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Mollusca of Assateague Island, Maryland and Virginia: Additions to the Fauna, Range Extensions, and Gigantism

ROBERT S. PREZANT,[1] CLEMENT L. COUNTS, III[2] AND ERIC J. CHAPMAN[1]

[1]Department of Biology and Molecular Biology, College of Science and Mathematics, Montclair State University, Upper Montclair, New Jersey 07043, USA

[2]Department of Natural Sciences, University of Maryland Eastern Shore, Princess Anne, Maryland 21853-1299, USA

Abstract. Collections of 108 species of marine and estuarine mollusks from and around Assateague Island, Maryland and Virginia, from 1991 to 1996, vary from and extend the known species lists generated by three previously published collections over the past 100 years. Extensive sampling, including benthic grabs, trawls, and hand collecting, has added 54 species of mollusks (20 bivalves, 31 gastropods, one polyplacophoran, and two cephalopods) to the 1914 list of Henderson & Bartsch and 46 (19 bivalves, 26 gastropods and one cephalopod) to that of Counts & Bashore from 1991. Homer et al. in 1997 provided a mollusk survey of Maryland coast bays and listed 73 molluscan species (including 10 species recorded as shells only and eight as taxonomic uncertainties). To the latter we have added 51 molluscan taxa they did not find (19 bivalves, 29 gastropods, one polyplacophoran, and two cephalopods). All collections represent a total described malacofauna of this region of 146 shallow-water species excluding undescribed or non-described taxa in earlier papers. Within the populations of some of the species collected were a few exceptionally large individuals, adding to previous records of unusually large specimens of mollusks from this region of the Atlantic coast. Additionally, some species of mollusks (*Tectura testudinalis, Eupleura semisulcata* [Gastropoda], *Tridonta borealis* [Bivalvia]) and some non-mollusks (the ascidian *Ecteinascidia turbinata* and a confirmation of an extension of the anthozoan *Peachia parasitica*) have been found in the waters surrounding Assateague, well outside of their previously reported geographic ranges. The results of the present study suggest the need for a re-evaluation of possible environmental shifts that could have taken place since the collections of the early 1900s and have elsewhere been implicated in the change of malacofauna of Assateague Island since that time. Additionally, range extensions reported could reflect a subtle geographic transition zone, newly introduced species, or, most likely, an understudied coastal area.

INTRODUCTION

Three previous notable surveys of marine and estuarine mollusks have been conducted at or just adjacent to Assateague Island along the Maryland and Virginia, USA, coast. The first, by Henderson & Bartsch (1914), reported 37 species of bivalves and 44 species of gastropods from nearby Chincoteague Island, Virginia, from collections made during the course of a week in the summer of 1913. Fourteen of the gastropods reported in their study were described as new species. In particular, among other gastropods, they described as new some very small snails including: *Bittiolum alternatum virginicum, Odostomia pocahontasae, O. virginica, Turbonilla pocahontasae, T. powhatani, T. toyatani,* and *T. virginica.* Among the 14 new species were three others they believed were new but of which the specimens were "too poor to serve for description" (Henderson & Bartsch, 1914). It is unlikely that these latter specimens truly represent new species. Within the individual genera, their other "new species" are often difficult to distinguish as morphologically unique, and some are likely subtaxa or ecophenotypes of other species, e.g., *Diastoma virginica* Henderson & Bartsch 1914 = *Bittiolum alternatum virginicum* = probably a variant of *Bittiolum varium* (Pfeiffer, 1840). The validity of several of their new species awaits detailed examination, as many other species described as new by Bartsch have already been placed in synonomy of previously described taxa. Counts & Bashore (1991) made similar collections between April 1988 and August 1989, but expanded their geographic coverage to include all of Assateague Island. They found 73 species of mollusks, 32 species of bivalves, 39 species of gastropods, and one species each of Polyplacophora and Cephalopoda. However, of the 81 valid or newly described species of Mollusca reported by Henderson & Bartsch, only 50 were reported as still present 75 years after their 1913 collection, and Counts & Bashore (1991) reported an additional 25 species not found during the study of Henderson & Bartsch. More recently, Homer et al. (1997) surveyed the mollusks of the Maryland coast in a "shellfish inventory" for the Maryland Department of Natural Resources. The latter study was intended to form a baseline for "future management needs" of the Maryland coast, in particular for commercially important mollusks (e.g., *Crassostrea virginica, Mercenaria mercenaria*) of the region. They recovered 63 live molluscan taxa during their study plus 10 species represented by shells only. Of their recovered species, 16 were previously unrecorded from the Maryland coast.

During several collections from 1994–1996, we found live representatives of 101 species and valves of an additional seven species of mollusks from along areas comparable to these other collections. Our data showed significant variation in the malacofauna reported in all previous studies plus some interesting range extensions, and evidence of "gigantism" among some of the mollusks in the area. This study collected 27 species of mollusks not recorded in the previous three major studies. Similarly, each of the studies had at least some species not found by the others. The faunal variations found among the various studies are significant, and while our overall collection most closely overlaps with that of Counts & Bashore (1991) (in terms of most species matches), interesting differences appear between various collections of gastropods and between all pairs of previous collections. If nothing else, it is clear this mid-Atlantic coastal region has a wide array of microhabitats that hold many hitherto unrecorded taxa.

METHODS

Quantitative and qualitative sampling was carried out during midsummer, late autumn, and early spring during 1994, 1995, and 1996. All primary shallow-water marine habitats along coastal Assateague and Chincoteague were sampled. Qualitative samples were taken at irregular sites along Assateague, Maryland, and Virginia (Figure 1) with kicknets, Yabby pumps, trawls, seines, and by hand collecting. Habitats sampled qualitatively included jetties, extensive mudflats (Tom's Cove, Little Tom's Cove, and Wash Flats), benthic trawls (especially in Cockle and Mosquito creeks), grabs to depths of 15 m (especially near the mouth of Chincoteague Bay at Turner's Lump and adjacent waters), and oyster beds. The rock jetty at Memorial Park, Chincoteague was also carefully searched for epifauna and crevice dwellers. Since the time of collection, the original rock jetty at Memorial Park has been replaced with a much more extensive wooden (treated) and rock structure and boat launch. Additionally, we sampled the eelgrass beds adjacent to nearby Greenbackville, Virginia.

As part of a larger survey of macroinvertebrates of Assateague Island (Counts & Prezant, 2001), sampling stations were established along transects at uniform distances from shore and/or water depths along the island to include ocean near-shore sandy bottom, bay sandy bottom, bay submerged aquatic seagrass beds, bay intertidal mudflats, fringing marshes, and bay muddy bottom/tidal gut/embayments. Specifically (Figure 1), along each of four separate oceanside transects (O-2, O-7, O-12, O-16), three sampling stations were established at mid-swash zones, 5 m from shore (subtidal), and 25 m from shore (also subtidal). Twelve transects within Chincoteague Bay were established (B-1 through B-4 and B-7 through B-16), each with four sampling stations that included: mid-swash zone, 0.5 m depth relative to mean high tide (subtidal), 1.0 m depth (subtidal), and 1.5 m depth (subtidal). Six replicates were taken at each site with a small box core sampler. These individual sites are described in the the next section.

All samples were preserved with 5% ($CaCO_3$) buffered formalin, washed in water and transferred to 70% ethanol for storage. Identifications were made in the laboratory using standard reference works. Collections have been deposited in the mollusk collections of Montclair State University, the University of Maryland Eastern Shore, and the American Museum of Natural History, New York.

Our qualitative data allowed a comparison with the few more complete compilations of molluscan taxa collected from the Assateague and Chincoteague coasts. We used a Bray-Curtis similarity index using PRIMER version 5.0 (Plymouth Routines in Multivariate Ecological Research, Carr [1997]) to compare our species list with those compiled by Henderson & Bartsch (1914), Counts & Bashore (1991), and Homer et al. (1997). Additionally, we used this program to perform cluster analyses among the various studies to find highest levels of similarity in collections. In all analytical work, we discounted any taxa not fully identified in previously published work (e.g., *Turbonilla* sp.).

RESULTS AND DISCUSSION

Description of the Study Area

Assateague Island is a barrier island system located on the southern Atlantic coast of Maryland extending southward to the northern coast of Virginia (Figure 1). The island is approximately 58 km in length and averages 0.8 km in width. It is bounded on the north by Ocean City Inlet (separating Assateague from Fenwick Island), on the south by Chincoteague Inlet, on the east by the Atlantic Ocean, and on the west by Sinepuxent and Chincoteague Bays. The average depth of Sinepuxent Bay ranges from 1.0 to 1.5 m, with a 2 m deep channel, and deepens to 5–6 m at Ocean City Inlet. The maximum width of Chincoteague Bay is 11.6 km, and the entire back bay system has an area of 428.9 km^2 (Biggs, 1970). The depth of Chincoteague Bay ranges from 1 to 3 m, deepening to 38 m at Chincoteague Inlet. The southern end of the island contains Tom's Cove, formed by an eastward-bending sand spit (Fishing Point) and the main body of the island. The average depth of Tom's Cove is 1 m.

