1 (BZM)	NW Pacific
	<i>Synidotea laevidorsalis</i>	NIS	1 (MCM)	NW Pacific
	<i>Carcinus maenas</i>	NIS	2 (CMH, KHM)	NE Atlantic
Crustacea: Decapoda: Brachyura (crabs)	<i>Hemigrapsus sanguineus</i>	NIS	2 (QH, CMH)	NW Pacific
Entoprocta (entoprocts)	<i>Barentsia benedeni</i>	NIS	2 (CMH, MCM)	NE Atlantic
Bryozoa: Cheilostomata (cheilostome bryozoans)	<i>Bugula neritina</i>	NIS	9 (QH, VW, CMH, OPM, IRM, AM, BZM, BWM, KHM)	Indo-Pacific
	<i>Conopeum</i> sp., cf. <i>seurati</i>	NIS	4 (OPM, BWM, KHM, MCM)	NE Atlantic
	<i>Cryptosula pallasiana</i>	NIS	1 (KHM)	NE Atlantic
	<i>Electra monostachys</i>	C	1 (BZM)	Unknown
	<i>Schizoporella pungens</i>	NIS*	6 (CMH, OPM, IRM, AM, BZM, KHM)	Caribbean
	<i>Tricellaria inopinata</i>	NIS	6 (CMH, OPM, IRM, BZM, BWM, KHM)	North Pacific
Bryozoa: Ctenostomata (ctenostome bryozoans)	<i>Amathia distans</i>	NIS*	3 (CMH, BZM, BWM)	Caribbean-SE USA
	<i>Amathia gracilis</i>	C	2 (CMH, BZM)	Unknown
	<i>Anguinella palmata</i>	C	1 (BWM)	Unknown

Table 1 (continued)

Taxon	Species	Status in mid-atlantic	Stations south to north (Number and Stations)	Origin
Chordata: Ascidiacea (sea squirts)	<i>Botrylloides violaceus</i>	NIS	5 (CMH, IRM, BZM, BWM, KHM)	NW Pacific
	<i>Didemnum vexillum</i>	NIS	2 (IRM, BZM)	NW Pacific
	<i>Diplosoma listerianum</i>	NIS	4 (OPM, IRM, BZM, KHM)	Uncertain
	<i>Distaplia bermudensis</i>	NIS*	1 (CMH)	Caribbean
	<i>Ecteinascidia turbinata</i>	NIS*	2 (VW, CMH)	Caribbean
	<i>Styela canopus</i>	NIS	4 (VW, CMH, BZM, BWM)	NW Pacific
	<i>Styela clava</i>	NIS	5 (CMH, IRM, AM, BZM, BWM)	NW Pacific
Chlorophyta (green algae)	<i>Styela plicata</i>	NIS*	3 (QH, CMH, OPM)	NW Pacific
	<i>Bryopsis hypnoides</i>	C	7 (VW, CMH, OPM, IRM, AM, BZM, BWM)	Unknown
	<i>Bryopsis maxima</i>	NIS	2 (QH, CMH)	NW Pacific
	<i>Bryopsis plumosa</i>	C	6 (QH, CMH, AM, BZM, BWM, KHM)	Unknown
	<i>Cladophora flexuosa</i>	C	1 (OPM)	Unknown
	<i>Cladophora sericea</i>	C	2 (KHM, MCM)	Unknown
	<i>Codium fragile</i> subsp. <i>fragile</i>	NIS	7 (QH, CMH, OPM, IRM, BZM, BWM, KHM)	NW Pacific
Rhodophyta (red algae)	<i>Grateloupia turuturu</i>	NIS	4 (CMH, IRM, BZM, BWM)	NW Pacific
	<i>Polysiphonia subtilissima</i>	C	2 (IRM, MCM)	Unknown

