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OBSERVATIONS ON THE BIOLOGY OF THE VEINED RAPA WHELK, *RAPANA VENOSA* (VALENCIENNES, 1846) IN THE CHESAPEAKE BAY

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ABSTRACT The recent discovery of the Veined Rapa whelk (*Rapana venosa*, Valenciennes, 1846) in the lower Chesapeake Bay provides an opportunity to observe the initial biological and ecological consequences of a novel bioinvasion. These large predatory gastropods occur in subtidal, hard bottom habitats in the lower Bay and are capable of feeding, mating, and moving while completely burrowed. Hard clams (*Mercenaria mercenaria*) are consumed preferentially in the laboratory when offered concurrently with oysters (*Crassostrea virginica*), soft clams (*Mya arenaria*), and mussels (*Mytilus edulis*). Chesapeake Bay *R. venosa* readily open and consume large hard clams (30 to 85 mm SH) leaving no visible signs of either drilling or boring behavior. Shell morphology and thickness may provide an inherent size-selective predation refuge for Rapa whelks in the Bay. These same shell characteristics may change the dynamics of shell selection by local hermit crabs, particularly the striped hermit crab, *Clibanarius vittatus*. Recent collections of striped hermit crabs from the Hampton Roads area indicate that very large striped hermit crabs are using empty *Rapana* shells as shelters.

KEY WORDS: *Rapana venosa*, Veined Rapa whelk, Muricidae, Thaididae, ballast water, bioinvasion, Chesapeake Bay, *Clibanarius vittatus*, *Mercenaria mercenaria*

INTRODUCTION

The Veined Rapa whelk, *Rapana venosa*, (Valenciennes, 1846) is a large, predatory gastropod that has recently been found in the lower portion of the Chesapeake Bay. As with other representatives of the Thaididae family [Earlier classifications of the Neogastropods place *Rapana* sp. in the family Muricidae. Recent taxonomic revisions include *Rapana* in the Thaididae (R. Germon, Smithsonian Institution, Washington, D.C., pers. comm.)], this animal is a carnivore whose principal prey items include many commercially valuable bivalves. *Rapana venosa* is one of several modern *Rapana* species including *R. bezoar* and *R. rapiformis*. Although *R. thomasiana* was originally described by Crosse in 1861 as a separate species (Thomas's Rapa whelk), it is currently recognized as a synonym for *R. venosa* (R. Germon, Smithsonian Institution, Washington, DC, pers. comm.).

Rapana venosa is native to the Sea of Japan, the Yellow Sea, the East China Sea, and the Gulf of Bohai (Tsi et al. 1983, Chung et al. 1993, Zolotarev 1996, Chung and Kim 1998). Three species of *Rapana* occur sympatrically in Chinese waters: *R. venosa*, *R. bezoar*, and *R. rapiformis* (Tsi et al. 1983). All three species are found in coastal subtidal habitats and are commercially harvested (Hwang et al. 1991, Chung et al. 1993, Morton 1994). Rapa whelks were discovered in the Black Sea in 1947 (Drapkin 1963) and have subsequently spread throughout the Black Sea and into the Sea of Azov as well as the Aegean (Koutsoubas and Voultsiadou-Koukoura 1990, Zolotarev 1996) and Adriatic (Bombace et al. 1994) Seas. *R. venosa* from Korean waters described by Chung et al. (1993) ranged from 32.5 to 168.5 mm shell length (the maximum distance from the tip of the spire to the bottom of the columella, SL).

Rapana venosa is easily distinguished from native gastropods of the Chesapeake Bay. It has a short spired, heavy shell with a large inflated body whorl and a deep umbilicus (Fig. 1). The slightly concave columella is broad and smooth. Small, elongate teeth are present along the edge of the large, ovate aperture's outer lip. External shell ornamentation includes smooth spiral ribs that end in regular blunt knobs at both the shoulder and the periphery of the body whorl. In addition, fine spiral ridges are crossed by low vertical riblets. Older specimens can be eroded, but the color is variable from gray to orange-brown (one specimen is atypically blonde), with darker brown dashes on the spiral ribs. The aperture and columbella vary from deep orange-red to yellow or off-white. Spiral, vein-like coloration, ranging from black to dark blue, occasionally occurs internally, originating at the individual teeth at the outer lip of the aperture.

The first collection of *Rapana venosa* in the Chesapeake Bay was made in the summer of 1998 during a routine trawl collection by the Virginia Institute of Marine Science (VIMS) trawl survey in the vicinity of the Monitor-Merrimac Tunnel (Fig. 2). This specimen was positively identified as *Rapana venosa* by Drs. Jerry Harasewych (Smithsonia Institution, Washginton, DC) and Yuri Kantor (Russian Academy of Science, Moscow). A subsequent sampling trip specifically for *Rapana venosa* in the same vicinity on August 24, 1998 yielded two masses of *R. venosa* egg cases (Fig. 3; a total of 50+ egg cases) but no live animals. The egg cases were returned to VIMS and maintained at ambient temperature and salinity conditions on a 14 h light:10 h dark regime. Within a week postcollection, individual egg cases began hatching with the last egg case hatching on September 21, 1998. Larvae were cultured and used in salinity tolerance experiments (Mann and Harding, in review). Given the size of the specimens collected to date from the lower Bay (68 to 165 mm SL) and the presence of viable egg cases, it seems reasonable to assume that the local Rapa whelk population is sexually mature and actively breeding.

As in the eastern Mediterranean and Black Seas (Zolotarev 1996), ballast water from commercial and/or military ship traffic is the probable source of introduction into the Chesapeake Bay. *R. venosa* larvae are planktonic for 14 to 17 days (Chung et al. 1993, Mann and Harding in review). Normal transit time to the Hampton Roads/Norfolk area from the Baltic, Black, Adriatic, or Aegean Seas is approximately 10 to 24 days (G. Ruiz, Smithsonian Environmental Research Center, pers. comm.). This time interval is well within the temporal window for survival of viable planktonic *R. venosa* larvae. At certain times during the year (e.g., May

