

Two new modern records of the southern oyster drill *Stramonita haemastoma floridana* (Conrad, 1837) in Chesapeake Bay, USA

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ABSTRACT

Live southern oyster drills, *Stramonita haemastoma floridana* (Conrad, 1837), have been collected from two Chesapeake Bay western shore tributaries. Four specimens were collected between Brown Shoal and Thomas Rock in the lower James River in February 2005. Thirteen live southern oyster drills were collected from Back River in April 2006. Identification of these drills as *Stramonita haemastoma floridana* has been confirmed using DNA bar-coding data. Southern oyster drills collected in Chesapeake Bay are genetically nearly identical to populations from the Atlantic coast, and differ significantly from populations from the Azores and from the Gulf of Mexico. These collections mark the first reported records of live southern oyster drills from within the Chesapeake Bay estuary. It is unknown if these drills represent isolated introductions or expansions of the northern range this species. Water temperature patterns in Chesapeake Bay and the Mid-Atlantic Bight from 1990–2005 are similar to those observed in the late 1950s when *Stramonita haemastoma floridana* was first found living in Chincoteague Bay, Maryland.

Additional Keywords: Range extension, water temperature, Cape Hatteras, zoogeography, DNA bar-coding

INTRODUCTION

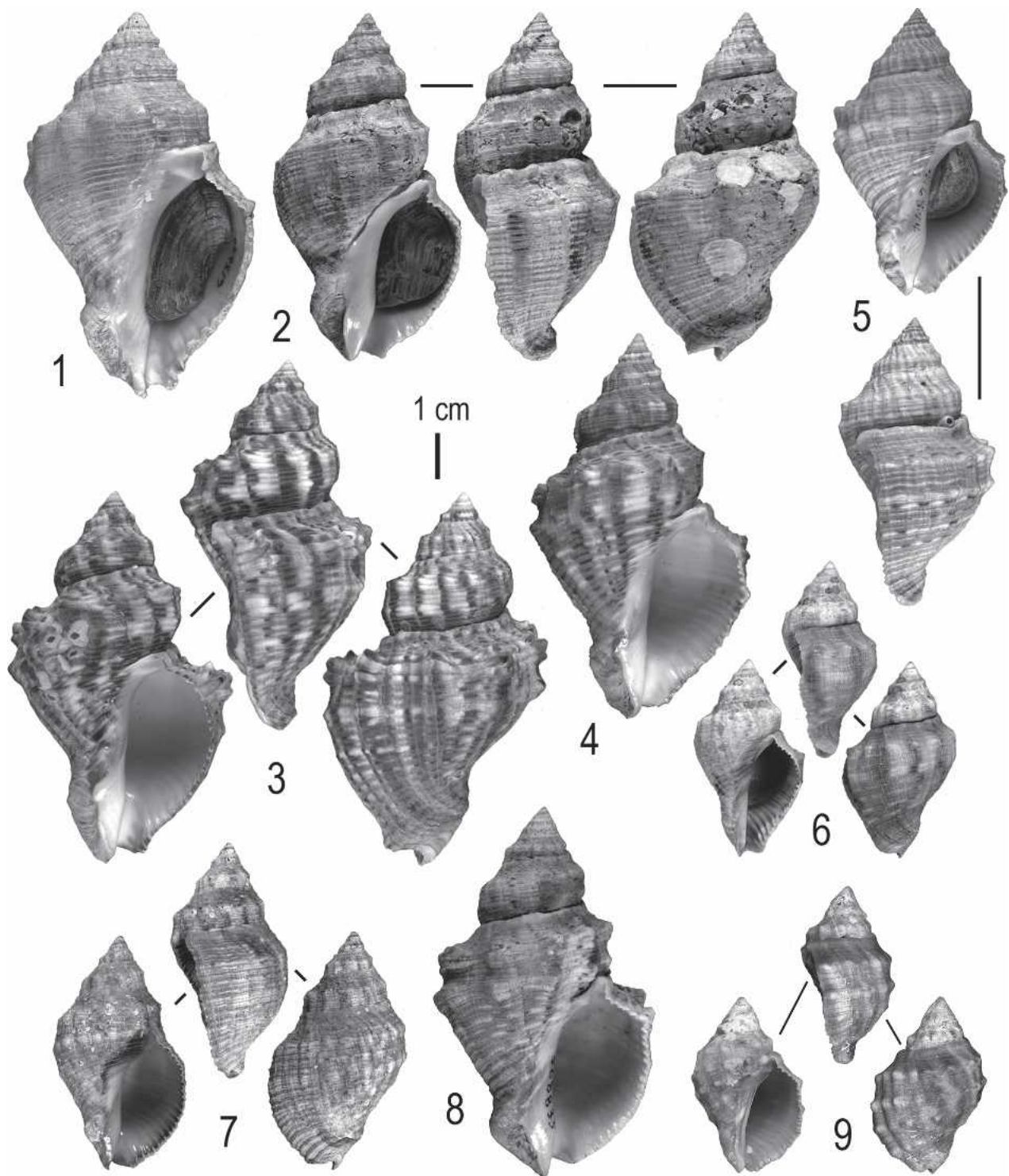
The southern oyster drill *Stramonita haemastoma floridana* (Conrad, 1837) is a predatory gastropod typically found in association with populations of the oyster *Crassostrea virginica* Gmelin, 1791 (e.g., Burkenroad, 1931; Butler, 1985). A population from the Atlantic coast of the United States was described as *Purpura floridana* Conrad, 1837, but later regarded to be a subspecies of the

broadly ranging *Stramonita haemastoma* (Linnaeus, 1767), a morphologically diverse taxon that has been reported to span the temperate and tropical coasts of the eastern and western Atlantic as well the eastern Pacific.

The name *Stramonita haemastoma haemastoma* (type locality: Tenerife, Canary Islands, fixed by Clench, 1947: 76) has been applied to the populations ranging from the Channel Islands southward to Senegal, the western Mediterranean, the Madeira, Canary and Cape Verde Islands in the eastern Atlantic (Clench, 1947: 76; Poppe and Goto, 1991: 141), the Azores (Morton et al., 1998), Trinidad southward to Uruguay in the western Atlantic (Clench, 1947: 76), and from Baja California southward to Peru in the eastern Pacific by some (e.g., Clench, 1947) but not all (e.g., Keen, 1971: 549) researchers. *Stramonita haemastoma floridana* (type locality: Hypoluxo Island, Lantana, Florida, see Clench, 1947: 77) was reported to range from North Carolina southward to Yucatan and the West Indies, and throughout the Caribbean as far south as Trinidad (Clench, 1947: 76), or extending to Brazil (Abbott, 1974: 180). The name *Stramonita haemastoma canaliculata* (Gray, 1839) (type locality originally but erroneously listed as China) has been applied to a distinctive morphological variant prevalent throughout the Gulf of Mexico (e.g., Abbott, 1974: 180). Some three dozen names have been variously partitioned and synonymized for the many geographically circumscribed shell phenotypes belonging to the *Stramonita haemastoma* complex (see Rosenberg, 2005).