C, Cryptogenic; NIS, Non-indigenous; NIS*, Caribbean Creep species; NIS+Chesapeake Creep species; NE, Northeast; NW, Northwest, SE, Southeast

using the universal primers 16Sar (CGCCTGTTT ATCAAAAACAT) and 16Sbr (CCGGTCTGA ACTCAGATCACGT) of Palumbi et al. (1991), as well as a ~650 bp region of the mitochondrial cytochrome c oxidase I (COXI) gene using the universal primers jgLCO1490 (TITCIAC IAAY CAYAARGAYATTGG) and jgHCO2198 (TAIACYTCIGGRTGICCAARAAYCA) of Geller et al. (2013). Amplification reaction cocktails contained 1 µl 10X reaction buffer (Bioline, Cincinnati, OH, USA), 0.3 µM each primer, 2.5 mM MgCl₂, 0.5 mM dNTP, and 0.5 units Biolase Taq (Bioline), in a 10 µl final volume. The thermocycler profile started with a denaturation at 95 °C for 7 min, followed by 35 cycles of 95 °C 30 s, 50 °C 30 s, 72 °C 45 s, finishing with an extension of 72 °C for 90 s. PCR products were purified with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA) following manufacturer's instructions. Sequencing was performed

using the BigDye Terminator 3.1 Cycle Sequencing Kit (Applied Biosystems, Waltham, MA, USA) following manufacturer's instructions. Sequencing was carried out with a 3730xl DNA Analyzer (Applied Biosystems) at the Laboratories of Analytical Biology (LAB), NMNH. Chromatograms were processed using Sequencher 5.0.1 (Gene Code Corporation, Ann Arbor, MI, USA). Each was subjected to the following, very conservative, trimming parameters: trim until the first and last 25 bp contain fewer than three ambiguities and trim until the first and last 10 bp contain fewer than three bases with a Phred score below 30. Only trimmed fragments greater than 200 bp in length and with overall confidence above 90% (as calculated by Sequencher) were used to construct the final sequences. Passing sequences were visually examined for errors.

Statistical analyses

To examine similarity/dissimilarity of our community composition from south to north across our 10 sites, we used a non-metric multidimensional scaling plot (nMDS) at three levels: native species only, NIS only, and aspect dominance (the latter could include native, NIS, cryptogenic, or unassigned species). We then created a Bray–Curtis similarity resemblance matrix, and nMDS plots using default values in Primer 7.0.23 (Primer-e). We also created a cluster matrix and overlaid these clusters onto the nMDS plots at a similarity of 45%. This allowed us to determine how similar/dissimilar our sites were in community composition across the study region.

Results

Biodiversity and biogeography

A total of 141 species were identified from Virginia to New Jersey (Table S2). Of these, we found 70 native species (49.6% of all taxa), 29 NIS (20.6%), 17 unassigned taxa (12.1%), and 25 cryptogenic species (17.7%) (Table S2). DNA barcoding allowed us to resolve the identities of three tunicates (*Botrylloides violaceus*, *Diplosoma listerianum*, *Styela canopus*), two isopods (*Ianiropsis serricaudis* and *Idotea metallica*), and two polychaetes (*Parasabella microphthalma* and *Syllis gracilis*). The majority (86.2%) of the 29 NIS belonged to one of four main taxonomic groups: ascidians (n=8), crustaceans (n=8), bryozoans (n=6), and macroalgae (n=3).

We found at least five NIS of both macroinvertebrates and macroalgae at each site, with the maximum number of 18 NIS found at Curtis Merritt Harbor (CMH) in Chincoteague, VA (Fig. 3a). Fourteen and thirteen NIS were found at Key Harbor Marina (KHM) in Barnegat Bay, NJ and Bree-Zee-Lee Marina (BZM) in Cape May, NJ, respectively, with 12 NIS found at Blue Water Marina (BWM) in Ocean City, NJ and 10 NIS found at Ocean Pines Marina (OPM) in Ocean Pines, MD and Indian River Marina (IRM) in Rehoboth Beach, DE. The remaining sites all supported less than 10 NIS. There was thus no latitudinal pattern in NIS numbers per site from Virginia to New Jersey (Fig. 3a).