Seiling (1954) described the physical characteristics of the waters surrounding Assateague Island. In summer months, water temperatures are cooler at the inlets and warmer in the shallow bays. In the winter, the pattern is

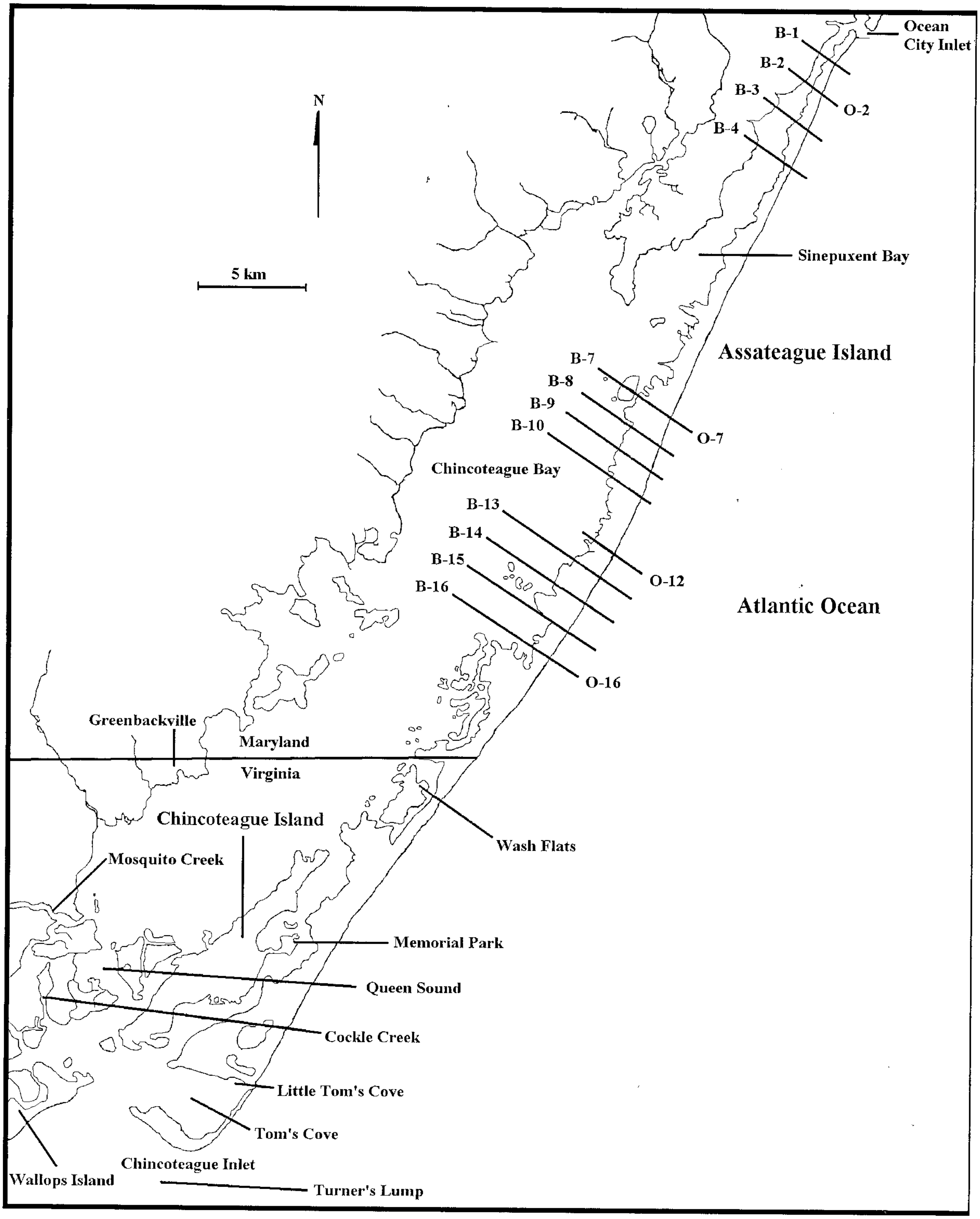

Figure 1. Assateague Island, Maryland and Virginia. The map shows transect lines along Chincoteague Bay (represented by B-transect lines) and ocean coast (represented by O-transect lines). See text for description of transect sites. Other sampling areas are labeled by name.

reversed, and occasionally the bays will freeze over. In summer, salinities decrease toward the inlets where tidal surge mixes seawater with high salinity bay water. The salinity pattern reverses during the winter and spring months. Summer salinity patterns result from a net loss from evaporation that is made up by tidal inflow and minimal freshwater inflow streams on the mainland (Pellenbarg & Biggs, 1970). Summer 1989 was characterized by higher than usual rainfall, and salinities ranged from 24 to 35 ppt in Chincoteague Bay, the highest salinities being measured at the inlets. Tidal amplitudes are not remarkable, being approximately 1 m at the inlets and 0.33 m in the bays. Tidal currents of Chincoteague and Sinepuxent bays are mostly independent of the non-tidal oceanic currents, and water flows away from the inlets at Ocean City and at Chincoteague as the tide rises (Pellenbarg & Biggs, 1970). Bay water circulation is such that the total water movement of the bays allows a daily water exchange of approximately 7.5% from outside sources (Pritchard, 1960). Pellenbarg & Biggs (1970) reported the bays to be essentially stagnant and intensely heated and stratified during the summer months. Seiling (1954) noted that currents throughout the bays, although of no great magnitude, could have some influence on shellfish larval distribution.

Atlantic coastal waters of Assateague Island are shallow, and Pellenbarg & Biggs (1970) noted that they become rapidly stratified by mid-April and that there is little mixing between thermally stratified waters. Summer surface currents are generally onshore, and the entire water mass has a northerly drift, perhaps due to the nearby Gulf Stream (Pellenbarg & Biggs, 1970).

While the overall exposed beach along Assateague was quite uniform (mid-energy medium course sand sediment), the bay side was somewhat variable. The sites used for transects (as indicated on Figure 1) include the following (B = Bay side; O = Ocean side):

B-1: 1 km south of Ocean City Inlet. A sandy shore bordering a *Spartina alterniflora* dominant marsh. Relatively firm substratum with some fragmented macroalgae accumulations. The 1.0 m depth site along the transect was located 40 m from shore indicating a relatively shallow beach slope. Sediments from deeper (0.5 and 1.0 m depths) sites were muddy with a diatom or cyanobacter coating (slippery surface over firm mud). Sediments from all depths had a hydrogen sulfide odor, which was strongest at the 0.5 m depth site.

B-2: 3 km south of Ocean City Inlet. The swash zone occurred as an overwash flat with soft sediments; sporadic algal clumps; swash zone sediment was dark colored with hydrogen sulfide odor; 0.5 m depth subtidal sediments had a muddy silt covering. The gently sloping beach dropped to the 1.0 m depth site at 50 m from the swash zone.

B-3: 5 km south of Ocean City Inlet. Swash zone is an eroding salt marsh perimeter. Substratum in swash had a hydrogen sulfide odor; no odor from subtidal sediments; No shell fragments. 1.0 m depth site located 50 m from shore.

B-4: 7 km south of Ocean City Inlet. Very shallow decline to about 0.75 m. Sandy sediments. No sulfide odors in sediments collected. 1.0 m depth station located 80–85 m from shore.

B-7: 13 km south of Ocean City Inlet. Swash zone along a *Spartina* marsh gut, other station sites within gut. Turbid water caused by suspended solids; sediment anaerobic close to surface. Steeper slope beach with 1.0 m depth located 10 m from shore. Some submerged vegetation at 1.0 m depth.

B-8: 15 km south of Ocean City Inlet. Very shallow sloping beach with swash zone within *Spartina* marsh and 0.5 and 1.0 m depth stations in embayment. 1.0 m depth station located 125 m from shore. Sandy, firm substratum; anaerobic in shallower stations.

B-9: 17 km south of Ocean City Inlet. Beach front a bit steeper with 1.0 m meter station located 30 m from shore. Swash zone at edge of shallow gut with 0.5 m and 1.0 m stations located within submerged aquatic vegetation (SAV). Soft sediments black to gray in color.

B-10: 19 km south of Ocean City Inlet. Swash zone along marsh front with deeper stations in shallow gut about 45 m from shore. Plant fragments in swash zone; swash zone sediments with hydrogen sulfide odor.

B-13: 25 km south of Ocean City Inlet. Very shallow beach with 1.0 m depth located 140 m beyond swash zone. Entire station part of a tidal flat with fine sand substratum; only swash zone sediment had a sulfide odor.

B-14: 27 km south of Ocean City Inlet. 1.0 m depth located only 15 m from shore, comparatively steep beach. Swash zone an eroding marsh front; 1.0 m depth station with SAV (*Zostera marina*). Swash zone sediment clumped mud grading to fine to medium sands with increasing depth.

B-15: 29 km south of Ocean City Inlet. Relatively steep beach with 1.0 m depth located 20 m from shore. Swash zone part of *Spartina* marsh; 1.0 m depth with SAV. Firm substratum with sulfide odor in swash zone sediments only.

B-16: 31 km south of Ocean City Inlet. Relatively steep beach with 1.0 m depth located 20 m from shore. Swash zone is part of Marsh Island Cove, a low *Spartina* marsh. Eelgrass beds at 0.5 and 1.0 m depths. Swash zone sediments with sulfide odor. Sediments in swash zone muddy with probable cyanobacter and/or diatom cover. Deeper sites with sandier substratum.

Ocean sites were located in direct line with bay sites B-2, 7, 12, and 17 and were nearly identical in general appearance: fine to medium sand, low to mid-energy beaches with mid-grade slope. Each ocean transect had samples taken (six replicates) at the swash zone, 0.5 and 1.0 m depths.

Malacofauna, Environment, and Changes through Time and among Studies

Assateague and Chincoteague Islands and their nearshore environments offer a wide array of soft sediment habitats ranging from mud flats to marshes, sea grass beds to sand beaches. Numerous jetties and piers add artificial hard substrata that are densely colonized by epifauna. Oyster beds, natural and planted, offer an additional hard surface and crevice habitat for various mollusks. A large number of variably detailed general surveys have included at least part of our study sites. Casey & Wesche (1981) examined the coastal benthos of Maryland's bays. Their seasonal collections included two locations in Chincoteague Bay. Using an otter trawl (6.35 mm mesh) and a Ponar grab (sieved at 1.0 mm), they recovered a total of 15 species of mollusks. They also collected another 142 species of non-molluscan benthic organisms. In all of their samples, *Mytilus edulis* dominated in terms of sheer numbers, composing 87% of all individuals collected (T = 50,033 in spring and winter samples). The bias toward *M. edulis* probably indicates a bias in sample sites and thus sampling substratum and habitat. Blue mussels are frequently not only dominant organisms in terms of sheer numbers in a community, but also can serve to inhibit settlement of other species, thus reducing overall diversity. Seasonally, however, the authors found a significant overall decline in the number of organisms and number of taxa recovered from their spring sampling period (late April to early May) to their summer sampling (late July to early August). In spring 1981, they collected 11 species of mollusks. This dropped to nine in the summer collection. In fall 1981, they collected nine species of mollusks (six gastropods, three bivalves) while in their winter collection this dropped to a total of five (two gastropods, three bivalves). The most commonly collected species for all seasons combined was the relatively small *Tellina agilis,* an infaunal bivalve usually inhabiting fine sand to mud. The likelihood that there were only 15 species of mollusks present during the latter study is remote. More likely, the low diversity reflects a combination of compromised sampling techniques (the authors allude to grab samples that lacked adequate "bite"), relatively infrequent sampling, and poor preservation (some specimens were difficult to identify because of preservation problems).