North American records of *Stramonita* have generally been divided into two subspecies, *Stramonita haemastoma floridana* from the Atlantic coastline, and *Stramonita haemastoma canaliculata* from the Gulf of Mexico; such division is based on shell characters (Abbott, 1974; Butler, 1985). *Stramonita haemastoma canaliculata* has been differentiated morphologically on

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Figures 1–9. *Stramonita* spp. 1–6. *Stramonita haemastoma floridaana* (Conrad, 1837). 1. USNM 618840, Willis Wharf, Hog Island Bay, Northumberland Co., Virginia, trapped in 2.4 m depth. September 15, 1955, ex-F. W. Sieling. 2. USNM 1091020, oyster reefs just below Deep Creek, Lower James River, Virginia, in approximately 3 m, February 2005. 3. Male and 4. female specimen, USNM 1091021, Back River, Virginia, in commercial crab pots set in 3 m, April 2006. 5. USNM 416874, Fort Macon, North Carolina. 6. USNM 1099258, Sand bar on north side of Fort Pierce Inlet, E of Little Jim Island, Ft. Pierce, Florida. 6 August 2004. 7. *Stramonita canaliculata* (Gray, 1839), USNM 1099259, St. Andrews Bay, Florida, rip-rap near campsites. 8. *Stramonita haemastoma haysae* (Clench, 1927), USNM 568834, Barataria Bay, Louisiana. 9. *Stramonita haemastoma haemastoma* (Linnaeus, 1767), USNM 1099260, intertidal rocks, Vila Franca do Campo, São Miguel, Azores, 26 July 2006.

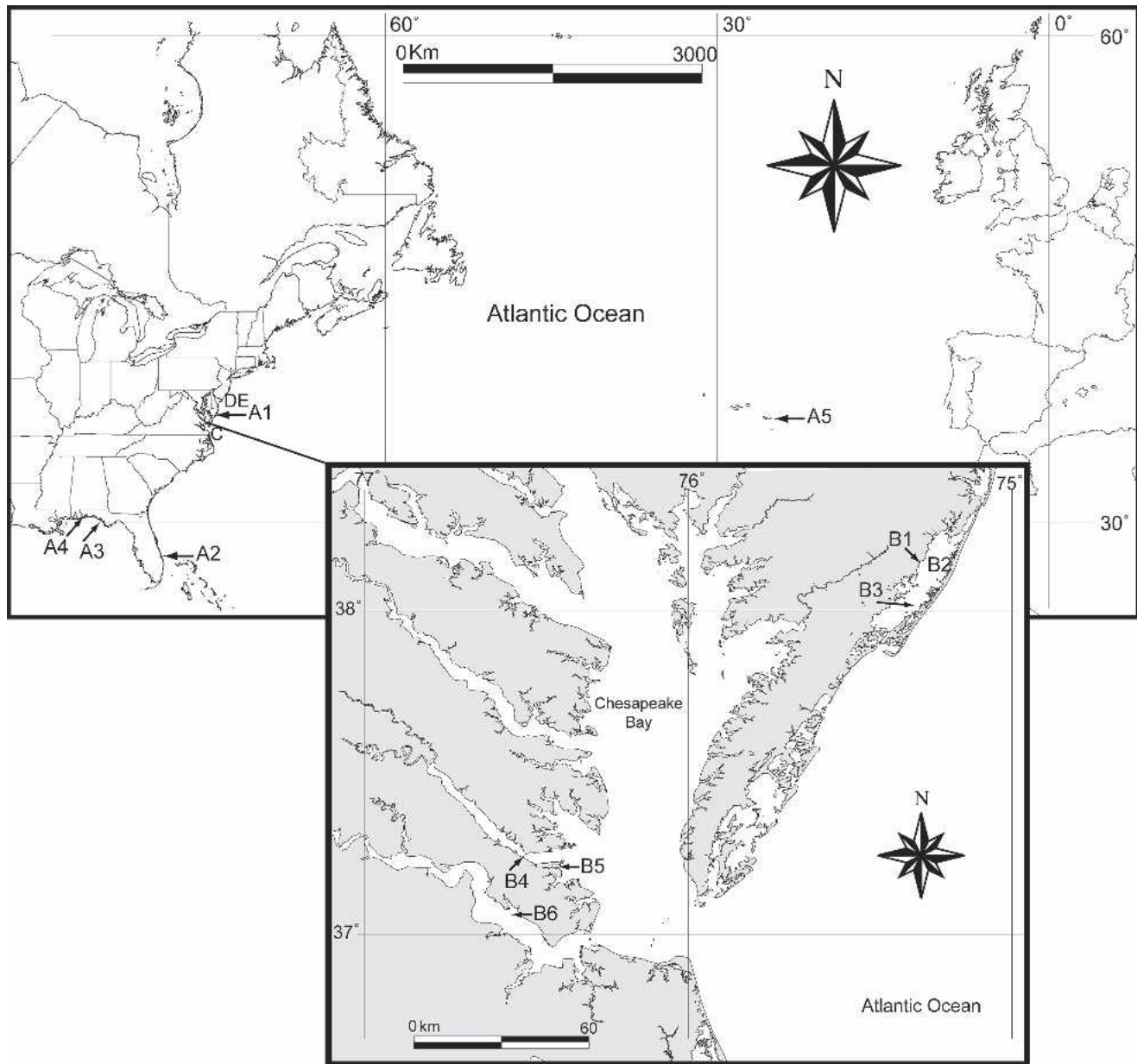


Figure 10. Map of the Atlantic Ocean depicting the southeastern coast of the United States, Chesapeake Bay region [inset], and the Azores Islands, showing collection sites for *Stramonita* specimens and water-temperature data. Sites are identified as follows: Delaware lightship and buoy stations (DE), Chincoteague, VA (A1), Chesapeake lightship and buoy stations (C), Fort Pierce Inlet, FL (A2), St. Andrew's Bay, FL (A3), Pensacola, FL (A4), and São Miguel, Azores (A5). Within the Chesapeake Bay region Chincoteague, VA (B1), Maryland DNR monitoring station XBM1849 (B2), Maryland DNR monitoring station XBM 1301 (B3), Virginia Institute of Marine Science, Gloucester Point, VA (B4), Back River, VA (B5), James River near Deep Creek (B6).

the basis of its larger size, presence of strong, rugose shoulder nodules, and its deeply channeled suture. Several authors (e.g., Butler, 1954; Gunter, 1979; Walker, 1982) had reported that differences in shell morphology are neither consistent nor concordant with geographical patterns and concluded that subspecific distinction was not warranted. More recently, Liu et al. (1991) confirmed that characters of shell and radula were not taxonomically informative, but demonstrated that *Stramonita*

from the northern Gulf of Mexico could be differentiated from populations of the Atlantic coast at "a level that is characteristic of congeneric species" using allozyme electrophoresis. Other recent studies have explored the effectiveness of the east Florida ecotone as a barrier to gene flow between Atlantic and Gulf coast populations for a variety of taxa (for reviews, see Avise, 2000; Wise et al., 2004). Vermeij (2001: 701) reviewed the Recent and fossil species of *Stramonita*, and suggested that the *Stramonita*

Table 1. Samples of *Stramonita* spp. used in this study.

Taxon	Locality	Voucher specimens USNM	Number of specimens sequenced	GenBank accession number
<i>Stramonita canaliculata</i> ⁽¹⁾	Pensacola, FL	888709	1	U86330
<i>Stramonita canaliculata</i>	St. Andrew's Bay, FL	1099259	1	EU073061
<i>Stramonita haemastoma haemastoma</i>	São Miguel, Azores	1099260	2	EU073051–EU073052
<i>Stramonita haemastoma floridana</i>	Ft. Pierce Inlet, FL	1099258	2	EU73053–EU073054
<i>Stramonita haemastoma floridana</i>	Deep Creek, VA	1091020	3	EU073055–EU073057
<i>Stramonita haemastoma floridana</i>	Back River, VA	1091021	3	EU073058–EU073060

⁽¹⁾ Sequence data from Harasewych et al., 1997

monita haemastoma complex may consist of as many as four western Atlantic and two eastern Atlantic species. He also noted similarities (bifid crenulations along the outer lip) between some specimens of *S. canaliculata* and *S. bifida* Vermeij, 2001, from the Cantare Formation (early Miocene, Venezuela).