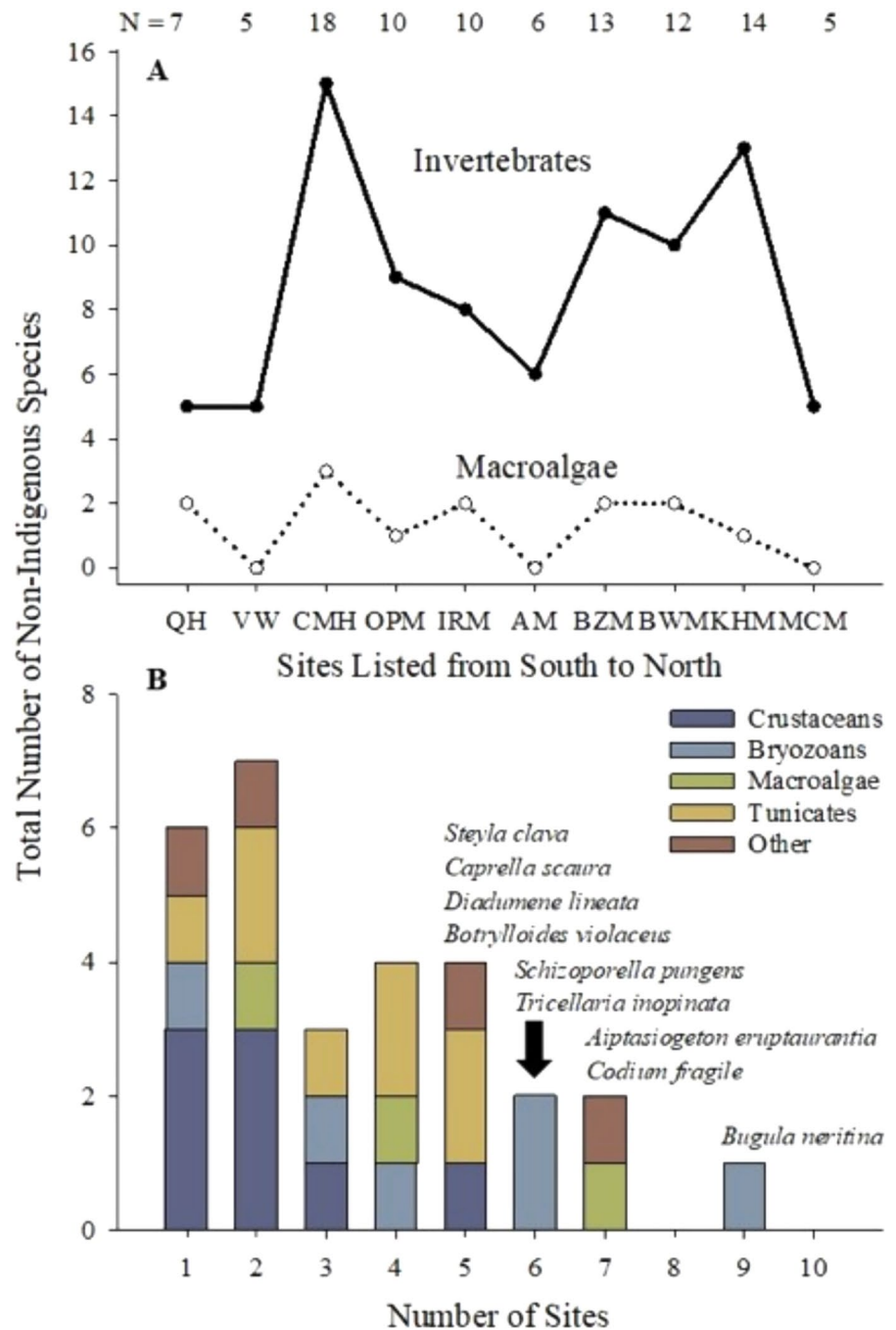
Only one NIS – the bryozoan *Bugula neritina* – was found at 90% of sites, while the macroalgae *Codium fragile* subsp. *fragile* and sea anemone *Aiptasiogeton eruptaurantia* were discovered at 70% of sites (Fig. 3b). Six other NIS were found at either 60% (the bryozoans *Schizoporella pungens* and *Tricellaria inopinata*) or 50% (the caprellid amphipod *Caprella scaura*, the sea anemone *Diadumene lineata* and ascidians *Botrylloides violaceus* and *Styela clava*) of sites (Fig. 3b). Several NIS were only found at a single site, including the polychaete *Ficopomatus enigmaticus* and the bryozoan *Cryptosula pallasiana* at Key Harbor Marina, the macroparasite cirriped *Loxothylacus panopaei*, found on its brachyuran crab host *Eurypanopeus depressus* in the fouling community at Wachapreague, Virginia, the isopods *Ianiropsis serricaudis* at Bree-Zee-Lee Marina and *Synidotea laevidorsalis* at Monmouth Cove Marina, and the ascidian *Distaplia bermudensis* at Curtis Merritt Harbor (Table S2).