Similar to the study noted above, Drobek et al. (1970), in a final report on the environment of Assateague Island, listed only 12 species of mollusks. These authors sampled 64 sites within Chincoteague Bay, from Ocean City Inlet to the Virginia border, using a shallow-water escalator harvester. They note that this "gear permits a quantitative removal from the bottom of all bottom-dwelling animals over approximately 1 cm in length." Thus, their sampling missed the smaller biota.

More comprehensive studies targeted the malacofauna specifically and revealed a much more diverse molluscan biota. Henderson & Bartsch (1914) reported 81 species (excluding two *Turbonilla* that they presumed new but did not describe) from Chincoteague Island. Counts & Bashore (1991) found 73. (Note: The text and tables in Counts & Bashore [1991] are not in agreement; the appropriate counts for that paper are taken from their Table 1.) Homer et al. (1997) reported a total of 73 molluscan taxa from the Maryland coast. We found 108 species of mollusks from this region (Table 1), a total greater than that in any previous study. In all studies combined, there are 146 species of mollusks listed from this region (also excluding undescribed or nondescribed taxa listed by Homer et al. [1997]). Homer et al. (1997) suggested that there were several factors that could be associated with the molluscan diversity found. These include the polyhaline environment that "allows the more tolerant marine species to exploit this system, adding to the true estuarine species." Additionally, they note the diversity of benthic habitats based on a wide array of sediment types as a possible factor accounting for the relatively high molluscan diversity. In our collections, mollusks were found in a wide array of habitats that reflect the diversity of substrata and other resources available in the region for initial settlement (see Table 2 for listing of general habitat distribution and specific localities based on transects). Lastly, Homer et al. (1997) suggested that the location of Chincoteague Bay offers a transitional zone, located at the south end of the Virginian province, allowing a blending with several Carolinian species. Nevertheless, among all studies through time, we see significant differences among total species listed.

We found 47 species of bivalves, compared to 32 by Counts & Bashore (1991), 37 by Henderson & Bartsch (1914), and 31 by Homer et al. (1997) (Table 3). Of these, we found 19 not reported by Counts & Bashore (1991), 20 not found by Henderson & Bartsch (1914), and 19 not reported by Homer et al. (1997) (Table 4). On the other hand, Counts & Bashore reported six bivalve species we did not discover, Henderson & Bartsch found 10 not on our present list, and Homer et al. (1997) reported three that we did not recover. These kinds of differences are evaluated more carefully below where we examine specific similarities and differences in malacofauna. In some cases they represent subspecies of questionable validity; in others, they could represent drift of empty valves (reported as such in our study but not differentiated from living mollusks by Henderson & Bartsch (1914) and Counts & Bashore (1991). In all, the three earlier studies and the present study have a total overlap of only 13 species of bivalves. We found nine species of bivalves not found by Henderson & Bartsch (1914), Counts & Bashore (1991), nor Homer et al. (1997). Thus only about 22% of the species of bivalves we found in the present study were found in all three previous studies.

Of the 58 reported gastropods in the present study, we

Table 1

Mollusca of Assateague Island, Maryland and Virginia. A comparison of results from Henderson & Bartsch (1914) (A), Counts & Bashore (1991) (B), Homer et al. [coastal Maryland study, 1993–1996] (1997) (C) and the present study (D). Notes are presented in right hand column. + = Present; – = Absent; **G** = "Giant" specimen(s); **R** = Range extension; **S** = Shell only. (Note: Counts Bashore [1991] did not distinguish live animals from shells only.) In cases where the taxonomic validity of a particular species is in question (either because of a debate or question in the literature; overviews in Turgeon et al., 1998), it is also indicated under the notes column. Undescribed species, species thought to be new, or nondescribed taxa (e.g., two species of *Turbonilla* in Henderson & Bartsch and seven species of gastropods in Homer et al. listed as sp.) are not included in this list nor in any numerical analyses.

Species	A	B	C	D	Notes
BIVALVIA					
Abra aequalis (Say, 1822)	+	–	–	–	
Aligena elevata (Stimpson, 1851)	–	–	+	+	
Anadara ovalis (Bruguière, 1789)	+	+	+	+	*Scapharca campechiensis pexata* in Henderson & Bartsch (1914)
Anadara transversa (Say, 1822)	+	+	+	+	*Scapharca transversa* Say in Henderson & Bartsch (1914)
Anomia simplex d'Orbigny, 1842	+	+	+	+	*Anomia glabra* also listed by Henderson & Bartsch (1914) but almost certainly an error
Argopecten gibbus (Linnaeus, 1758)	+	+	–	–	Henderson & Bartsch (1914) list as *Pecten gibbus irradians*—probably a juvenile *A. irradians irradians*
Argopecten irradians f. *concentricus* (Say, 1822)	–	+	–	–	Planted by M. Castagna, VIMS, Wachapreague, VA
Argopecten irradians irradians (Lamarck, 1819)	–	+	S	S	Planted by M. Castagna, VIMS, Wachapreague, VA
Astarte castanea (Say, 1822)	+	+	–	–	
Barnea truncata (Say, 1822)	–	+	–	+	
Brachidontes exustus (Linnaeus, 1758)	–	–	–	+	
Chione cancellata (Linnaeus, 1767)	+	+	–	S	
Circomphalus strigillinus (Dall, 1902)	–	–	–	+	
Cyrenoidea floridana (Dall, 1896)	–	–	–	+	
Corbula contracta Say, 1822	+	–	–	+	
Crassinella lunulata (Conrad, 1834)	+	+	–	–	
Crassostrea virginica (Gmelin, 1791)	+	+	+	+	
Cyclinella tenuis (Récluz, 1852)	–	–	R	–	
Cyclocardia borealis (Conrad, 1831)	+	+	–	–	*Venericardia granulosa* Say = *Cardita borealis* Henderson & Bartsch in Henderson & Bartsch 1914)
Cyrtopleura costata (Linnaeus, 1758)	+	+	+	+	
Dinocardium robustum (Lightfoot, 1786)	S	–	–	–	
Divaricella quadrisulcata (d'Orbigny, 1842)	+	+	–	S	
Donax variabilis Say, 1822	+	+	+	+	
Ensis directus Conrad, 1843	–	+	+	+	
Ensis minor Dall, 1900	+	–	–	–	
Gemma gemma (Totten, 1834)	–	+	+	+	Very common on mudflats, within *Limulus* depressions
Geukensia demissa (Dillwyn, 1817)	–	+	+	+	
Gouldia cerina (C.B. Adams, 1845)	–	–	–	+	
Ischadium recurvum (Rafinesque, 1820)	–	+	+	–	
Laevicardium mortoni (Conrad, 1830)	+	–	–	–	
Linga pensylvanica (Linnaeus, 1758)	S	–	–	–	*Phacoides aurantia* Deshayes in Henderson & Bartsch (1914)
Lyonsia hyalina Conrad, 1831	+	–	+	G	Rare intertidally
Macoma balthica (Linnaeus, 1758)	–	+	+	+	
Macoma tenta (Say, 1834)	+	–	+	+	*Psammacoma tenta* Say in Henderson & Bartsch (1914)

Table 1

Continued.

