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The intermingling of benthic macroinvertebrate communities during a period of shifting range: The "East of Nantucket" Atlantic Surfclam Survey and the existence of transient multiple stable states

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Abstract

A survey of the region eastward of Nantucket provided an opportunity to examine the cold temperate–boreal boundary along the high-energy Great South Channel. Here described are the benthic macroinvertebrate community types encountered, with a focus on the influence of climate change on the range boundaries of the benthic biomass dominants and the potential existence of transient multiple stable states. The survey identified three primary community types. The shallowest sites were occupied by a surfclam-dominated community, comprising an abundance of large (≥150 mm) surfclams, and a few common attached epibiota primarily attached to exposed surfclam shell. Two communities exist at intermediate depths, one dominated by submarket and small market-size surfclams (<150 mm) and the other, created by mussel mats and their attendant epibiota, crabs, sea urchins, and other mobile epifauna. Mussels are a foundational species, establishing a hard-bottom terrain conducive to these other denizens in soft-bottom habitat. Cobbles were nearly ubiquitous, rocks were routinely recovered, and boulders were encountered occasionally. Slow growing attached epibionts were exceedingly rare and mobile epifauna were not obviously associated with these large sedimentary particles; nor were the surfclam or mussel communities. The frequency of barnacle scars suggests sediment scour under the high-flow regime characteristic of the surveyed region, which voids the habitat potential of these sedimentary particles. The abundance of surfclam shell indicates that surfclams have inhabited the shoaler depths for an extended time; limited shell at deeper sites supports the inference from the absence of large animals that these sites are relatively newly colonized and represent further evidence of an offshore shift in range brought on by increasing bottom water temperatures. The dichotomous nature of the two primary community types at mid-depths suggests that these two communities represent multiple stable states brought on by the interaction of an invading cold temperate species with the receding boreal fauna resulting in a transient

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intermingling of species, which, however, structure the habitat into exclusionary stable states rather than overlapping in a co-occurrence ecotone.

KEYWORDS
climate change, cobble, community composition, mussel, range shift, *Spisula*

1 | INTRODUCTION

As the world continues to warm, range shifts by benthic species are increasingly documented (e.g., Southward, Hawkins, & Burrows, 1995; Oviatt, 2004; Lucey & Nye, 2010; Wethey, Woodin, Berke, & Dubois, 2016). The northwest Atlantic is a particularly interesting case history due to the rapid rate of warming in comparison to other regions (Saba et al., 2016) and the existence of a long-term survey time series of two long-lived benthic dominants, the Atlantic surfclam, *Spisula solidissima*, and the ocean quahog, *Arctica islandica* (NEFSC, 2017a, 2017b). These two species occupy the cold temperate (Virginian Province—Hale, 2010) and boreal (Acadian Province—Hale, 2010) sides of the north-temperate advancing temperature boundary. As the surfclam responds more rapidly to warming temperatures with an across shelf shift in range (Hofmann et al., 2018; Timbs, Powell, & Mann, 2018), the two species presently occupy an ecotone extending along much of the mid-Atlantic region (Powell, Ewing, & Kuykendall, 2019). The dynamics of this geographically extensive ecotone remain unstudied, save for its documentation. Along the northern boundary of the cold temperate habitat in the northwestern Atlantic, surfclam habitat presently also abuts a higher energy boreal habitat characterized by mussel beds and associated biota. This interface remains unstudied due to the difficulty of surveying the benthos in areas with high-velocity tidal currents, large-amplitude shifting sand waves, and boulder fields typical of the region between Nantucket and Georges Bank across the Great South Channel (Emery & Uchupi, 1965; Mann, Swift, & Perry, 1981).

Over the last year, two initiatives independent of climate change focused attention on the absence of benthic survey data for a portion of this high-velocity region east of the island of Nantucket eastward to the Great South Channel, the cold temperate portion of which provides significant catch of Atlantic surfclams. The first is a redesign of the U.S. Atlantic surfclam stock survey (Jacobson & Hennen, 2019). A survey design team identified this region east of Nantucket as the most important area supporting surfclams that fell outside of the historical survey stratum map (NEFSC, 2017a) used for the U.S. EEZ (exclusive economic zone) survey. The second was a newly created Habitat Management Area (HMA), within which the use of bottom-tending gear such as hydraulic dredges would be limited. Consequent of both reasons, a survey of the region eastward of Nantucket to the Great South Channel was undertaken, providing an opportunity to examine the cold temperate–boreal boundary along the high-energy Great South Channel. Survey results identified a post-2000 range shift offshore by Atlantic surfclams suggesting that the cold temperate–boreal boundary was in flux in this region and, in fact, might be characterized by the intermingling of community types as the dominant benthic sedentary and sessile species reposition in geographic space at varying rates. Herein, the community types encountered are described, with a focus on the benthic biomass dominants, followed by a further inquiry as to the potential existence of transient multiple stable states (for more on multiple stable states, see, e.g., Gray, 1977; Peterson, 1984; Coco, Thrush, Green, & Hewitt, 2006) as a characteristic of rapidly evolving range boundaries.

2 | METHODS

2.1 | Survey location and design

The survey domain is shown in Figure 1. Three regions are demarcated. The first, located on the upper left, is the shoaler region historically supporting significant surfclam landings. This region falls outside of the survey stratum map (NEFSC, 2017a), and consequently, the U.S. surfclam survey in the EEZ does not contain an historical record of this region. Note that the western boundary approximates the inshore EEZ boundary and that the southern boundary abuts on the lower left the Nantucket Lightship Habitat Closure Area, an area closed to bottom-tending gear. The larger region located in the center and to the right falls within the proposed Great South Channel Habitat Management Area. For ease of discussion, these last two regions will be referred to in the results section and identified on all maps of faunal distribution.

A fixed grid design was chosen to insure that the region was evenly and densely surveyed. Fixed grids are routinely used to evaluate regions initially for later inclusion into a stratified random survey design (e.g., van der Meer, 1997; Morehead, Montagna, & Kennicutt, 2008; HSRL, 2012; Powell, Mann, Ashton-Alcox, Kuykendall, & Long, 2017). A hub-and-spoke fixed grid design was implemented with spokes of 3-nm length (Figure 1), a sampling density approximating the densest sampling grid theoretically achievable under the NEFSC (1988) survey protocol. Six of the 63 stations (9.5%) were repositioned under a standard NEFSC protocol permitting repositioning within 1 nm of the designated position. Stations were moved for three reasons: (a) Some fell just inshore of the EEZ inshore boundary and were moved offshore across the boundary line; (b) some stations fell just inside the Nantucket Lightship Habitat Closure Area and were moved just north of that closure line; and (c) some stations fell on untowable bottom, always locations too shallow for the vessel to safely tow, and were moved laterally into deeper water.