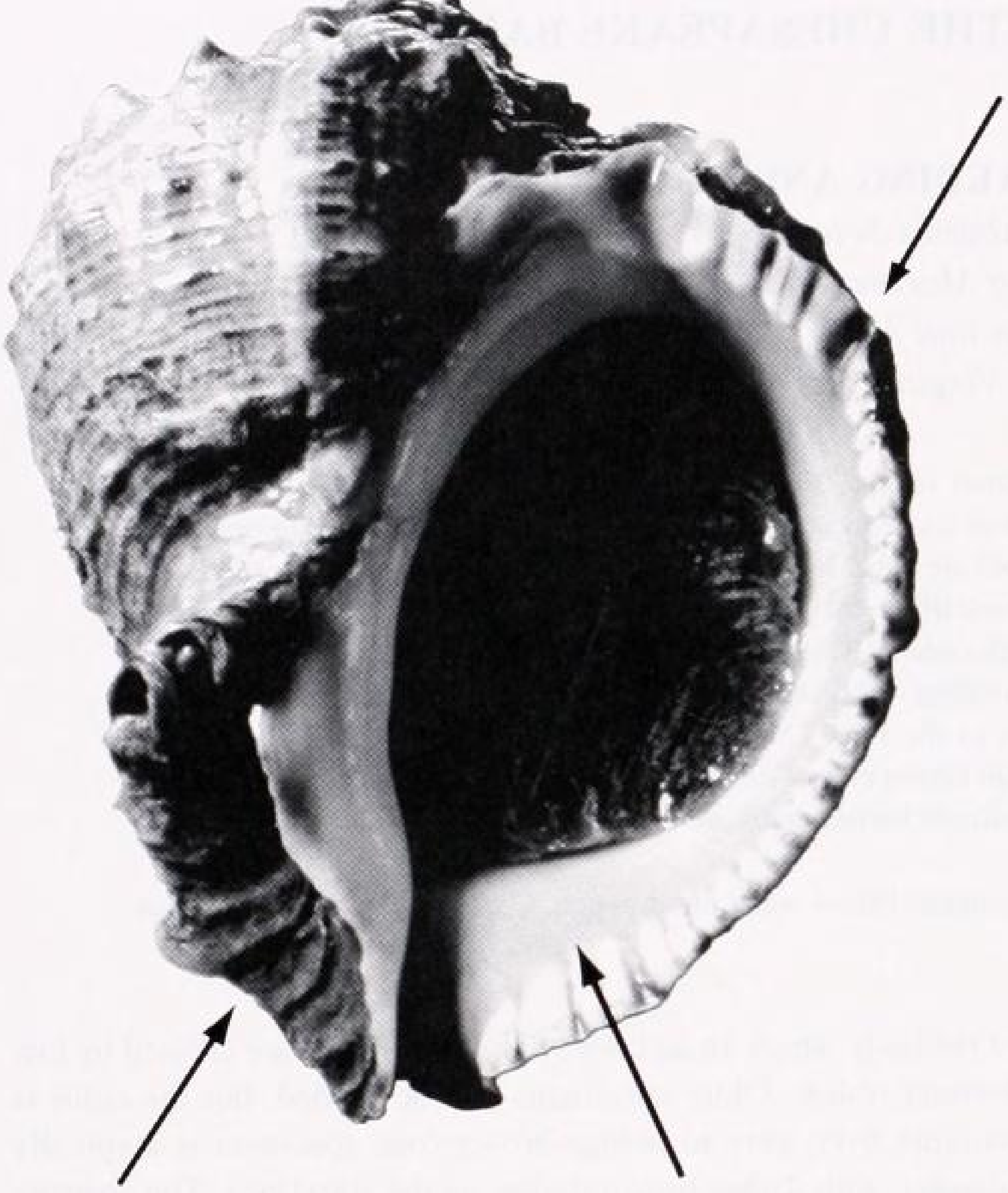


Figure 1. Picture of an adult *Rapana venosa* (150 mm SL) from the Chesapeake Bay. The arrows highlight the broad columella, opercular teeth, and bright orange aperture.

through October) temperature and salinity regimes on both ends of the trip are similar (see Mann and Harding, in review for a detailed discussion). The Hampton Roads/Norfolk area is a major foci of container, coal transport, and military ship activity. The area ranks third among U.S. ports in terms of volume of ballast discharged on an annual basis (G. Ruiz, Smithsonian Environmental Research Center, pers. comm.). Given the sheer volume of ballast water arriving in Chesapeake Bay annually from ports with active Rapa whelk populations (15 million metric tons; G. Ruiz, Smithsonian Environmental Research Center, pers. comm.), the possibility of obtaining sufficient numbers of Rapa whelk larvae needed to eventually establish a breeding population in the Chesapeake Bay may be quite high. International traffic aside, the Hampton Roads/Norfolk area is also a major hub for coastal shipping along the eastern seaboard of North America (G. Ruiz, Smithsonian Environmental Research Center, pers. comm.). If a local population of Rapa whelks becomes established in the Bay, it is likely that the Chesapeake would eventually become a source population for other coastal ports with similar habitat conditions. This scenario places ports throughout the Middle Atlantic Bight (e.g., New York, Boston) as well as the South Atlantic Bight (e.g., Charleston) at higher risk for introduction of the species in that they would be receiving both international and local inoculations.

Since the discovery of *Rapana venosa* in the Chesapeake Bay, live Rapa whelks have been under observation in wet laboratory tanks at VIMS. To date, 412 animals have been donated to VIMS (these numbers include live animals, dead animals with shells, or shells only), mostly by commercial watermen and seafood processing companies, indicating the presence of an established population of *Rapana venosa* in the lower portion of the Chesapeake Bay. Observations to date on the basic biology and ecology of *Rapana venosa* in the Chesapeake Bay are described herein and placed in the context of potential trophic interactions of this animal in the lower Chesapeake Bay.

Current Distribution

The current distribution of *Rapana venosa* in the Chesapeake Bay extends from the Chesapeake Bay Bridge Tunnel northward along the western shore line in a continuous swath across Little Creek, Ocean View, Fort Monroe, and Buckroe Beach (Figs. 2 and 4). Several unconfirmed reports from the Poquoson flats area are punctuated by two confirmed discoveries of *Rapana* at Tue Marshes Light in the York River (Fig. 2). The northernmost report of a Rapa whelk in the Bay is from Butler's Hole, a small oyster rock near the mouth of the Rappahannock River; this 130 mm SL

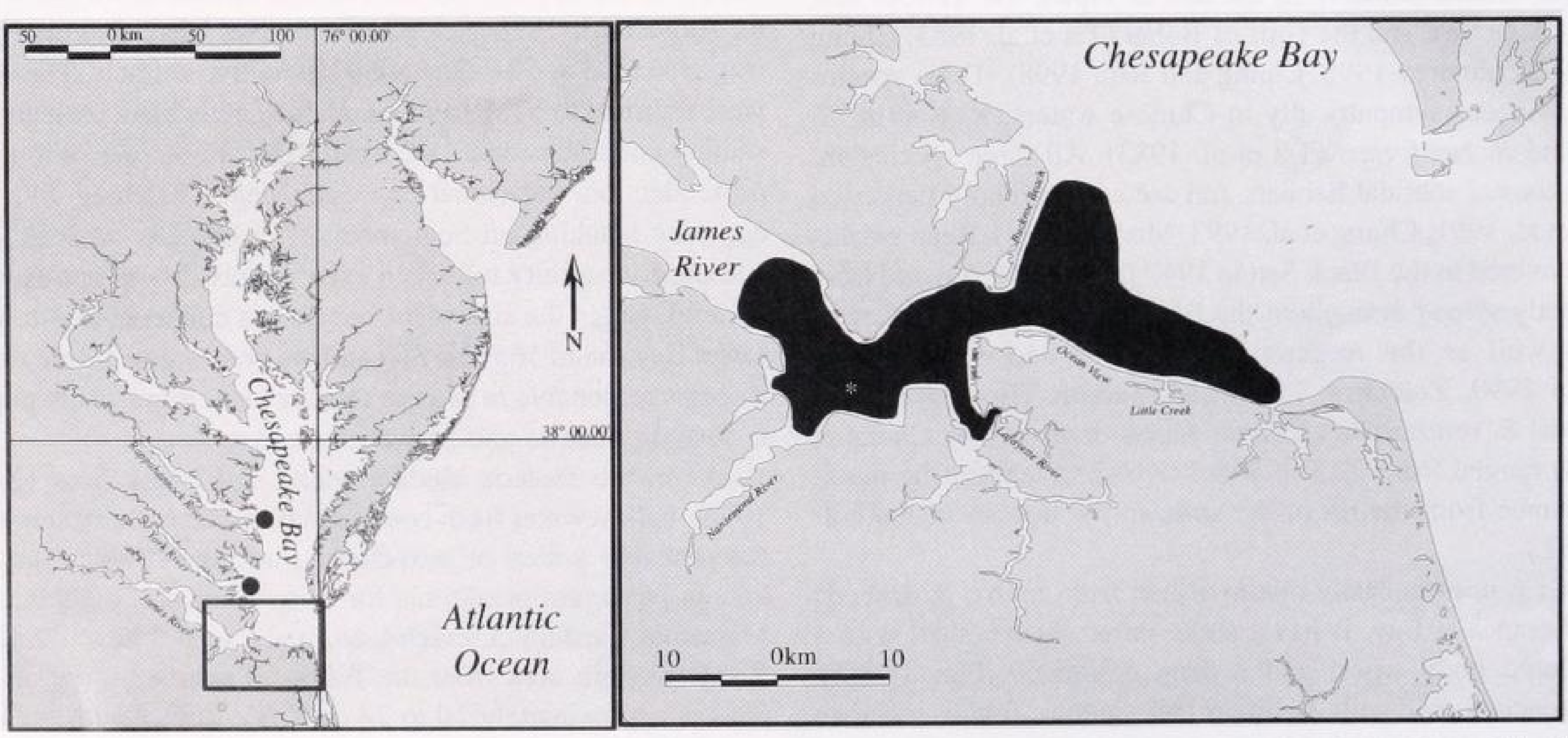


Figure 2. Map showing known *Rapana venosa* distribution as of March 1999 in the Chesapeake Bay proper (A.) and the Ocean View/Hampton Roads/James River region (B.). The black circles (A.) indicate the Rappahannock and York River collection sites. The black zone (B.) shows the known distribution within the lower Bay/Hampton Roads/James River. The first collection location is indicated with an asterisk (B.).

