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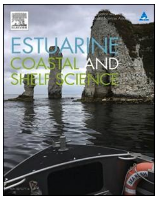

The conundrum of biont-free substrates on a high-energy continental shelf: Burial and scour on Nantucket Shoals, Great South Channel

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ABSTRACT

A survey of the adjacent waters east of Nantucket, Massachusetts provided an opportunity to evaluate the epibiota attached to cobbles, rocks, boulders, and Atlantic surfclam shell in a region of high tidal current velocity and sand scour where burial, exhumation, and scour may limit epibiont coverage on exposed, and thus otherwise highly preferred for attachment, substrates. Such conditions may confute the expectation that substrate complexity always adds significantly to ecosystem value by expanding the range of habitat options and consequently increasing species richness and trophic linkages. Sedimentary particles potentially providing good attachment substrate for erect sessile epibiota included surfclam shells, abundant at many locations, cobbles, nearly ubiquitous, rocks, routinely encountered, and occasional boulders. The attached epibiota fell into three categories based on their biases for particle types. Some preferred the largest particles or evidence of their occupation was best preserved on these particles: these included sponges, mussels, and barnacles and their scars. Some preferred intermediate and smaller terrigenous particles; these included tunicates and encrusting bryozoans. Some preferred surfclam shells, namely the slipper shells and erect hydroids. Slow-growing attached epibionts were exceedingly rare and all soft-bodied attached epibionts were rare. Only barnacles and their taphonomic scars and hydroids were common. The frequency of barnacle scars relative to intact barnacles suggests sediment scour under a high-flow regime. Mussels were rarely attached to larger sedimentary particles such as cobbles and rocks, though commonly occurring locally as mussel beds on sand and pebble, further supporting the ephemerality of exposed unscoured attachment sites. The absence of attached epibionts demonstrates that edaphic processes minimize the importance of cobbles, rocks, boulders, and shells in community structure in some subtidal high-energy regimes, defying expectations from their contribution to substrate complexity. Their apparent contribution to habitat complexity belies their resultant much more minor role in determining community composition, thereby limiting their ecosystem value.

1. Introduction

The Great South Channel and adjacent waters east of Nantucket, Massachusetts, is a region of high tidal current velocities, characterized by half-decameter-scale sand dunes and a cobble, rock, and boulder-rich sediment consequent of the presence of a terminal moraine from the last ice age (Emery and Uchupi, 1965; Trumbull, 1972; Twichell, 1983; Mann et al., 1981). The area is highly productive. Atlantic surfclams (*Spisula solidissima*), a species of interest in this study, grow to a size larger here than over the remainder of the species' range (Powell et al., 2020). Regions on the continental shelf of the type exemplified by the Great South Channel, characterized by high current velocities, sand dunes with amplitudes of many meters, and mobile sand-rich sediments with admixtures of larger grain sizes derived from the continental glaciers that receded at the end of the Pleistocene are relatively rare in the world's oceans. They are, however, not infrequent in localized regions of northern hemisphere boreal and subarctic waters (Bøe et al., 2009, 2015; Barrie et al., 2009; Bellec et al., 2010).

Substrate complexity is expected to add significantly to ecosystem value by expanding the range of habitat options and consequently increasing species richness and trophic linkages. The combination of rocks, cobbles, and boulders derived from glacial till, immersed in a sea of moving sand and prograding dunes, may however provide an unexpectedly rigorous habitat for benthos that normally should be

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advantaged by the availability of hard bottom for colonization and increased habitat complexity supporting increased species richness. Though the hydrodynamics and sedimentology of these high-current-velocity environments are well-studied, the epibiotic community of these rigorous habitats remains poorly known.

Off the Island of Nantucket, a portion of such a region has been designated as a Habitat Management Area (the Great South Channel HMA) due to the complex habitat rendered by the coarse substrates left by ice-age glaciation (Powell et al., 2019). The potential closure of an important fishing ground for Atlantic surfclam, *Spisula solidissima*, led to a survey of the region eastward of Nantucket to the Great South Channel (Powell et al., 2019, 2020). The survey provided an opportunity to evaluate the epibiota of the hard-substrate constituents in a region of prograding sand dunes, high tidal current velocities and sand scour on the continental shelf and to address the expectation that substrate complexity is a routinely useful surrogate for ecosystem value and thus a useful tool for identifying critical habitats on the continental shelf for ecosystem management.

The distribution of skeletal epibionts and their traces offer potential in the interpretation of paleo-communities (Nebelsick et al., 1997; Walker, 1998; Rodland et al., 2006; Brett et al., 2011; Peryt et al., 2012; Smrecak and Brett, 2014). Much attention has been given to epibiont communities on skeletal material such as bivalve shells (Black and Peterson, 1987; Lescinsky, 1993; Zuschin and Baal, 2007; Smyth and Roberts, 2010; Schejter et al., 2011), leading to the important concept of taphonomic feedback (Kidwell, 1986). Much less attention has been directed towards abiotic terrigenous and carbonate substrates with the exception of rocky shores (Daly and Mathieson, 1977; Littler et al., 1983; D'Antiono, 1986) and carbonate hardgrounds (Zuschin and Pervesler, 1996a, 1996b; Gherardi and Bosence, 1999; Brett et al., 2011). Among the more unique applications are ship wrecks (Hageman, 2001) and ghost fishing gear (Saldanha et al., 2003). Much attention has been paid to quiet water habitats wherein the rate of burial is a prime controller of epibiont coverage (Conover, 1975; Parsons-Hubbard et al., 1999; Gordillo and Aitken, 2000; Powell et al., 2011a; Brett et al., 2011) and in which taphonomic degradation of skeletal epibionts follows standard taphonomic outcomes based on the relationship of burial rate and the rigors of the taphonomically-active zone (TAZ; Davies et al., 1989). Receiving much less attention are high energy subtidal regimes where burial, exhumation, and sediment scour may limit epibiont coverage on exposed, and thus otherwise highly preferred for attachment, substrates. Identifying such conditions is critical for constraining the use of epibiont coverage in paleocommunity reconstruction, while also imposing caution on the assumed importance of substrate complexity in determining present-day community structure and in application to ecosystem management. Herein is examined the degree of epibiont coverage in a classic high-energy case of a substrate-rich environment on the continental shelf exposed chronically to burial, exhumation, and sediment scour. Inquiry focuses on the importance of substrate complexity as it influences community structure under these conditions.

2. Methods

2.1. Survey location and design

The survey took place in early August 2017. The survey domain is shown in Fig. 1. Three regions are demarcated for easy reference in a series of faunal maps that follow. The first, located on the eastern portion of the maps at the upper left, is a region historically supporting significant landings of Atlantic surfclams. The surfclam supports a major fishery on the continental shelf of the U.S. Mid-Atlantic coast (NEFSC, 2017). Note that the western boundary approximates the inshore boundary of the U.S. exclusive economic zone (EEZ) and that the southern boundary abuts on the lower left the Nantucket Lightship Habitat Closure Area. The larger region located in the center and to the right is the Great South Channel Habitat Management Area much of which was closed in 2019 to bottom-tending fishing gear otherwise expected to damage the complex habitat and susceptible epibiota presumed to co-occur as a consequence of substrate complexity in the HMA.

A fixed grid design was chosen for the survey to insure that the region was evenly and densely sampled. 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 et al., 2008; HSRL, 2012; Powell et al., 2017a). A hub-and-spoke fixed grid design was implemented with spokes of 3-nm (5.56-km) length (Fig. 1). Six of the 63 stations (9.5%) were repositioned within 1NM of the designated position. Stations were moved for three reasons: (1) some fell just inshore of the EEZ inshore boundary and were moved offshore across the boundary line; (2) some stations fell just inside the Nantucket Lightship Habitat Closure Area and were moved just north of that closure line; and (3) some stations fell on untowable bottom, always locations too shallow for the vessel to safely tow, and were moved laterally into deeper water.

2.2. Survey towing and on-deck processing protocol

The survey vessel was the *F/V Mariette*, homeport New Bedford, Massachusetts. This vessel fishes routinely in the area. The dredge was a 99-in (2.51-m) hydraulic dredge (for a description of this type of gear, see Lambert and Goudreau, 1996). Bar spacing was 1.875″ (4.76 cm) 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), that represent the dominant contributor of sedimentary skeletal material in the surveyed region (Powell et al., 2020), with selectivity steadily declining at smaller sizes. Only large whole surfclam shell or major fragments (Davies et al., 1990) of large surfclam shells were retained, as small fragments, very likely plentiful, were narrower than the dredge bar spacing. Round or oblate particles such as cobbles should be nearly 100% selected if larger in diameter than the 1.75″ bar spacing. 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.[1]

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 decreased tow time in a few cases. Total swept area averaged about 1250 m^2. The entire catch was sorted including all live surfclams, cobbles, rocks, boulders, associated invertebrates, and shell. All free-living invertebrates, except mussels, were tallied. Bushel volumes were recorded for mussels, cobbles, rocks, and boulders rather than counts. To limit processing time, invertebrates were identified to higher taxon (e.g., anemone, tunicate, sponge). In some cases (e.g., tunicates), these categories included a number of different species. Only common taxa are included in this report. A full dataset is available as supplementary material to Powell et al. (2019). All biota and sediment particles were standardized to per m^2 catch except attached bionts that were placed into a semiquantitative scale (viz., 0 = absent, 1 = present, 2 = predominant; where predominant refers to a taxon with considerably more coverage than other taxa within the sample as judged by visual inspection).

Ten haphazardly chosen each of cobbles (2–6″) (5.1–15.2 cm), rocks (6–12″) (15.2–30.5 cm), boulders (>12″), and surfclam shells were photographed, if ≥ 10 where present; otherwise all were photographed. Photos were biased towards the side of the particle with the largest coverage of attached bionts, if any were present. Photographs were analyzed in terms of percentages (e.g., percent of photographs with hydroids). The photographic analysis is biased against stations with

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[1] Throughout, vessel gear characteristics will be specified in inches, in conformance with standards used in the fishing industry. Sediment particle definitions that follow likewise will be specified in inches in conformance with definitions used by the National Marine Fisheries Service.