Although the northern limit of *Stramonita* along the eastern United States has generally been reported as Oregon Inlet, North Carolina (Wells and Grey, 1960; Butler, 1985), living individuals (Figure 1) and recent historical specimens (empty shells) were collected from locations in the Maryland and Virginia waters of Chincoteague Bay (Figure 10, A1) in 1955 and 1956 (Sieling, 1955; 1960), extending the northern range boundary for this animal along the US Atlantic coast. Sieling (1960) suggested that the southern oyster drills were introduced into Chincoteague Bay with transplanted oysters. Subsequent surveys of Assateague Island and Chincoteague Bay by Counts and Bashore (1991),

Homer et al. (1997), and Prezant et al. (2002) reported living *S. haemastoma floridana* from these habitats as recently as 1996 (Prezant et al., 2002). Counts and Bashore (1991) categorized *S. haemastoma floridana* as “rare” and linked the relative decline in abundance and distribution of this drill with the decline in local oyster resources from 1960 to 1989. Prezant et al. (2002) report living *S. haemastoma floridana* in their survey and collected specimen(s) from Memorial Park, Maryland.

Living species of *Stramonita* have not previously been reported from the interior of the Chesapeake Bay (Andrews, 1956; Wass, 1972) in modern time, although *S. h. canaliculatum* had occurred in Chesapeake Bay, Maryland, and *S. h. floridana* had reached southern New Jersey during the exceptionally warm Sangamonian Stage (80,000 to ca. 220,000 yr BP) of the Pleistocene (Petuch 1997: 53). Ruiz et al. (2000) reported *S. haemastoma* as an established resident in the Chesapeake Bay region on the basis of the Chincoteague Bay, Maryland-Virginia,

Table 2. Summary of water temperature data sources from 1950–2005 for Delaware (DE, Figure 10) and Chesapeake (C, Figure 10). Sea surface temperature (SST), bottom temperature (BT) and air temperature at the water surface (AT) were used.

Station	Year(s)	Data	Station type	Depth	Source
Delaware/Winter Quarter	1955–60	SST, BT	Winter Quarter lightship	24–29 m	1
	1961–70	SST, BT	Delaware lightship	30 m	2
	1970–84	SST	One degree quadrangles	NA	3, 4, 5
Chesapeake	1984–2005	AT, SST	NOAA buoy 44009	28 m	6
	1950–1971	SST	Chesapeake lightship	20 m	7, 8
	1971–84	SST	One degree quadrangles	NA	3, 4, 5
	1985–2005	AT, SST	NOAA buoy CHLV2	11.6 m	9

1. Winter Quarter lightship data archive. East Coast USCG lightship/Lightstations. MBLWHOI Library data archives, Woods Hole, MA. http://dlaweb.whoi.edu/lightship/lightships_winterqtr.html

2. Delaware lightship data archive. East Coast USCG Lightship/Lightstations. MBLWHOI Library data archives, Woods Hole, MA. http://dlaweb.whoi.edu/lightship/lightships_delaware.html

3. 1966–1974. The Gulf Stream. U.S. Naval Oceanographic Office, Vols 1–9.

4. 1975–1980. gulfstream. U.S. Dept. of Commerce, NOAA, National Weather Service. Vols. 1–6.

5. 1981–94. Oceanographic Monthly Summary. U.S. Dept. of Commerce, NOAA, National Weather Service/National Earth Satellite Service. Vols. 1–14.

6. Delaware Bay, Buoy 44009. <http://www.nodc.noaa.gov/BUOY/44009.html>.

7. Bumpus, D. 1957. Surface water temperatures along Atlantic and Gulf coasts of the United States. U.S. Fish and Wildlife Service Special Scientific Report—Fisheries No. 214.

8. Chesapeake lightship data archive. East Coast USCG Lightship/Lightstations. MBLWHOI Library data archives, Woods Hole, MA. http://dlaweb.whoi.edu/lightship/lightships_chespstn.html

9. Chesapeake Light, VA, Buoy CHLV2. <http://www.nodc.noaa.gov/BUOY/chlv2.html>.

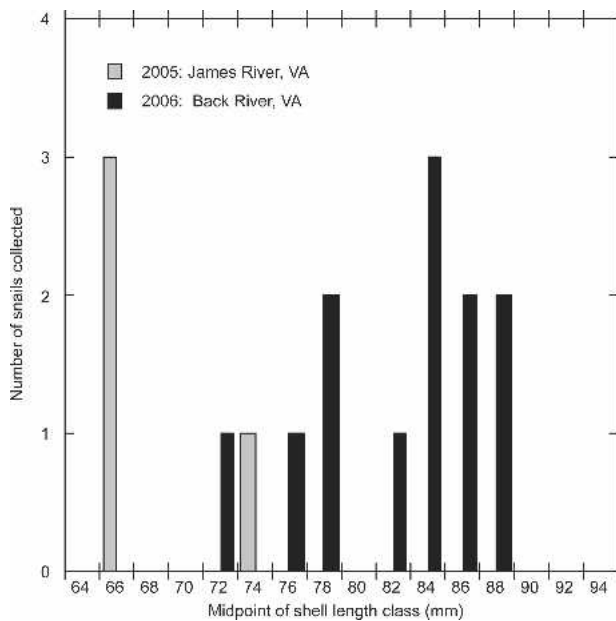


Figure 11. Length frequency distribution of live *Stramonita haemastoma floridana* specimens collected from Back River, VA (2006) and the James River, VA near Deep Creek (2005).

and Hog Island Bay, Virginia, collections reported by Sieling (1960) (P. Fofonoff, Smithsonian Environmental Research Center, personal communication). Distribution patterns of many molluscan species along the US Atlantic coast are directly related to water temperature with Cape Hatteras acting as a natural zoogeographic boundary (Franz and Merrill, 1980a, b). Wells and Gray (1960) reported *S. h. floridana* on two subtidal shipwrecks south of Cape Hatteras, North Carolina, but found none on the four shipwrecks they examined north of Cape Hatteras. Wells (1961) described regular collections of resident *S. h. floridana* from intertidal oyster reefs in the vicinity of Beaufort and Cape Lookout, North Carolina.

Southern oyster drills begin laying eggs at water temperatures between 20 and 30°C (Stickle, 1999). At water

temperatures less than 10–12.5°C southern oyster drills stop feeding on bivalves, bury into the substrate, and become inactive (Bulter, 1954; Gunter, 1979; Garton and Stickle, 1980; Stickle, 1999) until water temperatures rises. While the upper lethal thermal limit for southern oyster drills is 35 to 40° C (Brown and Stickle, 2002), the lower lethal thermal limit for southern oyster drills is unknown.