A. B.

Figure 3. *Rapana venosa* egg cases collected from Hampton Roads, VA in August 1998. The yellow egg case cluster was attached basally to a hydroid mat (A.). Note the broad phyllopodus egg case tops and egg pores shown in the top view (B.).

individual was collected by the authors during an annual oyster stock assessment dredge survey.

The majority of Rapa whelks have been collected by either commercial clammers or crab dredgers working in the lower Bay. In early September 1998, VIMS established an ongoing *Rapana* bounty system with the help of the Virginia Saltwater Commerical Fishing Develoment Fund and, as of January 1999, the Virginia Sea Grant program. A bounty is paid for each snail turned in to VIMS personnel, provided that collection information (i.e., location, gear, depth, and bottom type) are reported at the time of donation. The bounty program yielded an average of 8 to 10 animals per week through the end of November 1998 donated primarily by clammers working off Ocean View and Buckroe Beach (Fig. 2). Clammers in the lower Chesapeake fish for hard clams or quahogs (*Mercenaria mercenaria*) with patent tongs. Quahogs > 50 mm shell height are abundant (approximately 1 to 11 animals m^2) in portions of the lower bay (Roegner and Mann 1991), and the commercial hard clam fishery in the reigon is economically important, annually landing 1.1 million pounds with a dockside value of approximately $6 million (Kirkley 1997).

The lower Bay also supports a winter crab dredge fishery targeting blue crabs (*Callinectes sapidus*) that burrow into the sand/mud bottom to overwinter. When crab dredge season opened in the lower Bay on December 1, 1998, Bay water temperatures were still 8 to 12°C. During the first 2 weeks of December 1998, over 30 Rapa whelks/day were donated to the VIMS colleciton by crab

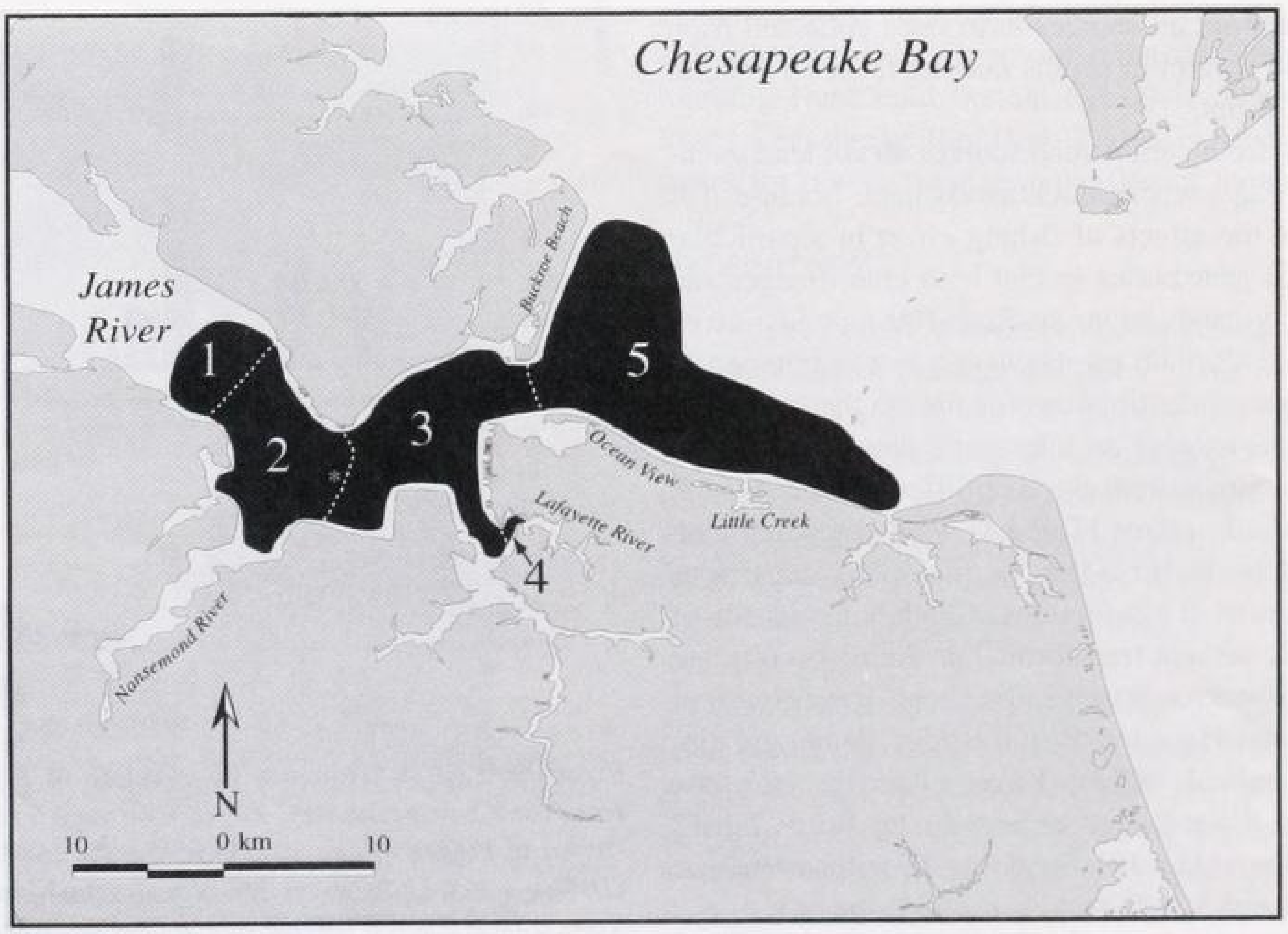


Figure 4. Distribution map of *Rapana venosa* from the lower Chesapeake Bay showing collection zones: 1.) Above the SR 258 James River Bridge, 2.) Between the James River Bridge and the Monitor-Merrimac Bridge Tunnel, 3.) Between the Monitor-Merrimac Bridge Tunnel and the Hampton Roads Bridge Tunnel, including the Hampton Bar area, 4.) the Lafayette River, and 5.) the Buckroe Beach, Fort Monroe, Ocean View, and Little Creek areas in the bay proper.

TABLE 1.

Summary of *Rapana venosa* collections through March 1, 1999 from the lower Chesapeake Bay and its tributaries.