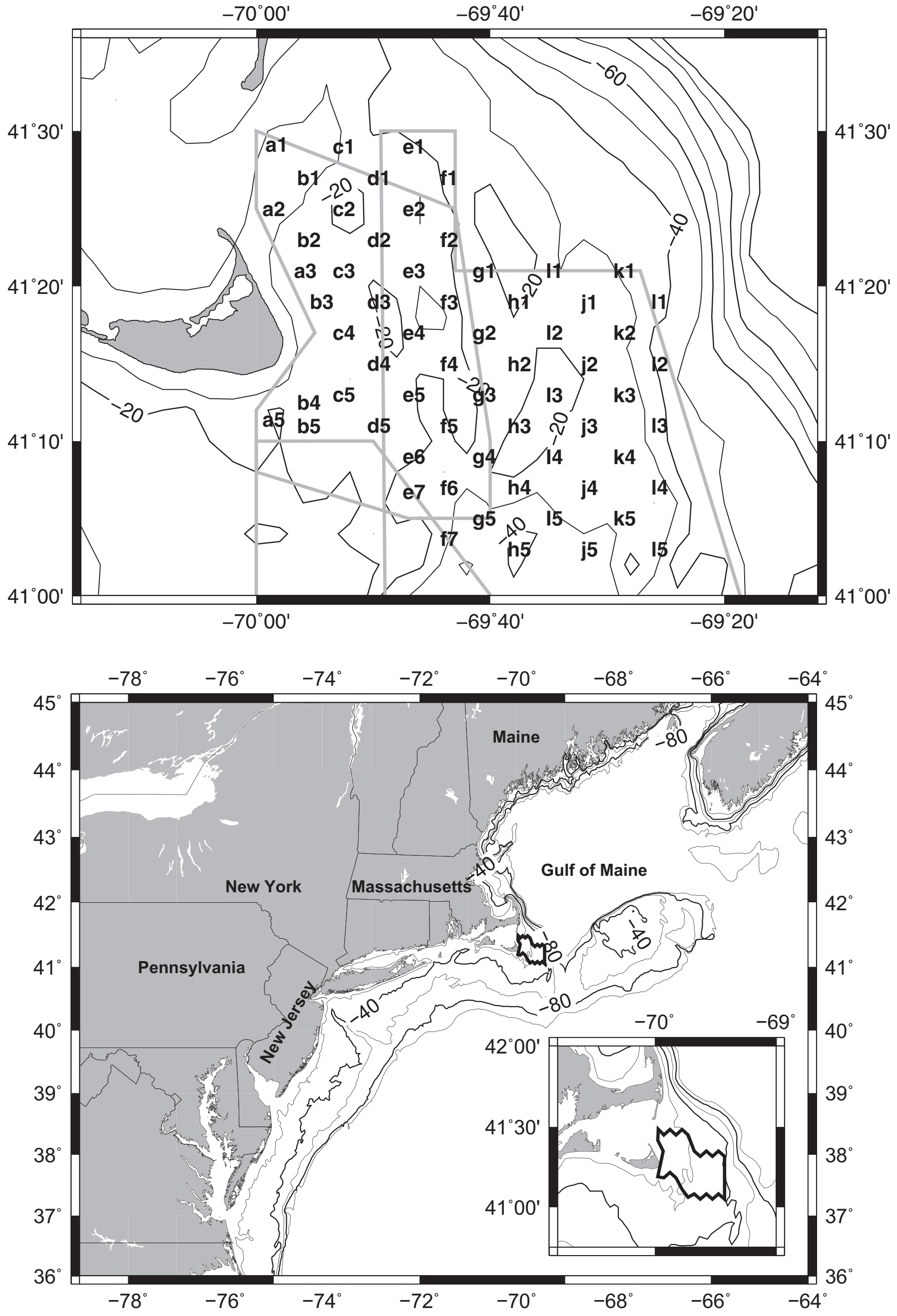

FIGURE 1 Above, the survey design. Gray lines outline (upper left) the sector historically contributing most of the Atlantic surfclam landings in the surveyed region, (lower left) the northern portion of the Nantucket Lightship Habitat Closure Area, and (right) the upper half of the Great South Channel HMA. Letters and numbers are station designations for the 63 stations in the survey. Depths are in meters. Below, the regional context with the surveyed area outlined in bold in the lower right insert

2.2 | Survey towing and on-deck processing protocol

The survey protocol followed the protocol used by NMFS-NEFSC for the 1982–2011 *R/V Delaware II* surveys in most respects. This protocol was chosen to permit comparison of "bycatch" data routinely collected during the *R/V Delaware II* surveys (see Powell, Kuykendall, & Moreno, 2017). The survey vessel was the *F/V Mariette*, homeport New Bedford, Massachusetts. The dredge was a 99-in hydraulic dredge of standard surfclam design (Lambert & Goudreau, 1996). Bar spacing was 1.875″ on the top, bottom, and knife shelf and 1.75″ on the sides. Selectivity is unknown, but experience with dredges of this type suggests that the dredge will be ~100% selective for market-size surfclams (≥120 mm) with selectivity steadily declining at smaller sizes. The *F/V Mariette* uses a shaker to clean up the catch. The shaker grate was closed to 0.75″ (~1.9 cm) for the survey.

Towing protocol was a 5-min tow in the direction of the next station except where large sand waves restricted towing direction. Tow speed was 3 knots. Most tows lasted for 5 min, but excessive catch or rapid shoaling occasionally decreased tow time. Tow swept area averaged about 1,250 m^2 tow^{-1} (Table 1). The survey in its entirety sampled about 78,500 m^2.

The entire catch was sorted including all surfclams, cobbles, rocks, boulders, associated invertebrates, and shell. To limit processing time, invertebrates were tallied by higher taxon (e.g., echinoid, crab, naticid gastropod). In some cases (e.g., crabs), these categories included a number of different species. Only common taxa are included in this report. In most cases, taxa were tallied. Bushel volume (U.S. standard bushel = 35.2 L) measurements were used for mussels, cobbles, rocks, and boulders. All tallied biota and sediment particles were standardized to per m^2 catch. Attached bionts were placed into a semiquantitative scale (viz., 0 = absent, 1 = present, 2 = predominant). Due to their rarity, anemones, tunicates, and sponges were combined into an attached biont category and enumerated as the sum of their individual semiquantitative scales. For presentation, surfclams were allocated to 4 size classes: <120 mm, 120–150 mm, 150–170 mm, and ≥ 170 mm. The 120-mm division marks the size-class boundary termed “fishable” in earlier NEFSC assessment reports (e.g., NEFSC, 2003). Animals smaller than 120 mm, although landed, are not targeted, and will be termed submarket in this report. Animals ≥ 150 mm are desired by companies that hand-shuck, hence the size-class boundary separating small-market and medium-market surfclams in this report. Animals ≥ 170 mm, termed large-market clams in this report, generally exceed the von Bertalanffy L_∞ for the remainder of the stock (Munroe et al., 2016).

Maps that follow compare two components of the catch. Circle diameters are linearly proportional to catch (in m^{-2}) or to the semiquantitative scale within each component, but are not comparable between components. Thus, for example, in a plot of submarket and medium-market surfclams (Figure 2), differential circle sizes for submarket surfclams show differences in catch of submarket surfclams between stations; ditto for medium-market surfclams. However, no valid quantitative comparison can be made between the circle sizes for submarket surfclam catch and the circle sizes for medium-market surfclam catch. Catch values are provided as supplementary data.

TABLE 1 Tow track statistics. The upper 4 metrics are given in terms of tow^{-1}. The sum is the total for all 63 stations occupied

	Distance (m)	Swept Area (m^2)
Mean	495.9	1,247.0
Standard deviation	52.9	133.0
Median	498.3	1,253.1
Interquartile range	70.8	178.0
Sum	31,242.0	78,561.2

Correspondence analysis was used to examine the entire dataset holistically because some data were categorical (e.g., attached bionts) (Clausen, 1998). In this case, quantitative data were classified into linearly incrementing categories. Correlations used the Pearson product–moment method. Statistical analyses were done with version 9.4 of SAS (SAS Institute, Cary, North Carolina).

3 | RESULTS

3.1 | Atlantic surfclams

Highest catches of surfclams were taken in the central portion of the surveyed region coincident with the north-central portion of the HMA and just outside of the region historically contributing most of the region's surfclam landings (Figure 2). Surfclam size frequency varied with depth. Submarket (<120 mm) and small-market (120–150 mm) surfclams were found in highest abundance in the central northern portion of the surveyed area coincident with the western half of the HMA and the eastern edge of the region demarcated by landings data (Figure 2). Few small surfclams were found inshore where most landings originate. The two size classes generally overlapped wherever they occurred. In contrast, medium-market (150–170 mm) and large-market (≥170 mm) surfclams were found on the most extreme southwestern edge of the HMA and inshore to the EEZ boundary (Figure 2). Animals 150 mm and larger were rarely encountered offshore of this region and extremely large animals (170 + mm) were very rare offshore of this region. Overall, submarket size animals dominate in water > 10.5 m deep in comparison to the larger clams generally found at shallower depths.

Deeper-water stations yielding primarily smaller clams were newly colonized with oldest animals borne post-2000, whereas the inshore stations were characterized by mature age frequencies (e.g., Weinberg, 1999) including clams exceeding 20 years in age (our unpubl. data). Further confirmation of the newness of offshore habitation comes from the distribution of surfclam shell . Surfclam shell generally was encountered where market-size surfclams were most

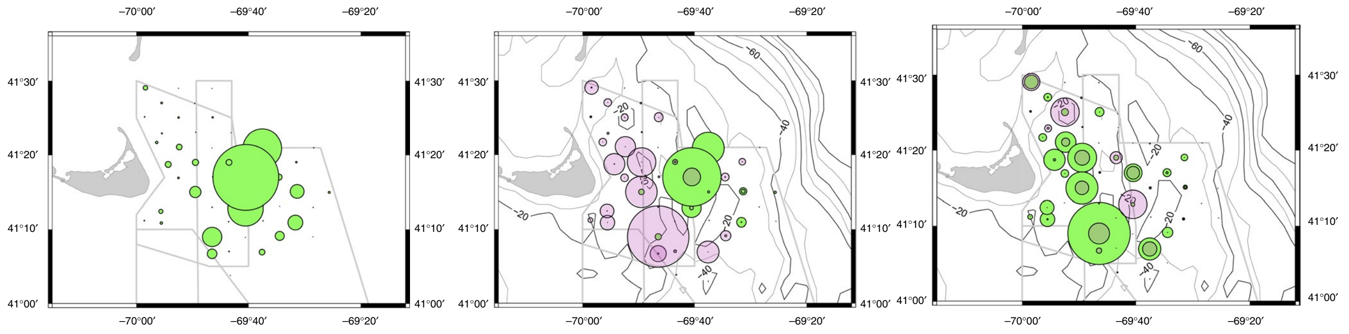

FIGURE 2 Left, catch of all sizes of Atlantic surfclams. Center, catch of submarket (green) and medium-market (purple) Atlantic surfclams. Right, catch of surfclam dead shell (purple) and medium-market (150–170 mm) surfclams (green). Circle diameters are linearly proportional to numbers m^{-2} within category but are not comparable between categories. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