Caribbean creep, Chesapeake creep, and range extensions

Our RAS detected 10 species that have expanded their ranges in the mid-Atlantic. Seven of these 10 species have expanded northwards from southern locations in the Caribbean or the western Atlantic, while three NIS have expanded southwards (Fig. 1; Tables 1, 2 and 3).

Among the northward-moving species are three species that we have termed “Chesapeake creepers” – southern species spreading north of the Chesapeake Bay region. These species include: (1) an anemone *Aiptasiogeton eruptaurantia*: native to Florida, the Gulf of Mexico, and the Caribbean and formerly undetected between Wachapreague, VA and Barnegat Bay, NJ (but detected in southern New England since 2009); (2) an ascidian *Ecteinascidia turbinata*: native to Florida and the Caribbean and now as far north as Chincoteague, VA; and (3) an ascidian *Styela plicata*, noted previously in North Carolina and now detected as far north as Ocean Pines, MD (Table 2). Other northward moving creepers include four species native or cryptogenic in subtropical and tropical waters (i.e. “Caribbean creepers”): (1) a bryozoan *Schizoporella pungens*, native to southern Florida, the Gulf of Mexico, and the Caribbean with a previous northern range edge

Fig. 3 The total number of non-indigenous species found during the June 2023 Mid-Atlantic Rapid Assessment Survey (A) by site, listed from south to north, and partitioned into invertebrates and macroalgae, and (B) frequency of occurrence of taxonomic groups of non-indigenous species. In (A), numbers (i.e., N=) above the graph indicate total number of non-indigenous species found per site. In (B), for instance, only 1 species of bryozoan was found at 1 site, while 2 bryozoans were found at 6 sites. Species names for those occurring at 5 or more sites are listed above the corresponding bar



at Fort Pierce, FL; (2) a bryozoan *Amathia distans*, native to Florida and the Caribbean with a previous northern range edge at Beaufort, NC; (3) an ascidian *Distaplia bermudensis*, native to Florida and the Caribbean with a previous northern range edge at Wrightsville Beach, NC; and (4) an amphipod

Caprella scaura, cryptogenic in the Western Atlantic, with a previous published northern range edge at Charleston, SC (although it was previously found by the Smithsonian Environmental Research Center in Wachapreague, VA in 2018) (Table 2).

Table 2 South to north bioinvasions: Caribbean Creep and Chesapeake Creep. NIS expanding north to new regions. * Chesapeake Creep

Species	Previous historic range	Recent distribution north of historical range	Northern range expansions	Comments
Southern species moving north				
* Anemone <i>Aiptasiogeton eruptaurantia</i>	Florida, Gulf of Mexico, and Caribbean (Fautin & Daly 2009; Glon et al. 2020)	1941–1942: Beaufort, NC (previously absent) (Field 1949) 1960s: Chesapeake Bay (Wass 1965) 2009: Point Judith, RI (Hobbs 2022; Pederson et al. 2021) 2018: Wachapreague, VA (Ritter 2018) 2019: NY (Pederson et al. 2021)	All stations QH to KHM except CMH	Range expansion north of ca. 280 km from Wachapreague, VA to Barnegat Bay, NJ. However, already known from Brooklyn, NY (2019) to RI (2009) (Pederson et al. 2021). This anemone may have moved north (but went undetected) between the 1960s and 2000s from Chesapeake Bay to NY. Its appearance in southern New England since 2009 may thus be linked to its undetected creep up the Delmarva Peninsula into NJ-NY, rather than to a jump to New England from Chesapeake Bay or from further south
* Bryozoan <i>Schizoporella pungens</i>	Southern Florida, Gulf of Mexico, and Caribbean (Winston 2005; McCann et al. 2007; Winston, 2012)	2003: Indian River Lagoon, Fort Pierce, FL (Winston 2005, 2012)	Stations from CMH to KHM	Range expansion north of ca. 1450 km from Fort Pierce, FL to Barnegat Bay, NJ
Bryozoan <i>Amathia distans</i>	Florida and Caribbean (Winston 1982)	1957: Beaufort, NC (Maturo 1957)	CMH, BZM, and BWM	Range expansion north of ca. 525 km from Beaufort, NC to Ocean City, NJ
* Ascidian <i>Ecteinascidia turbinata</i>	Florida and Caribbean (Van Name 1945)	1961: Wachapreague, VA (Fofonoff et al. 2018) 1966: Chesapeake Bay (Calder et al. 1966) 1996–1998: Chincoteague, VA (Prezant et al. 2002)	VM and CMH	Northern boundary confirmed herein as remaining at Chincoteague VA