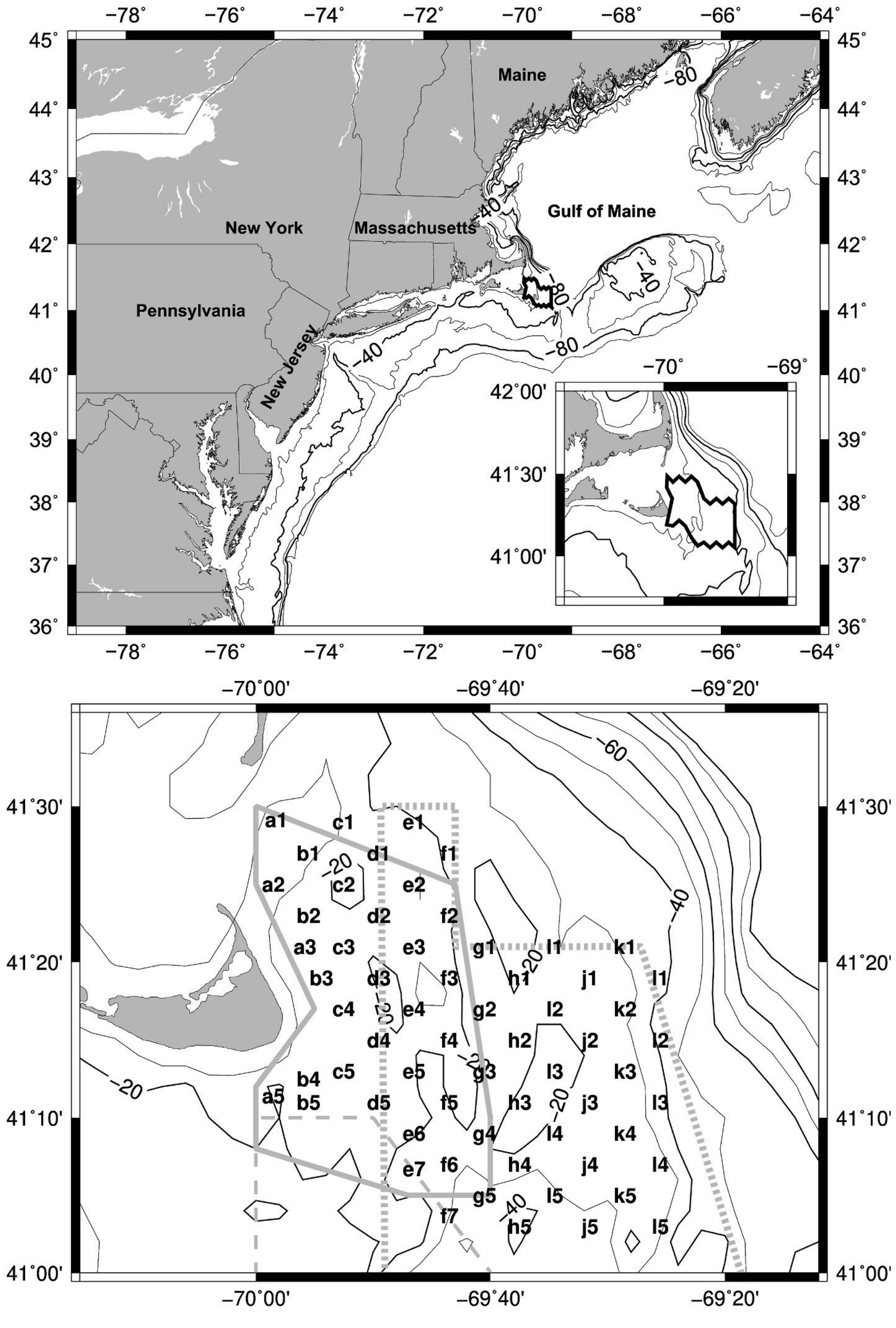

Fig. 1. Top, location of survey outlined by a solid black line just off Massachusetts just east of Nantucket. Bottom, close up of the survey design. Gray solid line outlines the sector historically contributing most of the Atlantic surfclam landings in the surveyed region. Gray dashed line outlines the northern portion of the Nantucket Lightship Habitat Closure Area. Gray dotted line outlines the upper half of the Great South Channel Habitat Management Area. Letters and numbers are station designations for the 63 stations in the survey. Depths are in meters.

large catches in that 10 photographs from those stations were usually a small subsample of the entire catch. However, standardizing to catch would have provided metrics dominated by a few stations and thus not be representative of the surveyed region. The photographic analysis is also biased against stations with low catches in that these stations provided fewer than 10 photographs of one or more sedimentary particle type. No standardization for under-representativeness is included. Chi-square was used for statistical analysis standardized to numbers per hundred. The limited number of boulders encountered resulted in chi-square tests incorporating this particle size failing standard cell number requirements for chi-square in some cases. These analyses are nevertheless included: *caveat lector*.

Figures that follow generally 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 surfclam shell and cobbles (Fig. 2), differential circle sizes for surfclam shell show differences in catch of surfclam shell between stations; ditto for cobbles. However, no valid quantitative comparison can be made between the circle sizes for the catch of surfclam shell and the catch of cobbles.

3. Results

3.1. Distribution of Atlantic surfclam shell

Rocks, cobbles, and boulders are relatively permanent components of the sedimentary environment. As the dredge was constructed to minimize the capture of most particles <120 mm, most shell recovered and all large shell recovered was whole shells and major shell fragments of the Atlantic surfclam, *Spisula solidissima*. The survey also encountered

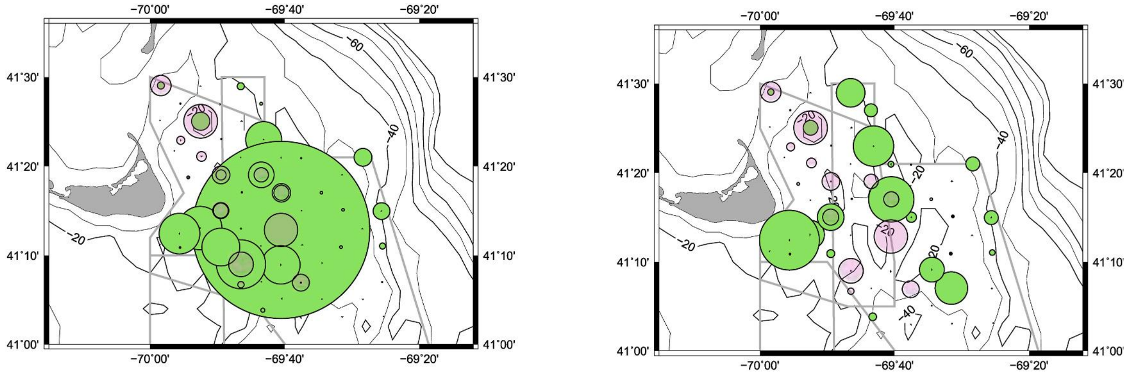

Fig. 2. Left, catch of cobbles (green) and surfclam shell (purple). Right, catch of rocks (green) and surfclam shell (purple). Variations in green and purple shading accrue from circle overlap. Circle diameters are linearly proportional to bu m^{-2} within category only. Abundance comparisons cannot be made across categories. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

shells of a number of small clams (e.g., *Astarte, Pitar*), that are poorly caught by the survey gear and thus not reported here. Bivalve shell enters into the taphonomic process after death. Stated simply, various degradative processes such as dissolution, abrasion, and bioerosion operate to destroy the shell (Staff et al., 1986; Powell et al., 1989; Davies et al., 1990) while it is at the surface or in the surficial sediments within the TAZ. Burial, on the other hand, removes shell from the TAZ, thereby preserving it for an extended period of time if not indefinitely (Powell, 1992; Tomašových et al., 2006; Powell et al., 2012). The robustness to taphonomic degradation of surfclam shell is unknown, but shells of similar clam species tend to be robust (Callender et al., 1994; Walker and Goldstein, 1999; Powell et al., 2011b,c). Thus, surfclam shell should remain intact for many decades after death (Powell et al., 2017b) and therefore should be a relatively permanent contributor to the complexity of the sedimentary environment. Herein, surfclam shells are treated equivalently with the larger terrigenous components of the substrate.

In the surveyed region, surfclam shell was generally encountered in the northwestern corner and then on a southeastward trend through the region historically supporting the surfclam fishery, thence through the eastern and central HMA, the central region being relatively newly colonized by surfclams (Powell et al., 2020) consequent of post-2000 warming of the bottom water along the Great South Channel (Pershing et al., 2015) (Fig. 2). Catches generally coincided with locations where surfclams >150 mm were most common (Powell et al., 2019), as would be anticipated by their source and high probability of preservation.

3.2. Distribution of cobbles, rocks, and boulders

Cobbles, rocks, and boulders are routinely encountered on the neighboring Georges Bank in regions occupied by surfclams (Powell et al. 2017b, 2019). Surfclams, however, are sand denizens and, presumably, do not require or benefit from the presence of such sedimentary components in their habitat. Cobbles, defined as particles 2–6″ in diameter, were commonly encountered at many sites in the surveyed region (Fig. 2), but were most common at intermediate depths in the west-central portion of the HMA and southeast of Nantucket. See Powell et al. (2019) for depth dependencies of the biota and sedimentary particles in the surveyed region. Although surfclam shell routinely co-occurred with cobbles, cobbles frequently did not co-occur with surfclam shell (Fig. 2).

Rocks, sediment particles 6–12″ in diameter, were 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 rarely common in locations where surfclam shell was abundant, however. Rocks were most common in the north and central portions of the HMA and southeast of Nantucket (Fig. 2).

Boulders, sediment particles >12″ in diameter, were sporadically and uncommonly encountered on the survey, but were more likely to be encountered at sites where rocks were common (Fig. 3). This too is consistent with the glacial origin of both.

3.3. Distribution of mussels

Mussels were abundant at a few sites. When abundant, they occurred in dense mats attached to pebbles and sand grains, which counterweighed their tendency towards saltation. Mats normally were a mixture of *Modiolus modiolus* and a *Mytilus* species or just *Mytilus*. 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 and Harper, 2009), with mussels collected south of central Maine on the East coast more likely to be *Mytilus edulis* as *M. edulis* is the predominant species from central Maine south (Hilbish et al., 2000; Rawson et al., 2001) to Cape Hatteras (Wells and Gray, 1960). No attempt was made to determine the species composition of the mytilids on this survey, however no large *Modiolus* were collected, consistent with the warming of the study region since 2000 with bottom water temperatures likely too high for long-term survival of this boreal species.

Highest mussel catches occurred in the northwestern portion of the HMA, with a single exception of one site in the south-central portion of the HMA (Fig. 4). The distribution of mussels along the northeast coast of the U. S. in the intertidal is noteworthy for being associated with rocky shores or manmade structures (Lauenstein et al., 1997; Cockrell et al., 2015), although they commonly occur in intertidal mats along the western European coast (Beukema and Cadée, 1996; Widdows et al., 2002; Diederich, 2006) and in the Bay of Fundy (Wildish et al., 2009). 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 (Fig. 4). Surprisingly, the mussels were rarely abundant at sites where cobbles, rocks, or boulders were common (Figs. 4 and 5), even though all four were frequently encountered in the same depth range. Thus, mussel beds did not depend on large sedimentary particles for their presence or integrity; rather, their cohesion was based on interwoven byssal threads, pebbles, and sand grains, as is typical of mussel beds on soft sediments (Wildish et al., 2009; Salas et al., 2016; wa Kangeri et al., 2014, 2016).

Although the vast majority of mussels occupied interwoven byssal mats, a few were found attached to shells, cobbles, and rocks. The percentage of such particles bearing attached mussels was low (Table 1, Fig. 5). Mussel coverage differed significantly among substrate types (Table 2). Attached mussels were somewhat more common on boulders, although by no means ubiquitous (Table 1) and significantly more

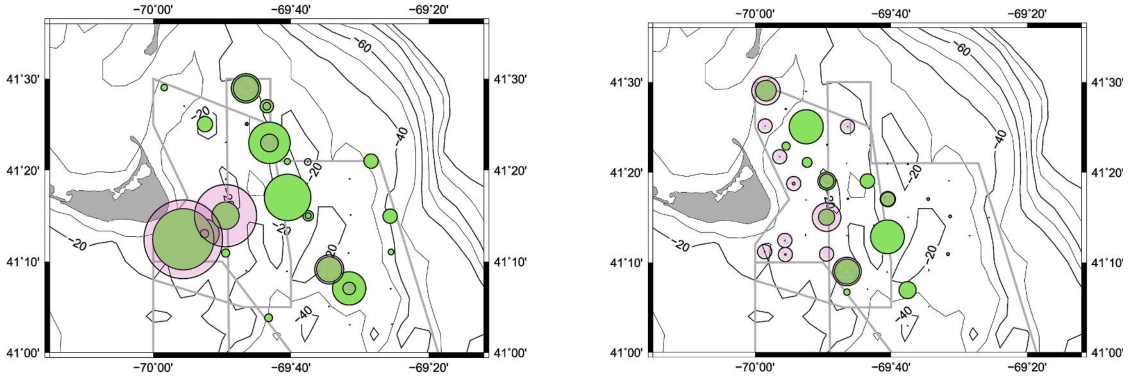

Fig. 3. Left, catch of rocks (green) and boulders (purple). Right, catch of surfclam shell (green) and slipper shells (purple). Variations in green and purple shading accrue from circle overlap. Circle diameters are linearly proportional to bu m^{-2} for surfclam shell and 1 = present and 2 = abundant for slipper shells. Abundance comparisons cannot be made across categories. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