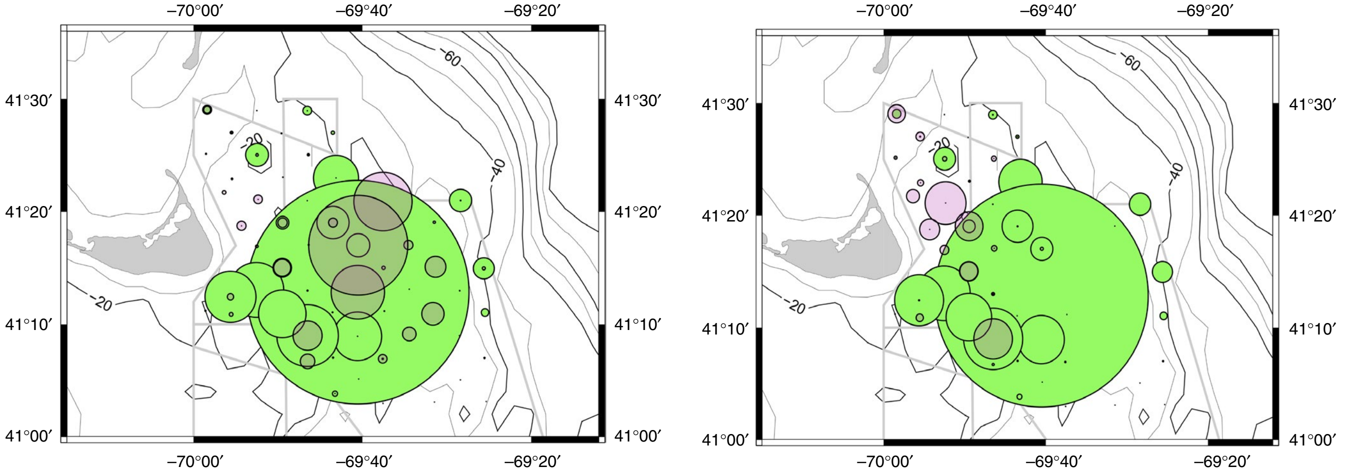

FIGURE 3 Left, catch of all, mostly submarket and small-market, Atlantic surfclams (purple) and cobbles (green). Right, catch of large-market Atlantic surfclams (purple) and cobbles (green). Circle diameters are linearly proportional to numbers m^{-2} for surfclams and bu m^{-2} for cobbles. Circle diameters are comparable within category, but not between categories. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

common (Figure 3), an indication that surfclams have been a dominant benthic inhabitant at these inshore depths for an extended period of time. How long is unclear, but the maximum life span of ~ 30 years would suggest that habitation has extended over half-century time scales or longer. In contrast, smaller surfclams, found offshore of this region, rarely were found in locales where surfclam shell was abundant. The inference that this deeper-water region has been inhabited only recently by surfclams is consistent with the failure to find animals borne earlier than 2004 at the offshore stations from which surfclams were aged (our unpubl. data).

3.2 | Distribution of cobbles, rocks, and boulders

Cobbles, rocks and boulders are routinely encountered on Georges Bank in regions occupied by surfclams (Powell, Kuykendall, et al., 2017). Surfclams, however, are sand denizens and, presumably, do not require or benefit from the presence of such sedimentary components in their habitat. Nonetheless, hydraulic dredges will catch these large sedimentary particles if present in the dredge path and if shallow enough in the sedimentary column to be intersected by the dredge knife. Cobbles, defined as particles 2–6″ (~5–15 cm) in diameter, were commonly encountered at many sites in the surveyed region (Figure 3). Cobbles were most common at intermediate depths in the west-central portion of the HMA and southeast of Nantucket. Medium-market and large-market surfclams are generally found inshore and north of the cobble-rich region. In contrast, submarket and small-market surfclams are most common within the depth range where cobbles are also frequently encountered (Figure 3). Assuming that the distribution of smaller surfclams indicates a range extension into deeper water, surfclams are becoming increasingly abundant at depths where cobbles are also common. However, closer inspection suggests that submarket and small-market surfclams tend to be more common in locales within this depth range where cobbles are less abundant, although overlap is clearly increased relative to the distributional dichotomy between cobbles and medium-market and large-market surfclams.

Rocks, sediment particles 6–12″ (~15–30 cm) in diameter, are much less common than cobbles; however, the distribution of rocks is similar to cobbles, as might be anticipated by the glacial origin of both (Trumbull, 1972). Rocks were most common in the north and central portions of the HMA and southeast of Nantucket (Figure 4). As with cobbles, the distribution of medium-market and large-market surfclams clearly diverged from that of rocks. The smaller surfclam sizes were most abundant at depths where rocks were often encountered, but closer inspection suggests that surfclams tend to be more common in locales within this depth range where rocks are less abundant (Figure 4). An equivalent conclusion is reached for boulders, sediment particles > 12″ (~30 cm) in diameter. Boulders were sporadically and uncommonly encountered on the survey, but were more likely to be encountered at sites where rocks were common (Figure 4).

3.3 | Distribution of mussels

Mussels were abundant in a few tows. When abundant, they occurred in dense mats attached to pebbles and sand grains, which counterweighed their tendency toward saltation (Figure 5). Mats normally were a mixture of *Modiolus modiolus* and a *Mytilus* species or just *Mytilus*. Large, and therefore old, *M. modiolus*, however, were not collected whereas large *Mytilus* were abundant. Two species of *Mytilus* are found along the northeast coast, *Mytilus edulis* and *Mytilus trossulus*, with the latter extending farther north and the former farther south. Considerable overlap in their ranges exists north of Cape Cod (Rawson & Harper, 2009). According to Hilbish et al. (2000), mussels collected south of central Maine on the East coast were likely *Mytilus edulis* as *M. edulis* is the predominant species from central Maine south (Rawson, Hayhurst, & Vanscoyoc, 2001) to Cape Hatteras (Wells & Gray, 1960). Regardless, no attempt was

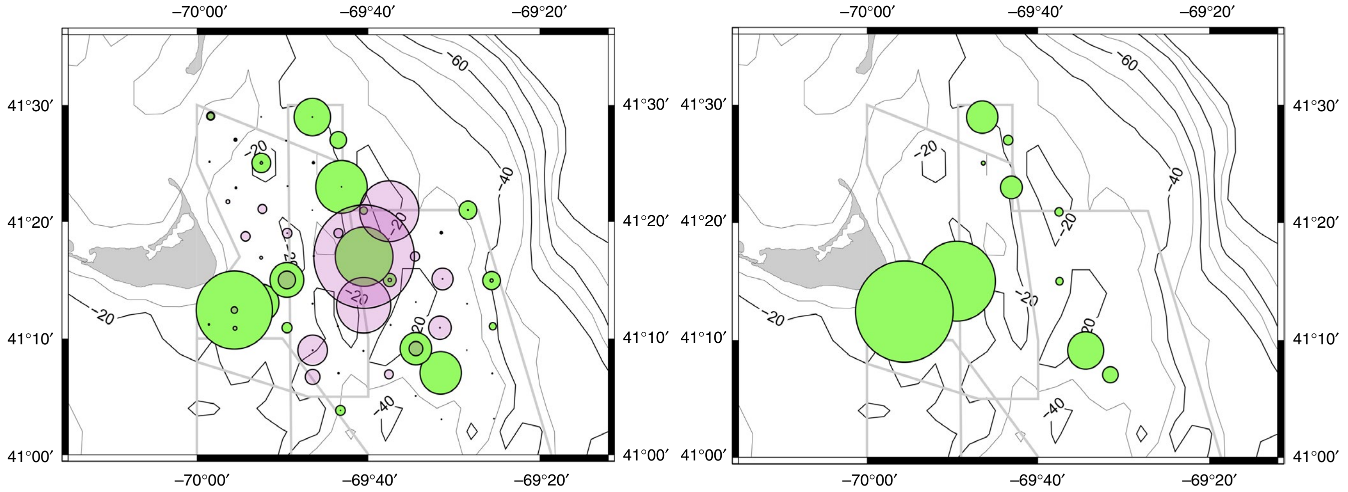

FIGURE 4 Left, catch of all, mostly submarket and small-market, Atlantic surfclams (purple) and rocks (green). Right, catch of boulders. Circle diameters are linearly proportional to numbers m^{-2} for surfclams and bu m^{-2} for rocks and boulders. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

FIGURE 5 Underside of a piece of mussel mat showing the interwoven byssal threads securing the mussels to pebbles and sand grains to achieve a cohesive mass with added weight to resist saltation under low current velocities

made to determine the species composition of the mytilids. Large mussel catches were characterized by a wide range of size classes including new recruits and adults; as a consequence, numbers caught were too large to permit tallying the catch numerically. Bushel volumes were used.