Table 2 (continued)

	Species	Previous historic range	Recent distribution north of historical range		Comments
				Northern range expansions	
Subtropical-tropical introductions or cryptogens in western atlantic moving poleward	Ascidian <i>Diaplia bermudensis</i>	Florida and Caribbean (Van Name 1945)	2014: Wrightsville Beach, NC (Villalobos et al. 2017)	CMH	Range expansion north of 480 km from Wrightsville Beach, NC to Chincoteague, VA. Detected at Chincoteague by the Smithsonian Environmental Research Center in 2016 (K. Larson, personal communication, 2023)
	*NIS Ascidian <i>Styela plicata</i>	Beaufort, NC (Van Name 1945)	1999: Near Chincoteague Island, VA (O'Beirn et al. 2004)	QH, CMH, and OPM	Range expansion north of ca. 100 km from Chincoteague Island, VA to Ocean Pines, MD
	Cryptogenic Amphipod <i>Caprella scaura</i>	Biscayne Bay, Florida (Fofonoff et al. 2018)	2002: Charleston Harbor, South Carolina (Foster et al. 2004)	CMH and OPM	Range expansion north of ca. 765 km from Charleston, SC to Ocean Pines, MD. Detected at Wachapreague, VA by the Smithsonian Environmental Research Center in 2018 (R. Aguilar, personal communication, 2025)

Table 3 North to South Bioinvasions: NIS Expanding South to New Regions within Their Presumed Temperature Tolerances

Species	Native Region	Previous Southern Limit in Northeast Atlantic	New Southern Record	Comments
Bryozoan <i>Tricellaria inopinata</i>	North Pacific Ocean	2019: Stamford, CT (Long Island Sound) (Pederson et al. 2021)	2023: Chincoteague Inlet, VA (CMH)	Range expansion south of ca. 450 km
Ascidian <i>Didemnum vexillum</i>	Japan	2004: Shinnecock Inlet, Long Island, NY (Bullard et al. 2007)	2016: Rehoboth Bay, DE (IRM)	Range expansion south of ca. 320 km from outer coast of Long Island. In Long Island Sound, south to Groton, CT (2023: J. T. Carlton, personal observation). Detected in Rehoboth Bay, DE by (Smithsonian Environmental Research Center in 2016 (Larson, pers. comm., 2023)
Amphipod <i>Caprella mutica</i>	Japan	2013: Ocean City Inlet, MD (M. Ros in Fofonoff et al. 2018)	2023: Chincoteague Inlet, VA (CMH)	Range expansion south of ca. 65 km

Moving in the southward direction are three NIS that have continued to expand their ranges along the eastern US coast. These include: (1) the bryozoan *Tricellaria inopinata*, native to the North Pacific Ocean, first found in southern New England in 2010 (Johnson et al. 2012), detected in Long Island Sound in 2019 (Table 3), and now detected during our RAS in Chincoteague, VA; (2) an ascidian *Didemnum vexillum*: native to Japan, first found in New England in 1982 (Dijkstra and Nolan 2011), then detected south in Long Island in 2004 (Table 3), and now detected in this RAS in Delaware; and (3) an amphipod *Caprella mutica*, native to Japan, first found in New England in 2000 (Ashton et al. 2007), then found in Ocean City, MD in 2013 (Table 3), and now detected in Chincoteague, VA (Table 3).

Community composition

Community composition and community similarity/dissimilarity analyses reveal several notable observations. When ‘all species’ were examined (including native, NIS, and unknown species classifications), all sample sites clumped together at a 45% similarity, except for the two most southern Virginia sites, Wachapreague (VW) and Quinby Harbor (QH), and the northernmost New Jersey location, Monmouth

Cove Marina (MCM) (Figure S1A). MCM was our lowest salinity site, with a resultant estuarine community that differed from all other sites in our study region (Table S1). For example, the native bryozoan *Conopeum tenuissimum* was the only dominant species at MCM (Table S2).