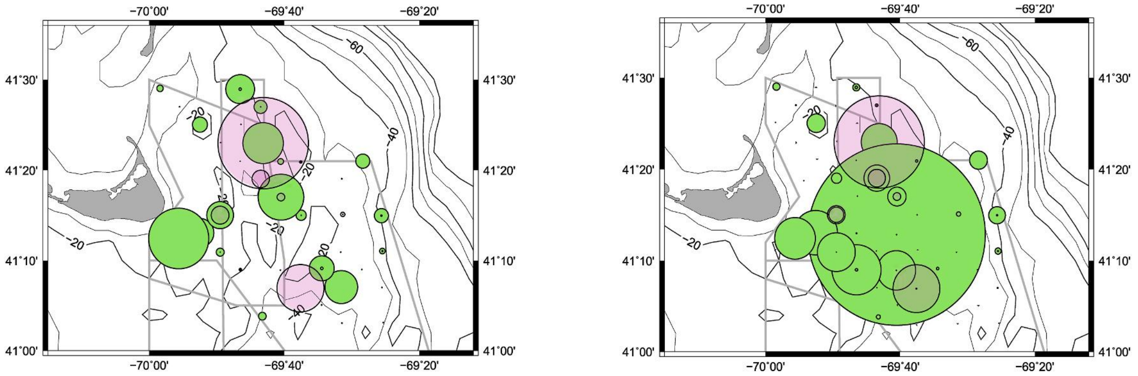

Fig. 4. Left, catch of rocks (green) and mussels (purple). Variations in green and purple shading accrue from circle overlap. Right, catch of cobbles (green) and mussels (purple). Circle diameters are linearly proportional to bu m^{-2}. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

common than on rocks, cobbles, and shells (Table 2), presumably due to the increased stability of boulders and their higher vertical extent above the sea floor. Mussels were also significantly more frequently attached to rocks than cobbles or shells (Table 2), but no more common on shells than on cobbles; however, mussels were never present in quantity on any of the four substrate types.

3.4. *Distribution of attached epibenthos*

Evaluation was made of large attached epibenthos on cobbles, rocks, boulders, and surfclam shell. No record was made of the occurrences of small encrusting organisms such as spirorbids, serpulids, and foraminifera; such small epibionts are frequent rapid colonizers of newly exposed substrate (Haderlie, 1969; Brett et al., 2011), but too small to be consistently identified under the conditions of this survey. Cobbles, rocks, boulders, and surfclam shell were most commonly free of the recorded suite of attached epibionts (Fig. 6), with the exception of barnacles and their scars (Table 1).

The most common and ubiquitous large epibiont was the barnacle. Barnacles were observed encrusting cobbles, rocks, boulders, and surfclam shells at almost every site where these particles were present (Fig. 7, Table 1), however barnacles and scars (the basal plate or attachment mark made by the basal plate) were equivalently distributed among these substrate types (Table 2). Barnacles and barnacle scars were least common on surfclam shells and most common on boulders, with frequency incrementing with particle size, consistent with an anticipated increasing likelihood of exposure of the particle above the sediment-water interface and immobility of the particle while exposed (Table 1, Fig. 8). This trend was significant, with the exception of cobbles and shells which, once again, did not differ significantly in coverage (Table 2).

Barnacles are common fouling organisms, widely reported present-day and in the fossil record (e.g., Haderlie, 1969, 1971; Scanland, 1979; Zuschin and Pervesler, 1996b; Parras and Casdío, 2005; Nielson and Funder, 2003; Schneider-Storz et al., 2008). The overwhelming majority of barnacle occurrences in this survey were in the form of barnacle scars rather than intact barnacles (Table 1). Barnacle fragments and scars are very likely commonplace on hard substrate, but are very rarely reported (Brett et al., 2011; see Aguirre et al., 2008 for a fossil example). Attached barnacles occurred with about equal frequency among the particle types (Table 1, Fig. 8), whereas barnacle scars occurred with increasing frequency with increasing particle size. The inference from the limited reporting of barnacle scars in the fossil record and limited evidence from recent studies (Brett et al., 2011; Powell et al., 2011a) is that these taphonomic remains rapidly degrade; thus implying near-term abrasive processes limiting survival of living barnacles and

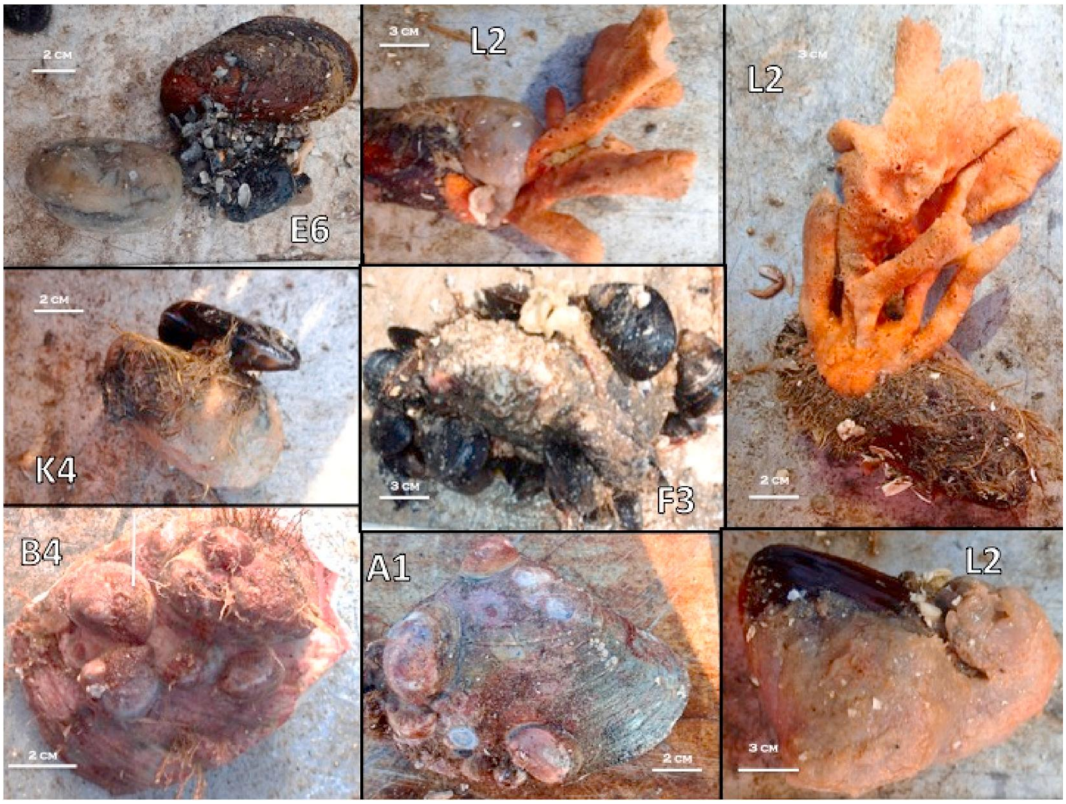

Fig. 5. Example surfclam shells, cobbles, rocks, and boulders with attached mussels, slipper shells, and sponges. Letter-number designations refer to sample sites as delineated in Fig. 1.

Table 1
Frequency of occurrence of mussels and barnacles and barnacle scars on shells, cobbles, rocks, and boulders. Frequencies are defined within column; between column comparisons are invalid. Note that photographic analyses are not normalized to substrate catch volume or by station: numbers are raw estimates based on the number of photographs taken. Note that substrate photographs emphasize the side with the most attached epibionts.

	PhotographsExamined	Percent with Attached Mussels	Percent with EncrustingBarnacles or Scars	Percent with EncrustingBarnacles	Percent with EncrustingBarnacle Scars
Shells	290	7.2%	56.9%	30.0%	51.4%
Cobbles	445	5.4%	61.8%	22.7%	59.6%
Rocks	140	13.6%	74.3%	28.6%	73.6%
Boulders	26	30.8%	80.8%	26.9%	76.9%
Total	901				

Table 2
Results of chi-square tests across all substrates and between designated substrate pairs. The comparison examines the differential distribution of substrates with and without each biont type. Percentage compositions are provided in Tables 1, 3 and 4. The category of erect hydroids includes erect hydroids and erect bryozoans which were not distinguished. -, no significant at $\alpha = 0.05$.

	Barnacles	Mussels	Tunicates	Encrusting Bryozoans	Erect Hydroids/
All Substrates	$P = 0.0011$	$P < 0.0001$	–	$P < 0.0001$	$P < 0.0001$
Boulder-Rock	–	$P = 0.029$	–	$P = 0.05$	$P = 0.05$
Boulder-Cobble	$P = 0.05$	$P < 0.0001$	–	$P = 0.04$	–
Boulder-Shell	$P = 0.018$	$P < 0.0001$	–	–	$P = 0.0026$
Rock-Cobble	$P = 0.007$	$P = 0.0012$	–	–	$P = 0.039$
Rock-Shell	$P = 0.0005$	$P = 0.034$	–	$P < 0.0001$	$P = 0.037$
Cobble-Shell	–	–	$P = 0.01$	$P < 0.0001$	$P < 0.0001$

preservation of their tests after death. One cannot exclude, however, that these scars record the longer-term colonization of sedimentary particles exposed and buried many times since the end of Pleistocene glaciation.

Sponges, anemones, and tunicates were rarely encountered. These attached epibionts were most often encountered in the north and northeastern sectors of the HMA (Fig. 9). Attachment to surfclam shells occurred less frequently than attachment to sedimentary particles (Figs. 5 and 9, Table 3), but these epibionts were exceedingly rare in comparison to barnacles and barnacle scars. Importantly, these epibionts do not leave long-lasting traces when detached or eroded off. The occurrence rate of whole barnacles was higher, but only about three

Fig. 6. Example surfclam shells, cobbles, rocks, and boulders free of attached epibionts. Letter-number designations refer to sample sites as delineated in Fig. 1.

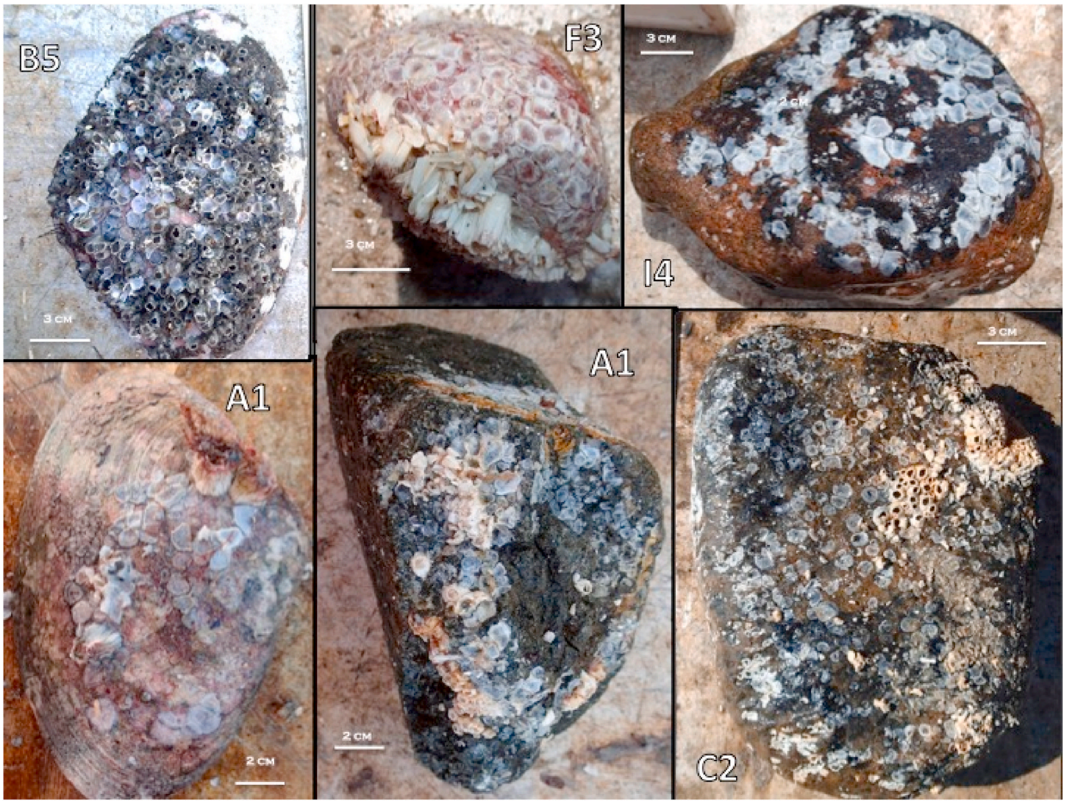

Fig. 7. Photographs of representative surfclam shell, cobbles, rocks, and boulders with barnacles and barnacle scars. Letter-number designations refer to sample sites as delineated in Fig. 1.