Species	A	B	C	D	Notes
Mercenaria mercenaria (Linnaeus, 1758)	+	+	+	+	
Mulinia lateralis (Say, 1822)	+	+	+	+	
Mya arenaria Linnaeus, 1758	+	+	S	+	
Mysella planulata (Stimpson, 1851)	−	−	+	−	
Mytilus edulis Linnaeus, 1758	+	+	+	+	
Noetia ponderosa (Say, 1822)	+	+	+	+	
Nucula proxima Say, 1822	+	−	+	+	Subtidal only at Turner's Lump
Nuculana acuta (Conrad, 1831)	+	−	−	+	
Petricola pholadiformis (Lamarck, 1818)	+	+	+	+	
Pitar morrhuanus (Linsley, 1848)	+	−	+	+	
Placopecten magellanicus (Gmelin, 1791)	−	−	−	S	
Pleuromeris tridentata (Say, 1826)	+	−	−	R	
Polymesoda caroliniana Bosc, 1802	−	−	−	+	
Raeta plicatella (Lamarck, 1818)	+	+	−	+	
Siliqua costata Say, 1822	−	−	−	S	
Solemya velum Say, 1822	−	+	+	+	Very common near Wash Flats, approx. 1–1.5 m depth
Solen viridis Say, 1821	−	+	+	+	
Spisula solidissima (Dillwyn, 1817)	+	+	+	+	
Spisula solidissima similis (Say, 1822)	+	−	−	−	Controversial subspecies, see Cargnelli et al. (1999)
Tagelus divisus (Spengler, 1794)	+	−	+	+	
Tagelus plebius (Lightfoot, 1786)	+	+	+	+	*Tagelus gibbus* Spengler in Henderson & Bartsch (1914)
Tellina aequistriata Say, 1824	−	−	−	+	
Tellina agilis Stimpson, 1857	+	+	+	+	*Angulus tenera* Say in Henderson & Bartsch (1914)
Tellina versicolor DeKay, 1843	−	−	−	+	
Teredo navalis Linnaeus, 1758	−	−	−	+	In wood debris on beaches
Tridonta borealis (Schumacher, 1817)	−	−	−	R	Subtidal only at Turner's Lump; Formerly *Astarte borealis*
Yoldia limatula (Say, 1831)	+	−	−	+	Subtidal only at Turner's Lump
GASTROPODA					
Acanthodoris pilosa (Müller, 1776)	−	+	−	+	
Acteocina bidentata (d'Orbigny, 1841)	+	+	+	+	In Henderson & Bartsch (1914) as *Cylichnella biplicata* & Homer et al. as *C. bidentata*
Acteocina canaliculata (Say, 1822)	+	+	+	+	*Tornatina canaliculata* Say in Henderson & Bartsch (1914)
Acteon punctostriatus Adams, 1840	−	−	−	+	
Assiminea succinea (Pfeiffer, 1840)	−	−	−	+	
Astyris lunata (Say, 1826)	+	+	+	+	Formerly *Mitrella lunata*
Bittiolum alternatum (Say, 1822)	−	−	−	+	*Zostera* beds; possibly an ecological variant of *B. varium. Fissurella alternata* Say in Henderson & Bartsch (1914)
Bittiolum alternatum virginicum (Henderson & Bartsch, 1914)	G	−	−	−	Probably not a valid (sub)taxon but a variant of *B. varium*
Bittiolum varium (Pfeiffer, 1840)	−	−	+	+	*Zostera* beds
Boonea bisuturalis (Say, 1822)	−	−	−	+	On *Crassostrea virginica*
Boonea impressa (Say, 1822)	+	−	S	+	On *Crassostrea virginica*
Boonea seminuda (C. B. Adams, 1839)	−	−	−	+	=*Odostomia toyatani* of Henderson & Bartsch (1914); On *Crassostrea virginica*
Buccinum undatum Linnaeus, 1758	−	+	−	−	
Busycon carica (Gmelin, 1791)	+	+	−	+	Very large specimen. *Fulgur carica* in Henderson & Bartsch (1914)

Table 1

Continued.

Species	A	B	C	D	Notes
Busycon sinistrum (Hollister, 1958)	+	+	−	−	*Fulgar perversa* Linnaeus in Henderson & Bartsch (1914)
Busycotypus canaliculatus (Linnaeus, 1758)	+	+	+	+	*Sycotypus canaliculatus* Say in Henderson & Bartsch (1914)
Cerithidea scalariformis (Say, 1826)	−	−	−	+	
Cerithiopsis emersoni (C.B. Adams, 1839)	−	−	S	−	
Cerithiopsis greenii (C.B. Adams, 1839)	+	−	+	+	
Clathurella jewetti (Stearns, 1873)	+	−	−	−	Uncertain taxon
Conchiolepis parasitica Stimpson, 1858	−	−	−	+	
Costoanachis avara (Say, 1822)	+	+	+	+	*Anachis avara* in other reports
Cratena pilata (Gould, 1870)	−	+	−	−	
Crepidula convexa Say, 1822	+	+	+	G	
Crepidula fornicata (Linnaeus, 1758)	+	+	+	+	Very large specimens
Crepidula plana (Say, 1822)	+	+	+	+	
Cresis virgula (Rang, 1828)	−	+	−	−	
Crucibulum striatum Say, 1824	−	+	−	S	
Diodora cayenensis (Lamarck, 1822)	+	+	S	S	
Doris verrucosa Linnaeus, 1758	−	−	+	−	Chincoteague only
Elysia chloritica (Gould, 1870)	−	−	−	+	*Zostera* beds
Epitonium angulatum (Say, 1830)	−	+	−	−	
Epitonium humphreysi (Kiener, 1838)	+	+	−	+	*E. sayana* Dall in Henderson & Bartsch (1914)
Epitonium multistriatum (Say, 1826)	+	+	+	+	
Epitonium rupicolum (Kurtz, 1860)	+	+	+	+	*E. lineata* Say in Henderson & Bartsch (1914)
Eptinioum virginicum (Henderson & Bartsch, 1914)	+	−	−	−	Uncertain taxonomic validity
Eupleura caudata (Say, 1922)	+	+	+	+	
Eupleura sulcidentata Dall, 1890	−	−	−	R	Possible imports with oysters
Haminoea solitaria (Say, 1822)	−	−	+	+	
Hydrobia totteni Morrison, 1954	−	−	−	+	
Inodrillia dalli (Verrill & Smith, 1882)	−	+	−	+	
Kurtziella cerina (Kurtz & Stimpson, 1851)	+	+	−	+	*Mangilia cerina* Kurtz & Stimpson in Henderson & Bartsch (1914)
Kurtziella limonitella (Dall, 1884)	−	−	−	R	
Littoraria irrorata Say, 1822	+	+	−	+	
Littorina littorea (Linnaeus, 1758)	−	+	−	+	
Littorina saxatilis (Olivi, 1792)	−	+	−	+	
Lunatia heros (Say, 1822)	+	+	−	−	
Lunatia pallida (Broderip & Sowerby, 1829)	+	−	−	−	
Lunatia triserata (Broderip & Sowerby, 1829)	−	+	−	−	
Marginella roscida Redfield, 1860	+	−	−	−	*Marginella apicina borealis* Verrill in Henderson & Bartsch (1914)
Melampus bidentatus Say, 1922	−	+	+	+	
Melanella intermedia (Cantraine, 1835)	+	+	+	+	Usually found on sea cucumber *Holothuria impatiens* (Abbott, 1974); Henderson & Bartsch (1914) list *M. oleacea*—almost certainly *M. intermedia*
Nassarius obsoletus (Say, 1822)	+	+	+	+	
Nassarius trivittatus (Say, 1826)	+	+	+	+	*Tritia trivittata* Say in Henderson & Bartsch (1914)
Nassarius vibex (Say, 1822)	+	+	+	+	
Natica pusilla Say, 1822	+	−	−	−	Listed by Henderson & Bartsch (1914) but not so indicated in Table 1 in Counts & Bashore (1991)
Neverita duplicatus (Say, 1822)	+	+	+	+	
Odostomia pocahontasae Henderson & Bartsch, 1914	+	−	+	+	Uncertain taxonomic validity; on *Crassostrea virginica*

Table 1

Continued.

Species	A	B	C	D	Notes
Odostomia toyatani Henderson & Bartsch, 1914	+	−	−	−	Uncertain taxonomic validity
Odostomia virginica Henderson & Bartsch, 1914	+	−	−	−	
Olivella mutica (Say, 1822)	−	+	−	+	
Ovatella myosotis (Draparnaud, 1801)	−	−	−	+	
Pyramidella candida Mörch, 1875	−	−	−	+	
Pyramidella crenulata (Holmes, 1860)	−	−	R	+	Found in Chincoteague Bay in 1981 by Casey & Wesche (1982)
Pyrgocythara plicosa (C.B. Adams, 1850)	−	−	+	+	
Retusa obtusa (Montagu, 1807)	−	−	−	+	
Sayella fusca (C.B. Adams, 1839)	−	−	−	+	Population with variable eyes; under rocks, Chincoteague
Seila adamsi (H.C. Lea, 1845)	−	−	+	S	
Sinum perspectivum (Say, 1831)	+	+	−	+	*Sigaretus perspectivus* Say in Henderson & Bartsch (1914)
Stramonita haemastoma floridana (Conrad, 1837)	−	+	S	+	Formerly *Thais haemastoma*
Tectura testudinalis (Müller, 1776)	−	−	−	R	Very small specimens
Terebra concava Say, 1827	+	−	−	−	
Terebra dislocata (Say, 1822)	+	+	−	+	
Triphora nigrocincta (C.B. Adams, 1839)	+	−	S	−	
Triphora pyrrha Henderson & Bartsch, 1914	+	−	−	−	
Turbonilla interrupta (Totten, 1835)	−	−	+	+	
Turbonilla pocahontasae Henderson & Bartsch, 1914	+	−	S	−	Described by Henderson & Bartsch (1914) in their original collection; questionable taxonomic validity
Turbonilla powhatani Henderson & Bartsch, 1914	+	−	+	−	Described by Henderson & Bartsch (1914) in their original collection; questionable taxonomic validity
Turbonilla toyatani Henderson & Bartsch, 1914	+	−	−	−	Described by Henderson & Bartsch (1914) in their original collection; questionable taxonomic validity
Turbonilla virginica Henderson & Bartsch, 1914	+	−	−	−	Described by Henderson & Bartsch (1914) in their original collection; questionable taxonomic validity
Urosalpinx cinerea (Say, 1822)	G	+	+	+	Very large specimens reported by Baker, 1951, Chincoteague
CEPHALOPODA					
Loligo pealeii Lesueur, 1821	−	+	−	+	
Loliguncula brevis (Blainville, 1823)	−	−	−	+	
POLYPLACOPHORA					
Chaetopleura apiculata (Say, 1830)	−	+	−	G	

matched the list of Henderson & Bartsch (1914) with 27 (Table 5). Our list and that of Counts & Bashore (1991) overlapped with 32 species and there was an overlap of 29 species with Homer et al. (1997). All three lists matched with 22 species. We found 14 species of gastropods not found by Henderson & Bartsch (1914), Counts & Bashore (1991), nor Homer et al. (1997). On the other hand, Henderson & Bartsch (1914) noted 17 species of gastropods that our list lacks; Counts & Bayshore (1991) listed seven not on the current list, and Homer et al. (1997) found five species of gastropods we did not find (Table 4).