When comparing the community of species that contributed to the ‘aspect dominance’ at each site, we identified three groupings of sites at 45% similarity: (1) Curtis Merritt Harbor (CMH) in Virginia and Indian River Marina (IRM) in Delaware, which were dominated by bryozoans, ascidians, and the macroalgae *Ulva* spp.; (2) Ocean Pines Marina (OPM) in Maryland and Key Harbor Marina (KHM) in Barnegat Bay, which were dominated by the polychaetes *Parasabella microphthalma* and *Potamilla neglecta* and the sponge *Halichondria* sp.; and (3) QH and VW, which were dominated by only two taxa—*Halichondria* sp. and ascidians *Styela plicata* at QH and *Ecteinascidia turbinata* at VW (Figure S1B; Fig. 2; Table S2). The rest of the sites did not group with any others; instead, these sites were characterized by different dominant species (Table S2), including the following: the isopod *Jassa marmorata* at AM (Anglers Marina, Delaware); the ascidian *Didemnum vexillum* and sea anemone *Diadumene leucomela* at BZM (Bree-Zee-Lee Marina, Cape May, New

Jersey); the sponge *Clathria prolifera* at BWM (Blue Water Marina, Ocean City, NJ); and the sea anemone *Diadumene lineata* and bryozoan *Conopeum tenuissimum* at MCM (Fig. 2).

‘Native only’ community comparisons had the same large clumping of sites (45% similarity) and outliers as in the ‘all species’ comparison (Figure S1C). For the ‘NIS only’ comparison, there was once again a large clumping of sites (at 45% similarity) from the central part of our study region, except for Anglers Marina (AM) in Delaware which was more similar to Quinby Harbor (QH) in Virginia. Both QH and AM had only one non-indigenous ascidian species, in comparison to the other sites within the clumped group where multiple NIS were detected (Table S2). There were also two outlier sites (MCM and VW), which had the fewest NIS among all our sites, with 4 and 5 species, respectively (Fig. 3).

Discussion

While individual reports have documented the presence and distribution of a number of new species introductions in the region between Chesapeake Bay and Sandy Hook Bay, New Jersey, our report is the first rapid assessment survey across this 350 km region of Mid-Atlantic waters of the United States. All 10 communities were distinctly different, and species dominance varied by latitude and by site. At more southern stations, the non-indigenous ascidians *Styela plicata* and *Ecteinascidia turbinata* were predominant, but these were largely replaced from Delaware north by other non-indigenous and native ascidians, including the non-indigenous *Styela clava*, botryllids (a mixture of native and non-indigenous species), and, at one site, the non-indigenous *Didemnum vexillum*. The yellow cryptogenic sponge *Hali-chondria* sp. was predominant in two southern Virginia stations, but re-appeared as a prominent species to the north at only one station (Ocean City, New Jersey). Macroalgae were abundant in water-line fouling communities at only two stations—Rehoboth Beach, Delaware and Cape May, New Jersey.

This baseline survey of 10 sites documented 29 NIS in the shallow-water biofouling communities on floating and suspended structures. Of these, six species are indigenous or cryptogenic to waters to the south of the RAS study area, and the remaining 23

are non-indigenous in all of the Northwest Atlantic. More than half (56%) of the NIS have origins from the Pacific Ocean. Non-indigenous invertebrate species were among the dominant taxa at 9 of the 10 communities sampled, including the ascidians *Botrylloides violaceus*, *Didemnum vexillum*, *Ecteinascidia turbinata*, *Styela clava*, and *Styela plicata*, the bryozoans *Schizoporella pungens*, *Tricellaria inopinata*, and *Bugula neritina*, and the sea anemone *Diadumene lineata*. At one site (Indian River Marina in Delaware), the non-indigenous macroalgae *Grateloupia turuturu* was also prominent. Peaking in NIS presence were fouling communities in Chincoteague, Virginia and Rehoboth Beach, Delaware, with five dominant NIS invertebrate taxa at each site.

Additional NIS are doubtless present at or near our study sites. Seventeen taxa, only resolved to genus level, were categorized as unassigned, meaning that we do not yet know if they are native, cryptogenic, or non-indigenous. These include four invertebrate species (1 sponge, 2 flatworms, and 1 hydroid) and 13 algal species (taxa shown in Table S2 as “spp.” are conservatively counted as two species). Further, a large number of biofouling groups are omitted from our work, including most protists, most flatworms, nematodes, oligochaetes, benthic copepods, and mites, as well as most parasites. We also omit fish and planktonic communities closely associated with the fouling assemblages. Among these groups, too, NIS are likely to be found.