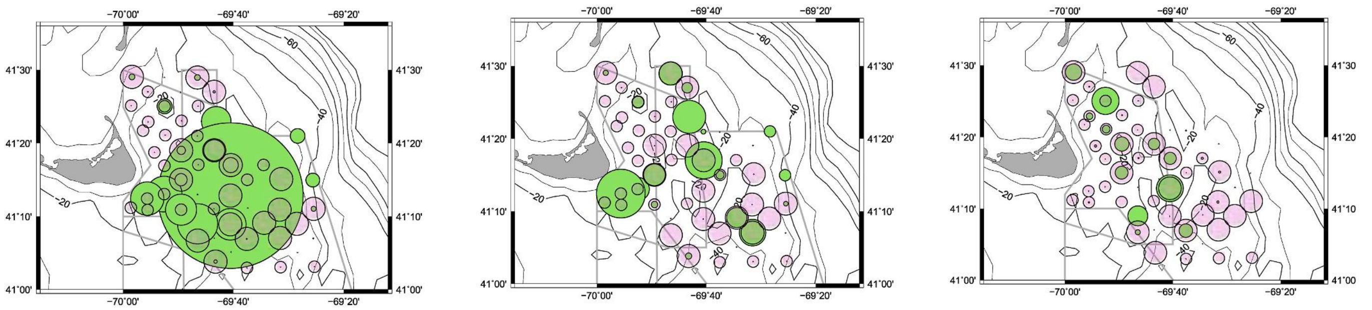

Fig. 8. Left, catch of cobbles (green) and barnacles and barnacle scars (purple). Middle, catch of rocks (green) and barnacles and barnacle scars (purple). Right, catch of surfclam shell (green) and barnacles and barnacle scars (purple). Circle diameters are linearly proportional to bu m^{-2} for cobbles, rocks, and surfclam shell. Circle values for barnacles are 1 = present and 2 = abundant. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

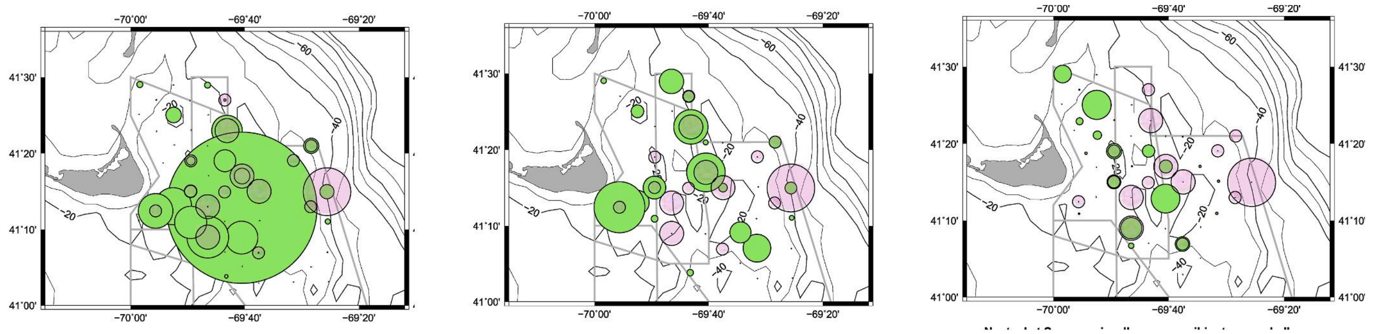

Fig. 9. Left, catch of cobbles (green) and miscellaneous epibionts (purple). Middle, catch of rocks (green) and miscellaneous epibionts (purple). Right, catch of surfclam shell (green) and miscellaneous epibionts (purple). Circle diameters are linearly proportional to bu m^{-2} for cobbles, rocks, and surfclam shell. Circle values for miscellaneous epibionts are the sum of individual values of 1 = present and 2 = abundant for tunicates, anemones, and sponges. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Frequency of occurrence of tunicates, anemones, and sponges on shells, cobbles, rocks, and boulders. Frequencies are defined within column; between column comparisons are invalid. Note that photographic analyses are not normalized to substrate catch volume or by station: numbers are raw estimates based on the number of photographs taken. Note that substrate photographs emphasize the side with the most attached epibionts.

	Photographs Examined	Percent with Tunicates + Anemones + Sponges	Percent with Tunicates	Percent with Anemones + Sponges
Shells	290	4.8%	4.8%	0.0%
Cobbles	445	11.2%	10.1%	1.3%
Rocks	140	8.6%	7.9%	1.4%
Boulders	26	7.7%	3.8%	3.8%
Total	901			

times as high in comparison to the factor of 10 difference for barnacle scars. Thus, the impact of taphonomy was recorded for the barnacles, but not for the other epibionts.

Nearly all occurrences of anemones, tunicates, and sponges were provided by the tunicates (Table 3). Sponges and anemones were exceedingly rare. Their rarity is consistent with an analysis for a neighboring region on Georges Bank and also the southern part of the Great South Channel HMA south of the surveyed region (Powell et al., 2017a). Tunicates were unevenly distributed among the substrate types (Table 2). They were least often encountered on boulders and surfclam shells and most often encountered on rocks and cobbles (Tables 2 and 3). Rocks and cobbles did not differ significantly in the frequency of tunicate occurrence (Table 2), although, often, though not always, encrusting tunicates displayed high coverage on the sedimentary particles on which they were found. Sponges and anemones were never encountered on surfclam shells and were distinctly more frequent, though still very rare, on boulders, suggesting that the larger sediment particles provided some degree of temporal stability above the sediment-water interface allowing these slower growing epibionts to populate.

In contrast to the tunicates, sponges, and anemones, the attached hydroids[2] were considerably differentially distributed (Fig. 10). Hydroids were commonly encountered at many sites. Many such sites were locations yielding surfclam shell (Fig. 9). Hydroids, though found attached to cobbles, rocks, and boulders, were distinctly differentially distributed from these sedimentary particles. Distribution was uneven in its occurrence among substrate types, with the occurrence rate on shells being significantly higher than other substrate types (Table 2), emphasizing the importance of surfclam shell for this epibiont (Figs. 10 and 11). Photographic analysis confirmed the ubiquity of hydroids as attached epibionts (Fig. 11, Table 4), though less common than barnacles and barnacle scars (Table 1).

Encrusting bryozoans and bryozoan remnants were encountered with some frequency on rocks and cobbles and with much lower frequency on shells and boulders (Table 4). Distribution was uneven in its occurrence among substrate types, with the occurrence rate on shells being significantly lower than on rocks and cobbles, which themselves

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[2] Erect bryozoans and hydroids could not be differentiated during the survey. Most organisms encountered were likely hydroids, but confirmation is lacking; nonetheless, for brevity, this type of epibiont will be referred to as "hydroid" throughout this report.

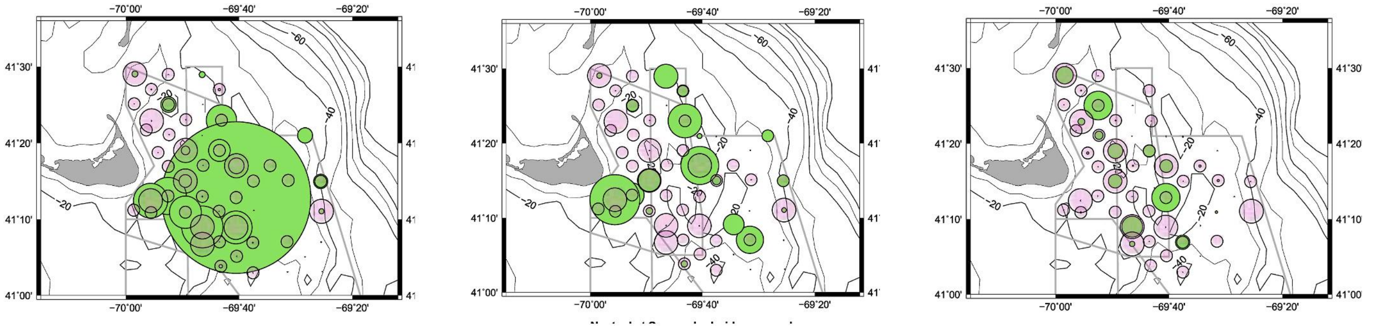

Fig. 10. Left, catch of cobbles (green) and hydroids (purple). Middle, catch of rocks (green) and hydroids (purple). Right, catch of surfclam shell (green) and hydroids (purple). Circle diameters are linearly proportional to bu m^{-2} for cobbles, rocks, and surfclam shell. Circle values for hydroids are 1 = present and 2 = abundant. Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 11. Representative hydroids attached to a surfclam shell and a cobble. Note that hydroids and erect bryozoans were not discriminated; thus reference here and elsewhere to 'hydroid' should not be interpreted as a definitive identification.

Table 4
Frequency of occurrence of slipper shells, encrusting bryozoans and their remnants, and encrusting hydroids on shells, cobbles, rocks, and boulders. The category of erect hydroids includes erect hydroids and erect bryozoans which were not distinguished. Frequencies are defined within column; between column comparisons are invalid. Note that photographic analyses are not normalized to substrate catch volume or by station: numbers are raw estimates based on the number of photographs taken. Note that substrate photographs emphasize the side with the most attached epibionts.

	Photographs Examined	Percent with Slipper Shells	Percent with Encrusting Bryozoans and Remnants	Percent with Erect Hydroids
Shells	290	1.7%	13.4%	50.0%
Cobbles	445	0.2%	30.3%	29.9%
Rocks	140	0.0%	30.0%	39.3%
Boulders	26	0.0%	11.5%	19.2%
Total	901			

did not differ (Table 2), Encrusting bryozoans were not distinguished from their remnants. Like the barnacle scars, the presumption that bryozoan remnants document recent occupation is assumed. Slipper shells (*Crepidula* sp.) were uncommon, but more frequently encountered on shells than on other substrates (Table 4, Fig. 5), and most common inshore of the region supporting mussel beds (Fig. 3). The preference of slipper shells for large surfclam shells, found in highest concentrations inshore, was striking.

3.5. *Distribution of epibionts across substrate types*

Epibionts were not distributed randomly among substrate types (Table 5). Some part of this bias accrued from a differential distribution of particle type by depth; however, rocks, cobbles, boulders, and shell were widely distributed across the depth range and thus available for colonization in most depths (Powell et al., 2019). Barnacles and their scars and mussels occurred significantly more commonly on boulders than the other epibiont taxa (Table 5). Barnacles and their scars were significantly more commonly encountered on rocks than other epibiont taxa (Table 5); tunicates and mussels were significantly less common. The same pattern existed for cobbles. Surfclam shells evinced a relatively unique pattern in the significantly higher incidence of erect hydroids, a similar incidence with the occurrence of barnacles and their scars, relative to the remaining epibiont taxa (Table 5). Whether this is a depth or substrate preference is unclear as surfclam shells were more common at shallower depths, as were the erect hydroids.