Collection Location	n	Average Shell Length (mm)	Standard Error (SE, mm)
Lower Bay: Little Creek/Ocean View/Buckroe Beach	185	141.8	0.93
James River: Hampton Bar	7	138.8	5.23
James River: between Monitor-Merrimac Bridge Tunnel and the James River Bridge	198	132.7	0.84
James River: above the James River Bridge	11	131.3	3.63
Lafayette River	7	102.7	4.9
Nansemond River	1	135.0	——
York River: Tue Marshes Light	2	149.0	9.00
Rappahannock River: Butler's Hole	1	130.0	——

"n" refers to the number of animals collected from each location. Locations are shown in relation to the mainstem Chesapeake Bay and each other in Figures 2 and 4.

dredgers and seafood processing companies. The arrival of a cold front just before Christmas 1998 caused water temperatures to fall below 5°C and coincided with a reduction in both fishing activity and *R. venosa* donations. Throughout January and February 1999, crab dredgers working the lower Bay have reported few *R. venosa*. Presumably, the sustained colder temperatures have driven them either into deeper waters as reported in their home range (Wu 1988) or deeper into the sediment below the zone of dredging activity.

Although donations from crab dredgers in the lower Bay essentially stopped in January 1999, Rapa whelk donations from clammers working in the James River continued until the closing of the area to commercial fishing in mid-March at an average rate of 6 animals/day^{-1}. As of this writing, there have been no *R. venosa* reported by commercial oystermen working on extant oyster beds in the James River upstream of the Route 258/17 James River bridge (Haven and Whitcomb 1983). A majority of the animals collected to date from all sources have been collected from regions with hard sand bottom in depths ranging from 10 to 60 m at salinities of 18 to 28 ppt.

The collection data from commercial sources do not lend themselves to an accurate Rapa whelk stock assessment, because it is impossible to separate the effects of fishing effort in a particular location from potential gear biases in that both crab dredges and patent tongs selectively catch larger snails (>100 mm SL) given standard ring size for both (0.06 m). However, an examination of *R. venosa* length-frequency distributions for sites in the lower Bay and Hampton Roads area yields an interesting pattern. The shell lengths (SL, mm) of animals from the five different regions with >5 confirmed Rapa whelk reports (Table 1) were compared with an ANOVA followed by Fisher's test for multiple comparisons (per Zar 1996). Data satisfied assumptions of both homogeneity of variance and normality without transformation. Animals collected from the Ocean View/Buckroe Beach/Little Creek area (Fig. 4) or from regions outside the Hampton Roads Bridge tunnel are significantly larger than animals collected from either the Lafayette River, above the James River Bridge, or between the Route 258/17 James River bridge (hereafter JRB) and the Monitor-Merrimac bridge tunnel (Figs. 4 and 5; ANOVA, $p < .05$; Fisher's test, $p < .05$). Animals collected from the Lafayette River are significantly smaller than Rapa whelks collected from any other site (Figs. 4 and 5; ANOVA, $p < .05$; Fisher's test, $p < .05$). It is interesting to note that the Little Creek/Ocean View area is immediately adjacent to

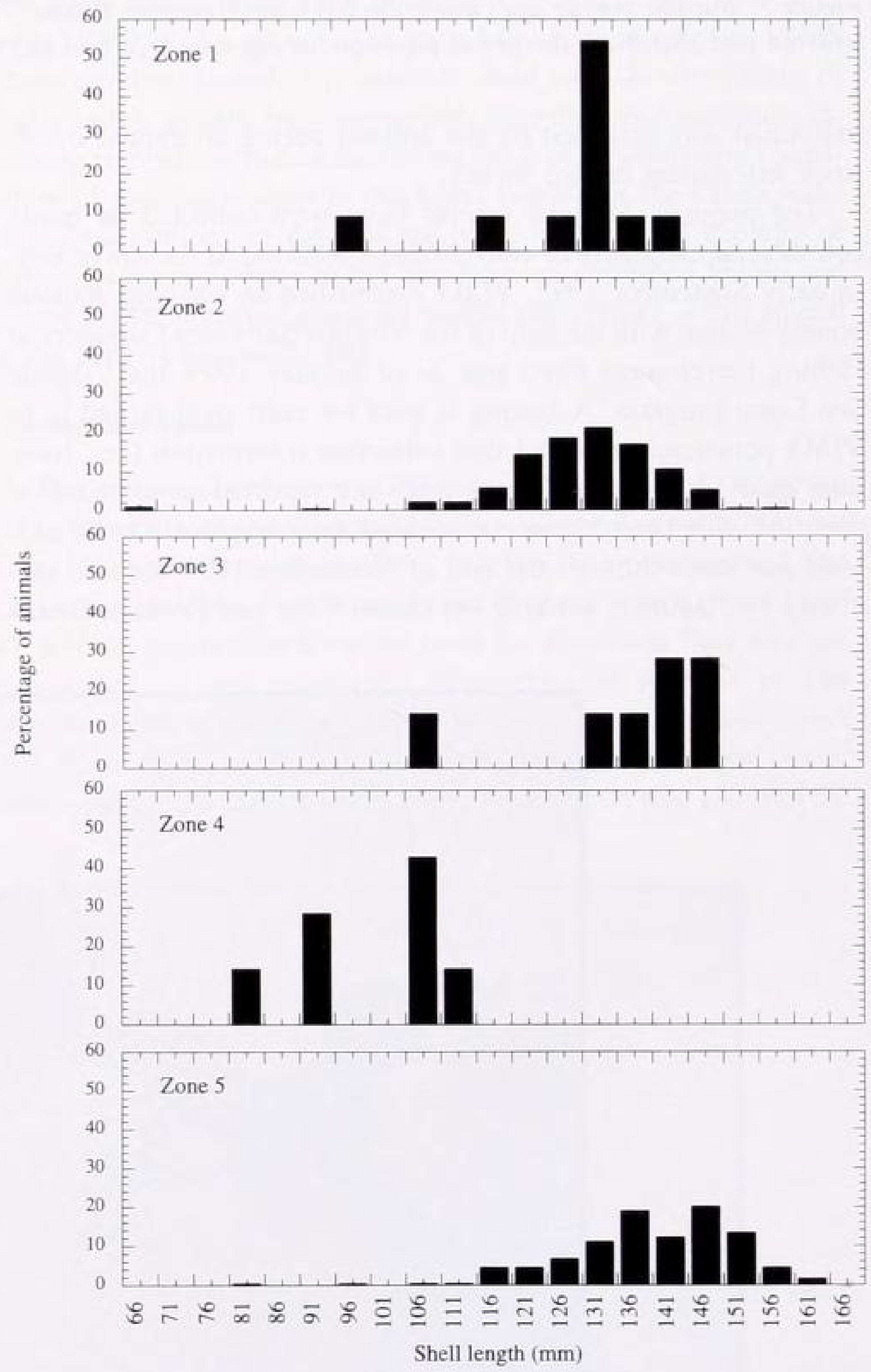


Figure 5. Length-frequency distribution of *Rapana venosa* collected from the Chesapeake Bay. Zones 1 through 5 correspond to the zones shown in Figure 4; i.e., 1.) Above the SR 258/17 James River Bridge (JRB, n = 11), 2.) Between the JRB and the Monitor-Merrimac Bridge Tunnel (n = 194), 3.) Between the Monitor-Merrimac Bridge Tunnel and the Hampton Roads Bridge Tunnel, including the Hampton Bar area (n = 7), 4.) the Lafayette River (n = 7), and 5.) the Buckroe Beach, Fort Monroe, Ocean View, and Little Creek areas in the Bay proper (n = 181).

both the anchorage for commercial and military ships awaiting pilots and clearance to enter the port and the Thimble Shoals shipping channel (Figs. 2 and 4). The area between the JRB and the Monitor-Merrimac bridge tunnel includes the Newport News coal container terminal, a major site of deballasting for international ships awaiting coal.