This report documents the first collections of living *Stramonita haemastoma floridana* from within the Chesapeake Bay estuary. We characterize both groups of southern oyster drills collected in the Chesapeake Bay genetically (cytochrome *c* oxidase I “DNA bar-coding”) and compare these data to sequences derived from representative specimens from the southeastern (Indian River Inlet) and northwestern (St. Andrew’s Bay, Pensacola) coasts of Florida, as well as from samples from São Miguel, Azores. The presence of these drills in Chesapeake estuarine habitats is analyzed in the context of a long term (1950–2005) coastal bottom water temperature data set and two independently collected estuarine bottom water temperature data sets (Chincoteague Bay, Maryland and Virginia, 1951–56; McGary and Seiling, 1953; Seiling, 1957; York River, Virginia, 1986–2005; VIMS, 2006) in order to relate the observed Chesapeake collections with environmental/climate conditions in known drill habitats along the Atlantic coast and in Chincoteague Bay.

MATERIALS AND METHODS

Sample Collection: Four living *S. haemastoma* (Figure 2) were collected in the lower James River, Virginia, in the Chesapeake Bay from oyster (*Crassostrea virginica*) reefs just below Deep Creek (Figure 10, B6) at a depth of approximately 3 m in February 2005 and were turned in to the Virginia Institute of Marine Science (VIMS) rapa whelk [*Rapana venosa* (Valenciennes, 1846)] bounty program (see Harding and Mann, 2005, for bounty program details). All four *Stramonita* speci-

Table 3. Nucleotide (above diagonal) and amino acid (below diagonal) differences between samples in the portion of the cytochrome *c* oxidase I gene (591 aligned positions, corresponding to positions 73 to 664 in the complete mitochondrial genome of *Ilyanassa obsoleta* [Genbank NC 007781]).

Sample	1	2	3	4	5	6	7	8	9	10	11	12
1) <i>S. canaliculata</i> Pensacola, FL	—	0	126	126	123	123	123	122	124	124	123	122
2) <i>S. canaliculata</i> St. Andrew’s, FL	0	—	126	126	123	123	123	122	124	124	123	122
3) <i>S. h. haemastoma</i> Azores 1	8	8	—	5	56	55	55	58	56	56	56	56
4) <i>S. h. haemastoma</i> Azores 2	7	7	1	—	57	56	56	61	57	57	57	57
5) <i>S. h. floridana</i> Ft. Pierce Inlet, FL1	7	7	3	2	—	2	2	7	3	5	3	3
6) <i>S. h. floridana</i> Ft. Pierce Inlet, FL2	7	7	3	2	0	—	0	5	1	3	1	1
7) <i>S. h. floridana</i> Deep Creek, VA1	7	7	3	2	0	0	—	5	1	3	1	1
8) <i>S. h. floridana</i> Deep Creek, VA2	8	8	2	3	1	1	1	—	6	8	6	6
9) <i>S. h. floridana</i> Deep Creek, VA3	7	7	3	2	0	0	0	1	—	4	2	2
10) <i>S. h. floridana</i> Black River, VA1	7	7	3	2	0	0	0	1	0	—	4	4
11) <i>S. h. floridana</i> Black River, VA2	7	7	3	2	0	0	0	1	0	0	—	2
12) <i>S. h. floridana</i> Black River, VA3	7	7	3	2	0	0	0	1	0	0	0	—

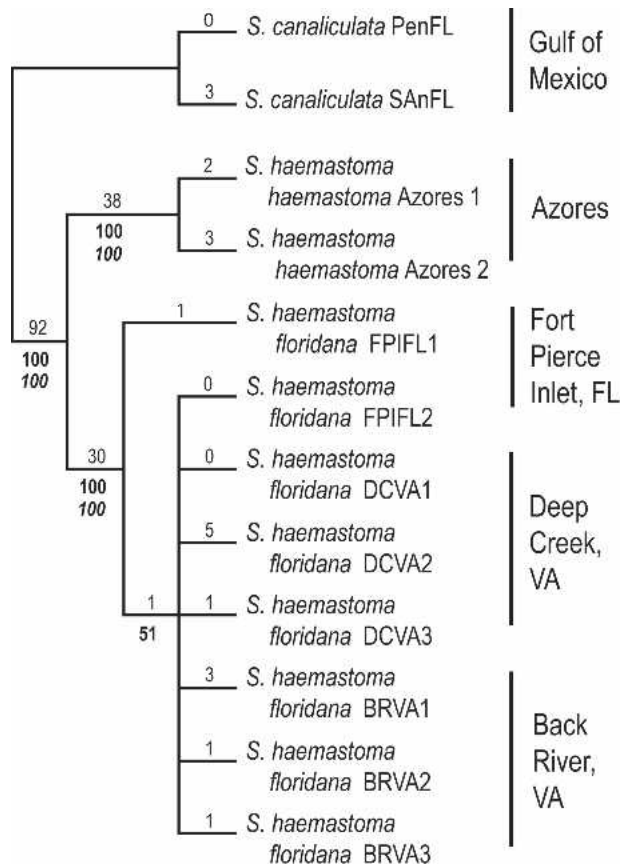


Figure 12. Strict consensus of four most parsimonious trees ($l = 176$; $ci = 0.955$; $ri = 0.960$) resulting from an exhaustive search using maximum parsimony (PAUP 4.0b10) based on 591 bp of cytochrome *c* oxidase I sequences. Branch lengths from one of the four most parsimonious trees are above the branches, bootstrap (**bold**) and jackknife (**bold italic**) proportions are below the branches.

mens were collected in a single oyster dredge tow. Thirteen living *S. haemastoma* (Figures 3–4) were collected in Back River, Virginia, (Figure 10, B5) in April 2006 and were also turned into VIMS via the rapa whelk bounty program. The 2006 collection was made using commercial crab pots (wire mesh cubes with approximately 0.5 m sides) baited with northern quahogs [*Mercenaria mercenaria* (Linnaeus, 1758)] deployed at a depth of 3 m. Shell lengths of specimens (mm, maximum dimension tip of the spire to bottom of the siphonal canal) were measured upon receipt at VIMS. Voucher specimens from both Chesapeake collections have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM, Table 1).

DNA Bar-coding: Three specimens from each Chesapeake collection were frozen and transported to the laboratory, where DNA was extracted from red buccal muscles of each animal using Qiagen DNEasy kits according to the manufacturer's protocol. A portion of the mitochondrial gene for the DNA bar-coding region of

the cytochrome *c* oxidase I gene was amplified using Sigma JumpStart RedTaq ReadyMix and Meyer's (2003) degenerated versions of the Folmer et al. (1994) HCO and LCO primers for the samples listed in Table 1. The resulting PCR products were cleaned using magnetic beads [Agencourt, manufacturer's protocol] and sequencing reactions were run on ABI 3730 sequencers that were set up according to manufacturer's instructions. Sequences were manually checked/corrected and assembled using Sequencer™ 4.1 (Gene Codes Corp.), then aligned with Clustal W (Higgins et al., 1994) using default settings, and their relationships analyzed using PAUP 4.0b10 (Swofford, 2002). Pairwise comparisons of sequences and amino acids were performed using Mega 3.1 (Kumar et al., 2004).

Water Temperature Data: COASTAL HABITATS: Water temperature data from 1950–2005 were used to describe mean monthly bottom water temperatures (BT, $^{\circ}\text{C}$) for two stations in the Mid-Atlantic Bight (Delaware/Winter Quarter and Chesapeake) (Figure 10, Table 2). Daily sea surface and bottom water temperature data from the Delaware/Winter Quarter (1961–70) and Chesapeake (1958–71) lightship stations were used to calculate the average monthly observed difference between sea surface temperature (SST) and bottom water temperature (BT) on a site-specific basis. The observed average monthly SST-BT differences from the daily lightship data were used to estimate average monthly BT at these sites during years after 1971 when only SST was available (Table 2).