Table 5

Results of chi-square tests across all epibionts and between designated epibiont pairs. The comparison examines the differential distribution of epibionts on each substrate type. Percentage compositions are provided in Tables 1, 3 and 4. The category of erect hydroids includes erect hydroids and erect bryozoans which were not distinguished. -, not significant at α = 0.05.

	Boulders	Rocks	Cobbles	Shell
All Epibionts	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Encrusting Bryozoans-Tunicates	–	$P < 0.0001$	$P < 0.0001$	$P = 0.0003$
Encrusting Bryozoans-Erect Hydroids	–	–	–	$P < 0.0001$
Encrusting Bryozoan-Mussels	–	$P = 0.0009$	$P < 0.0001$	$P = 0.014$
Encrusting Bryozoans-Barnacles	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Tunicates-Erect Hydroids	–	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Tunicates-Mussels	$P = 0.01$	–	$P = 0.0085$	–
Tunicates-Barnacles	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Erect Hydroids-Mussels	–	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
Erect Hydroids-Barnacles	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$	–
Barnacles-Mussels	$P = 0.0003$	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

4. Discussion

4.1. Hydrodynamics and burial

The Great South Channel region is characterized by high rates of tidal current flow with a net flow to the south (Chen et al., 1995). Flow rates are sufficient to support the creation and migration of multi-meter amplitude sand waves (Harris et al., 2012). Conditions of this sort are unusual on the continental shelf, but not unprecedented (e.g., Bøe et al., 2009, 2015; Barrie et al., 2009; Bellec et al., 2010).

The surveyed area is noteworthy for the commonplace encounter of sedimentary particles potentially providing good attachment substrate for erect sessile epibiota. Atlantic surfclams were abundant over much of the region and reached unusually large size (Powell et al., 2020). Not surprisingly, surfclam shells were also abundant at many locations. Cobbles were nearly ubiquitous. Though very common at a smaller proportion of stations, rocks were routinely encountered, and boulders were encountered occasionally. These larger sedimentary constituents originate from the presence of a terminal moraine from the last Pleistocene glaciation; their near ubiquity is therefore not unexpected. For surfclams, in contrast, death occurs at the sediment-water interface, as the species is infaunal. Thus, the shell initially is mostly or completely buried. Even a dusting of sediment will prevent attachment of most encrusters, the small skeletal polychaetes and certain encrusting foraminifera being exceptions (Parsons-Hubbard et al., 1997, 2001; Powell et al., 2008). Thus, encrustation on surfclam shell was anticipated to be relatively rare due to their infaunal tier (Rodland et al., 2004). Surprisingly, perhaps, encrustation was also rare on cobbles, rocks, and boulders, with the exception of barnacle scars, suggesting that these sedimentary constituents are also persistently or frequently buried. In particular, slow-growing attached epibionts such as sponges were exceedingly rare and most soft-bodied attached epibionts were rare, the exception being the erect hydroids.

The frequency of barnacle scars relative to intact barnacles is suggestive of burial and exhumation and the abrasive impact consequent of sediment scour in a high-flow regime, which is a 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 often buried, and are scoured by resuspended and saltating sediment when exposed (Lewis, 1964; Daly and Mathieson, 1977; D'Antonio et al., 1986). The commonplace occurrence of barnacles, given the hydrodynamic conditions, can be explained by their rapid growth rates (Haderlie, 1971; Goren, 1979; Bertness et al., 1991; Sanford et al., 1994; Nishizaki and Carrington, 2015), permitting successful colonization during relatively short periods of substrate exposure and limited scour, and their ability to withstand a degree of instability of the attached substrate (Boessenecker, 2013). The frequency of scars indicates the importance of sand scour (Schneider-Storz et al., 2008). The oddity of hydroids also may be explained by their rapid growth rates (Gili and 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 remain 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).

4.2. Community types

The shallowest sites were occupied by a distinct surfclam-dominated community, comprising an abundance of large surfclams (Powell et al., 2019, 2020), and a few common attached epibiota, the hydroids and slipper shells, that were primarily found attached to exposed surfclam shell. The presence of common attached organisms on surfclam shell, despite the hydrodynamic regime facilitating resuspension and burial, suggests that a mechanism exists maintaining exposure of some fraction of the shell resource. Shell left to natural bottom conditions will normally be buried, often rapidly, in soft-sediment environments (van Straaten, 1952; Clifton and Hunter, 1973; Conover, 1975; Trewin and Welsh, 1976; Parsons-Hubbard et al., 1997), unless transiently uncovered by the passage of sand waves (Diaz et al., 2003), as may well be the case in the surveyed region. Regardless, shell routinely will have few or no epibionts due to limited exposure time (e.g., Rodland et al., 2006; Powell et al., 2008; Brett et al., 2011: compare these examples to that of exposed scallops, oysters, epifaunal clams, and hermatized gastropods, Walker, 1988; Lescinsky, 1993; Smyth and Roberts, 2010; Souto et al., 2012; Vicentuan-Cabaitan et al., 2014). Possibly, the activities of the fishery are responsible. Hydraulic dredges resuspend the bottom, but some shell is retained while the remaining smaller sedimentary constituents rapidly settle back to the bottom. The retained shell is subsequently discarded overboard and can be expected to remain for a time on the sediment surface providing potential habitat for fast growing epibionts such as slipper shells (Johnson, 1972; Wall et al., 2013) and hydroids (Gili and Hughes, 1995). The consistent association of hydroids and surfclam shell provides support for this possibility.

At deeper depths, hydroids are present, but surfclam shell is not abundant, and slipper shells are consequently rare. Mussel mats occur at these depths. Mussels are a foundational species, establishing a hard-bottom terrain both through their presence living and the production of shell in a soft-bottom milieu conducive to the support of a variety of mobile epifauna (see Goddard and Love, 2010; Manoukian et al., 2010; van der Zee et al., 2015; Powell et al., 2019). Mussels, however, are not dependent upon rocks, cobbles, or boulders; in fact, the distribution of these sedimentary particles, though common at the same depths, does not track the distribution of concentrations of mussels, nor does it track the distribution of surfclams and their shell (see also Powell et al., 2019).

Mussel beds on soft sediments are constructed to resist erosion and this is 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 et al., 2016): current velocities in the surveyed region reach such velocities (Harris et al., 2012; Dalyander et al., 2013) and, so, one might anticipate that mussel beds are more or less mobile over time. Such a capability is essential for species that are relatively long-lived (Heller, 1990). The dynamics of mussel mat formation and saltation 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. What is clear is that mussels are much less commonly attached to larger sedimentary particles such as cobbles and rocks, whose lack of mobility and small size would expose mussels to scour without saltation. The somewhat increased frequency of attachment to boulders attests to the somewhat greater size and vertical extent of these particles and thus the lower exposure to scour permitting longer-term occupation. Boulders, however, supported a very small fraction of all mussels as shown by the disparate geographic distribution of the two (Powell et al., 2019).

4.3. The rarity of attached epibenthos

A stunning observation is the limited coverage of exposed large particles, whether shells, cobbles, rocks, or boulders, by attached epibionts, whether skeletal bionts such as barnacles and encrusting bryozoans or fleshy bionts such as tunicates and sponges. Setting aside the barnacles, these taxa are distinctly uncommon in comparison to the apparent availability of substrate, and even the barnacles are uncommon in comparison to coverages often observed elsewhere (Connell, 1961; Goren, 1979; Haderlie, 1971; Caffey, 1985; Soniat et al., 2004; Davis and Ward, 2009; Munroe and Noda, 2009). Ephemeral substrates can be rapidly occupied by fast growing opportunists (Lewis, 1964; Haderlie, 1969; Branscomb, 1976; Goren, 1979; Littler et al., 1983; Nebelsick et al., 1997; Brett et al., 2011). Among these are the barnacles and encrusting bryozoans which are distinctly more common than other biont taxa on substrates observed in this study. Longer-lived attached biota are extremely rare. By inference from a range of studies, these substrates must be buried and exhumed frequently and exposed to scour by moving sand, all of which would be anticipated from the known tidal currents in the region and the presence of large mobile sand waves (see Twichell, 1983 for a nearby equivalency and Bøe et al., 2009 and Bellec et al., 2010 for photographs of lag deposits in the troughs of moving sand waves); otherwise occupation by attached epibionts would be much more common and a wider range of taxa would be expected (Haderlie, 1971; Zuschin and Pervesler, 1996a; Collie et al., 1997; Nebelsick et al., 1997; Glasby, 1999; Fraschetti et al., 2001; Cranfield et al., 2003; Brett et al., 2011; Bassi et al., 2012; Altieri and Witman, 2014). The uncommonness of attached mussels is particularly striking as these animals typically attach to such substrates (Harger, 1972; Braby and Somero, 2006; Elliott et al., 2008; Manoukian et al., 2010) and they are plentiful within the region (Powell et al., 2019). Their tendency to have limited resistance to scour and prolonged burial (Landahl, 1988; Newell, 1989; Seed and Suchanek, 1992; McQuaid et al., 2013) is consistent with their infrequent collection on these substrates in this survey. Thus, the rarity of long-lived attached epibionts suggests the ephemerality of exposed surfaces reminiscent of some intertidal sand-scoured rocky shores (Lewis, 1964; Daly and Mathieson, 1977; D'Antonio et al., 1986) and that cobbles, rocks, and boulders contribute little to the community composition in the surveyed region, which is composed almost exclusively of infaunal clams, less commonly, mat-forming mussels, and exclusive of the mussel mats, infrequent gastropods and other mobile fauna (Powell et al., 2019).

The limited presence of mobile fauna throughout much of the surveyed region is itself interesting, even though such epibenthos as regular sea urchins, crabs, and buccinid gastropods were abundant in association with mussel mats, often occurring at the same depths as cobble, rocks, and boulders (Powell et al., 2019). This scarcity of mobile epibenthos distinguishes this form of habitat complexity off Nantucket from other areas where mobile fauna are commonplace (e.g., Davis and VanBlaricom, 1978; Eleftheriou and Robertson, 1992; Ellis et al., 1996; Zuschin et al., 1999; Buhl-Mortensen et al., 2012).

4.4. Cobbles, rocks, boulders, and surfclam shells

Each of the four particle types exists in a high energy environment subjected to sand scour and likely frequent episodes of burial and exhumation, yet the attached biota vary considerably. Some portion of this may be variations in particle distribution with depth, but cobbles and rocks, in particular, are nearly ubiquitous and surfclam shell is widely distributed, though less commonly encountered in deeper water. Boulders are likely the more stable of the 4 particle types and the more likely to be exposed for longer periods of time. Mussels, when not associated with mussel mats, and sponges are most likely to be found on boulders as might be anticipated as both require relatively long-term stability and exposure of their attachment site. The limited coverage by mussels, sponges, and most other epibiota relative to barnacles is consistent with their relative low resistance to scour. Barnacle scars are more common on boulders and rocks, but barnacles are distributed across all particle types. Barnacle scars are occasionally reported as the taphonomic remnants of attached barnacles (Miller and Brown, 1979; Walker, 1988; Brett et al., 2011; Boessenecker, 2013). Perhaps scars are more easily eroded off the smaller and likely more mobile cobbles and surfclam shells. Regardless of explanation, the bias favoring larger particle sizes is clear, as is the preponderance of scars in comparison to intact barnacle tests.