Counts & Bashore (1991) suggested that changes in the back-bay circulation and resultant salinity changes could account for differences in malacofauna over time. This speculation was based, in part, on the work of Castagna & Chanley (1973) who examined the distribution of mollusks along coastal Virginia as influenced by salinity. In addition to other stochastic events that forced opening of new inlets through the island, in 1933 a hurricane opened the Ocean City Inlet, and this new opening was secured by a series of jetties and maintained by dredging. The result of this major inlet was increased flow to, and thus salinity in, the back-bay waters. Specifically, Counts & Bashore (1991) found no pyramidellids, and suggested this was a result of a shift in salinity in the bay due to the inflow of seawater. Pyramidellids were recorded by Henderson & Bartsch (1914) and more recently by Ho-

Table 2

Habitat and local distribution of malacofauna recovered from Assateague and Chincoteague during this study. Habitat distribution is representative and does not indicate total distribution; sites indicated in middle column are from transects described in text. Greenbackville, Virginia is the closest town to a small eelgrass bed; Locations listed as "Assateague Island" represent species common along the long stretch of sand beaches in the state park on Assateague.

Species (Taxon)	Representative collection locations	Habitat note
BIVALVIA		
Aligena elevata (Stimpson, 1851)	Tom's Cove	fine sand-mud; associated with *Diopatra* tubes
Anadara ovalis (Bruguière, 1789)	Queen Sound attached by byssus to *Ulva*	muddy sand in shallow water subtidally
Anadara transversa (Say, 1822)	B-16	muddy bottom below low tide line
Anomia simplex d'Orbigny, 1842	B-14, B-16; Cockle Creek	epifaunal on mollusk values
Argopecten irradians irradians (Lamarck, 1819)	Assateague Island; Greenbackville,	seagrass beds, shallows
Astarte borealis (Schumacher, 1817)	B-3	subtidal, benthic in mud and fine sand
Barnea truncata (Say, 1822)	Wash flats	consolidated mud
Brachidontes exustus (Linnaeus, 1758)	Memorial Park	nestled among rocks
Chione cancellata (Linnaeus, 1767)	Assateague Island	beaches
Circomphalus strigillinus (Dall, 1902)	B-3, B-7, B-8, B-15	medium coarse sand with heavy clam clumps
Cyrenoidea floridana (Dall, 1896)	B-14	brackish water species
Corbula contracta Say, 1822	B-15	medium coarse sand with heavy clay clumps
Crassostrea virginica (Gmelin, 1791)	Memorial Park	oyster beds, pilings, rock jetties
Cyclinella tenuis (Récluz, 1852)	Assateague Island	beaches
Cyrtopleura costata (Linnaeus, 1758)	Greenbackville	firm mud
Deminucula atacellana Schenck, 1939	Turner's Lump; Chincoteague Inlet	fine sand-mud
Divaricella quadrisulcata (d'Orbigny, 1842)	Assateague Island	beaches
Donax variabilis Say, 1822	O-2, O-7, O-12, O-16	high to mid-energy sand beaches
Ensis directus Conrad, 1843	B-4,B-7, B-8; Tom's Cove	low energy embayments in fine to mid sand
Gemma gemma (Totten, 1834)	B-1, B-2, B-3, B-4, B-7, B-8, B-10, B-11, B-13	quiet embayments, mud to fine sand, often in depressions
Geukensia demissa (Dillwyn, 1817)	B-4, B-8, B-14	*Spartina* marshes, often nested among roots
Gouldia cerina (C.B. Adams, 1845)	Tom's Cove	found attached to loose shell material
Lyonsia hyalina Conrad, 1831	Tom's Cove	less than 2 m depth in fine sand
Macoma balthica (Linnaeus, 1758)	B-14, B15	common intertidal
Macoma tenta (Say, 1834)	B-2, B-3, B-14	common in shallow sandy water
Mercenaria mercenaria (Linnaeus, 1758)	B-1, B-4, B-8, B-13, B-16	common in shallow sand and mud bays
Mulinia lateralis (Say, 1822)	B-1, B-4, B-7, B-14, B-15; Tom's Cove	shallow sandy quiet waters
Mya arenaria Linnaeus, 1758	Tom's Cove	shallow sandy intertidal to just subtidal
Mytilus edulis Linnaeus, 1758	B-1, B-2, B-8, B-9, B-14	attached to solid objects in marshes
Noetia poderosa (Say, 1822)	Cockle Creek	among shell "litter"
Nucula acuta (Conrad, 1831)	Turner's Lump	fine sand-mud
Nucula proxima Say, 1822	Turner's Lump	fine sand-mud
Petricola pholadiformis (Lamarck, 1818)	Cockle Creek	shell mix
Pitar morrhuanus (Linsley, 1848)	Assateague Island	beaches
Placopecten magellanicus (Gmelin, 1791)	Wash Flats	washed into embayment
Pleuromeris tridentata (Say, 1826)	Cockle Creek	among shell "litter"
Polymesoda caroliniana Bosc, 1802	B-4	sandy-mud
Raeta plicatella (Lamarck, 1818)	Assateague Island	beaches
Siliqua costata Say, 1822	B-4	shallow water sand flats
Solemya velum Say, 1822	B-3, B-7, B-8, B-9, B-10, B-13, B-14, B-15, B-16	shallow water in mud
Solen viridis Say, 1821	B-1; Wallops Beach	shallow water sand flats
Spisula solidissima (Dillwyn, 1817)	O-2, O-12, O-16; Wallops Beach (North)	subtidal on beaches
Tagelus divisus (Spengler, 1794)	B-1, B-8, B-9, B-13, B-14, B-15, B-16, O-16	shallow water
Tagelus plebius (Lightfoot, 1786)	B-4, B-13, B-15, B-16	shallow water in mud-sand intertidal area
Tellina aequistriata Say, 1824	Wash Flats	fine sand/mud
Tellina agilis Stimpson, 1857	B-1, B-2, B-3, B-4, B-8	common in medium to fine sand

Table 2

Continued.

Species (Taxon)	Representative collection locations	Habitat note
Tellina versicolor DeKay, 1843	B-1, B-2, B-3, B-4, B-7, O-2	common subtidal to 150 ft
Yoldia limatula (Say, 1831)	benthic Turner's Lump	infaunal, soft sediments
GASTROPODA		
Acanthodoris pilosa (Müller, 1776)	Cockle Creek	on sulfur sponges (*Halichondria*)
Acteon punctostriatus Adams, 1840	Assateague Island	beach
Acteocina bidentata (d'Orbigny, 1841)	Chincoteague Inlet	fine sand
Acteocina canaliculata (Say, 1822)	B-9, B-15, B-16	estuarine
Assiminea succinea (Pfeiffer, 1840)	Memorial Park	fine sand between rocks
Astyris lunata (Say, 1826)	B-1, B-2, B-3, B-10, B-14, B-15, B-16	found at low tide line
Bittiolum alternatum (Say, 1822)	B-8, B-9, B-14, B-15; Memorial Park	sand bottoms in quiet water from low tide line
Bittiolum varium (Pfeiffer, 1840)	B-7, B-8, B-9, B-10, B-13, B-14, B-15, B-16	exceptionally common in eelgrass
Boonea bisuturalis (Say, 1822)	Memorial Park jetty; Queen Sound	on oyster *Crassostrea virginica*
Boonea impressa (Say, 1822)	Memorial Park jetty	on oyster *Crassostrea virginica*
Boonea seminuda (C.B. Adams, 1839)	Memorial Park jetty	on oyster *Crassostrea virginica*
Busycon carica (Gmelin, 1791)	Wallops Beach (North); Assateague Island	beaches
Busycotypus canaliculatus (Linnaeus, 1758)	Assateague Island; Tom's Cove; Wash Flats	beaches
Cerithidea scalariformis (Say, 1826)	B-4	medium sand
Cerithiopsis greenii (C.B. Adams, 1839)	Assateague Island	beaches
Conchiolepis parasitica Stimpson, 1858	Memorial Park	subumbrella Scyphozoan *Chrysaora*
Costoanachis avara (Say, 1822)	Assateague Island; Tom's Cove	beaches, shallow calm waters
Crepidula convexa Say, 1822	Cockle Creek	on shell rubble
Crepidula fornicata (Linnaeus, 1758)	B-16; Tom's Cove; Wash Flats	attached to hard surfaces, including horseshoe crabs, shell rubble, etc.
Crepidula plana (Say, 1822)	O-2, O-7, O-12, O-16; Cockle Creek	frequently near internal edge of conch shell inhabited by hermit crab
Crucibulum striatum Say, 1824	Assateague Island	washed up on beach
Diastoma alternatum (Say, 1822)	Greenbackville	seagrass beds
Diodora cayensis (Lamarck, 1822)	Assateague Island	washed up on beaches
Elysia chloritica (Gould, 1870)	Greenbackville	seagrass beds
Epitonium humphreysi (Kiener, 1838)	B-4	fine sand/mud
Epitonium multistriatum (Say, 1826)	Chincoteague Inlet	among coarse sediments and shell rubble
Epitonium rupicolum (Kurtz, 1860)	Assateague Island	beaches
Eupleura caudata (Say, 1922)	Cockle Creek	among shell rubble
Eupleura sulcidentata Dall, 1890	Mosquito Creek; Memorial Park	oyster beds
Haminoea solitaria (Say, 1822)	B-15	white fine sand
Hydrobia totteni Morrison, 1954	B-8, B-9	shallow pools or marshes
Inodrillia dalli (Verrill & Smith, 1882)	Turner's Lump	usually deeper benthos
Kurtziella cerina (Kurtz & Stimpson, 1851)	Greenbackville	seagrass beds
Kurtziella limonitella (Dall, 1884)	Turner's Lump	mud
Littoraria irrorata Say, 1822	B-2, B-3, B-4, B-7, B-8, B-13, B-14	on (*Spartina*) and mud flat surfaces
Littorina littorea (Linnaeus, 1758)	Ocean City Inlet Jetty	cold water species found on rocks or other hard surfaces
Littorina saxatilis (Olivi, 1792)	Memorial Park	rocky surfaces and crevices
Melampus bidentatus Say, 1822	B-15; Chincoteague marsh	intertidal in marshes
Melanella intermedia (Cantraine, 1835)	Chincoteague Inlet	dredged in mixed sediment; shell mix to fine sand
Nassarius obsoletus (Say, 1822)	B-1, B-2, B-3, B-4, B-7, B-8, B-9, B-10, B-13, B-14; Chincoteague Inlet	very common on oozy, warm mud flats
Nassarius trivittatus (Say, 1826)	Turner's Lump	benthic, fine-medium sand
Nassarius vibex (Say, 1822)	B-8; Cockle Creek	common in sand and mudflats
Neverita duplicatus (Say, 1822)	Assateague Island (north end beach)	infaunal predator, just beneath sand surface
Odostomia pocahontasae Henderson & Bartsch, 1914	B-16	fine to very fine sand, some clay present at 1.0 m station
Olivella mutica (Say, 1822)	Assateague Island	beaches
Ovatella myosotis (Draparnaud, 1801	Memorial Park	in sand between rocks
Pyramidella candida Mörch, 1875	Memorial Park	shallow bays, oyster "parasite"
Pyramidella crenulata (Holmes, 1860)	B-3, B-7, B-8, B-14, B-15, B-16; Chincoteague Bay	shallow bays on sand, mud, or grass

Table 2

Continued.