Mussels did not occur at sites where medium-market and large-market surfclams were found (Figure 6). Large mussel catches occurred primarily offshore of the region where these larger surfclams were common, with highest catches in the northwestern portion of the HMA, with a single exception of one site in the south-central portion of the HMA (Figure 6). On the other hand, sites where submarket and small-market surfclams abounded fell within the same depth range as sites yielding quantities of mussels. Nonetheless, although the two taxa overlapped in their offshore depth range, at no site were both caught in large quantities. The two distributions were clearly locally disjunct (Figure 6).

The distribution of mussels along the northeast coast of the United States in the intertidal is noteworthy for being associated with rocky shores or manmade structures (Cockrell, Bernhardt, & Leslie, 2015; Lauenstein et al., 1997), although they commonly occur in intertidal mats along the western European coast (Beukema & Cadée, 1996; Diederich, 2006). The abundance of cobbles and rocks at some survey sites suggests ideal substrate exists for mussels and sites yielding mussels or cobbles and rocks in abundance were often located in a similar depth range along a southeast trending line from the northwestern corner of the HMA south to the central region of the HMA (Figure 7). Surprisingly, the mussels were rarely abundant at sites where cobbles, rocks, or boulders were common (Figure 7), although all four were frequently encountered at the same depths. Thus, mussel beds did not depend on large sedimentary particles for their presence or integrity; rather, their cohesion was based on interwoven byssal threads and embedded pebbles and sand grains (Figure 5), as is typical of mussel beds on soft sediments (Salas, Defeo, & Narvarte, 2016; wa Kangeri et al., 2014; wa Kangeri, Jansen, Joppe, & Dankers, 2016).

3.4 | Distribution of miscellaneous megabenthos—mostly mobile

Crabs and regular sea urchins occurred commonly at a few sites (Figure 8), typically coincident with mussels. Naticid snails were also commonly encountered at most, except the deepest, depths. Naticids are bivalve predators (Boggs, Rice, Kitchell, & Kitchell, 1984; Powell, Staff, Stanton, & Callender, 2001; Stanton, Powell, & Nelson, 1981; Visaggi & Kelley, 2015). The expectation based on known predatory proclivities (Dietl & Alexander, 1997; Quijón, Grassle, & Rosario, 2007) that the naticids should covary with surfclams is not supported, however, as their distribution did not obviously coincide with the distribution of large or small surfclams

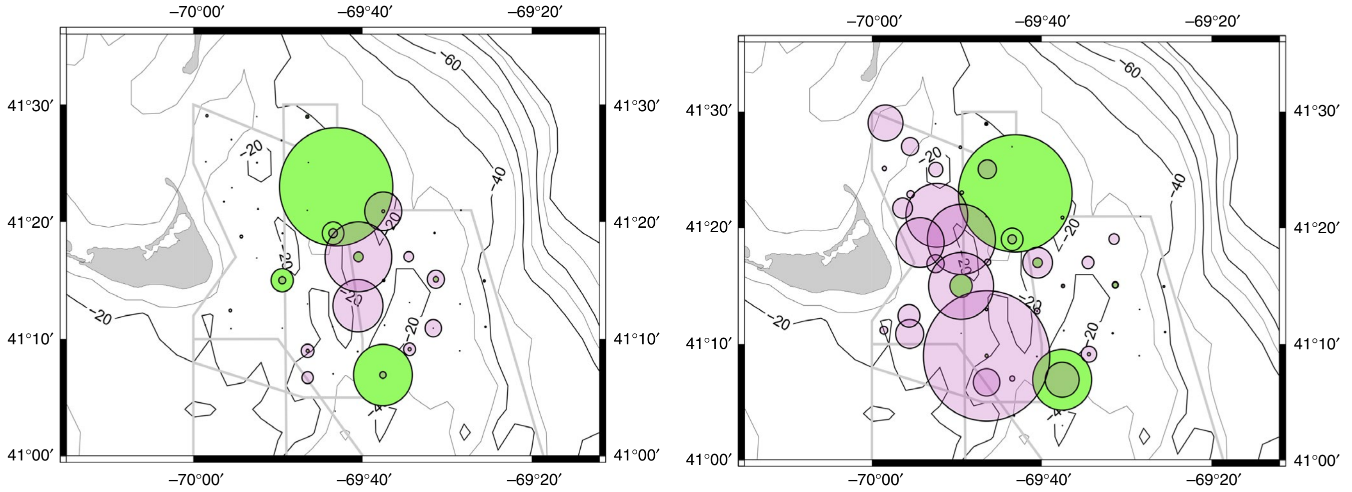

FIGURE 6 Left, catch of small-market Atlantic surfclams (purple) and mussels (green). Right, catch of medium-market and large-market Atlantic surfclams (purple) and mussels (green). Circle diameters are linearly proportional to numbers m^{-2} for surfclams and bu m^{-2} for mussels. Circle diameters are comparable within category but not between categories. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

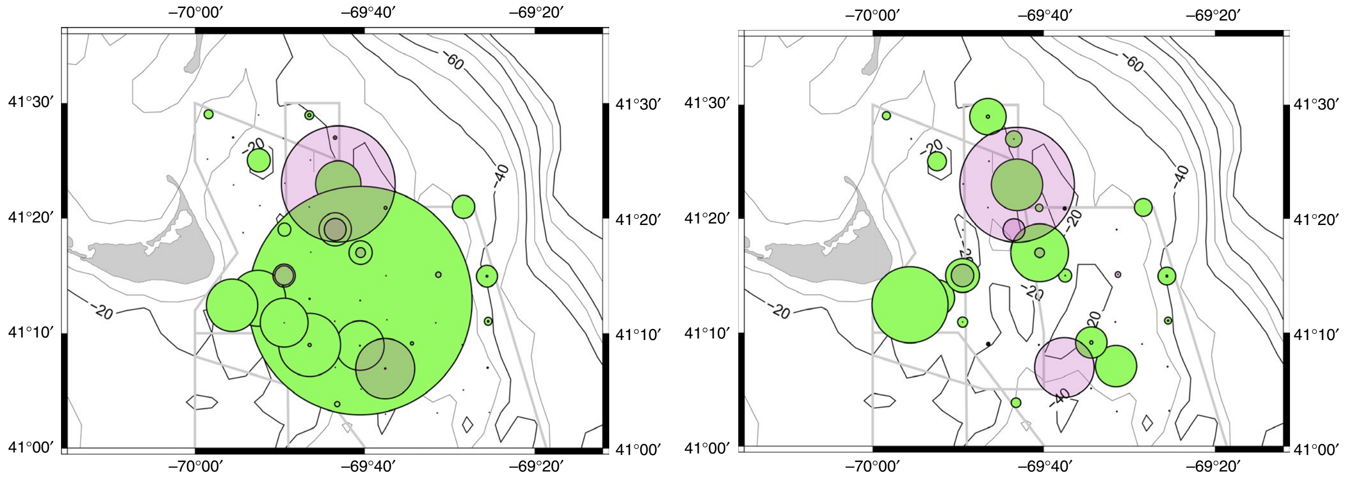

FIGURE 7 Left, catch of cobbles (green) and mussels (purple). Right, catch of rocks (green) and mussels (purple). Circle diameters are linearly proportional to bu m^{-2} within category but are not comparable between categories. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

(Figure 9), nor did the distribution of naticids obviously coincide with the distribution of mussels. The survey encountered a number of small clams (e.g., *Astarte*, *Pitar*), which are poorly caught by the survey gear and thus not reported here. Likely these clams are the primary prey of the naticids. Sea cucumbers were caught at a few sites (Figure 10). All of these were in deeper water, distinctly deeper than the depth range of mussels, surfclams, and their associated biota. *Buccinum* gastropods were often caught in the central and northeast portion of the HMA (Figure 10). Slipper shells (*Crepidula* spp.) were commonly caught inshore at sites where large surfclams and surfclam shells were abundant (Figure 10). *Crepidula* has a propensity to attach to certain bivalve species (e.g., Peterson, 1983).