Hourly air temperature (AT) and SST data from NOAA buoys (1985–2005) were used to calculate the observed difference between average monthly AT and average monthly SST for Delaware Light and Chesapeake Light. The observed average monthly AT-SST differences from the buoy data were used to estimate hourly SST for these sites during months after 1984 when only AT was available.

Average residuals for annual BT from the long-term (1950–2005) average annual BT were calculated for each site in which at least 9 months of data were available. Monthly average bottom water temperatures (with standard error of the mean) were calculated for each of 12 months for all sites. Monthly BT estimates from 1970 to 1983 (Delaware) and 1984 (Chesapeake Light) use a single published monthly average (Table 2) while monthly BT estimates from NOAA buoys (Table 2) are averages calculated from hourly readings with n values >400 per month.

Estuarine Habitats: Water temperature data collected at Public Landing, Maryland, in Chincoteague Bay from McGary and Sieling (1953) and Sieling (1957) were used to calculate average monthly water temperatures (with standard error of the mean) during the period 1951–1956. Modern (2001–2004) water temperature data from Chincoteague Bay stations south of Robins Marsh (XBM8149) (Figure 10, B2) and near the MD-VA border (XBM1301) (Figure 10, B3) were obtained from

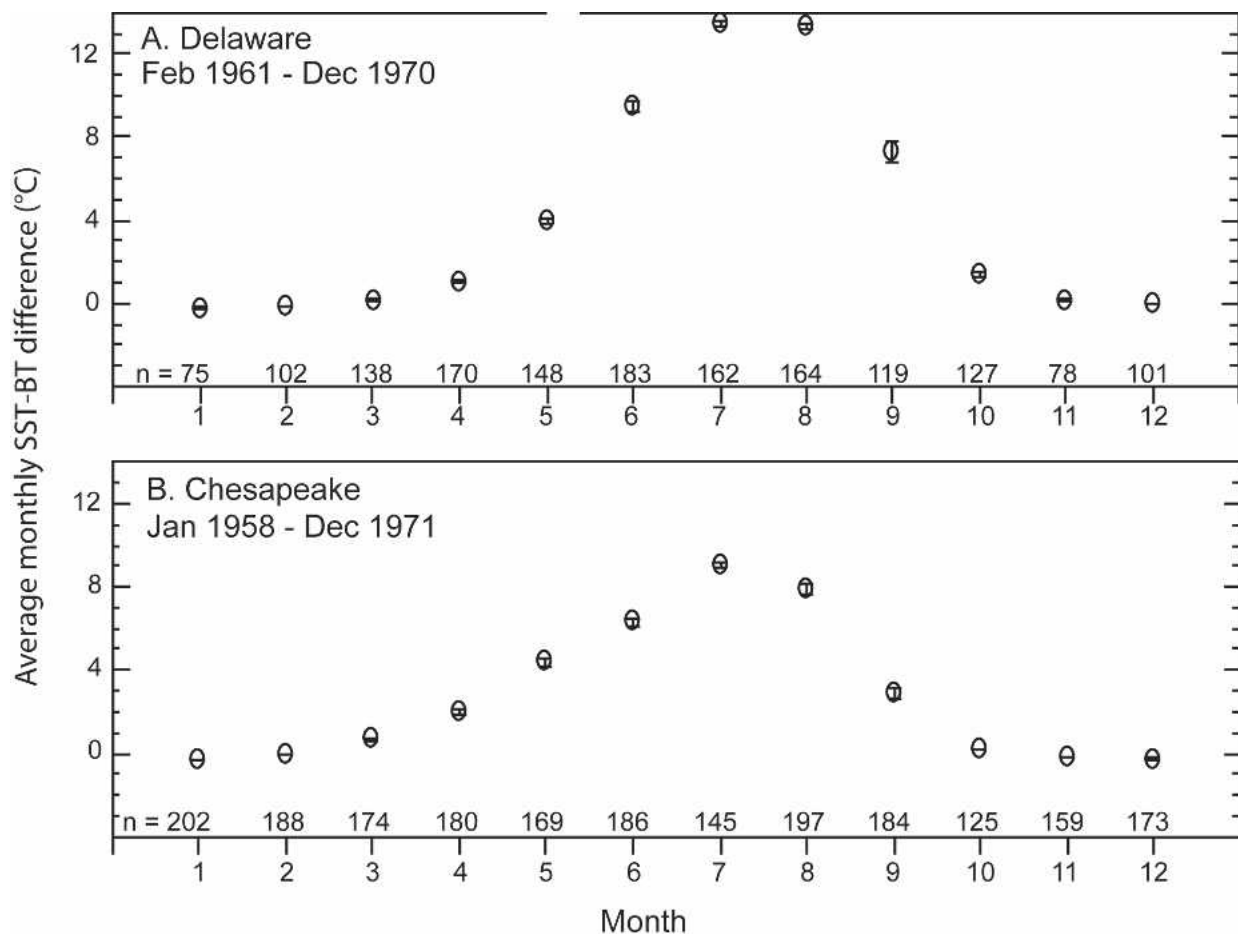


Figure 13. Average monthly difference between sea surface temperature (SST) and bottom water temperature (BT) from lightship data (Table 2) for Delaware (A) and Chesapeake (B) lightships. Error bars indicate standard error of the mean. N values (number of daily SST-BT pairs used to estimate the SST-BT differences) at each site are presented above the X axis in each panel.

the Maryland Department of Natural Resources Eyes on the Bay web site (http://mddnr.chesapeakebay.net/bay_cond/). Water depth at all (historical and modern) of these Chincoteague Bay sites is 3 m or less. Seiling (1954) reported less than a degree Celsius variation between surface and bottom water temperatures and the data presented in McGary and Seiling (1953) and Seiling (1957) from sites throughout the estuary confirm the well-mixed nature of these non-channel habitats.

The Virginia Institute of Marine Science (VIMS) at Gloucester Point, Virginia (Figure 10, B4) maintained a water temperature monitoring station from 1986 through September 18, 2003, (arrival of Hurricane Isabel) that recorded bottom water temperatures (°C) at a depth of 2–3 m. The VIMS Molluscan Ecology program has maintained an environmental monitoring station located within 200 m of the original VIMS station since January 2005 that records bottom water temperatures (°C) at depths of 2 m. Hourly water temperature averages were obtained from the VIMS data archive (1986 to Sep 2003) and the VIMS Molluscan Ecology program environmental data archive (2005) and used to calculate monthly residuals from the 1986–2005 mean and average monthly

bottom water temperatures (with standard error of the mean).

RESULTS

Morphology: The southern oyster drill specimens collected from the James River in February 2005 ranged in size from 66.4 to 75.6 mm shell length with an average shell length of $69.0 \pm$ standard error of the mean 2.21 mm. Southern oyster drills collected in April 2006 from Back River had shell lengths ranging from 73 to 89 mm with an average shell length of 83.3 ± 1.41 mm. Size frequency distributions for both collections (Figure 11) indicate that all specimens were adults (sexually mature; Burkenroad, 1931; Butler, 1985) and represent the upper end of the size distribution typically found in Louisiana habitats (Brown and Richardson, 1987; Brown et al., 2004). These large individuals have probably reached a size refuge from most local predators including blue crabs (*Callinectes sapidus*, see the work of Turra et al., 2005, using *C. danae* preying on *S. haemastoma*) and are certainly capable of eating oysters >50 mm shell height (Garton, 1986; Brown and Richardson, 1987).