Species (Taxon)	Representative collection locations	Habitat note
Pyrgocythara plicosa (C.B. Adams, 1850)	B-16; Memorial Park	fine to very fine sand, some clay present at 1.0 m station
Retusa obtusa (Montagu, 1807)	B-3, B-7, B-9, B-14, B-15, B-16	fine to very fine sand, some clay present at 1.0 m station
Sayella fusca (C.B. Adams, 1839)	B-4, B-7, B-9, B-13; Memorial Park	under rock and shell rubble, intertidal
Seila adamsi (H.C. Lea, 1845)	B-4, B-7, B-9, B-13; Chincoteague Channel	medium to fine sand with very fine sand at 1.5 m station
Sinum perspectivum (Say, 1831)	Assateague Island	mud to fine sand, just subtidal
Stramonita haemastoma floridana (Conrad, 1837)	Memorial Park	oyster and barnacle predator
Tectura testudinalis (Müller, 1776)	B-8, B-14; Cockle Creek	cold water species found on rocks or other hard surfaces
Terebra dislocata (Say, 1822)	O-12	shallow water
Turbonilla interrupta (Totten, 1835)	O-2	shallow water
Urosalpinx cinerea (Say, 1822)	B-16; Indian River Inlet	intertidal to a depth of 25 ft
CEPHALOPODA		
Loligo pealei Lesueur, 1821	Cockle Creek; Walker Point	nektonic
Loliguncula brevis (Blainville, 1823)	Cockle Creek; Turner's Lump	nektonic
POLYPLACOPHORA		
Chaetopleura apiculata (Say, 1830)	Cockle Creek; Queen Sound	benthic on shell rubble

mer et al. (1997). Our study found four species of pyramidellids, three associated with oyster beds. While it is possible that these small gastropods were absent during the 1991 study, it is more likely that they were present and overlooked in the oyster bed refugia. Additionally, a large population of a larger pyramidellid, *Sayella fusca,* was found under rocks at the Chincoteague Memorial Park jetty in 1994 and 1995. Interestingly, these small gastropods had a large number of eye variations. *Sayella fusca* normally has two small, circular, black basal eyes, but in this population a number of snails had only a left or right eye, sometimes a single central eye, and rarely no eyes. In more recent years, i.e., 1996 and 1997, these pyramidellids were absent at this site, and the original site has now been significantly modified by construction of a pier.

Table 3

Comparative number of total molluscan species recorded from Assateague and Chincoteague from Henderson & Bartsch (1914), Counts & Bashore (1991), Homer et al. (1997), and the present study. Species identified by Henderson & Bartsch (1914), especially among the very small gastropods, are included in their counts although some remain to be resolved taxonomically. The table also includes taxa identified from valves only (dead shells) as well as taxa that could represent unresolved ecomorphs but are listed in the literature as species. The table does not include the four taxa Henderson & Bartsch list as possible new species or the seven non-described taxa listed by Homer et al.

	Henderson & Bartsch (1914)	Counts & Bashore (1991)	Homer et al. (1997)	Present study
Bivalvia	37	32	31	47
Gastropoda	44	39	34	58
Polyplacophora	0	1	0	1
Cephalopoda	0	1	0	2
Total	81	73	65	108

It is relatively easy to account for some of the differences in malacofauna recovered in the four studies. Some small bivalves were likely overlooked previously (e.g., *Aligena elevata, Cyrenoidea floridana*). Others are probably of very patchy, perhaps rare occurrence (e.g., *Lyonsia hyalina*). It appears that Henderson & Bartsch (1914) did not carefully explore adjacent salt marshes, as indicated by the absence of common marsh fauna (*Geukensia demissa* and *Melampus bidentatus*) from their lists. On the other hand, Henderson & Bartsch (1914) found some larger bivalves not recovered in present collection or in those of Counts & Bashore (1991) (e.g., *Dinocardium robustum, Abra aequalis*), and it is more difficult to account for these differences. In some cases, the taxonomy of a group has not been firmly resolved and this could show itself as differences on our respective lists (e.g., pyramidellids, *Bittium-Bittiolum,* and Turridae, etc.). Additionally, the very small size of many of the gastropods (including species of *Odostomia* and *Turbonilla*) described by Henderson & Bartsch (1914) could lead to misidentifications or severe "splitting" of taxa (perhaps

Table 4

Comparative number of species uniquely found in each study compared to each other study. The number to the left of the diagonal line in each box represents the number of species found in the study listed at the top of the tables versus that on the left. The number to the right of the diagonal line, on the other hand, represents the number of species found uniquely in the study noted on the left of the table versus that on the top. For example, Henderson & Bartsch (1914) found 18 gastropods not found by Counts & Bashore (1991), whereas Counts & Bashore found 13 gastropods not collected by Henderson & Bartsch.

	Henderson & Bartsch		Counts & Bashore		Homer et al.	
	Bivalve	Gastropod	Bivalve	Gastropod	Bivalve	Gastropod
Counts & Bashore	15/10	18/13	xxxx	xxxx	xxxx	xxxx
Homer et al.	17/11	19/10	9/8	19/14	xxxx	xxxx
Present Study	10/20	17/31	9/19	7/26	3/19	5/29

based on ecophenotypes) and demand additional taxonomic examination using modern techniques. These presumed species are often difficult to distinguish based on shell alone, and the shell was the source of the prime characters used by Henderson & Bartsch. Henderson & Bartsch also identified a very large number of small mollusks they defined as new; many of these are now regarded as synonomies of other species. It is clear that the cluster of species described by Henderson & Bartsch is in dire need of re-examination in the future.

Taxonomic uncertainties, however, are not limited only to the small mollusks. Neither the present study nor other recent studies isolate *Spisula solidissima similis* as a valid subspecies of *S. solidissima.* This species is under taxonomic evaluation. *S. raveneli,* an example of the taxonomic problems within this genus, is found in the southernmost range of *S. solidissima* but of questionable species validity (Cargnelli et al., 1999) as well. We are probably looking at a series of ecophenotypes along the North American eastern seaboard. It is clear that there are taxonomic issues in all the lists used in this study and that many critical issues, at least at the species level, remain to be resolved.

The variability and large array of microhabitats, small size of many of the mollusks, temporal variability of some habitats (fringing marshes, seagrass beds, etc.), cryptic habits of some species, continued changes to and additions of artificial substrata (i.e., new piers, docks, pilings, etc.), examination of previously unexplored subtidal sites, and relative collection efforts among the various studies, could account for at least some of the differences among the studies. These same factors ensure that additional species will be found in the future. Certainly the creation and loss of inlets cutting through the island influences circulation, salinity, temperature, and predator access, and could thus shift species distributions. Major shifts in salinity altered the region's previously extensive oyster beds and coincidentally its associated fauna. For a review see Counts & Bashore (1991) and Homer et al. (1997).

Study Similarities and Differences

There are notable differences and similarities between and among the primary studies examined in this paper. Table 4 shows the uniqueness of specific studies as defined as species collected in one study and not a comparable study. Ignoring taxa listed as possibly new by Henderson & Bartsch (1914) and unidentified by Homer et al. (1997), the largest difference is between the present study and that of Henderson & Bartsch (1914). For instance, we collected 31 species of gastropods not listed

Table 5

Overlap of species between collections (Henderson & Bartsch [1914], Counts & Bashore [1991], Homer et al. [1997] and Present Study). The last column represents the total number of molluscan species (including cephalopods and chitons) found in common between the two studies noted in the left column.

	Bivalves	Gastropods	Total
Henderson & Bartsch and Counts & Bashore	22	26	50
Henderson & Bartsch and Homer et al.	20	24	44
Henderson & Bartsch and Present Study	27	27	57
Counts & Bashore and Homer et al.	23	29	54
Counts & Bashore and Present Study	26	32	60
Homer et al. and Present Study	28	29	60

Table 6

Similarity indices using Bray-Curtis analysis for molluscan taxa recovered from the present study and those of Henderson & Bartsch (1914), Counts & Bashore (1991) and Homer et al. (1997). A. Indices for all molluscan fauna. B. Indices for bivalves only. C. Indices for gastropods only.

	Henderson & Bartsch (1914)	Counts & Bashore (1991)	Homer et al. (1997)
A. ALL MOLLUSKS			
Counts & Bashore	62.338	xxxxx	xxxxx
Homer et al.	60.274	62.319	xxxxx
Present study	57.447	66.667	66.279
B. BIVALVIA			
Counts & Bashore	67.768	xxxxx	xxxxx
Homer et al.	58.824	73.016	xxxxx
Present study	64.286	65.823	71.795
C. GASTROPODA			
Counts & Bashore	63.415	xxxxx	xxxxx
Homer et al.	61.539	55.556	xxxxx
Present study	54.000	65.957	64.444

by Henderson & Bartsch. Perhaps of equal importance in total analysis is the similarity of species found between studies (Table 5). The highest similarity of bivalves (same species collected) can be found between Homer et al. (1997) and the present study. Counts & Bashore (1991) and the present study matched with a total of 60 species of mollusks.