Age Estimates

In the absence of age and growth estimates for Chesapeake Bay *Rapana venosa,* age and growth estimates for a Knobbed whelk (*Busycon carica*) population from Virginia's Eastern Shore may offer a conservative estimate of potential Rapa whelk growth rates. Kraeuter et al. (1989) and Castagna and Kraeuter (1994) provide growth and length-at-age estimates for *B. carica* from both laboratory and field studies extending over a 14-year period. Growth rates for *B. carcia* were greatest during the first year (approximately 32 mm/y^{-1}) and then subsequently decreased to 14.4 mm/yr^{-1} for the first 10 years followed by growth rates of 6.5 to 9.5 mm/y^{-1} for animals older than 10 y and/or greater than 160 mm SL (Fig. 6; Kraeuter eta l. 1989, Castagna and Kraeuter 1994). In the absence of any data on *Rapana* growth rates in the Chesapeake Bay, it is reasonable to consider growth rates of such sympatric species as *B. carica* for initial estimates of Rapa whelk age. Ninety-five percent of all *R. venosa* collected thus far in the Chesapeake Bay are between 110 and 160 mm SL. If this range of *Rapana* shell lengths is overlaid onto the *B. carica* growth curve presented by Kraeuter et al. (1989) and Castagna and Kraeuter (1994), the resulting age distribution extends from approximately 7.5 to 13 years (Fig. 6). These are conservative growth estimates when considered in relation to the growth rates for Black Sea *Rapana* reported by Chukhchin (1984).

Rapa whelk length-at-age relationships have been described by

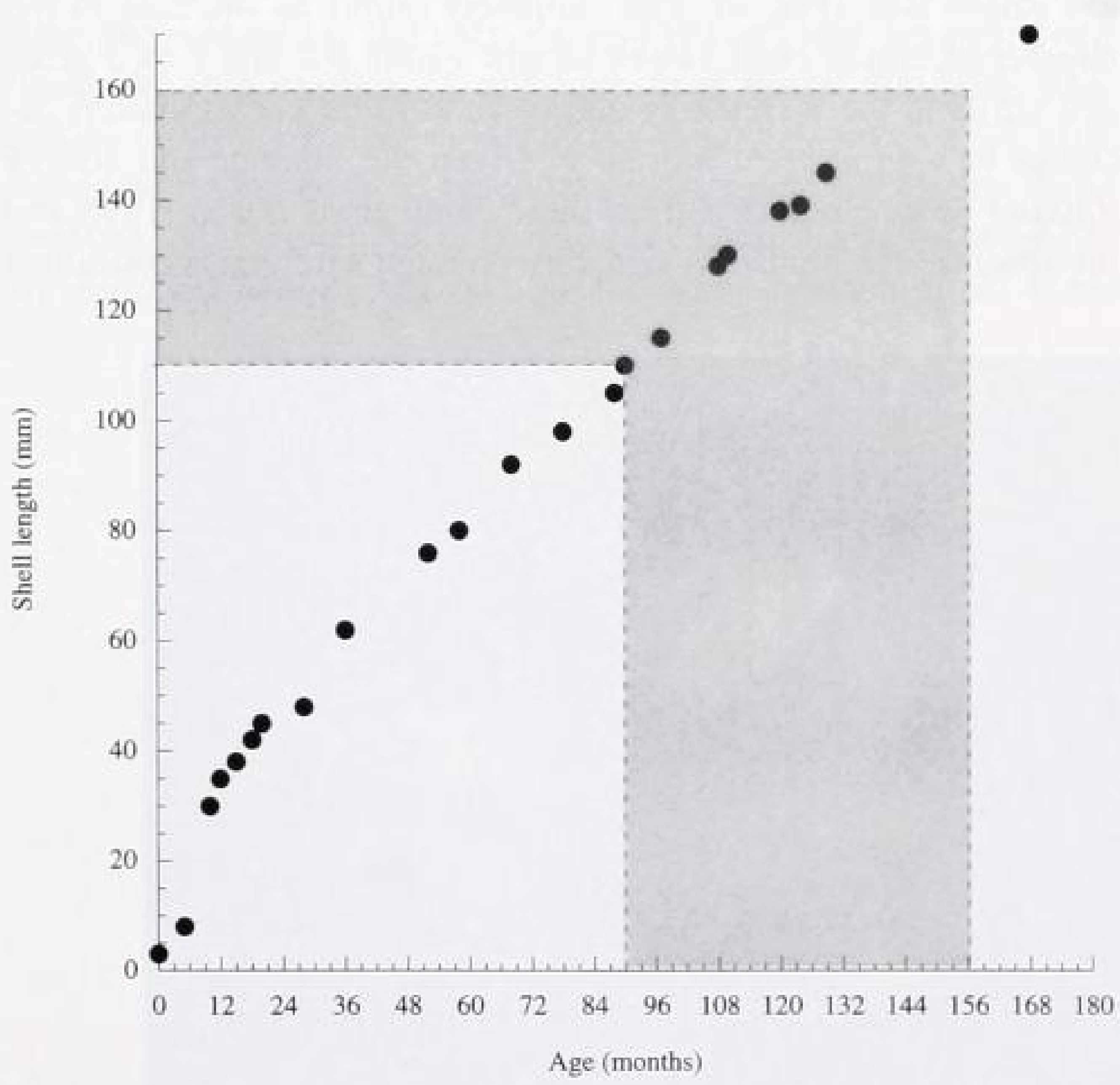


Figure 6. Plot of *Busycon carica* length-at-age relationship from laboratory and field observations of an Eastern Shore, VA *B. carica* population after Kraeuter et al. (1989) and Castagna and Kraeuter (1994). The shaded zone indicates the size range (SL, mm) and corresponding age estimate for 95% of the *Rapana venosa* collected in the Chesapeake Bay thus far.

Chukhchin (1984) for animals from the Black Sea. Chukhchin (1984) estimates reports growth rates for individuals in Sevastopol Bay of 20 to 40 mm during year 1, with mean shell length (SL) values of 64.6 mm, 79.4 mm, 87.5 mm, and 92.1 mm in years 2 through 6, respectively. This terminal size is smaller than the maximum SL of 120.1 mm reported by Smagowicz (1989) for a specimen in a collection from Bulgaria and Georgia, whose exact collection location was not reported. Chukhchin (1984) correlates shell thickening with spawning events and notes that the first spawning occurs in the second year at sizes ranging from 35 to 78 mm SL with a mean value of 58 mm SL.

Habitat Preferences

Both field collections and laboratory observations confirm that *Rapana venosa* prefers hard sand bottom habitats. These animals are avid burrowers and remain completely burrowed for more than 95% of the time in the laboratory. A 150 mm SL *R. venosa* can burrow into a sand bottom so that its shell is completely covered in less than 1 h. The only visible sign of a burrowed Rapa whelk is the maroon U-shaped siphon that is usually extended 1 to 3 cm above the surface of the sand. Rapa whelk siphons are sensitive to both light and motion and are retracted immediately at the slightest disturbance. Siphonal sensitivity combined with the animal's burrowing speed and low visibility conditions in the Bay may make conventional benthic survey methods that relay on direct observation of the animal (diver transects, video surveys) difficult as non-invasive stock assessment techniques. Bombace et al. (1994) observed an apparent increase in *R. venosa* biomass after artificial reef deployment in the Adriatic Sea. It is possible that there were burrowed *Rapana* at the sites at the time of reef deployment and that increases in *Rapana* sightings after reef construction are attributable to the emergence of local snails to feed on the reefs not the arrival of snails from other areas.

Laboratory observations indicate that Rapa whelks are capable of both feeding and mating while burrowed. They move reasonably quickly while burrowed (approximately 1 body length per minute). Hard sand bottom habitat is relatively common in the lower Chesapeake Bay (Fig. 7) and is not likely to be a limiting factor for potential range expansion of the animal in the bay.