Interestingly, tunicates and encrusting bryozoans and their remnants are more common on cobbles and rocks than on boulders or surfclam shell, even though both are often recorded attached to exposed bivalve shell (e.g., Powell et al., 2008; Brett et al., 2011) and are common fouling organisms on a variety of hard substrates (e.g., Haderlie, 1969, 1971; Goren, 1979; Hageman, 2001; Rodríguez and Ibarra-Obando, 2008). In comparison, slipper shells and hydroids are distinctly more common on surfclam shell. Part of the latter bias is likely related to depth, as slipper shells tend to be common in shallow waters (Marsh, 1976; Peterson, 1983; Wall et al., 2013), although differential degrees of predation cannot be excluded (Pechenik et al., 2010; but see Thieltges, 2005). Erect hydroids and erect bryozoans are often encountered attached to bivalve shells (Boekschoten, 1967; McKinny, 1996; Soniat et al., 2004; Brett et al., 2011; Almeida et al., 2018). These erect forms may be able to better withstand light sediment coverage, once established, which commonly occurs with shells exposed on the sediment surface (e.g., Parsons-Hubbard et al., 1997), and which might explain their commonplace occurrence on surfclam shell; why cobbles, rocks, and boulders support these taxa with lower frequency is unclear.

4.5. The ambiguity of substrate complexity

Substrate complexity often is a useful surrogate for ecosystem value and thus a useful tool for identifying critical habitats for ecosystem management when detailed ecological data are insufficiently available. This is based on the expectation that complexity in the range of available substrates adds ecosystem value. For shells, this is consistent with the taphonomic feedback hypothesis of Kidwell (1986) and the recognition of the importance of shell as a component of sandy and muddy sediments (Gutiérrez et al., 2003). For edaphic constituents such as cobbles, rocks, and boulders, this is consistent with a range of observations from rocky shores and hardgrounds wherein hard substrate increases species richness through the colonization of sessile and mobile epibiota not normally components of soft-bottom habitats (e.g., Neumann et al., 1977; Peckal and Searles, 1984; Zuschin and Pervesler, 1996a, 1996b; Cusson and Bourget, 2005). The survey of the region westward of the Great South Channel provided an opportunity to evaluate the verity of this assumption in a region of the continental shelf characterized by prograding sand dunes, high tidal current velocities, and sand scour.

Such conditions, though uncommon on the continental shelf, are well described across a range of continental shelves, particularly in boreal regions typified by the presence of glacial till left by Pleistocene glaciation.

Between Nantucket and the Great South Channel, the attached epibiota fall into three categories based on their biases for substrate types. Some prefer the largest particles or evidence of their occupation is best preserved on these particles: these include sponges, mussels, and the barnacles and their scars. Some prefer intermediate and smaller terrigenous particles; these include tunicates and encrusting bryozoans. Some prefer surfclam shells, namely the slipper shells and erect hydroids. Unlike the factors controlling distributions of attached epibionts which often involve colonization timing, competitive interactions, and predatory controls, the distribution of the attached epibiota in this study appear to be controlled by the physical rigors of the environment. Although little is known of the timing of colonization in the surveyed habitat, coverage was insufficient to permit competition for space as a primary determinant, and the gear used was efficient at catching large mobile predators such as crabs. These predators were abundant in mussel beds, but notable in their rarity elsewhere. Whereas the resistance of bivalve shells to abrasive forces is well studied (Driscoll and Weltin, 1973; Smith and Nelson, 2003; Ford and Kench, 2012), unfortunately little is known of the adaptability of various attached epibiota to these conditions, save perhaps the mussels; too little to unequivocally associate taxon, particle type, and adaptive ambit, thereby resolving the principal edaphic controls on the distribution of the attached epibionts observed in this study. What is clear is that the most common condition, the absence of attached epibionts, and the secondarily common condition, the presence solely of opportunistic fast-growing epibionts, demonstrates that hydrodynamic and edaphic processes minimize the importance of substrate complexity in community structure. The anticipated contribution of shell, cobbles, rocks, and boulders to habitat complexity belies their resultant much more minor role in determining community composition.

The community composition between Nantucket and the Great South Channel shows that under conditions of high current velocity and the continual bed-load movement of sand, the presence of substrate complexity, whether contributed recently by the deaths of species with carbonate skeletons, or over geological time by the retreat of continental glaciers, cannot be used as a surrogate for ecosystem value in ecosystem management. Additionally, the same characteristics of community structure show that the paleoecological interpretations derived from limited epibiont coverage must be carefully evaluated in terms of the sedimentary facies present for evidence of high current velocity and scour. These regions of the continental shelf characterized by high current velocity and scour do not lend themselves to the standard assumptions of the relationship of substrate complexity to ecosystem value expressed in terms of epifaunal/epibiont species richness, biomass, and trophic linkage. What is present is an interestingly austere community composition that remains poorly studied today and which relies disproportionately on the resident soft-bottom biota rather than the epifauna on hard substrates.

CRediT authorship contribution statement

Eric N. Powell: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Visualization, Funding acquisition. **Roger L. Mann:** Conceptualization, Methodology, Investigation, Writing - review & editing, Supervision. **M. Chase Long:** Investigation, Writing - review & editing, Data curation. **Jeremy R. Timbs:** Investigation, Writing - review & editing. **Kelsey M. Kuykendall:** Methodology, Investigation, Writing - review & editing, Visualization, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Altieri, A.H., Witman, J.D., 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere 5 (10). https://doi.org/10.1890/ES14-00018.1, 124, 11.

Almeida, A.C.S., Souza, F.B.C., Farias, J., Alves, O.F.S., Vieira, L.M., 2018. Bryozoa on disarticulated bivalve shells from Todos os Santos Bay, northeastern Brazil, with the description of two new species. Zootaxa 4434, 401–428.

Barrie, J.V., Conway, K.W., Picard, K., Breene, H.G., 2009. Large-scale sedimentary bedforms and sediment dynamics on a glaciated tectonic continental shelf: examples from the Pacific margin of Canada. Continent. Shelf Res. 29, 796–806.

Bassi, D., Iryu, Y., Humblet, M., Matsuda, H., Machiyama, H., Sasaki, K., Matsuda, S., Arai, K., Inoue, T., 2012. Recent macroids on the Kikai-jima shelf, central Ryukyu Islands, Japan. Sedimentology 59, 2024–2041.

Bellec, V.K., Bøe, R., Rise, L., Slagstad, D., Longva, O., Dolan, M.F.J., 2010. Rippled scour depressions on the continental shelf bank slopes off Nordland and Troms, northern Norway. Continent. Shelf Res. 30, 1056–1069.

Bertness, M.D., Gaines, S.D., Bermudez, D., Sanford, E., 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Mar. Ecol. Prog. Ser. 75, 91–100.

Beukema, J.J., Cadée, G.C., 1996. Consequences of the sudden removal of nearly all mussels and cockles from the Dutch Wadden Sea. P.S.Z.N.I: Mar. Ecol. 17, 279–289.

Black, R., Peterson, C.H., 1987. Biological vs. physical explanations for the non-random pattern of host occupation by a macroalga attaching to infaunal bivalve molluscs. Oecologia 73, 213–221.

Bøe, R., Bellec, V.K., Dolan, M.F.J., Buhl-Mortensen, P., Bulh-Mortensen, L., Slagstad, D., Rise, L., 2009. Giant sandwaves in the Hola glacial trough off Verterålen, north Norway. Mar. Geol. 267, 36–54.

Bøe, R., Skarðhamar, J., Rise, L., Dolan, M.F.J., Bellec, V.K., Winsborrow, M., Skagseth, Ø., Knies, J., King, E.L., Walderhaug, O., Chand, S., Buenz, S., Mienert, J., 2015. Sandwaves and sand transport on the Barents Sea continental slope offshore northern Norway. Mar. Petrol. Geol. 60, 34–53.

Boekschoten, G.J., 1967. Palaeoecology of some Mollusca from the Tielrode Sands (Pliocene, Belgium). Palaeogeogr. Palaeoclimatol. Palaeoecol. 3, 311–362.

Boessenecker, R.W., 2013. Taphonomic implications of barnacle encrusted sea lion bones from the Middle Pleistocene Port Orford Formation, coastal Oregon. J. Paleontol. 87, 657–663.

Braby, C.E., Somero, G.N., 2006. Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. Mar. Biol. 148, 1249–1262.

Branscomb, E.S., 1976. Proximate causes of mortality determining the distribution and abundance of the barnacle *Balanus improvisus* Darwin in Chesapeake Bay. Chesap. Sci. 17, 281–288.

Brett, C.E., Parsons-Hubbard, K.M., Walker, S.E., Ferguson, C., Powell, E.N., Staff, G., Ashton-Alcox, K.A., Raymond, A., 2011. Gradients and patterns of sclerobionts on experimentally deployed bivalve shells: synopsis of bathymetric and temporal trends on a decadal time scale. Palaeogeogr. Palaeoclimatol. Palaeoecol. 312, 278–304.

Buhl-Mortensen, L., Buhl-Mortensen, F., Dolan, M.F.J., Dannheim, J., Bellec, V., Holte, B., 2012. Habitat complexity and bottom fauna composition of different scales on the continental shelf and slope of northern Norway. Hydrobiologia 685, 191–219.

Caffey, H.M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol. Monogr. 55, 313–332.

Callender, W.R., Powell, E.N., Staff, G.M., 1994. Taphonomic rates of molluscan shells placed in autochthonous assemblages on the Louisiana continental slope. Palaios 9, 60–73.

Chen, C.S., Beardsley, R.C., Limeburner, R., 1995. Variability of currents in late spring in the northern Great South Channel. Continent. Shelf Res. 15, 451–473.

Clifton, H.E., Hunter, R.E., 1973. Bioturbational rates and effects in carbonate sand, St. John, U.S. Virgin Islands. J. Geol. 81, 253–268.

Cockrell, M.L., Bernhardt, J.R., Leslie, H.M., 2015. Recruitment, abundance, and predation on the blue mussel (*Mytilus edulis*) on northeastern estuarine rocky shores. Ecosphere 6 (1). https://doi.org/10.1890/ES14-00176.1, 18, 24 pp.

Collie, J.S., Escanero, G.A., Valentine, P.C., 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Mar. Ecol. Prog. Ser. 155, 159–172.

Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31, 61–104.

Conover, M.R., 1975. Prevention of shell burial as a benefit hermit crabs provide to their symbionts (Decapoda, Paguridea). Crustaceana 29, 311–313.

Cranfield, H.J., Manighetti, B., Michael, K.P., Hill, A., 2003. Effects of oyster dredging on the distribution of bryozoan biogenic reefs and associated sediments in Foveaux Strait, southern New Zealand. Continent. Shelf Res. 23, 1337–1357.

Cusson, M., Bourget, E., 2005. Global patterns of macroinvertebrate production in marine benthic habitats. Mar. Ecol. Prog. Ser. 297, 1–14.

Daly, M.A., Mathieson, A.C., 1977. The effects of sand movement on intertidal seaweeds and selected invertebrates at Bound Rock, New Hampshire, USA. Mar. Biol. 43, 45–55.

Dalyander, P.S., Butman, B., Sherwood, C.R., Signell, R.P., Wilkin, J.L., 2013. Characterizing wave- and current-induced bottom shear stress: U.S. Middle Atlantic continental shelf. Continent. Shelf Res. 52, 73–86.

D'Antonio, C.M., 1986. Role of sand in the domination of hard substrata by the intertidal alga *Rhodomela larix*. Mar. Ecol. Prog. Ser. 27, 263–275.

Davies, D.J., Powell, E.N., Stanton Jr., R.J., 1989. Relative rates of shell dissolution and net sediment accumulation - a commentary: can shell beds form by the gradual accumulation of biogenic debris on the sea floor? Lethaia 22, 207–212.