Chesapeake Creep and Caribbean Creep

While we did not document any NIS new to the Northwest Atlantic, we found seven species that have expanded their range northward in responding to climate change as either “Caribbean Creep” (n=4) or “Chesapeake Creep” (n=3). These species represent four different taxonomic groups in four different phyla with a variety of life history strategies, feeding types, mobility, larval dispersal, and habitat preferences. “Caribbean Creep” species include the bryozoans *Schizoporella pungens* and *Amathia distans*, the ascidian *Distaplia bermudensis*, and the amphipod *Caprella scaura*, while the “Chesapeake Creep” species were the sea anemone *Aiptasiogeton eruptaurantia* and the ascidians *Ecteinascidia turbinata* and *Styela clava*.

Aiptasiogeton eruptaurantia and *Schizoporella pungens* are here documented for the first time to have proceeded up the Delmarva Peninsula to New Jersey (*A. eruptaurantia* had appeared in southern New England by 2009). *Styela plicata* has expanded north from Virginia to Maryland and *Caprella scaura* has extended north from South Carolina to Maryland. In addition, three species not native to the Western Atlantic are here documented to have expanded their ranges from north to south as expected, post-invasion, within their natural temperature limits. These species included the bryozoan *Tricellaria inopinata* (previously documented as far south as Long Island Sound, now found south to Chincoteague Island, Virginia), the amphipod *Caprella mutica* (expanded from Maryland to Virginia) and the ascidian *Didemnum vexillum* (expanded south from Long Island Sound to the Indian River Marina in Delaware). Southward post-invasion range expansions within thermal limits reflect a species' ability to colonize habitats that are already environmentally suitable (e.g., the introduced rhizocephalan barnacle *Loxothylacus panopaei*, and the European green crab *Carcinus maenas*, both on the east coast of the United States) (Roman 2006; Kruse and Hare 2007). These expansions are influenced by a mix of physiological tolerance, dispersal mechanisms, ecological interactions, and anthropogenic factors (Walther et al. 2009; Sunday et al. 2012). Understanding these patterns is essential for predicting future spread and managing invasive species impacts in both terrestrial and marine environments.

Records of range expanding species, especially of introduced species, have been common in the literature over the past few decades (Nye et al. 2009; Poloczanska et al. 2013; Hiddink et al. 2015; Hale et al. 2017). While there are many variables that contribute to the success of marine organisms colonizing new areas (including currents, ecological history, species interactions, trophic level, salinity and more), increasing ocean temperatures are the most likely explanation for the northward shifts we observed. In addition to lower latitude species moving poleward, as coastal waters continue to warm, species may also begin to experience increasing mortality at the southern end of their ranges and higher incidences of temperature-dependent reproductive failure (Crickenberger and Wethey 2018). As we have underscored here, many such expansions may include species that

are native or cryptogenic in southern regions, but are now colonizing higher latitudes as novel invasions. Hidden in modern literature may be numerous reports of the poleward movements of such species that are documented as new arrivals in a region (for example, Hale et al. 2017, 2018), but are not framed as biological invasions (Carlton and Schwindt 2024).

Comparisons to historical datasets

Comparisons to previous studies conducted ~50 years ago, as well as in more recent years (up to 2015), near some of our 2023 RAS stations suggest that significant changes in species composition have likely occurred. For example, Humphries (1973) studied bryozoans in a fouling community in 1967–1968 at Rehoboth Bay Marina in Dewey Beach, Delaware (9.5 km north of our Indian River Marina study site). In her survey 57 years ago, she did not record *Schizoporella pungens* (not known north of Fort Pierce, Florida before 2005), *Bugula neritina* (not known north of Cape Hatteras at that time), nor *Tricellaria inopinata* (which only arrived in the Northwest Atlantic in the early 2000s), whereas we recorded all three in this region in 2023.