The Bray-Curtis Index of Similarity was used to compare presence/absence and overlap of molluscan species between and among the four studies. Similarities between each pair of collections can also be found in Table 6. A comparison of degree of similarity between the present and each previous study can be found in the hierarchical clusters in Figure 2 (including total malacofauna and bivalves and gastropods examined separately). As can be seen in the clusters in Figure 2A, for overall mollusks the present study most closely aligns with Counts & Bashore (1991), and the latter two form a cluster with Homer et al. (1997). Only Henderson & Bartsch (1914) remain isolated with a total similarity index to all the other studies of about 65. For bivalves alone, Homer et al. (1997) cluster with Counts & Bashore (1991), and these two then form a cluster with the present study. Again, Henderson & Bartsch (1914) remain isolated. However, for gastropods alone, the present study most closely aligns with Counts & Bashore (1991).

The greatest similarity for all mollusks collected resides among the present study, Counts & Bashore (1991) and Homer et al. (1997) [similarity = 66.667 and 66.279, respectively]. Henderson & Bartsch (1914) and the present study had a similarity index of 57.447. Thus the earliest and the latest studies had the lowest degree of similarity, whereas the three more recent studies, with collections entailing more extensive effort and duration, were more similar. In the earliest study, the fauna were collected over a shorter period of time and using only the shore as the staging area for collections. The greatest similarity in bivalves collected was found between Counts & Bashore (1991) and Homer (1997) (similarity index = 73.016) (Table 6B). However, Counts & Bashore (1991) and the present study showed the highest similarity in gastropods collected (similarity index = 65.957) (Table 6C). The latter could reflect the careful perusal of varied habitats by these authors but more likely reflects the relatively lower number of gastropods by Counts & Bashore (1991) (39) with most being the more common species encountered. Additionally, the Bray-Curtis index does not overly weigh the overlap of 32 species (Table 5) and the relatively small number (seven; Table 4) of unique species collected by Counts & Bashore compared to the present study. Recall that the present study collected 108 species in toto compared to the next highest number of species collected (81 by Henderson & Bartsch, 1914). Thus the large number of non-overlapping taxa could create the lower levels of similarity in the newer studies when compared to each other or the earlier surveys. A large number of overlapping species could create the higher levels of similarity in the newer studies outweighing additional non-overlapping species.

Range Extensions and New Records

Discovery of hitherto unrecorded taxa in this region is not surprising. The very limited number of surveys along this coast easily accounts for some of the variances in molluscan taxonomic lists. The range extensions noted herein (Table 7) can also be accounted for by the dearth of published faunal surveys of this region. Some species found in the present study but not recorded by Counts & Bashore (1991) or Henderson & Bartsch (1914) are readily related to collection effort; the present study ran a course of several years and had an extended and large (though variable) collection team. Henderson & Bartsch made their collection during 1 week. Additionally, present collections included benthic surveys from slightly deeper waters not accessible to the former authors. In some cases, the small size and relative rarity of the species demanded intensive collection efforts or luck. For instance, the small lasaeid bivalve *Aligena elevata* was found in very shallow (wading) water of Tom's Cove, Assateague Island, Virginia only once. *Aligena elevata* is sometimes associated with the parchment tube of the polychaete *Diopatra cuprea,* a species quite common along the edge of Tom's Cove. It is possible that intensive sampling of the home tubes of these polychaetes would turn up additional specimens.

Homer et al. (1997) noted northern extensions in the ranges of three mollusks. *Pyramidella crenulata,* first

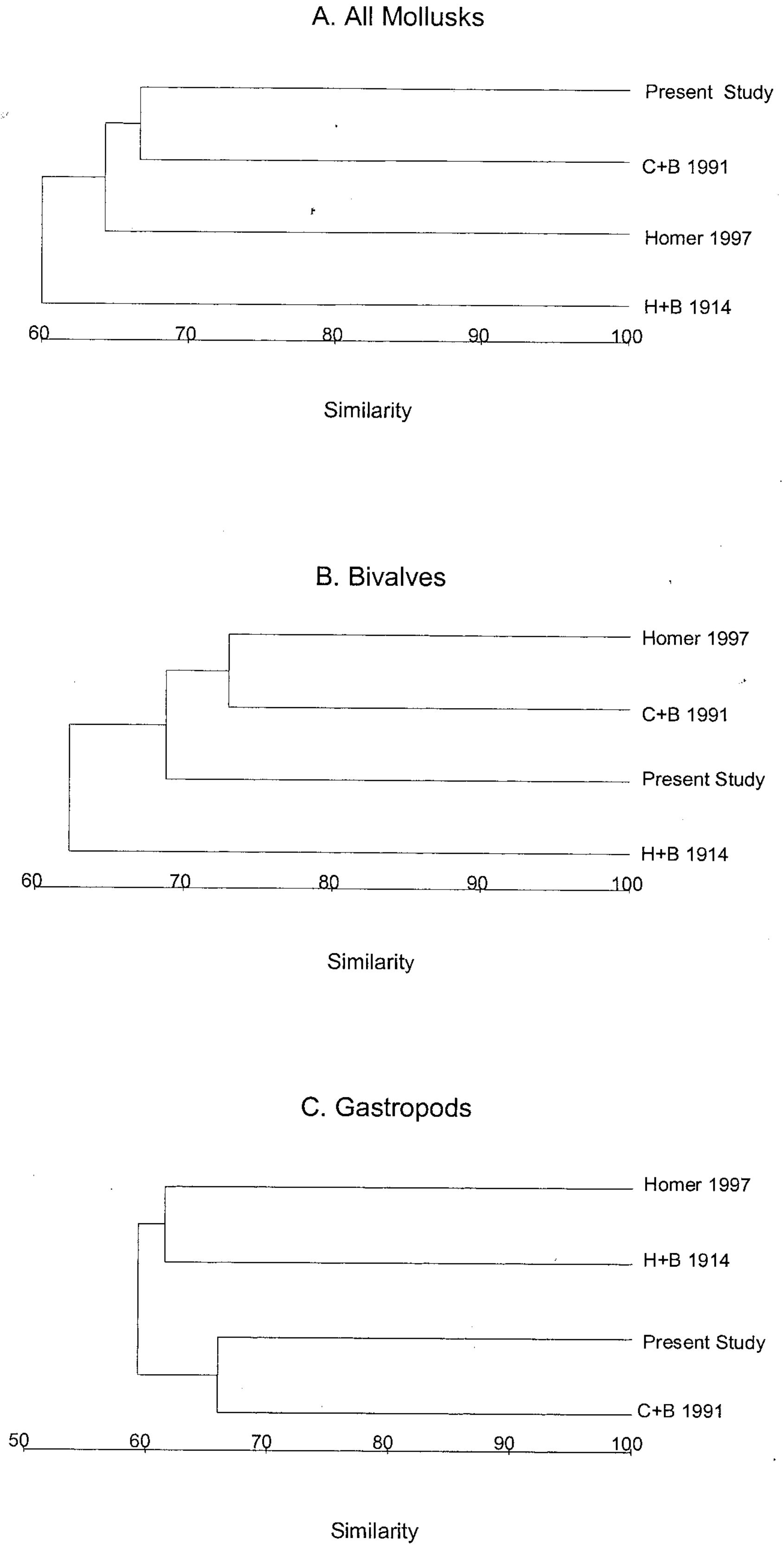

Figure 2. Hierarchical cluster analysis of the present study and Henderson & Bartsch (1914) ("H+B 1914"), Counts & Bashore (1991) ("C+B 1991"), and Homer et al. (1997) ("Homer 1997") using Bray-Curtis similarity indices. Figure 2A clusters studies using all molluscan taxa recovered. Figure 2B clusters for bivalves only; Figure 2C clusters for gastropods only.

Table 7

Species (mollusk and non-mollusk) from Assateague and Chincoteague Islands with range extensions. Source of previous range is noted. Two web sites are given: Fautin 2001: http://deuteron/kgs.ukans.edu/KWRC/anemone2/classification/current_classification.htm and Hardy 2001: http://www.gastropods.com/shell_pages/index.html

Species	Previously reported range
BIVALVIA	
Pleuromeris tridentata	North Carolina to all of Florida (Abbott, 1974); unconfirmed collection from "Long Island," New York in field guide of Long Island shells
Tridonta borealis	Arctic seas to Massachusetts Bay (Abbot, 1974)
GASTROPODA	
Eupleura sulcidentata	Florida, Bimini (Abbott, 1974; Lyons, 1977; Hardy, URL above)
Kurtziella limonitella	North Carolina to both sides of Florida; Jamaica (Abbott, 1974; Hardy, URL above)
Tectura testudinalis	Arctic seas to Long Island Sound, New York (Abbott, 1974)
ANTHOZOA	
Peachia parasitica	Adult anemones of this species typically not found south of Eastport, MA (Gosner, 1971); oceanic along northernmost coast of eastern United States up into southern Canadian coast (Fautin, URL above); occurrence noted in lower Chesapeake Bay (McDermott et al., 1982); associated with subumbrella of scyphozoan medusae
ASCIDIACEA	
Ecteinascidia turbinata	South Florida to Texas (Meinkoth, 1981; Plough, 1978); live-bearing tunicates

found in Chincoteague Bay in 1981 by Casey & Wesche (1982), was previously known only north to North Carolina (Abbott, 1974). *Cyclinella tenuis* was found in Chincoteague Bay (Homer et al., 1997) and considered a range extension from Cape Hatteras. Boss & Wass (1970), however, found this species in the lower Chesapeake Bay. Lastly, Homer et al. (1997) found *Acteocina bidentata* in Chincoteague Bay, whereas it was previously recorded north only to North Carolina (Abbott, 1974). The latter is somewhat confusing as the taxonomy has changed and it is assumed that Henderson & Bartsch (1914) had found this snail in their work but listed it under an earlier name.