3.5 | Distribution of attached epibenthos

The survey focused on large attached epibionts on cobbles, rocks, boulders, and surfclam shell and did not record the occurrences of small encrusting organisms such as spirorbids, serpulids, and foraminifera. The most common and ubiquitous large epibiont was barnacles which were observed encrusting cobbles, rocks, boulders, and surfclam shells at almost every site where these particles were present (Figure 11). Sponges, anemones, and tunicates were rarely encountered (Figure 11), but encountered most often in the north and northeastern sectors of the HMA. Overlap with medium-market and large-market surfclams was very limited. Overlap increased with the smaller surfclams due to their predominance in deeper water, but at only one site

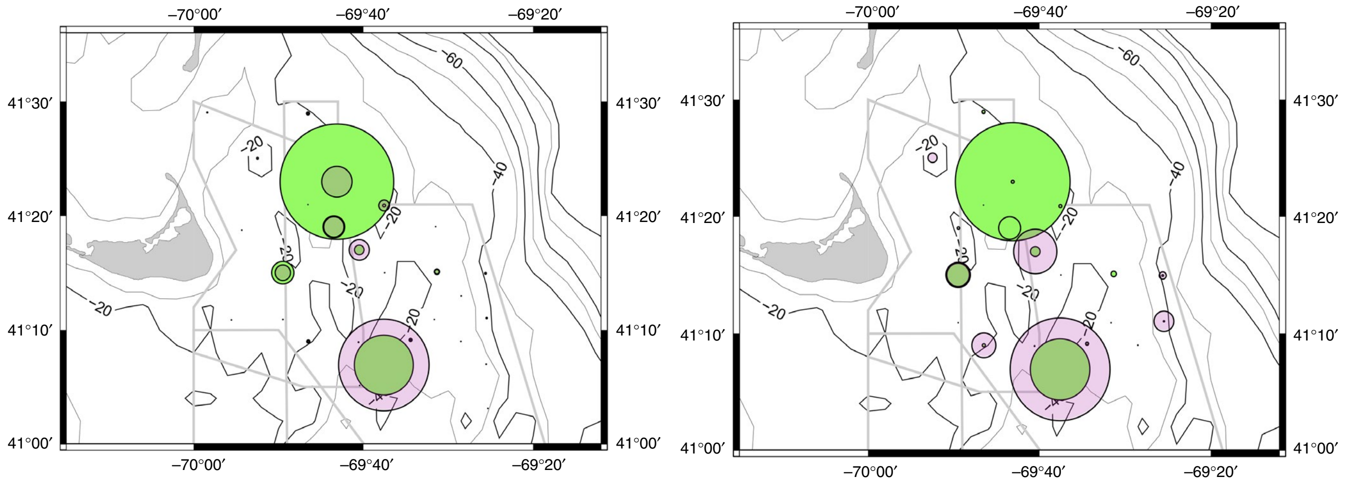

FIGURE 8 Left, catch of crabs (purple) and mussels (green). Right, catch of regular echinoids (purple) and mussels (green). Circle diameters are linearly proportional to numbers m^{-2} for crabs and echinoids and bu m^{-2} for mussels. Circle diameters are comparable within category but not between category. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

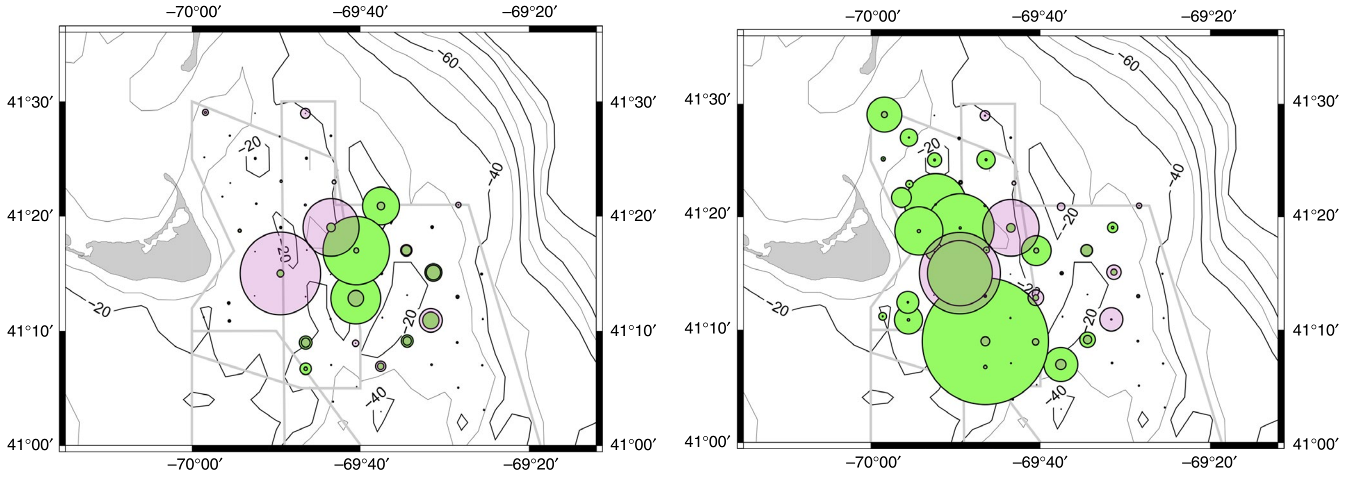

FIGURE 9 Left, catch of naticid gastropods (purple) and small-market Atlantic surfclams (green). Right, catch of naticid gastropods (purple) and medium-market and large-market Atlantic surfclams (green). Circle diameters are linearly proportional to numbers m^{-2} for naticids and surfclams. Circle diameters are comparable within category but not between categories. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

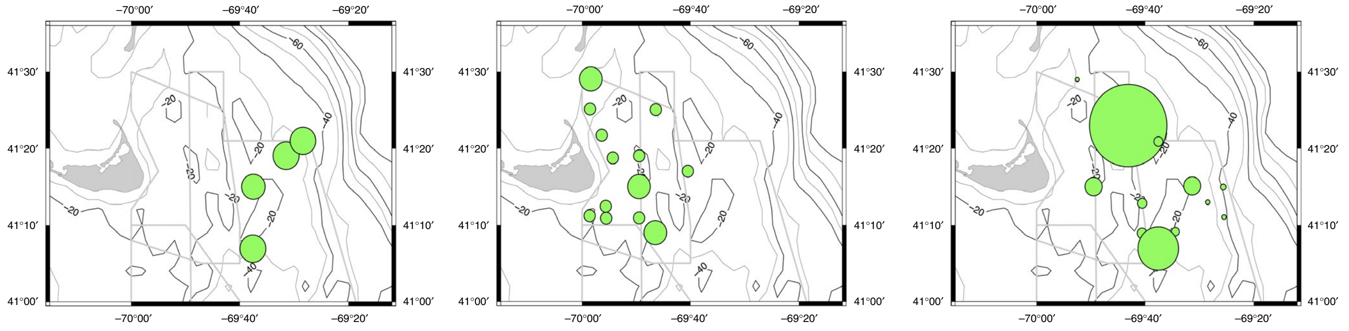

FIGURE 10 Presence of sea cucumbers (left), slipper shells (*Crepidula* spp.) (center), and *Buccinum* gastropods (right). Circle values for slipper shells and sea cucumbers are 1 = present and 2 = abundant. Circle diameters for *Buccinum* are linearly proportional to numbers m^{-2}. Zero catch stations are not shown (see Figure 1 for full station complement). Depths in m

were these epibionts caught coincident with a large number of small surfclams (Figure 11). In part, this tendency accrued from the differential distribution of surfclams and rocks and boulders, upon which most large epibionts were attached. After barnacles, tunicates were most commonly encountered: Sponges and anemones were exceedingly rare. Tunicates were least often encountered on boulders and surfclam