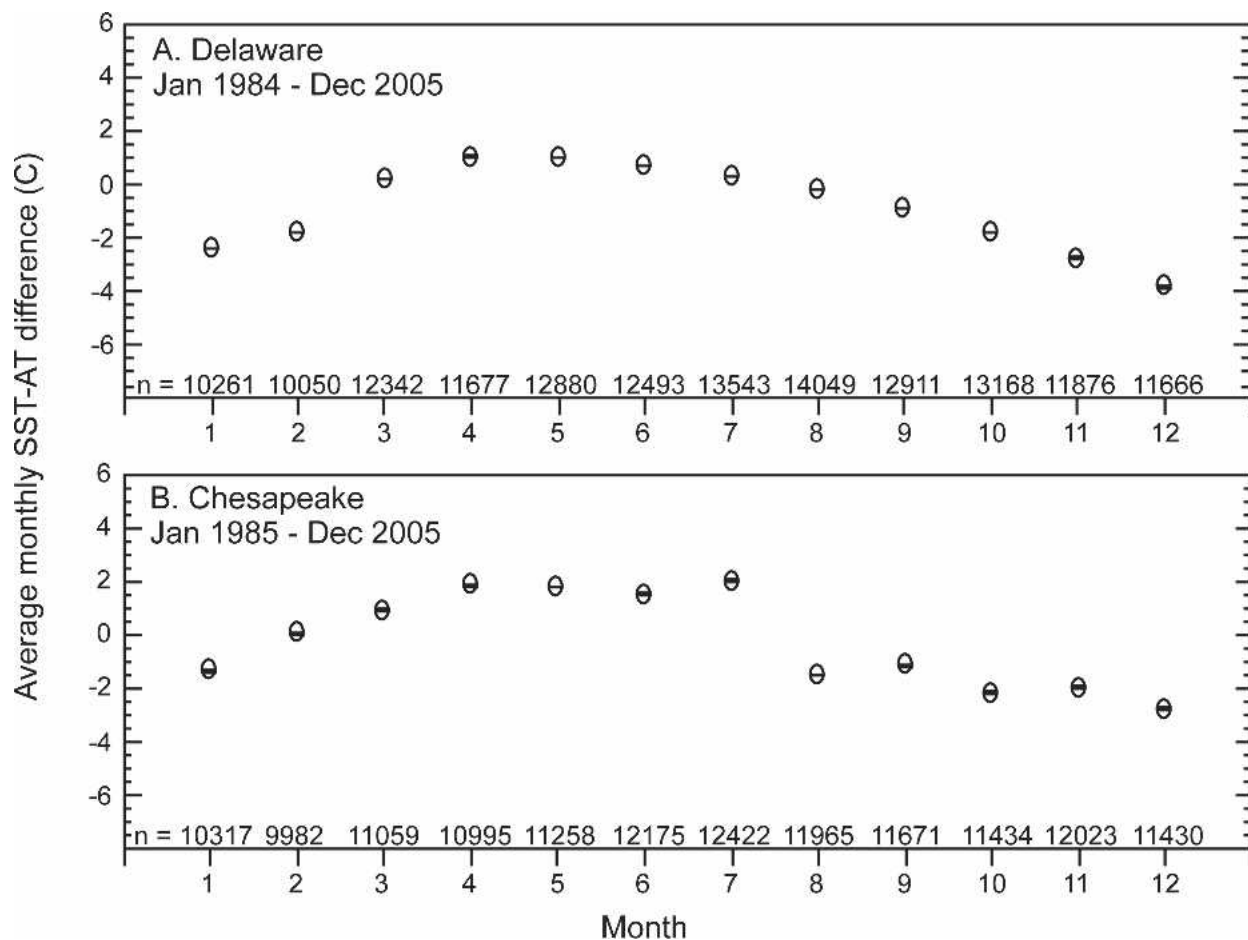


Figure 14. Average monthly difference between sea surface temperature (SST) and air temperature (AT) from NOAA buoys (Table 2) for Delaware (A) and Chesapeake (B) buoys. Error bars indicate standard error of the mean. N values (number of daily SST-AT pairs used to estimate the SST-AT differences) at each site are presented above the X axis in each panel.

DNA Bar-coding: Comparisons of a 591 base-pair portion of the mitochondrial gene for cytochrome *c* oxidase I from the samples listed in Table 1 revealed that specimens of *Stramonita* collected within Chesapeake Bay were genetically very similar or identical to specimens collected from Fort Pierce Inlet, on the southeastern coast of Florida, but differed substantially from Azorean samples and even more so from specimens from the northwestern coast of Florida (Table 3). Maximum parsimony analyses of the 144 phylogenetically informative sites using the exhaustive search algorithm yielded four equally parsimonious trees (length = 176; ci = 0.955; ri = 0.960). Figure 12 illustrates strict consensus tree of these four trees, including results of bootstrap and jackknife analyses.

Water Temperature Data: COASTAL HABITATS: Average annual bottom water temperatures in the period 1950–2005 for the two stations along the US Atlantic coast followed a latitudinal trend and were lower (9.81°C, SEM = 0.15, 600 months of data) at Delaware than at Chesapeake (12.30°C, SEM = 0.21, 596 months of data). The differences between SST and BT recorded

by the lightships (approximately 1956–71) show the seasonal development of the thermocline at Delaware and Chesapeake beginning in April and persisting until October with the most pronounced differences between surface and bottom water temperatures occurring in July and August (Figure 13) when these stations experience surface temperatures that are at least 7° C higher than bottom temperatures. Air temperatures recorded by the Delaware and Chesapeake NOAA buoys (Table 2) are 1–2° warmer than SST from April through July (Figure 14).

Examination of annual average residual bottom water temperatures from the average long-term (1950–2005) bottom water temperatures at coastal stations (Figure 15) shows that both sites experienced above average water temperatures during the late 1950s. Multiple consecutive years between 1970–1980 and, again, in the period 1995–2005. Estimated bottom water temperatures for 2002 were among the highest observed during the period 1950–2002 for Delaware and Chesapeake Bays. Delaware and Chesapeake, both north of Cape Hatteras, experience water temperatures of 10°C or less eight and five months out of the year, respectively (Table 4A).