Some of the noted range extensions in our study, as in that of Homer et al. (1997) are minor and not surprising. It is also true that publications denoting range extensions are today relatively infrequent. Conceptually historical zoogeographic boundaries, while still a useful concept in distribution studies, are often "ignored" by otherwise isolated taxa; this is especially true for species with a narrow distribution and nearby congeners. Some extensions, however, have evident significance. We found the limpet *Tectura testudinalis* in Cockle Creek, Chincoteague, Virginia on oyster rubble at about 4 m depth. Previously the southernmost known range of this limpet was Long Island Sound, New York. All specimens of this limpet found in Virginia waters were quite small and subtidal. In this case, the small size could reflect relatively young specimens that had yet to survive an entire year in this southern location. Additionally, the subtidal location is not unusual for a southern range extension since this would represent cooler and perhaps more tolerable waters for the typically northern species.

Eupleura sulcidentata was found in Mosquito Creek, Chincoteague, at a depth of about 2 m on rocky rubble and also intertidally on shell and rock rubble in Memorial Park, Chincoteague. This represents a significant range extension; *E. sulcidentata* is typically found along the west coast of Florida and Bimini (Lyons, 1977). Lyons (1977) suggested that Lake Worth Inlet on the Florida east coast could be the northernmost range limit for this species. Various species associated with oyster beds are frequently transplanted along with oysters, and this is a possible route for this gastropod to the Maryland and Virginia coast. More typical extensions can result from occasional shifts in prevailing coastal currents. This is demonstrated by the rare appearance of the scyphozoan dwelling anemone *Peachia parastica* (Agassiz, 1859) from the north and the viviparous ascidian *Ecteinascidia turbinata* from the south in the central location of Chincoteague. Although as recently as 2001, D. G. Fautin noted in an on-line database (http://deuteron.kgs.ukans.edu/KWRC/anemone2/classification/current_classification.htm) this "oceanic" anthozoan as being distributed in the extreme northeast of the United States and up along the Canadian coast, *Peachia parasitica* had been recorded from the lower Chesapeake Bay in the early 1980s (McDermott et al., 1982) as a "symbiont" of *Cyanea capillata.*

"Gigantism"

Rex & Etter (1997) discussed a recent spate of papers showing a renewed interest in the question of body size. Body size has clear implications in ecological and evolutionary studies, with these perhaps serving as the stimuli for the resurgence in size studies. Variation in intraspecific size is most commonly attributed to a combination of parameters that include diet, competition, preda-

Table 8

Molluscan species demonstrating "gigantism" (or exceptionally large size) at Assateague Island. Dimensions of Assateague specimens from present study or as noted. Size of specimens denoted from literature have not been verified here. True "giants" (here defined as at least 25% larger than previously recorded maximum size) are indicated with an asterisk.

Species	Previously reported dimensions	Dimensions of assateague specimens
BIVALVIA		
**Lyonsia hyalina*	12.68 to 19.02 mm shell length (Abbott, 1974)	25.5 mm shell length, 14.2 mm shell height; rate in area
GASTROPODA		
Bittiolum alternatum virginicum	Possibly a giant ecological form of *Bittiolum alternatum* (Say, 1822); shell height of 6.3 mm (Abbott, 1974)	Exceptionally large specimens of 8.3 mm from Chincoteague recorded in Henderson & Bartsch (1914) as *Diastoma virginica* n. sp.
Busycon carica	125.85 to 228.33 mm in length (Abbott, 1974) (but recorded at 281 mm from S. Carolina in Hutsell et al. 1999)	253 mm shell length
**Crepidula convexa*	6.34 mm to 12.68 mm (Abbott, 1974)	24.5 mm
Crepidula fornicata	19.02 to 51.74 mm (Abbott, 1974) (but recorded at 66.7 mm (no locality data) in Hustell et al., 1999)	Many large specimens, largest being 58.7 mm; all female stage
Urosalpinx cinerea folleyensis	68.3 mm from Washington noted (Hutsell et al., 1999)	Exceptionally large Delmarva specimens reported by Baker (1951) and from Chincoteague by Henderson & Bartsch (1914)
POLYPLACOPHORA		
**Chaetopleura apiculata*	7 to 20 mm in length (Abbott, 1974)	30.5 and 40.0 mm in length, four remarkably large specimens; rare in area

tion, environmental energetics (i.e., high wave intertidal versus quiescent mud flat), population density, offspring size, temperature, and other environmental variables (Branch & Branch, 1980; Branch, 1981; Underwood, 1984a, b; Bowling, 1994; Schindler et al., 1994; Sibly & Atkinson, 1994; Strayer, 1994; Atkinson, 1995; Takada, 1995; Kozlowski, 1996; Yampolosky & Schneiner, 1996). Homer et al. (1997) noted that coastal bay populations of *Nassarius vibex* tend to reach larger sizes than usually reported (they found that *N. vibex* in Chincoteague Bay averaged 15.8 mm long with a range between 9.0–18.0 mm, whereas "shell guides" typically report them to be smaller). Causative effects of within-habitat variation in size of relatively sedentary mollusks can reflect tide level and differences in microhabitat (Sutherland, 1970; Creese, 1980; Fletcher, 1984; Takada, 1995). Öst & Kilpi (1997) and Kautsky (1982) discussed a variety of environmental parameters that influence the maximum size of the blue mussel *Mytilus edulis* in Baltic waters. These include temperature, salinity, wave and light exposure, food supply, and population structure. Parasitism is also an occasional cause of gigantism in some snails (Mouritsen & Jensen, 1994). For example, trematodes of "low-pathogenecity" have been shown to cause gigantism in *Hydrobia* spp. (Gorbushin, 1997). De Jong-Brink (1995) suggested that trematodes could influence neuroendocrine functions in snails (in this case *Lymnaea stagnalis*) and induce increased growth. Baker (1951) reported a case of "gigantism" of *Urosalpinx cinerea folleyensis* from Chincoteague. Similarly, Henderson & Bartsch (1914) noted the "enormous size" of specimens of this gastropod taken from Chincoteague oyster beds. In the present study, we found exceptionally large specimens of two species of bivalve, four species of gastropod, and the chiton *Chaetopleura apiculata* (Table 8). These mollusks range from filter feeders (*Lyonsia hyalina* and *Crepidula convexa*) to grazing herbivores (*Chaetopleura apiculata*) to predatory carnivores (*Busycon carica*). None were found in particularly large numbers and there was little evidence of disproportionately intense predation of smaller cohorts of the filter feeders or grazers, although only large *Chaetopleura apiculata* and *Lyonsia hyalina* were found. The list includes both infaunal and epifaunal species, subtidal and intertidal species, and common and rare species. Nevertheless, *L. hyalina* and *C. apiculata* are noteworthy for their extreme sizes.

Tablado et al. (1994) found that the pulmonate limpet *Siphonaria lessoni* grew to larger sizes in sewage polluted areas of Argentina. These authors suspected the cause of larger snails was either directly or indirectly a result of organic enrichment. The anthropogenic input in the Assateague region is relatively high, especially during summer tourist season. However, the larger specimens found in our study represented only a small minority of the total population (except for *Chaetopleura apiculata,* which had an overall small population), and it seems unlikely that any general environmental factor could be causative.

Recent studies by Rex & Etter (1997) showed that both larval and adult shells increase in size with depth into the abyss. They suggested that the decreased input of nutrients into these deep waters will select for the larger specimens that would have a competitive or metabolic advantage. Whether this is accurate or not, it is clear that location plays a significant role in size distribution. Chincoteague and Assateague are in the Boreal province and Virginian subprovince. The region offers a wide array of temperate marine and estuarine habitats that are not as warm as those to the south or as seasonally cool as those to the north. While not a delineated provincial zone, this region offers a blend or transition between the Carolinian province and the Boreal. Although Cape Hatteras is the identified division between these provinces, temporal variations in the Gulf Stream can bring decisively Carolinian fauna up along Assateague. Similarly, shifts in the Labrador Current can bring cooler water species south. Such displaced species are common along northern coastal Virginia and southern Maryland (see list of range extensions; also note that during these collections several species of semitropical fish [e.g., *Chaetodon*] were found along our field sites). Does the integrative nature of this region influence growth rates or longevity as well as allowing an out-of-range existence?

The possibility, in all studies that reveal "gigantism," that sampling artifact plays a role cannot be overlooked. It is easy to envision an artificial selection of larger specimens in any collection. Here, however, our collections were over many years, and the "giants" included species that are considered uncommon in the region (e.g., *Lyonsia hyalina, Chaetopleura apiculata*). The extensive sampling (in terms of number of individuals doing the surveys plus time allotments) would certainly have revealed larger populations of these species through time. In most cases, the specimens of a particular species, large or not, were only rarely collected. Smaller specimens of the same species were equally atypical in these communities. Along the opposite spectrum, Prezant (1979, 1981) reported a "dwarfed" population of *Lyonsia hyalina* from Nahant Bay, Massachusetts. This population was composed of significantly smaller individuals, averaging half or less the size of those from more southerly populations (e.g., Cape Cod). The exact reason for this smaller size was not determined; however, the Nahant population was consistently infected with dense populations of coccidia that almost occluded the proximal limbs of their kidneys. In this case, as opposed to the "gigantism" apparently induced by trematode-infected *Hydrobia* (Gorbushin, 1997), it is possible that a parasitic infestation reduced maximum growth attained.

High seasonal primary productivity, coupled with the large array of protected natural and manmade habitats, offers conditions for a rich and stable food supply. The question then is, at least in part, not why a few species in this region have a few specimens that are large, but why the hundreds of other species lack these unusually large representatives and why so few within a population grow to unusually large sizes? Aside from the obvious ease with which the larger specimens are found, the answer probably rests with a few genetic anomalies confined within overall genetic constraints.

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