Prey preferences

Rapana bezoar was described by Morton (1994) as "a generalist predator of subtidal molluscs." This description is certainly apt for *R. venosa* in the Chesapeake Bay. In laboratory feeding studies, Chesapeake Bay *R. venosa* prefer hard clams to oysters (*Crassostrea virginica*), soft clams (*Mya arenaria*), or local mussels (*Mytilus edulis*), although they will eat these other bivalves when hard clams are rare or unavailable (Fig. 8). A 140 mm SL Rapa whelk is capable of consuming a 75 to 80 mm hard clam in less than 1 h.

Previous reports on the feeding behavior of *R. thomasiana* (now recognized as *R. venosa*) from the Black Sea place *R. venosa* among the gastropods that drill their prey (Gomoiu 1972, Carriker 1981) or use paralytic toxins during feeding (Chukhchin 1984). Morton (1994) describes feeding behavior of *R. bezoar* in terms of boring or crude rasping usually on the posterioventral shell margin. Similar rasping behavior has been observed for Chesapeake Bay *Rapana venosa* feeding on small hard clams [<30 mm shell height, SH (distance from hinge to the opposite shell margin)]. Small chips or rasp marks are visible on the posterioventral shell margin

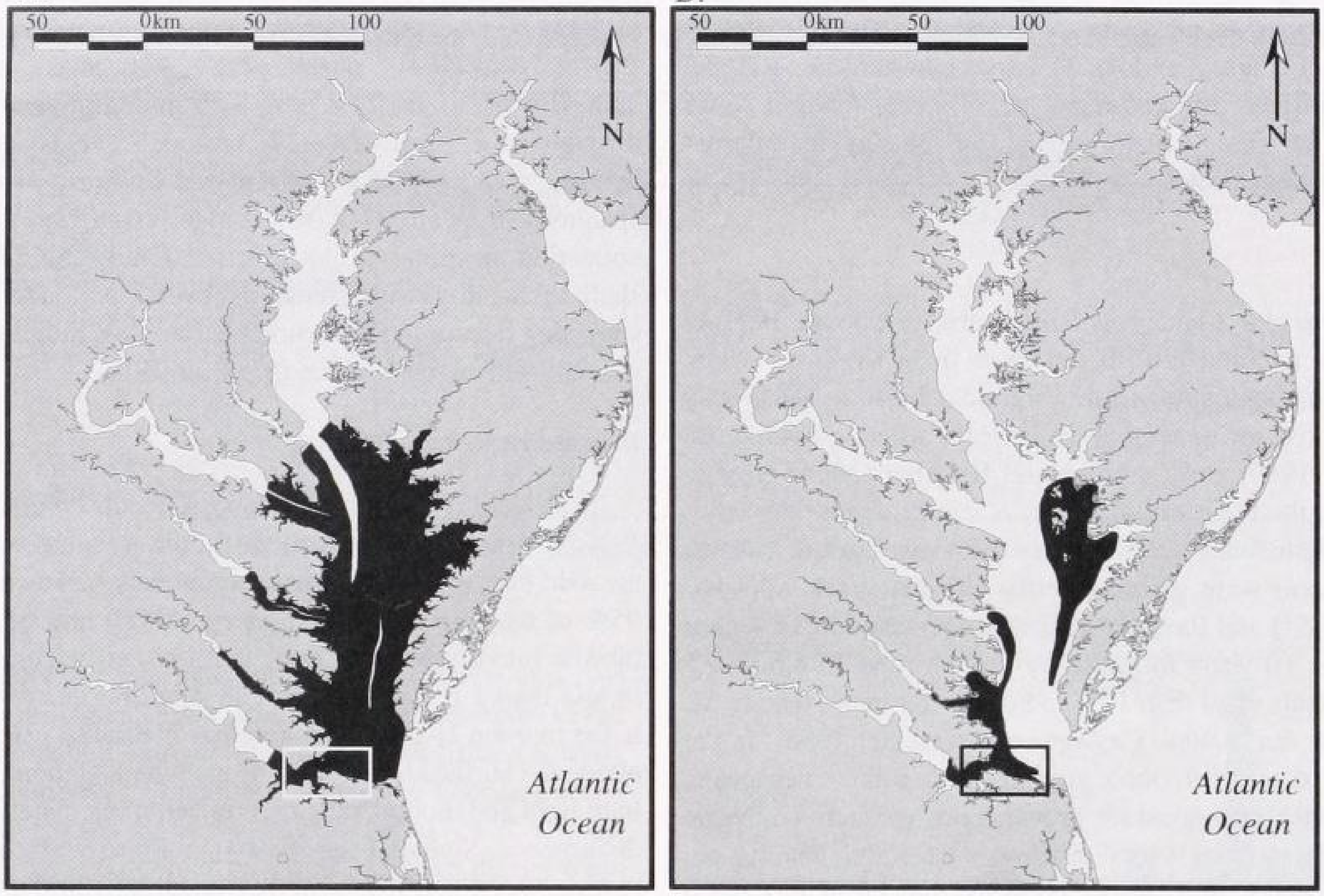
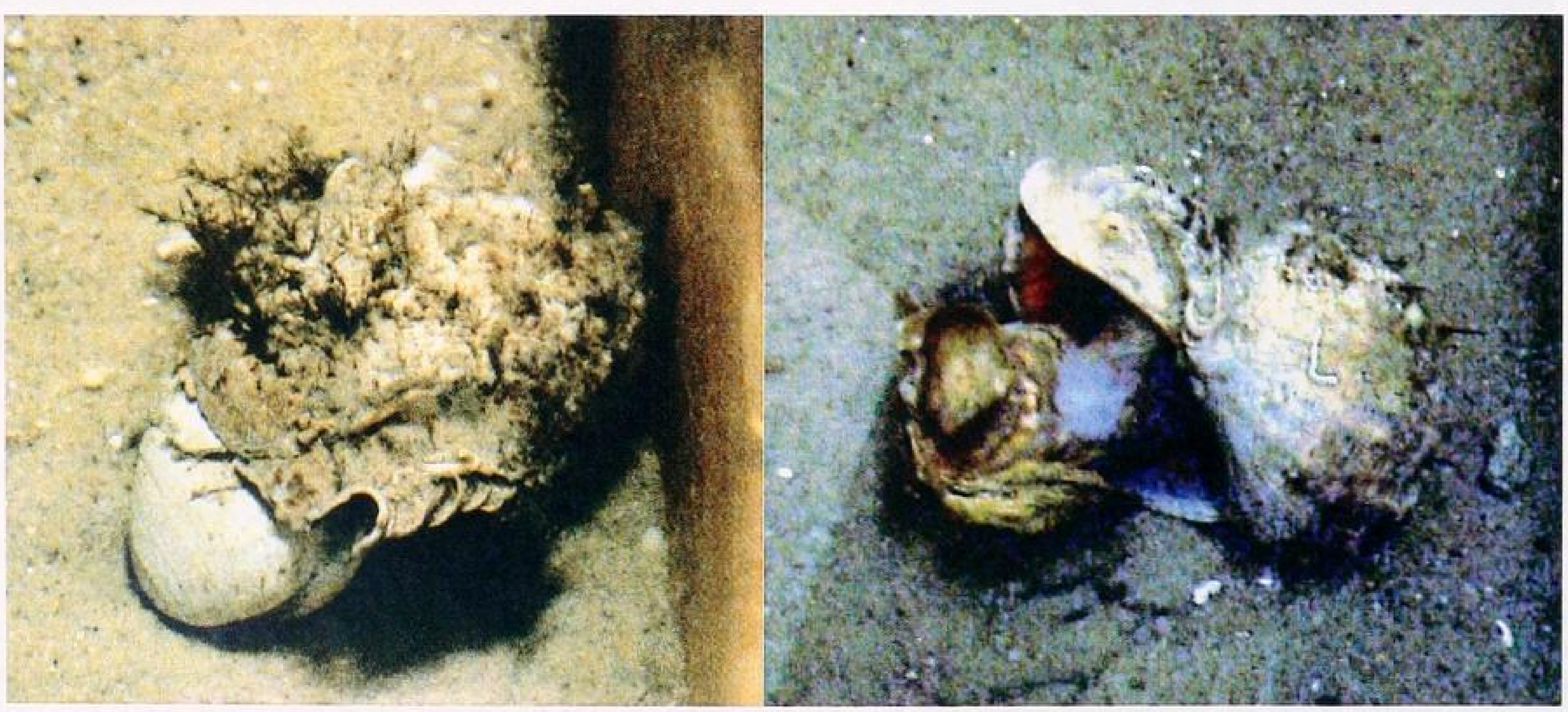