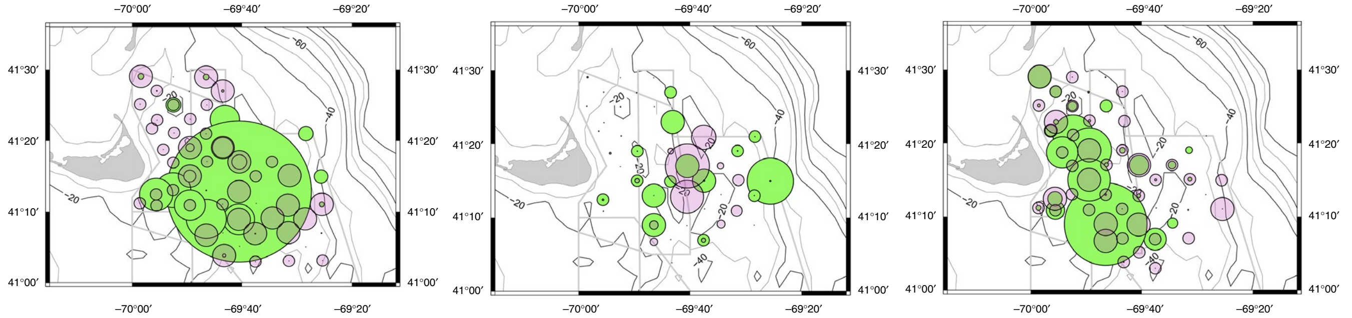

FIGURE 11 Left, occurrence of barnacles and barnacle scars (purple) and cobbles (green). Middle, occurrence of anemones, tunicates, and sponges (green) and small-market Atlantic surfclams (purple). Right, occurrence of hydroids (purple) and medium-market and large-market Atlantic surfclams (green). Circle diameters are linearly proportional to bushels m^{-2} for cobbles and numbers m^{-2} for surfclams. Circle values for barnacles and hydroids are 1 = present and 2 = abundant. Circle values for anemones, tunicates, and sponges are the summary designations of 1 = present and 2 = abundant for each taxon. Values range from 1 to 6; largest value obtained was 4

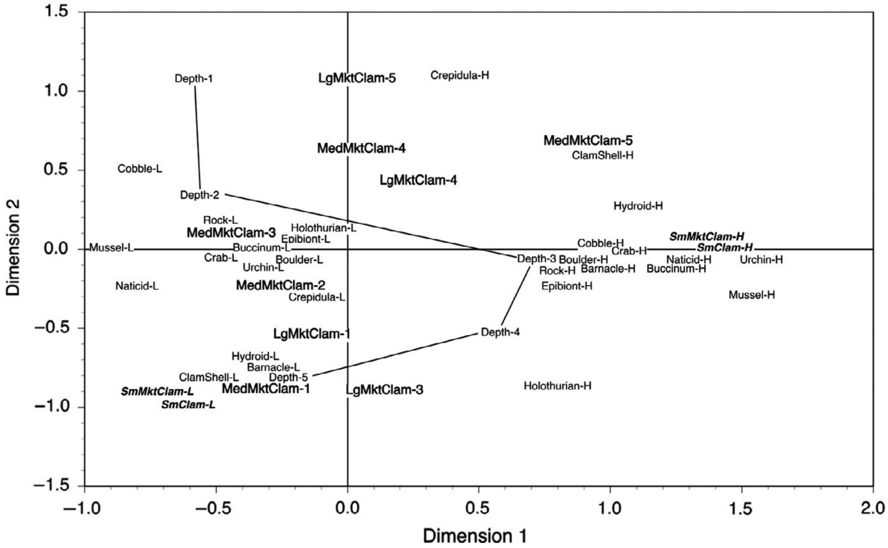

FIGURE 12 Correspondence analysis for the survey dataset. Categorical values for biota and sedimentary constituents were constructed by classifying catch values into quintiles (surfclams, mussels, cobbles), quartiles (rocks, naticids, crabs, surfclam shells), terciles (hydroids, barnacles/scars), and halves (boulders, anemones + sponges+tunicates, echinoids, slipper shells, sea cucumbers). Depth divisions were 10.5, 16.5, 22.5, and 27 m. For surfclams: Sm, submarket; Mkt, small-market; Med, medium-market; Lg, large-market. Values following the surfclam designations Med and Lg and depths represent positions in the quintile/quartile/tercile/half. For the remaining constituents, L refers to the lowest and H to the highest quintile/quartile/tercile/half

shells and most often encountered on rocks and cobbles. In contrast, hydroids were considerably differentially distributed (Figure 11). (Erect bryozoans and hydroids could not be differentiated during the survey. Most organisms encountered were likely hydroids, but conformation is lacking; nonetheless, for brevity, this type of epibiont will be referred to as “hydroid” throughout this report.) Hydroids were commonly encountered at many sites, particularly sites yielding medium-market and large-market surfclams and surfclam shell (Figure 11).

3.6 | Community relationships

The first two axes of the correspondence analysis (Figure 12) explained most of the variation in the dataset. Dimension 1 (x-axis) was specified by the relative abundance of the various survey constituents, with lower abundance sites on the left (negative values) and higher abundance sites on the right (positive values). Dimension 2 (y-axis) was specified by depth, with shallower sites having positive values and deeper sites having negative values. Accordingly, the upper left quadrant was occupied by sites with rare constituents in shallow water; the upper right, by abundant constituents in shallow water; the lower left, by rare constituents in deeper water; and the lower right, by abundant constituents in deeper water.

The host of low-abundance constituents in deeper water (lower left quadrant) identifies the limited biota present at the deepest sites. Surfclam shell and surfclams, hydroids, barnacles, naticids, and slipper shells, for example, were rarely collected at deeper-water sites. In the lower right-hand quadrant are the sea cucumbers; these were the only large animals collected commonly at the deepest depths.

TABLE 2 Pearson product–moment correlations: The regression coefficient is listed above the P value. Correlations were run after deleting zero–zero pairs

	<120 mm surfclams	Surfclams 120–150 mm	Surfclams 150–170 mm	Surfclams 170–200 mm	Mussels	Cobbles
Surfclams 120–150 mm	0.93 $p < 0.0001$					
Surfclams 150–170 mm	0.15 $p > 0.05$	0.21 $p > 0.05$				
Surfclams 170–200 mm	−0.0095 $p > 0.05$	−0.0095 $p > 0.05$	0.80 $p < 0.0001$			
Mussels	0.032 $p > 0.05$	0.045 $p > 0.05$	0.093 $p > 0.05$	−0.041 $p > 0.05$		
Cobbles	0.32 $p = 0.0115$	0.53 $p < 0.0001$	0.13 $p > 0.05$	0.0037 $p > 0.05$	0.12 $p > 0.05$	
Rocks	0.29 $p = 0.022$	0.22 $p > 0.05$	0.11 $p > 0.05$	−0.09 $p > 0.05$	0.33 $p = 0.0079$	0.24 $p = 0.06$

In the upper right quadrant are the larger size classes of surfclams, surfclam shell, slipper shells which were found in greatest abundance on surfclam shells, and to some extent hydroids which are distributed more broadly across the depth range of the survey than the slipper shells. The medium-market and large-market surfclams and the remaining aforementioned taxa represent the characteristic community elements at the shallow water sites.

Mussels and smaller surfclams fall near zero on the y-axis and at distinctly positive values on the x-axis. These taxa were abundant at moderate depths, along with *Buccinum* gastropods, naticids, sea urchins, crabs, and the attached epibiota (anemones, tunicates, sponges). Depth is not a discriminator for these taxa, although the distributions of surfclams, mussels, and attached epibiota rarely overlap substantively within this depth range. Cobbles, rocks, and boulders are also abundant at intermediate depths. These three constituents fall closely together on the x-axis, consistent with their common origin from the terminal moraine of the Wisconsinan glaciation (Uchupi & Bolmer, 2008). Note in Figure 12 the translation of depth along the x-axis (abundance) from depth = 1 (<10.5 m) and depth = 2 (10.6–16.5 m) to depth = 3 (16.6–22.5 m) and the translation back from depth = 4 (22.6–27 m) to depth = 5 (>27 m). Biota are scarce at depths deeper than 27 m. Mussels and the submarket and small-market surfclams are most abundant at 16.6–22.5 m. The larger surfclams are most abundant at < 10.5 m.

Pearson product–moment correlations showed, as expected, that the larger two size classes of surfclams were significantly correlated, as were the smaller two size classes (Table 2). The larger two size classes and the smaller two size classes were not significantly correlated (Table 2). Mussels, although falling close to the smaller surfclam size classes on the correspondence analysis axes, did not correlate significantly with any surfclam size class (Table 2), nor did they correlate with the cobbles, and indeed, correspondence analysis indicates a modest difference in depth between the mussels and cobbles (Figure 12), due primarily to the absence of mussels in shoaler waters where cobbles were also found (Figure 7). The abundance of cobbles was correlated significantly with that of the two smaller size classes of surfclams. This was driven primarily by the stations where both constituents were present in low abundance. The same was true for the unanticipated correlation between rocks and mussels which was driven primarily by their coincident rarity at many stations, in comparison to the expected correlation between rocks and cobbles accruing from their common origin. Thus, correlation analysis corroborates the dissimilarity of the distributional patterns inferred from correspondence analysis within the mid-depth range where all three habitat icons, surfclams, mussels, and cobbles/rocks, were most commonly encountered.