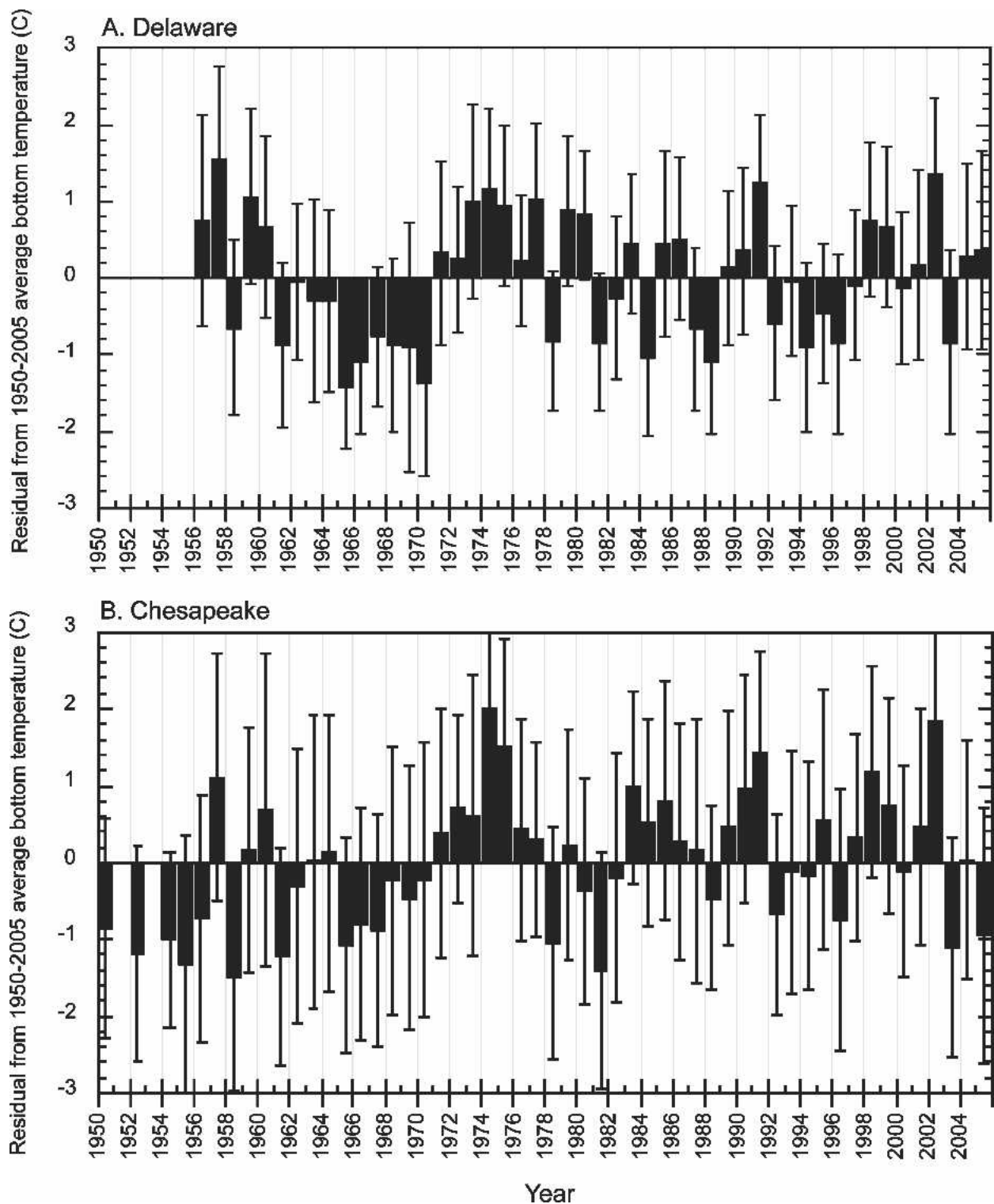


Figure 15. Annual average residual bottom temperature (BT) from the long term (1950–2005) average bottom temperatures for Delaware (A) and Chesapeake (B). Long term average data for each site are presented in Table 4. The error bars represent the standard error of the mean in degrees Celsius.

Table 4. Summary of average monthly bottom water temperatures for coastal stations (A, 1950–2005) and estuarine stations (B) shown in Figure 10 and discussed in text. Standard error of the mean for each value is given in parentheses.

A.

Month	Delaware	Chesapeake
Jan	6.99 (0.22)	6.96 (0.24)
Feb	5.25 (0.20)	5.60 (0.23)
Mar	5.58 (0.18)	6.12 (0.21)
Apr	7.02 (0.15)	8.31 (0.20)
May	8.88 (0.22)	11.02 (0.21)
Jun	9.33 (0.18)	14.34 (0.21)
Jul	9.45 (0.15)	14.93 (0.20)
Aug	10.69 (0.20)	16.72 (0.25)
Sep	14.62 (0.29)	20.27 (0.20)
Oct	16.56 (0.20)	19.11 (0.21)
Nov	13.57 (0.15)	11.02 (0.21)
Dec	10.06 (0.18)	10.41 (0.23)

B.

Month	Chincoteague Bay, Public Landing, MD (1951–56)	Chincoteague Bay, XBM8149 (2001–04)	Chincoteague Bay, XBM1301 (2001–04)	York River, Gloucester Point, VA (1986–2005)
Jan	4.14 (0.36)	5.3	5.7	5.32 (0.36)
Feb	6.22 (0.33)	5.25	5.38	5.55 (0.47)
Mar	9.76 (0.35)	9.65	9.9	8.46 (0.33)
Apr	14.57 (0.43)	15.53	15.85	13.61 (0.30)
May	20.1 (0.38)	18.65	18.87	18.86 (0.26)
Jun	24.08 (0.38)	27.25	26.33	23.91 (0.26)
Jul	27.77 (0.32)	26.1	25.85	26.96 (0.18)
Aug	27.2 (0.26)	27.42	27.65	27.11 (0.18)
Sep	23.6 (0.40)	22.95	22.93	23.99 (0.59)
Oct	17.32 (0.50)	14.55	14.6	19.28 (0.33)
Nov	10.72 (0.38)	15.1	15.68	13.56 (0.24)
Dec	5.64 (0.39)	5.2	5.5	8.36 (0.54)

ESTUARINE HABITATS: Annual average residual bottom water temperatures from the York River at Gloucester Point, Virginia were higher than the 1986–2005 annual average ($16.23 \pm 0.56^\circ\text{C}$) in 10 of the 18 years for which data are available (Figure 16) including 2005.

The relatively shallow (3 m or less) estuarine habitats examined in Chincoteague and Chesapeake Bays experience a seasonal average monthly water temperature cycle appropriate for their latitudes (Table 4B) with water temperatures less than 10°C observed December through March. The same pattern was observed in Chincoteague Bay during 1951–1956 (Table 4B).

DISCUSSION

The collections of live *Stramonita* from the James River (2005) and Back River (2006) mark the first modern record of this predatory gastropod from the Chesapeake Bay interior. The morphology of these specimens, particularly their larger size, deeply channeled suture, and the presence of strong, rugose shoulder nodules in the Back River samples, is similar to that of some populations from the northern Gulf of Mexico [particularly the form named *Stramonita haemastoma haysae* (Clench, 1927)

(Figure 8)]. This, in turn, has raised questions about whether these animals were introduced into Chesapeake Bay, and the possible source of such introductions. However, the results of the “DNA bar-coding” study clearly indicate that the Chesapeake *Stramonita haemastoma floridana* are genetically very similar to, and in one case indistinguishable from, a population of *Stramonita haemastoma floridana* from southeastern Florida. There seems little doubt that the source of the Chesapeake *Stramonita haemastoma floridana* populations lies along the eastern seaboard of the United States. Less clear is whether these populations were introduced into Chesapeake Bay with oysters, as had been suggested by Sieling (1960) for the Chincoteague *Stramonita*, or if their presence is due to a northward expansion of the range of *Stramonita haemastoma floridana* due to warmer ocean temperatures.