Davies, D.J., Staff, G.M., Callender, W.R., Powell, E.N., 1990. Description of a quantitative approach to taphonomy and taphofacies analysis: all dead things are not created equal. In: Miller III, W. (Ed.), Paleocommunity Temporal Dynamics: the Long-Term Development of Multispecies Assemblages, vol. 5. Spec. Publ. (Paleontol. Soc.), pp. 328–350.

Davis, N., VanBlaricom, G.R., 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 23, 417–427.

Davis, A.R., Ward, D.W., 2009. Establishment and persistence of species-rich patches in a species-poor landscape: role of a structure-forming subtidal barnacle. Mar. Ecol. Prog. Ser. 380, 187–198.

Diaz, R.J., Cutter Jr., G.R., Able, K.W., 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26, 12–20.

Diederich, S., 2006. High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. J. Exp. Mar. Biol. Ecol. 328, 211–227.

Driscoll, E.G., Weltin, T.P., 1973. Sedimentary parameters as factors in abrasive shell reduction. Palaeogeogr. Palaeoclimatol. Palaeoecol. 13, 275–288.

Eleftheriou, A., Robertson, M.R., 1992. The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. Neth. J. Sea Res. 30, 289–299.

Elliott, J., Holmes, K., Chambers, R., Leon, K., Wimberger, P., 2008. Differences in morphology and habitat use among the native mussel *Mytilus trossulus*, the non-native *M. galloprovincialis*, and their hybrids in Puget Sound. Mar. Biol. 156, 39–53. Washington.

Ellis, M.S., Wilson-Ormond, E.A., Powell, E.N., 1996. Effects of gas-producing platforms on continental shelf macroepifauna in the northwestern Gulf of Mexico: abundance and size structure. Can. J. Fish. Aquat. Sci. 53, 2589–2605.

Emery, K.O., Uchupi, E., 1965. Structures of Georges Bank. Mar. Geol. 3, 349–358.

Ford, M.R., Kench, P.S., 2012. The durability of bioclastic sediments and implications for coral reef deposit formation. Sedimentology 59, 830–842.

Fraschetti, S., Bianchi, C.N., Terlizzi, A., Fanelli, G., Morri, C., Boero, F., 2001. Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. Mar. Ecol. Prog. Ser. 212, 1–12.

Gherardi, D.F.M., Bosence, D.W.J., 1999. Modeling of the ecological succession of encrusting organisms in recent coralline-algal frameworks from Atol das Rocas, Brazil. Palaios 14, 145–158.

Gili, J.-M., Hughes, R.G., 1995. The ecology of marine benthic hydroids. Oceanogr. Mar. Biol. Annu. Rev. 33, 351–426.

Glasby, T.M., 1999. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. Estuar. Coast Shelf Sci. 48, 281–290.

Goddard, J.H.R., Love, M.S., 2010. Megabenthic invertebrates on shell mounds associated with oil and gas platforms off California. Bull. Mar. Sci. 86, 533–554.

Gordillo, S., Aitken, A.E., 2000. Palaeoenvironmental interpretation of Late Quaternary marine molluscan assemblages, Canadian Arctic Archipelago. Géogr. Phys. Quaternaire 54, 301–315.

Goren, M., 1979. Succession of benthic community on artificial substratum at Elat (Red Sea). J. Exp. Mar. Biol. Ecol. 38, 19–40.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101, 79–90.

Haderlie, E.C., 1969. Marine fouling and boring organisms in Monterey Harbor II. Second year of investigations. Veliger 12, 182–192.

Haderlie, E.C., 1971. Marine fouling and boring organisms at 100 feet depth in open water of Monterey Bay. Veliger 13, 249–260.

Hageman, S.J., 2001. Encrusting invertebrate faunas and shipwreck histories: ballast stones from North Carolina shipwreck 03BUI (Queen Anne's Revenge). SE. Geol. 40, 65–73.

Harger, J.R., 1972. Competitive coexistence: maintenance of interacting associations of the sea mussels *Mytilus edulis* and *Mytilus californianus*. Veliger 14, 387–410.

Harris, B.P., Cowles, G.W., Stokesbury, K.D.E., 2012. Surficial sediment stability on Georges Bank, in the Great South Channel and on eastern Nantucket Shoals. Continent. Shelf Res. 49, 65–72.

Heller, J., 1990. Longevity in molluscs. Malacologia 31, 259–295.

Hilbish, T.J., Mullinax, A., Dolven, S.I., Meyer, A., Koehn, R.K., Rawson, P.D., 2000. Origin of the antitropical distribution pattern in marine mussels (*Mytilus* spp.): routes and timing of transequatorial migration. Mar. Biol. 136, 69–77.

HSRL, 2012. Report of the 2012 Stock Assessment Workshop (14th SAW) for the New Jersey Delaware Bay Oyster Beds. Haskin Shellfish Research Laboratory, Rutgers Univ., Port Norris, NJ, p. 168.

Hutchison, Z.L., Hendrick, V.J., Burrows, M.T., Wilson, B., Last, K.S., 2016. Buried alive: the behavioural response of the mussels, *Modiolus modiolus* and *Mytilus edulis* to sudden burial by sediment. Plos ONE v 1 (3), 21 e0151471.

Johnson, J.K., 1972. Effect of turbidity on the rate of filtration and growth of the slipper limpet *Crepidula fornicata* Lamarck 1799. Veliger 14, 315–326.

Kidwell, S.M., 1986. Taphonomic feedback in Miocene assemblages: testing the role of dead hardparts in benthic communities. Palaios 1, 239–255.

Lambert, J., Goudreau, P., 1996. Performance of the New England hydraulic dredge for the harvest of Stimpson's surf clams (*Mactromeris polynyma*). Can. Ind. Rep. Fish. Aquat. Sci. 235, 1–28.

Landahl, J., 1988. Sediment-level fluctuation in a mussel bed on a 'protected' sand-gravel beach. Estuar. Coast Shelf Sci. 26, 255–267.

Lauenstein, G.G., Cantillo, A.Y., Kokkinakis, S., Frew, S., Jobling, H.J., Fay, R.R., 1997. Mussel Watch project site descriptions, through 1997. NOAA Tech. Memo. NOS ORCA 112, 354.

Lescinsky, H.L., 1993. Taphonomy and paleoecology of epibionts on the scallops *Chlamys hastata* (Sowerby 1843) and *Chlamys rubida* (Hinds 1845). Palaios 8, 267–277.

Lewis, J.R., 1964. The Ecology of Rocky Shores. Hodder and Stoughton, London, p. 323.

Littler, M.M., Martz, D.R., Littler, D.S., 1983. Effects of recurrent sand deposition on rocky intertidal organisms: importance of substrate heterogeneity in a fluctuating environment. Mar. Ecol. Prog. Ser. 11, 129–139.

Mann, R.G., Swift, D.J.P., Perry, R., 1981. Size classes of flow-transverse bedforms in a subtidal environment, Nantucket Shoals, North American Atlantic shelf. Geo Mar. Lett. 1, 39–43.

Manoukian, S., Spagnolo, A., Scarcella, G., Punzo, E., Angelini, A., Fabi, G., 2010. Effects of two offshore gas platforms on soft-bottom benthic communities (northwestern Adriatic Sea, Italy). Mar. Environ. Res. 70, 402–410.

Marsh, G.A., 1976. Ecology of the gastropod epifauna of eelgrass in a Virginia estuary. Chesap. Sci. 17, 182–187.

McKinny, F.K., 1996. Encrusting organisms on co-occurring disarticulated valves of two marine bivalves: comparison of living assemblages and skeletal residues. Paleobiology 22, 543–567.

McQuaid, C.D., Porri, F., Nicastro, K.R., Zardi, G.I., 2013. Simple, scale-dependent patterns emerge from very complex effects – an example from the intertidal mussels *Mytilus galloprovincialis* and *Perna perna*. Oceanogr. Mar. Biol. Annu. Rev. 53, 127–156.

Miller III, W., Brown, N.A., 1979. The attachment scars of fossil balanids. J. Paleontol. 53, 208–210.

Morehead, S., Montagna, P., Kennicutt II, M.C., 2008. Comparing fixed-point and probabilistic sampling designs for monitoring the marine ecosystem near McMurdo Station, Ross Sea, Antarctica. Antarct. Sci. 20, 471–484.

Munroe, D.M., Noda, T., 2009. Spatial pattern of rocky intertidal barnacle recruitment: comparison over multiple tidal levels and years. J. Mar. Biol. Assoc. U. K. 89, 345–355.

Nebelsick, J.H., Schmid, B., Stachowitsch, M., 1997. The encrustation of fossil and recent sea urchin tests: ecological and taphonomic significance. Lethaia 30, 271–284.

NEFSC, 2017. 61st Northeast Regional Stock Assessment Workshop (61st SAW) assessment report. NEFSC Ref. Doc. 17–05, 466.

Neumann, A., Kofoed, J., Keller, G., 1977. Lithoherms in the straits of Florida. Geology 5, 4–10.

Newell, R.I.E., 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North and Mid-Atlantic blue mussel). U S Fish Wildl. Serv. Biol. Rep. 82 (11.102). USACE TR EL-82-4, 25 pp.

Nielsen, J.K., Funder, S., 2003. Taphonomy of Eemian marine molluscs and acorn barnacles from eastern Arkhangelsk region, northern Russia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 191, 139–168.

Nishizaki, M.T., Carrington, E., 2015. The effect of water temperature and velocity on barnacle growth: quantifying the impact of multiple environmental stressors. J. Therm. Biol. 54, 37–46.

Parras, A., Casadío, S., 2005. Taphonomy and sequence stratigraphic significance of oyster dominated concentrations from the San Julián Formation, Oligocene of Patagonia, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 217, 47–66.

Parsons, K.M., Powell, E.N., Brett, C.E., Walker, S.E., Callender, W.R., 1997. Shelf and slope experimental taphonomy initiative (SSETI): Bahamas and Gulf of Mexico. Proc. 8th Int. Coral Reef Symp. 2, 1807–1812.

Parsons-Hubbard, K.M., Powell, E.N., Staff, G.M., Callender, W.R., Brett, C.E., Walker, S. E., 2001. The effect of burial on shell preservation and epibiont cover in Gulf of Mexico and Bahamas shelf and slope environments after two years: an experimental approach. In: Aller, J.Y., Woodin, S.A., Aller, R.C. (Eds.), Organism-sediment Interactions. Belle W. Baruch Library in Marine Science #21. University of South Carolina Press, pp. 297–314.

Pechenik, J.A., Ambrogio, O.V., Untersee, S., 2010. Predation on juveniles of *Crepidula fornicata* by two crustaceans and two gastropods. J. Exp. Mar. Biol. Ecol. 384, 91–98.

Peckal, P., Searles, R.B., 1984. Temporal and spatial patterns of growth and survival of invertebrate and algal populations of a North Carolina continental shelf community. Estuar. Coast Shelf Sci. 18, 133–143.

Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Bris, A. le, Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwod, G.D., Thomas, A.C., 2015. Slow adaptation in the face of rapid warming leads to collapse of the Gulf of Maine cod fishery. Science 350, 809–812.

Peryt, D., Peryt, T.M., Raczyński, P., Chlódek, K., 2012. Foraminiferal colonization related to the Zechstein (Lopingian) transgression in the western part of the Wolsztyn Palaeo-Ridge area, western Poland. Geol. Q. 56, 529–546.

Peterson, C.H., 1983. Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* Sowerby and *Cancer anthonyi* (Rathbun). J. Exp. Mar. Biol. Ecol. 68, 145–158.

Powell, E.N., 1992. A model for death assemblage formation. Can sediment shelliness be explained? J. Mar. Res. 50, 229–265.