4 | DISCUSSION

4.1 | Community types

The survey region supports four primary community types. The deepest depths yield few mega-epifauna or mega-infauna: The characteristic taxon is the sea cucumber, which is essentially the sole representative at these depths. At the other end of the depth spectrum, the shallowest sites are occupied by a distinct surfclam-dominated community, comprising an abundance of surfclams mostly ≥ 150 mm, and a few common attached epibiota, the hydroids and slipper shells, that are primarily found attached to exposed surfclam shell.

Two communities exist at intermediate depths. One is dominated by submarket and small-market surfclams (<150 mm). Hydroids are present, but surfclam shell is not abundant, and slipper shells and mobile epifauna are rare. Although no other taxa characteristically co-occur, naticids are frequently collected, as they are at most shallow and moderately deep sites. The other community is created by the presence of mussel mats. Crabs, sea urchins, and other mobile epifauna abound; this is an expected faunal composition (e.g., Kent et al., 2007). Mussels are a foundational species, establishing through their presence living or the production of shell, a hard-bottom terrain conducive to occupation by these other denizens in an otherwise soft-bottom expanse (see Goddard & Love, 2010; Manoukian et al., 2010; van der Zee et al., 2015).

Neither of these community types is dependent upon rocks, cobbles, or boulders; in fact, the distribution of these sedimentary particles, although common at the same depths, does not track the distribution of concentrations of surfclams or mussels. In fact, no major community type tracks these sedimentary particles in correspondence analysis and only one correlation coefficient exceeding 0.5, between small-market surfclams and cobbles, supports any such relationship despite the normal occurrence of edaphic factors structuring the benthos (e.g., Sanders, 1958; Rhoads & Young, 1971; Calnan & Littleton, 1989; Aller, 1995) and the commonplace encounter with sedimentary particles potentially providing good attachment substrate for erect sessile epibiota. Surfclam shells were abundant at many locations. Cobbles were nearly ubiquitous. Although very common at a smaller proportion of stations, rocks were routinely encountered, and boulders were encountered occasionally. In contrast, slow growing attached epibionts such as sponges were exceedingly rare and most soft-bodied attached epibionts were rare. Mobile epifauna were not obviously associated with these large sedimentary particles either.

The frequency of barnacle scars suggests sediment scour in the high-flow regime characteristic of the region between Nantucket and the Great South Channel. The absence of a well-developed attached epibiont community strongly suggests that cobbles, rocks, and boulders are normally buried (Powell, Brett, et al., 2011c).; Rodland, Kowalewski, Carroll, & Simões, 2006). The commonplace occurrence of barnacles, given the hydrodynamic conditions, can be explained by their rapid growth rates in high current velocities (Bertness, Gaines, Bermudez, & Sanford, 1991; Goren, 1979; Nishizaki & Carrington, 2015; Sanford, Bermudez, Bertness, & Gaines, 1994), permitting successful colonization during relatively short periods of substrate exposure and limited scour. The oddity of hydroids also may be explained by their rapid growth rates (Gili & Hughes, 1995). That is, only this type of epibiont could reach a large size in the short time that these sedimentary constituents are exposed and unscoured. The relatively high proportion of cobbles, rocks, and boulders without attached biota or with only barnacle scars is particularly instructive in supporting the hypothesis that these sedimentary constituents remain buried much of the time or are repeatedly scoured (Wilson, 1987). As a consequence, cobbles, rocks, and boulders contribute little to the community composition in the surveyed region, and their influence is predominately one of exclusion; the mussel and surfclam communities tended to be found in locations not characterized routinely by these large sedimentary particles.

4.2 | Surfclam range shift dynamics

Mid-Atlantic Bight water temperatures have been warming for at least the last 200 years, with a distinct increase in rate since 1970 (Fulweiler, Oczkowski, Miller, Oviatt, & Pilson, 2015; Nixon, Granger, Buckley, Lamont, & Rowell, 2004; Pace, Powell, & Mann, 2018; Steinman, Mann, & Miller, 2015). The influence of warming bottom water temperatures promoting an offshore shift in the surfclam's range is well described (see review in Hofmann et al., 2018). This process has been ongoing since the 1970s and is well documented off New Jersey by a shift in the range core (Timbs et al., 2018; Weinberg, Powell, Pickett, Nordahl, & Jacobson, 2005) and mass mortality along the inshore range boundary (Kim & Powell, 2004) off Delmarva. Powell, Kuykendall, et al. (2017) and NEFSC (2017a) documented the same trends as far north as Georges Bank. This nearly stock-wide shift in range is due to the narrow temperature window between optimal and the upper lethal limit (Munroe, Powell, Mann, Klinck, & Hofmann, 2013; Narváez et al., 2015). Consequences of this physiology include lower condition offshore (Marzec, Kim, & Powell, 2010), declining maximum size (L_∞: Munroe et al., 2016), and a differential distribution of surfclam shell and living surfclams (Powell, Kuykendall, et al., 2017). In the latter case, a characteristic of recent colonization is living surfclams with little co-occurring shell whereas the opposite is indicative of habitat abandonment, the timing of which is dependent upon the degree of time averaging (Bizjack, Kidwell, Velarde, Leonard-Pingel, & Tomašových, 2017; Flessa & Kowalewski, 1994; Kidwell, 2002; Powell & Davies, 1990).

Throughout much of this region, the offshore shift in the surfclam's range has initiated recruitment within the area occupied by ocean quahogs. This cohabited ecotone is well described. Powell, Kuykendall, et al. (2017) recently documented this phenomenon on Georges Bank (see also Powell et al., 2019). The finding of smaller surfclams offshore in this survey east of Nantucket is consistent with the expectation of recent colonization in deeper water. The alternative that surfclams are simply growing slower along the deeper portion of their onshore–offshore range can be excluded by their young age (our unpubl. data), although differential growth rates might be anticipated as temperature plays a major role determining maximum size (Munroe et al., 2016, 2013).

Bivalve shell enters into the taphonomic process after death. Stated simply, various degradational processes such as dissolution, abrasion, and bioerosion operate to destroy shell (Davies, Staff, Callender, & Powell, 1990; Powell, Staff, Davies, & Callender, 1989; Staff, Stanton, Powell, & Cummins, 1986) while it is at the surface or in the surficial sediments within the taphonomically active zone (TAZ; Davies, Powell, & Stanton, 1989). Burial, on the other hand, removes shell from the TAZ, thereby preserving it for an extended period of time if not indefinitely (Parsons-Hubbard et al., 1999; Powell, 1992; Tomašových, Fürsich, & Olszewski, 2006). The robustness to taphonomic degradation of surfclam shell is unknown, but shells of similar clam species tend to be robust (Callender, Powell, & Staff, 1994; Powell, Brett, et al., 2011c; Powell et al., 2011a, 2011b; Walker & Goldstein, 1999). Thus, surfclam shell should remain intact for many decades after death.

The abundance of surfclam shell indicates that surfclams have inhabited the shoaler surveyed depths for an extended period of time; whereas the limited shell content at deeper sites supports the inference from the absence of large animals that these sites are relatively newly colonized . The observation of a species present living, but not in the death assemblage is unusual and normally explained by rarity of occurrence or poor preservability (e.g., Callender & Powell, 2000;

Albano, 2014; Martinelli, Madin, & Kosnik, 2016), neither of which is true for Atlantic surfclams in the surveyed region. Long post-mortem shell half-lives impose taphonomic inertia into the system which permits the death assemblage to track the history of occupation (Kidwell, 2008; Poirier, Sauriau, Chaumillon, & Bertin, 2010), but which also imposes a time delay between initial colonization and representation in the death assemblage (Olszewski, 2012) and a variable signal of range relinquishment depending on the degree of time averaging (e.g., Perry, 1996; García-Ramos, Albano, Harzhauser, Piller, & Zuschin, 2016). No evidence of range relinquishment exists in this survey despite the wealth of evidence of such farther to the south (Powell et al., 2019), whereas range expansion is documented by multiple evidences including differential size frequencies shallow and deep (large vs. small surfclams), and varying distributions of surfclam shell content.