Additionally, three previous surveys (Dean and Hurd 1980; Dean 1981; Smedes and Hurd 1981) documented the biofouling communities between 1974 and 1976 in the Broadkill River Estuary, a few km from our site at Anglers Marina, Lewes, Delaware, in the same estuary. Broadkill River was the only site where we found the native hydroid *Ectopleura crocea* as an aspect dominant member of the community, as did these studies 49 years ago. However, unlike our survey, they found the barnacle *Amphibalanus improvisus* to be abundant, whereas we found the slightly more saline *Amphibalanus eburneus* to be abundant, and did not detect *A. improvisus*. This is unlikely to be a site difference within the estuary, as these previous surveys were performed further down-river toward the ocean. Thus, it may be that salinity regimes have shifted in this region.

In another example, Meixler et al. (2019) sampled five stations in the Great Bay–Barnegat Bay estuarine system from 2006 to 2013 and referenced earlier work from 1971 to 1972 and 1982. Notably absent as of 2013 – only 12 years ago – and in all prior years, were the bryozoans *Tricellaria inopinata*, *Bugulina stolonifera*, and *Schizoporella pungens*, as well as

the sponge *Halichondria*. All these taxa were found at our station Key Harbor Marina in Barnegat Bay in 2023.

Lastly, Peterson (1979) studied intertidal epifaunal communities at Barnegat Inlet, New Jersey from 1972 to 1974, opposite our station Key Harbor Marina in Barnegat Bay. While Peterson's work is in the intertidal, there is considerable species overlap, which may bear comparison. Of potential interest is that Peterson (1979) found the cooler-water bryozoan "*Schizoporella unicornis*" (now treated in the Northwest Atlantic as *Schizoporella variabilis*), while we found *Schizoporella pungens* in Barnegat Bay in 2023. It may be that *S. variabilis* has retreated due to warming water, or that *S. pungens* has outcompeted *S. variabilis*, or a combination of both.

Conclusions

Rapid assessment surveys represent vital scientific data because they not only document community changes that have occurred as a result of human-induced global change, but they can also provide important baseline data that may be missing in many ecological investigations. Continued and frequent monitoring is also key to discovering introduced species and range expansions, as it may allow for a more effective response to novel species invasions than detecting species many years after their likely establishments. We therefore look forward to repeating the current work in the summer of 2028, five years after this current survey. We predict a continuing cornucopia of lower latitude species invading the Mid-Atlantic shores of the United States (and, concomitantly, species continuing poleward expansions in northern states). At the same time, while we found no new invasions into the Western Atlantic within our survey region, it is possible that we may have missed species that were difficult to access or in low abundances, and thus it is important to revisit and resample these sites especially given increasing global shipping traffic (Naghash et al. 2024). Indeed, we also emphasize that we sampled only one habitat, and did not explore rocky shores, sand-mud flats, salt marshes, or other communities.

Even though our study emphasizes the clear need for surveys that track and document how coastal

ocean biodiversity is changing, it has become increasingly challenging to secure adequate funding to support the travel, housing, supply, and equipment costs for a field team of professional scientists and students (none of whom are paid to participate in an RAS) (Carlton and Fowler 2018). Further, we rely heavily on the availability of expert systematists, whose numbers continue to decline (Carlton and Fowler 2018). The alternative, sending numerous preserved specimens to taxonomic specialists, hoping for *pro bono* services, is increasingly unfeasible, the more so since the few available specialists often have many years of back-logged samples to identify. Additionally, for those just learning taxonomy of specialized groups, such as hydroids, the most comprehensive references for the Atlantic coast of North America are now more than 80 years old (e.g., Fraser 1944), although more recent works have continued to clarify the systematics and taxonomy of hydroids in the surrounding Atlantic region (e.g., Calder 2017; Calder and Choong 2018). We recognize that in the coming years alternative approaches, such as eDNA metabarcoding, may be employed to detect and monitor NIS. However, at this time, these approaches still have considerable challenges (Beng and Corlett 2020), although providing potentially valuable supplemental data. Nevertheless, we remain optimistic about our ability to continue to muster the resources to keep our fingers on the pulse of changes in coastal zone communities in 2028, and in the years to come.

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Data availability Data are available from the author upon request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval This work was conducted under scientific collecting permits from the States of Virginia, Maryland, Delaware, and New Jersey and from the Monmouth County Park System (New Jersey) and Indian River Marina Park (Delaware). The authors have complied with all policies relative to the collection and handling of marine species, and no ethics approval was required.

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