Powell, E.N., Brett, C.E., Parsons-Hubbard, K.M., Callender, W.R., Staff, G.M., Walker, S. E., Raymond, A., Ashton-Alcox, K.A., 2011. The relationship of bionts and taphonomic processes in molluscan taphofacies formation on the continental shelf and slope: eight-year trends: Gulf of Mexico and Bahamas. Facies 57, 15–37.

Powell, E.N., Callender, W.R., Staff, G.M., Parsons-Hubbard, K.M., Brett, C.E., Walker, S. E., Raymond, A., Ashton-Alcox, K.A., 2008. Mollusc shell condition after eight years on the sea floor – taphonomy in the Gulf of Mexico and Bahamas. J. Shellfish Res. 27, 191–225.

Powell, E.N., Hu, X.P., Cai, W.J., Ashton-Alcox, K.A., Parsons-Hubbard, K.M., Walker, S. E., 2012. Geochemical controls on carbonate shell taphonomy in northern Gulf of Mexico continental shelf and slope sediments. Palaios 27, 571–584.

Powell, E.N., Kuykendall, K.M., Moreno, P., 2017a. The death assemblage as a marker for habitat and an indicator of climate change: Georges Bank, surfclams and ocean quahogs. Continent. Shelf Res. 142, 14–31.

Powell, E.N., Mann, R., Ashton-Alcox, K.A., Kuykendall, K.M., Long, M.C., 2017b. Can we estimate molluscan abundance and biomass on the continental shelf? Estuar. Coast Shelf Sci. 198, 213–224.

Powell, E.N., Mann, R., Kuykendall, K.M., Long, M.C., Timbs, J.R., 2019. 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. Mar. Ecol. 40 (4), e12456.

Powell, E.N., Staff, G.M., Callender, W.R., Ashton-Alcox, K.A., Brett, C.E., Parsons-Hubbard, K.M., Walker, S.E., Raymond, A., 2011b. Taphonomic degradation of molluscan remains during thirteen years on the continental shelf and slope of the northwestern Gulf of Mexico. Palaeogeogr. Palaeoclimatol. Palaeoecol. 312, 209–232.

Powell, E.N., Staff, G.M., Callender, W.R., Ashton-Alcox, K.A., Brett, C.E., Parsons-Hubbard, K.M., Walker, S.E., Raymond, A., 2011c. The influence of molluscan taxon on taphofacies development over a broad range of environments of preservation: the SSETI experience. Palaeogeogr. Palaeoclimatol. Palaeoecol. 312, 233–264.

Powell, E.N., Staff, G.M., Davies, D.J., Callender, W.R., 1989. Macrobenthic death assemblages in modern marine environments: formation, interpretation and application. Crit. Rev. Aquat. Sci. 1, 555–589.

Powell, E.N., Trumble, J.M., Mann, R.L., Long, M.C., Pace, S.M., Timbs, J.R., Kuykendall, K.M., 2020. Growth and longevity in surfclams east of Nantucket: range expansion in response to the post-2000 warming of the North Atlantic. Continent. Shelf Res. 195, #104059.

Rawson, P.D., Harper, F.M., 2009. Colonization of the northwest Atlantic by the blue mussel, *Mytilus trossulus* postdates the last glacial maximum. Mar. Biol. 156, 1857–1868.

Rawson, P.D., Hayhurst, S., Vanscoyoc, B., 2001. Species composition of blue mussel populations in the northeastern Gulf of Maine. J. Shellfish Res. 20, 31–38.

Rodland, D.L., Kowalewski, M., Carroll, M., Simões, M.G., 2004. Colonization of a 'lost world': encrustation patterns in modern subtropical brachiopod assemblages. Palaios 19, 381–395.

Rodland, D.L., Kowalewski, M., Carroll, M., Simões, M.G., 2006. The temporal resolution of epibiont assemblages: are they ecological snapshots or overexposures? J. Geol. 114, 313–324.

Rodríguez, L.F., Ibarra-Obando, S.E., 2008. Cover and colonization of commercial oyster (*Crassostrea gigas*) shells by fouling organisms in San Quntin Bay, Mexico. J. Shellfish Res. 27, 337–343.

Salas, M.C., Defeo, O., Narvarte, M., 2016. Attachment features of mytilids in ecosystems with mobile substrate: *Brachidontes rodriguezii* in San Antonio Bay (Patagonia, Argentina). J. Mar. Biol. Assoc. U. K. 96, 1449–1456.

Saldanha, H.J., Sancho, G., Santos, M.N., Puente, E., Gaspar, M.B., Bilbao, A., Monteiro, C.C., Gomez, E., Arregi, L., 2003. The use of biofouling for ageing lost nets: a case study. Fish. Res. 64, 141–150.

Sanford, E., Bermudez, D., Bertness, M.D., Gaines, S.D., 1994. Flow, food supply and acorn barnacle population dynamics. Mar. Ecol. Prog. Ser. 104, 49–62.

Scanland, T.B., 1979. The epibiota of *Arca zebra* and *Arca inbricata*: a community analysis. Veliger 21, 475–485.

Schejter, L., Escolar, M., Bremec, C., 2011. Variability in epibiont colonization of shells of *Fusitriton magellanicus* (Gastropoda) on the Argentinean shelf. J. Mar. Biol. Assoc. U. K. 91, 897–906.

Schneider-Storz, B., Nebelsick, J.H., Wehrmann, A., Federolf, C.M.F., 2008. Comparative taphonomy of three bivalve species from a mass shell accumulation in the intertidal regime of North Sea tidal flats. Facies 54, 461–478.

Seed, R., Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In: Gosling, E. (Ed.), The Mussel Mytilus: Ecology, Physiology, Genetics and Culture, vol. 25. Dev. Aquacult. Fish. Sci., pp. 87–169

Smith, A.M., Nelson, C.S., 2003. Effects of early sea-floor processes on the taphonomy of temperate shelf skeletal carbonate deposits. Earth Sci. Rev. 63, 1–31.

Smrecak, T.A., Brett, C.E., 2014. Establishing patterns in sclerobionts distribution in a Late Ordovician (Cincinnatian) depth gradient: toward a sclerobiofacies model. Palaios 29, 74–85.

Smyth, D., Roberts, D., 2010. The European oyster (*Ostrea edulis*) and its epibiotic succession. Hydrobiologia 655, 25–36.

Soniat, T.M., Finelli, C.M., Ruiz, J.T., 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. J. Exp. Mar. Biol. Ecol. 310, 163–182.

Souto, V.S., Schejter, L., Bremec, C.C., 2012. Epibionts on *Aequipecten tehuelchus* (d'Orbigny, 1846) (Pectinidae) in shelf waters off Buenos Aires, Argentina. Am. Malacol. Bull. 30, 261–266.

Staff, G.M., Stanton Jr., R.J., Powell, E.N., Cummins, H., 1986. Time-averaging, taphonomy and their impact on paleocommunity reconstruction: death assemblages in Texas bays. Geol. Soc. Am. Bull. 97, 428–443.

Thieltges, D.W., 2005. Benefit from an invader: American slipper limpet *Crepidula fornicata* reduces star fish predation on basibiont European mussels. Hydrobiologia 541, 241–244.

Tomašových, A., Fürsich, F.T., Olszewski, T.D., 2006. Modeling shelliness and alteration in shell beds: variation in hardpart input and burial rates lead to opposing predictions. Paleobiology 32, 278–298.

Trewin, N.H., Welsh, W., 1976. Formation and composition of a graded estuarine shell bed. Palaeogeogr. Palaeoclimatol. Palaeoecol. 19, 219–230.

Twichell, D.C., 1983. Bedform distribution and inferred sand transport on Georges Bank, United States Atlantic continental shelf. Sedimentology 30, 695–710.

Trumbull, J.V.A., 1972. Atlantic continental shelf and slope of the United States - sand-size 861 fraction of bottom sediments, New Jersey to Nova Scotia. U. S. Geol. Surv. Prof, p. 45, 529-K.

van der Meer, J., 1997. Sampling design of monitoring programmes for marine benthos: a comparison between the use of fixed versus randomly selected stations. J. Sea Res. 37, 167–179.

van der Zee, E.M., Tielens, E., Holthuijsen, S., Donadi, S., Eriksson, B.K., van der Veer, H. W., Piersma, T., Olff, H., van der Heide, T., 2015. Habitat modification drives benthic trophic diversity in an intertidal soft-bottom ecosystem. J. Exp. Mar. Biol. Ecol. 465, 41–48.

van Straaten, L.M.J.U., 1952. Biogene textures and the formation of shell beds in the Dutch Wadden Sea. Koninl. Nederl. Akad. Wetenschappen Ser. B Proc. 55, 500–516.

Vicentuan-Cabaitan, K., Neo, M.L., Eckman, W., Teo, S.L.M., Todd, P.A., 2014. Giant clam shells host a multitude of epibionts. Bull. Mar. Sci. 90, 795-76.

wa Kangeri, A.K., Jansen, J.M., Barkman, B.R., Donker, J.J.A., Joppe, D.J., Dankers, N.M. J.A., 2014. Perturbation induced changes in substrate use by the blue mussel *Mytilus edulis*, in sedimentary systems. J. Sea Res. 85, 233–240.

wa Kangeri, A.K., Jansen, J.M., Joppe, D.J., Dankers, N.M.J.A., 2016. *In situ* investigation of the effects of current velocity on sedimentary mussel bed stability. J. Exp. Mar. Biol. Ecol. 485, 65–72.

Walker, S.E., 1988. Taphonomic significance of hermit crab (Anomura: Paguridea): epifaunal hermit crab–infaunal gastropod example. Palaeogeogr. Palaeoclimatol. Palaeoecol. 63, 45–71.

Walker, S.E., 1998. Endobionts on modern and fossil *Turritella* from the northern gulf of California region. Ichnos 6, 99–115.

Walker, S.E., Goldstein, S.T., 1999. Taphonomic tiering: experimental field taphonomy of molluscs and foraminifera above and below the sediment water interface. Palaeogeogr. Palaeoclimatol. Palaeoecol. 149, 227–244.

Wall, C.C., Gobler, C.J., Peterson, B.J., Ward, J.E., 2013. Contrasting growth patterns of suspension-feeding molluscs (*Mercenaria mercenaria, Crassostrea virginica, Argopecten irradians* and *Crepidula fornicata*) across a eutrophication gradient in the Peconic Estuary, NY, USA. Estuar. Coast 36, 1274–1291.

Wells, H.W., Gray, I.E., 1960. The seasonal occurrence of *Mytilus edulis* on the Carolina coast as a result of transport around Cape Hatteras. Biol. Bull. 119, 550–559.

Widdows, J., Lucas, J.S., Brinsley, M.D., Salkeld, P.N., Staff, F.J., 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. Helgol. Mar. Res. 56, 3–12.

Wildish, D.J., Fader, G.B.J., Parrott, D.R., 2009. A model of horse mussel reef formation in the Bay of Fundy based on population growth and geological processes. Atl. Geol. 45, 157–170.

Wilson, M.A., 1987. Ecological dynamics on pebbles, cobbles, and boulders. Palaios 2, 594–599.

Zuschin, M., Baal, C., 2007. Large gryphaeid oysters as habitats for numerous sclerobionts: a case study from the northern Red Sea. Facies 53, 319–327.

Zuschin, M., Pervesler, P., 1996a. Secondary hardground-communities in the northern Gulf of Trieste, Adriatic Sea. Senckenberg. Maritima 28, 53–63.

Zuschin, M., Pervesler, P., 1996b. Estimated preservation potential of secondary hardground communities in the northern Gulf of Trieste. Com. Reun. Tafon. Fossil. 421–424.

Zuschin, M., Stachowitsch, M., Pervesler, P., Kollmann, H., 1999. Structural features and taphonomic pathways of a high-biomass epifauna in the northern Gulf of Trieste, Adriatic Sea. Lethaia 32, 299–317.