4.3 | Mussel mats and a possible range shift

The boundaries of the biogeographic range of a species are typically delineated by the thermal tolerance of the organism with range contraction and range shifts being the common response to evade regions where temperatures have reached or exceeded the upper bounds of tolerance (Hutchins, 1947; Lucey & Nye, 2010; Weinert et al., 2016). Interestingly, another species that has shown a contraction and poleward shift in range over the past several decades is *Mytilus edulis* (Hutchins, 1947). In 1943, *M. edulis* was found as far south as Beaufort, North Carolina (McDougall, 1943). By 1960, the southern boundary of the range had contracted poleward to Cape Hatteras, North Carolina, due to increasing water temperature with increasing abundances and sizes to the north and mortality to the south of Cape Hatteras (Wells & Gray, 1960). Moving forward to 2005, the *M. edulis* population along the entire North Carolina coast no longer persisted year-round owing to increasing water temperatures (Jones, Mieszkowska, & Wethey, 2009). In total, the southern boundary of *M. edulis* had contracted roughly 350 km poleward as the decade of the 2000s neared its end (Jones, Lima, & Wethey, 2010).

Unfortunately, the option of using the death assemblage to inform recent colonization and range relinquishment is not available for mussels. Unlike most bivalve species, save oysters (Powell, Kraeuter, & Ashton-Alcox, 2006), mussels are poorly preserved. Shell half-lives typically are much less than 10 years (Callender et al., 1994; Powell, Brett, et al., 2011c).; Powell et al., 2008, 2011b). As a consequence, mussel shells rarely are recovered in death assemblages other than very shortly after death or under circumstances permitting rapid burial (Valentine, 1989).

Thus, the historical distribution of mussels in the surveyed region, lacking earlier survey data, can only be speculative. The temperature tolerances of the two species (Atlantic surfclam and blue mussel) are relatively similar; both would be identified as cold temperate species. Both extend into the Gulf of Maine (Newell, 1989; Palmer, 1991), with *Mytilus edulis* being the better established, at least partially due to an abundance of hard substrate. The differentials of the southern and inshore range boundary for the two species are unclear; however, one might consider that if the smaller surfclams offshore represent a relatively recent range extension, then this may presage a future withdrawal of *M. edulis* from the region. The other mussel, *Modiolus modiolus*, is a boreal species (e.g., Wildish, Fader, Lawton, & MacDonald, 1998; Lindenbaum et al., 2008) occupying a temperature range similar to the ocean quahog, *Arctica islandica* (compare Mann, 1982 with Gormley, Porter, Bell, Hull, & Sanderson, 2013; Hutchison, Hendrick, Burrows, Wilson, & Last, 2016). As of this writing, no evidence exists that the ocean quahog is withdrawing from its inshore boundary as a consequence of the Mid-Atlantic warming that has produced the surfclam invasive front (NEFSC, 2017b), but ocean quahogs have the ability to estivate during the warmer months, something not available to *M. modiolus* or *M. edulis*. No large *M. modiolus* were collected on the survey suggesting that the region is too warm now for this species, as might also be inferred from the presence of surfclams at these depths. Certainly evidence from this survey suggests that community dynamics in the 10.5–27 m depth range are in flux off Nantucket, west of the Great South Channel.

4.4 | Transient multiple stable states—do they exist?

Multiple stable states often refer to cases where biological influences alone limit simultaneous occupation of several species in a common habitat, although the inclusion of mediating environmental constraints and external influences in promoting faunal shifts within the concept of stable states has been variously included or debated (Choi, Frank, Leggett, & Drinkwater, 2004; Coco et al., 2006; Gray, 1977; Peterson, 1984; Sousa & Connell, 1985). The concept of multiple stable states is confounded by regime shifts generating shifts in species range and the transient intermingling of faunas (Carpenter et al., 2011; Collie, Richardson, & Steele, 2004; Hughes, Linares, Dakos, van de Leemput, & van Nes, 2013). During these transitions, multiple stable states may occur through the interaction of species that normally might have limited contact.

Although the distribution of newly colonized surfclam beds and mussel beds is visually distinctive, neither was obviously associated with locations where cobbles, rocks and boulders were common, these sedimentary constituents being one of the few potentially important habitat discriminators at mid-depths in the surveyed region. As might be expected, correspondence analysis only partially distinguished regions characterized by high concentrations of cobbles, rocks, or boulders from regions with high numbers of mussels or small-to-medium-size surfclams, nor did correspondence analysis readily distinguish the two species as they all fell within the same depth zone, yet correlations were mostly non-significant. The apparent indiscriminate distribution of large sedimentary particles relative to the two community types is consistent with the lack of dependency upon either on these sedimentary constituents and the likelihood that many cobbles, rocks, and boulders were actually buried. Of more interest is the failure of correspondence analysis to clearly identify the origin of the dichotomous nature of the two primary community types at mid-depths in the surveyed region, although the two were modestly separated along the x-axis. One possibility is that these two communities represent multiple stable states (see Gray, 1977; Peterson, 1984; Knowlton, 1992) within the same thermal, depth, and hydrodynamic range.

While speculative, a mussel mat might be expected to prevent settlement of surfclams, thereby excluding them (see a case for razor clams: van der Heide et al., 2014). Certainly, once established, mussel beds can maintain themselves by facilitating their own recruitment (Commito et al., 2014; Saraiva, Fernandes, van der Meer, Neves, & Kooijman, 2017). Thus, once established, mussel beds would tend to be self-perpetuating and exclusionary of infaunal filter-feeding bivalves. Salas et al. (2016), wa Kangeri et al. (2014), and wa Kangeri Jansen Joppe and Dankers (2016) note that mussel beds on soft sediments are constructed to resist erosion, a product of byssal thread interweaving and the incorporation of shell fragments, pebbles, and other small sedimentary constituents. High current velocities can resuspend and move mussel beds (wa Kangeri, Jansen, Joppe, & Dankers, 2016): Current velocities in the surveyed region reach such velocities (Dalyander, Butman, Sherwood, Signell, & Wilkin, 2013; Harris, Cowles, & Stokesbury, 2012) and so one might anticipate that mussel beds are more or less mobile over time. The dynamics of this process are not studied in the surveyed region; however, *Mytilus* can survive shallow burial and return to the sediment surface (Hutchison et al., 2016), thus providing two mechanisms (mat transport and exhumation) to recover from hydrodynamic events. Regardless, a mussel mat might be expected to prevent surfclam settlement and smother any surfclams that by happenstance were overtopped by a saltated mussel mat.

What might control the exclusion of mussels by surfclams is more difficult to rationalize. The differential spatial distribution may simply be a result of amensalism whereby mussel beds limit surfclam recruitment and the limited capacity of mussel beds to expand laterally over the time scale of surfclam recruitment and growth. On the other hand, active filtration and sediment disturbance by surfclams might limit initial mussel settlement, thereby establishing the competing multiple stable state. Infaunal filter-feeding bivalves affect the bottom boundary layer (Jones, Pilditch, Bryan, & Hamilton, 2011) and bivalve species have been shown to compete for food and space (e.g., Peterson & Andre, 1980; Freitas et al., 2009). Surfclam mobility may also physically disrupt the surface sediment, increasing porosity and ease of resuspension (for analogy, see Myers, 1977; Meadows & Meadows, 1991; Gutiérrez & Iribarne, 1999; Nikora, Green, Thrush, Hume, & Goring, 2002). As erosion of forming mussel beds increases when surface coverage is limited (Widdows, Lucas, Brinsley, Salkeld, & Staff, 2002), increasing ease of resuspension may limit mussel mat development.

Regardless of the explanation, overlap of surfclams and mussels is minimal in a region where both exist. The interaction of species thrown together by climate change, transiently as ranges shift at differing rates, is little understood. The Atlantic surfclam and the ocean quahog co-occur over an extensive boundary as surfclams invade ocean quahog habitat (Powell et al., 2019). What interaction occurs remains unknown, but both species are routinely found together along the invasion front, indicating that competitive exclusion is not occurring, at least on a time scale amenable to survey monitoring. The opposite seems to be a safe inference for the invasion of surfclams into habitat occupied by mussels, wherein the two species overlap little in space while occupying the same edaphic regime. Although the dynamics of species' invasions, by introduction or a shift in species' range are well considered (e.g., Holt, Keitt, Lewis, Maurer, & Taper, 2005; Oborny, Vukov, Csányi, & Mezzéna, 2009; Rawson & Harper, 2009; Karatayev, Burlakova, Mastitsky, & Padilla, 2011), the interaction with the extant species are much less studied (Troost, 2010; With, 2002) and the outcome with respect to the transient distribution of species meeting along an invasion front may dictate the spatial and temporal rate of progression of a species' range. During such times, transient multiple stable states may play an important role in structuring the advancing and receding communities along the interacting range boundaries.

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DATA AVAILABILITY

The data supporting this analysis are provided as supplementary material.

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