Figure 7. Maps of the lower Bay showing sand bottom habitat (A.) and hard clam populations (B.) in black per Roegner and Mann (1991). The Ocean View/Hampton Roads/James River region is indicated by a square in both maps.

of some small clams attacked and eaten by large *R. venosa*. However, Chesapeake Bay *R. venosa* readily open and consume large hard clams (30 to 85 mm SH) leaving no visible signs of either drilling or boring behavior. *R. venosa* grasps its prey along the shell margin and covers the clam with its foot until the clam gapes slightly (Fig. 8). When the clam gapes, the *Rapana* inserts its proboscis between the clam valves and begins feeding. The entire clam is consumed leaving clean, empty, articulated valves with no visible predation signature as the end product. Food is not likely to be a limiting factor for *Rapana venosa* in the Chesapeake Bay. Rapa whelks seem to share habitat preferences with their favored food item; the preferred habitat for both hard clams and Rapa whelks is sand bottom. The known *Rapana venosa* distribution overlaps regions of moderate to high hard clam densities in the lower bay (Fig. 7).

The absence of a predation signature on large hard clams consumed by Rapa whelks is troubling in light of recent conversations with commercial clammers working in the Ocean View and Hampton Roads area (Fig. 4). The clammers report an increase in the number of empty shell valves caught within the last 1 to 2 years and attribute the increase in empty valves to a corresponding increase in natural clam mortality. Given the number and size of *Rapana venosa* reported from these same areas during 1998 and the absence of a predation signature on large hard clams consumed



A. B.

Figure 8. Adult *Rapana venosa* consuming a hard clam (A.) and an oyster (B.).

in the laboratory, it is possible that the recent increase in empty, articulated shell valves observed by local watermen is attributable to Rapa whelk predation and not natural mortality.

Rapa whelks have also been described as scavengers consuming carrion (Chukhchin 1984, Morton 1994). Laboratory observations indicate that Rapa whelks prefer to capture and kill their own food; they will not feed on carrion in the presence of live prey. However, Chesapeake Bay *Rapana* have been caught incidentally by recreational fishermen that were using fresh squid as bait.

Potential Predators: Rapa Whelks

Rapana venosa are prey for native octopods in their native waters. Few of the habitats that *Rapana* have invaded include resident octopods as upper-level predators enabling *Rapana* populations to grow quickly and inflict considerable damage on local shellfish resources; for example, the decimation of the Black Sea oyster population as described by Chukhchin (1984). Within the Chesapeake Bay, the only upper-level or apex predators that might be capable of using Rapa whelks as a food resource are those that currently eat the local whelk species; that is, Channeled whelks (*Busycotypus canaliculatus*) and Knobbed whelks (*Busycon carica*). Crabs and other gastropod species are potential predators for very small *Rapana*. Sea turtles may be capable of eating Rapa whelks <100 mm SL.

Benthic communities in the lower Chesapeake Bay include several crustacean species that may be capable of crushing very small (<30 to 40 mm) Rapa whelks. Blue crabs, mud crabs (e.g., *Eurypanopeus depressus*), and two species of hermit crabs [flat clawed (*Pagurus pollicaris*) and striped (*Clibanarius vittatus*)] are common in lower Bay intertidal and subtidal habitats. Drapkin (1963) suggests that hermit crabs may be able to kill or remove very small Rapa whelks [Although Drapkin (1963) describes habits of *R. bezoar* from the Black Sea, it is now recognized that *R. venosa* (also previously described as *R. thomasiana* and *R. thomasiana thomasiana*) is the only *Rapana* species that has ever been introduced into the Black Sea.) from their shells. Similarly, Magalhaes (1948) describes stone crabs (*Menippe mercenaria*), blue crabs, and hermit crabs as potential predators on *Busycon* sp. from Beaufort, NC. Oyster drills (*Urosalpinx cinera*) and moon snails (*Neverita duplicata*) may be able to catch and drill small Rapa whelks in areas where they co-occur. However, neither crushing nor drilling are realistic threats once a Rapa whelk exceeds a certain size, given the thickness and strength of a *Rapana* shell. Magalhaes (1948) reports old growth shell thicknesses for 160 mm SL specimens of *Busycotypus canaliculatus* and *Busycon carica* as 1.6 mm and 4.5 mm, respectively. Preliminary observations on shell thicknesses for Rapa whelks 145 to 155 mm SL indicate that Rapa whelk shells are twice as thick as Knobbed whelk shells and up to six times thicker than Channeled whelk shells.

Small to medium Rapa whelks (40 to 100 mm SL) may be vulnerable to predation by sea turtles (e.g., loggerhead sea turtle, *Caretta caretta*). Sea turtles in the lower Bay consume local whelk species as indicated by the presence of Knobbed and Channeled whelk opercular plates in sea turtle gut contents. Similar crushing of a Rapa whelk shell would be possible, provided that turtle gape width was sufficient to reach around the shell. Given that *Rapana* have thicker shells (see above), are morphologically more compact or "boxy" than either Knobbed or Channeled whelks (Fig. 9), *Rapana* are probably vulnerable to predation by sea turtles for a shorter temporal window than local whelks. The maximum necessary "bite" or gape shell dimension on a Channeled (150 mm SL) or Knobbed whelk (165 mm SL) is less than the same dimension on a 140 mm SL *Rapana* (Fig. 9). Both local whelk shells have numerous locations that are vulnerable to turtle predation, because the bite or gape width is smaller than the maximum dimension; whereas the *Rapana* profile is essentially square, with all dimensions greater than the maximum bite dimension of a local whelk (Fig. 9). Chesapeake Bay *Rapana venosa* probably reach a size-selective predation refuge from all potential predators at a reasonably small size (e.g., 100 mm) because of their shell morphology and thickness.

Potential Predators: Egg Masses

Female *Rapana venosa* seasonally produce mats or masses of individual egg cases that are 30 to 40 mm tall and basally attached to firm substrate (Fig. 3). The egg cases are <3 mm in diameter at the dorsal or basal end and taper to a wide, phyllopodus-looking top or ventral surface with an anterior opening or pore through which the veliger larvae emerge (Chung et al. 1993, Mann and Harding, in review; Fig. 3). Immediately after deposition, indi-