The “bar-coding” data also indicate that the east-coast *Stramonita* are well differentiated from, yet more similar to *Stramonita* from the Azores than to specimens from the northern Gulf of Mexico (Figure 12). Provisional taxonomic consequences of this study are to recognize the Azorean populations as *Stramonita haemastoma haemastoma*, to retain the usage of *Stramonita haemastoma*

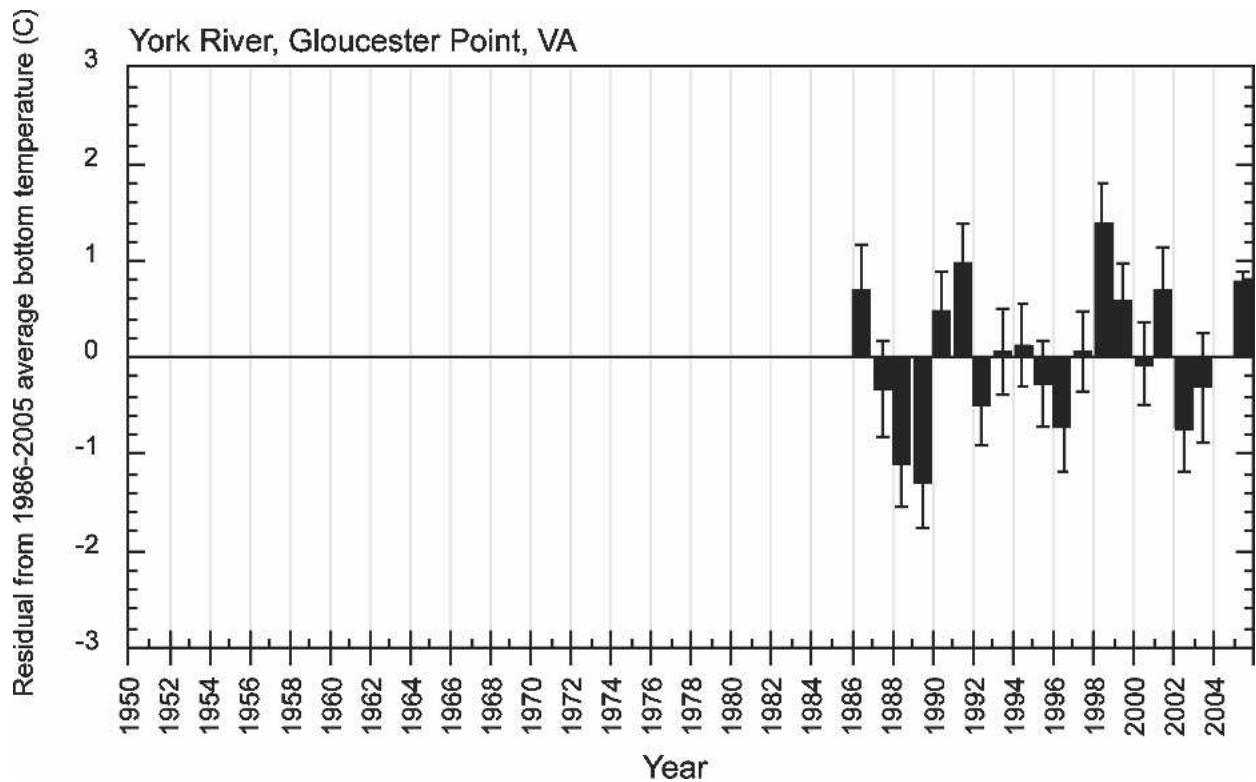


Figure 16. Annual average residual bottom temperature (BT) from the long term (1986–2005) average bottom temperatures (16.23 °C, standard error of the mean 0.56 °C) recorded at Gloucester Point, Virginia. The error bars represent the standard error of the mean in degrees Celsius.

floridana for the populations from the eastern United States, and to distinguish the populations from the northern Gulf of Mexico as *Stramonita canaliculata*, as advocated by Liu et al. (1991). Detailed analyses of this species complex over its entire geographic range are clearly required to better understand its biogeography and taxonomy.

Water temperature patterns in Chesapeake Bay habitats and along the coast of the lower Mid-Atlantic Bight since the late 1990s have been above average as were water temperature trends observed in the period 1955–1957 when live *Stramonita* were collected on the Atlantic coast of Maryland and Virginia (Sieling, 1960). Although the lower thermal lethal limit for southern oyster drills is unknown, the fact that observed seasonal trends in bottom water temperatures in Chincoteague Bay during the period 1951–56 are within 1 to 2°C of bottom water temperatures observed in the lower York River from 1986–2005 suggests that Chesapeake Bay tributaries may have seasonal temperature regimes conducive to survival of this animal. Living southern oyster drills were collected from Chincoteague Bay by Prezant et al. (2002) during surveys between 1991 and 1996, some 40 years after the initial collection (Sieling, 1956). The very low population levels (“rare”, Counts and Bashore, 1991) of southern oyster drills observed in Chincoteague Bay since 1988–89 have been attributed to a decline in local oyster resources (Counts and Bashore, 1991) rather than

unfavorable water temperatures. The tributaries of the lower Chesapeake Bay have resident populations of bivalves commonly eaten by *Stramonita* including mussels and oysters (Butler, 1985; Garton, 1986; Brown and Richardson, 1987). Several of these tributaries are also sites of focused oyster restoration efforts that incorporate addition of either spat on shell or broodstock oysters further expanding the potential prey field for southern oyster drills.

If these collections represent the beginning of an invasion into Chesapeake Bay tributaries, the persistence of *Stramonita haemastoma floridana* in Chesapeake Bay will be dictated by thermal tolerances as subjected to seasonal temperature cycles, while the geographic distribution will be set by salinity tolerances of adult and larvae. Adult *Stramonita haemastoma* may survive at salinities as low as 5–7 ppt (Gunter, 1979; Stickle, 1999). *Stramonita haemastoma* egg capsules survive and release viable larvae at salinities down to at least 7.5 ppt and possibly as low as 3.5 ppt (Stickle, 1999). Veliger larvae may survive up to 5 days when exposed to 10 ppt (Wells, 1961) but Roller and Stickle (1989) reported very low survival at salinities less than 15 ppt. In June 1972, heavy rains from Tropical Storm Agnes in combination with summer temperatures killed essentially all of the native oyster drills [*Urosalpinx cinerea* (Say, 1822), *Eupleura caudata* (Say, 1822)] in the upper reaches of Chesapeake Bay tributaries and reset the distributional range of the

native drills to the high salinity, lower reaches of the Chesapeake Bay where natural oyster populations currently persist in only limited regions and numbers. Re-establishment of these native gastropod species to their former habitats is occurring slowly over decadal time scales and is limited by the lack of planktonic larvae for both *Urosalpinx cinerea* and *Eupleura caudata*. Reinvansion of their historic habitats by the native drills is confounded by the fact that the historically widespread distribution of oyster reef habitat has been drastically reduced in areal coverage since the early 1960s by a combination of diseases and environmental degradation. Competition for the niche vacated by the native drills during Tropical Storm Agnes already includes one large non-native gastropod, the veined rapa whelk (*Rapana venosa*) (Harding and Mann, 1999; 2005), which has planktonic veliger larvae like *Stramonita haemastoma* and is equally long-lived. Regardless of how these *Stramonita haemastoma* got to these Chesapeake tributaries, the presence of adult individuals in these tributaries adds yet another competitor for this vacant niche as well as additional predation pressure on local oyster resources.

Successful invasion of a habitat requires a breeding population and the presence of all life history stages in the new habitat (Williamson, 1996). Southern oyster drills live from 5–20 yr in Florida (Butler, 1985) with generation times on the order of 12 months (Burkenroad, 1931; Butler, 1954). The small number of specimens collected to date combined with the absence of these animals in annual fishery independent surveys of oyster reefs in the James River conducted by Harding and colleagues at VIMS and the Virginia Marine Resources Commission since the early 1990s may be an indicator that the observed southern oyster drills specimens represent small, isolated introductions that have not yet established local populations.

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