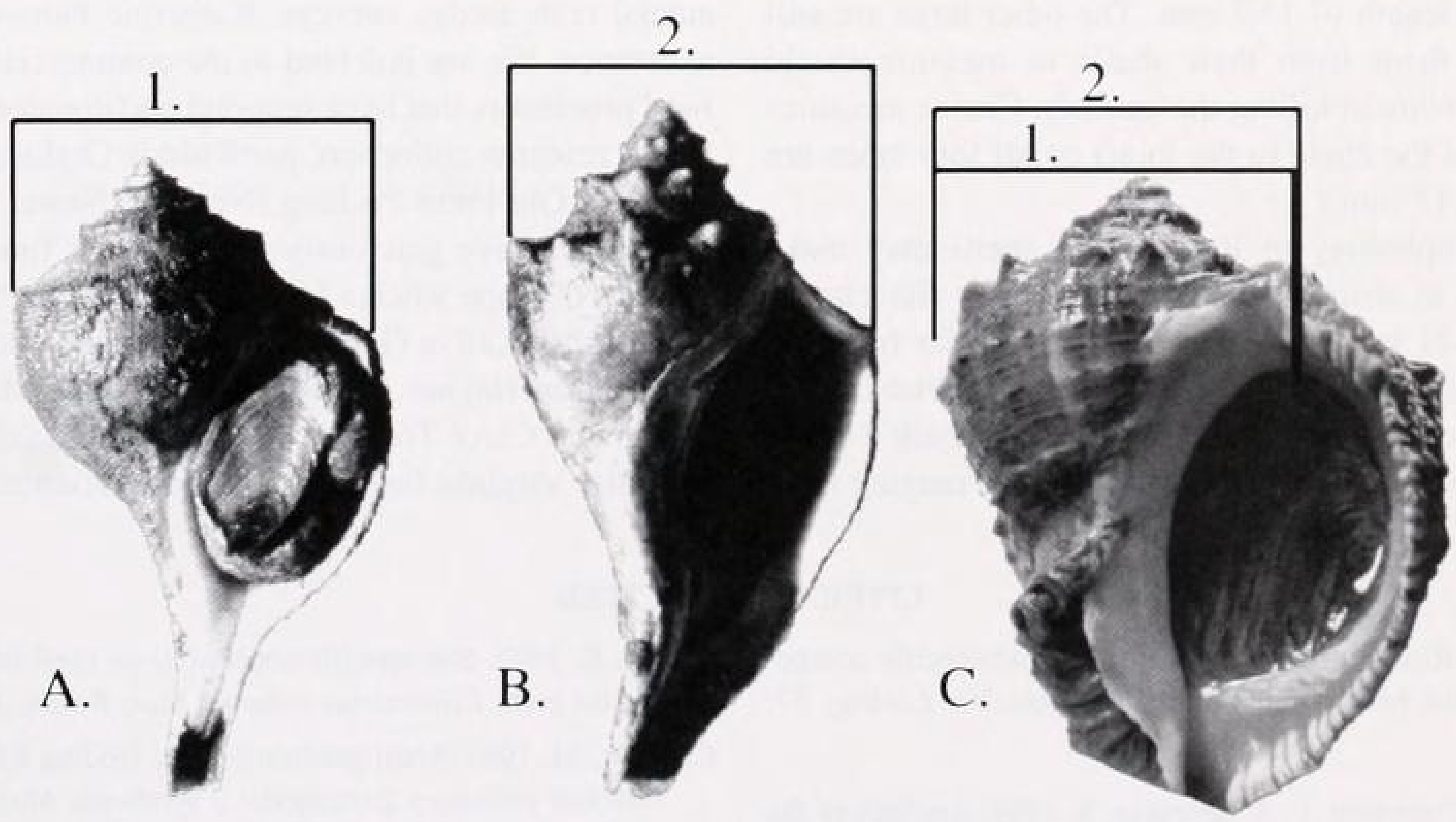


Figure 9. Profiles of Channeled (A.), Knobbed (B.) and Rapa (C.) whelks showing the maximum horizontal or "bite" dimension for a 150 mm SL Channeled (1.) and a 165 mm SL Knobbed (2.) whelk in relation to the same dimension of a 150 mm SL Rapa whelk.

vidual egg cases are lemon yellow. During development (12 to 17 day per Chung e al. 1993), egg cases change from lemon yellow to pale gray, then black, and finally deep purple when the egg case is dying. The gray-black color shift occurs as the shells of the individual veligers within develop before hatching (Mann and Harding in review). Hatching usually occurs during the black color phase but may occur successfully up until the completion of the black-to-purple color transition (Mann and Harding in review).

The egg cases that were collected from Hampton Roads, Virginia in August 1998 (see above) were attached to a hydroid mat. Commercial watermen and divers have observed egg cases attached to bridge pilings and commercial crab pots deployed in the Hampton Roads/Ocean View area (Fig. 4). Freshly laid egg cases, with their lemon yellow color and three-dimensional extension above the substrate, are unlike any native egg cases or organisms. The combination of egg case morphology and coloration may attract benthic feeding fishes that are seasonally abundant in the lower Chesapeake Bay including Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), white perch (*Bairdiella chrysoura*), and yearling striped bass (*Morone saxatilis*). These fishes are probably capable of consuming whole egg cases or at least dislodging them from the mat and damaging them. Local crab species (blue crabs, mud crabs, hermit crabs) and cownose rays (*Rhinoptera bonasus*) may also disturb or damage egg cases while feeding, accidentally or otherwise. Damage to an egg case may be as lethal to the enclosed veliger larvae as complete consumption, because successful veliger release depends upon a functional egg pore (Fig. 3). If the egg pore is damaged or blocked, the larvae have no other exit route and will suffocate as the egg case dies.

Effects of Rapana venosa *shells in the Chesapeake Bay*

The presence of a novel large gastropod in the lower Chesapeake Bay provides a new supply of shells for species of local hermit crabs; for example, flat-clawed (*Pagurus pollicaris*) and striped (*Clibanarius vittatus*) hermit crabs. Striped hermit crabs from the Lafayette River have been collected in Rapa whelk shells ranging from 80 to 110 mm SL. These striped hermit crabs are large and will readily consume oyster spat, mussels, mud crabs, and blue crabs (<50 mm carapace width) in laboratory experiments. [We have collected four live striped hermit crabs living in *Rapana* shells. One crab died postcollection and has been measured; it has a shield length of 13.7 mm. The other three are still alive and removing them from their shells to measure shield lengths is impossible without killing the animals. Chelae measurements (from the tip of the chela to the joint) on all four crabs are in the range of 12 to 13 mm.]

The particular morphology of Rapa whelk shells may make them more attractive to striped hermit crabs than to flat clawed hermit crabs. Of the 71 hermit crabs collected thus far from the lower Chesapeake Bay, 93% have been flat-clawed. Flat-clawed hermit crabs have been collected in Channeled whelk (13%), Knobbed whelk (61%), and moon snail shells (26%) ranging from 50 to 190 mm SL (whelks) or 30 to 50 mm shell diameter (maximum dimension across the shell; moon snails). All of the striped hermit crabs observed thus far have been collected in Rapa whelk shells. Previous studies have shown that large shells may be a limiting resource for hermit crabs (Bach 1976, Lively 1989, Lancaster 1990, Borwn 1992). Rapa whelk shells are thicker, have taller spires and are less elongate than local whelk or moon snail shells (see above). The favorable characteristics of larger shells in relation to hermit crab occupancy that were summarized by Brown (1992); that is, larger shells are less vulnerable to predators, increase female clutch sizes, and allow further growth may enhance the success of local striped hermit crabs. Similar increases in hermit crab size subsequent to the introduction of *Rapana* have been reported from the Black Sea by Drapkin (1963).

SUMMARY

Although current distribution estimates of *Rapana venosa* in the Chesapeake Bay are biased by both fishing effort and gear, it is clear that a substantial population is present in the lower Bay. The post-World War II invasions of the Black, Adriatic, and Aegean Seas as well as the Sea of Azov by this animal indicate that it is capable of significantly affecting local shellfish and benthic communities in relatively short periods of time (e.g., Drapkin 1963, Bombace et al. 1994, Zolotarev 1996). Given that the lower Chesapeake Bay supports both hard clam and oyster fisheries, the presence of an animal credited with the "destruction of the Gudauta oyster bank" per Drapkin (1963) has significant economic and ecological ramifications. Continuing research on the basic biology of this animal in the Chesapeake Bay in combination with a fishery-independent stock assessment program for the Chesapeake Bay *Rapana* (both in progress at VIMS) will provide necessary information for successful management and control strategies.

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