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Invasion of the North American Atlantic coast by a large predatory Asian mollusc

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Abstract

The large Asian gastropod mollusc *Rapana venosa* Valenciennes 1846 (Neogastropoda, formerly Muricidae, currently Thaididae) is reported for eastern North America in the lower Chesapeake Bay and James River, Virginia, USA. This record represents a transoceanic range expansion for this carnivorous species. This species has previously been introduced to the Black Sea, Adriatic Sea, and Aegean Sea. Ballast water transport of larval stages from the eastern Mediterranean or Black Sea is the suspected vector of introduction into the Chesapeake Bay; 650 adult specimens in the size range 68–165 mm shell length (SL) have been collected from hard sand bottom in depths ranging from 5 to 20 m at salinities of 18–28 ppt. The absence of small individuals from local collections is probably related to bias in collection methods. Age of the specimens could not be determined. *R. venosa* is probably capable of reproducing in the Chesapeake Bay. Egg cases of *R. venosa* were collected from Hampton Roads, a section of the James River, in August 1998, and hatched over a 21-day period under laboratory conditions to release viable bilobed veliger larvae. Four lobed larvae developed 4 days post-hatching and apparent morphological metamorphic competency was observed 14–17 days post-hatching. Despite the provision of live substrates and/or metamorphic inducers no metamorphosis to a crawling form was observed for larvae cultured on the monospecific diet. In work performed during 1999 settlement was observed for larvae cultured on a diet of mixed flagellates and diatoms and subsequently exposed to local epifaunal species. Salinity tolerance tests were performed on larvae at 1–6 days post-hatching. No deleterious effects were observed at salinities as low as 10 ppt with limited survival to 7 ppt at 6 days post-hatch. Current distribution is considered in context with larval salinity tolerance tests and literature describing native Asian and introduced populations to assess potential for establishment and further range extension both within the Chesapeake Bay and along the Atlantic coast of North America. Establishment within the Bay mainstem to the Rappahannock River with minor incursions into the mouths of the southerly subestuaries is considered feasible. A projected breeding range on the Atlantic seaboard extending from Cape Cod to Cape Hatteras is considered as tenable. Potential impact of *R. venosa* on commercially valuable shellfish stocks throughout the projected range is cause for serious concern. Boring by the polychaete *Polydora websteri* is more prevalent in the younger whorls of the shell, and absent in shell laid down later in life. This pattern suggests that juvenile animals may prefer hard substrates and not adopt an infaunal lifestyle until a size in excess of 50 mm SL, or after reaching maturity.

Introduction

Carlton (1999) reviews the history of molluscan invasions in marine estuaries and communities and emphasizes how such invasions, both accidental and intentional, have markedly altered communities as we now observe them. Examination of the estimated 100 species that have successfully survived introduction

to regions beyond their native ranges identifies both potential vectors of assisted dispersal, and dominant regions of origin (donor regions) as opposed to regions susceptible to invasion (receptor regions). Over historical time both premeditated, intentional introductions (for fishery and aquaculture purposes) and accidental (via hull fouling in various forms, and in rock, sand, and water ballast) have emphasized the western Pacific Ocean as a donor region, with resultant spread of donated species to the eastern Pacific and Atlantic Oceans, the Mediterranean and Black Seas, and parts of Australasia. With the notable exception of the large predatory gastropod *Rapana venosa* Valenciennes 1846, the donated western Pacific gastropods are mostly small and susceptible to dispersal as a component of surface fouling communities or within rock ballast. *R. venosa* was introduced to the Black Sea in the 1940s (Drapkin 1963), arguably as an associated species with oysters transported from the Orient in support of an oyster culture or fishery enhancement exercise. With this exception, the dispersal of large predatory muricid gastropods has been modest for a number of reasons: their habit is often infaunal, their large adult size serves them poorly in maintaining attachment to exposed fouling communities, and maturation at a large size prevents continued and frequent recruitment to exposed and disturbed fouling communities in transit. Further, the maturation at a large size and production of egg capsules that produce planktonic larvae, rather than crawling juveniles, of some muricid gastropods exacerbates their ability to form stable components of mobile, attached fouling communities.

The emergence of ballast water as a major vector in facilitating invasions has, however, provided gastropod species characterized by large adult size, late maturation, and planktonic larval dispersal phases with a means to join the ranks of actively, if inadvertently, dispersed species participating in the global experiment of marine and estuarine introductions. We report a remarkable transoceanic invasion by a large carnivorous marine gastropod with these life history characteristics. Receptor regions must now be considered susceptible to continued exposure to these predatory species as well as the ecological and economic impacts associated with their arrival and possible establishment.

We here report aspects of the invasion biology and ecology of the large carnivorous Asian muricid gastropod mollusc *R. venosa* Valenciennes, 1846 (Neogastropoda, formerly Muricidae, currently Thaididae), whose discovery in 1998 in Chesapeake Bay, on the mid-Atlantic coast of the United States, was reported by Harding and Mann (1999). This whelk is a well-known predator in both its native waters and in the Black Sea (Drapkin 1963, and discussion, below). We present a summary of adult distribution in the Bay, evidence of breeding, and laboratory experiments on salinity tolerance of early larval stages. We also consider the vectors that may have brought *Rapana* to the Atlantic American coast, and analyze its potential latitudinal range in North America.

Methods

Description of the species

Rapana venosa Valenciennes 1846 has also been described with the junior synonyms *Rapana thomasiana* Crosse 1861, and *Rapana thomasiana thomasiana* (Thomas' rapa whelk). For simplicity *R. venosa* is consistently used in the current text. The taxonomic status of the genus *Rapana* has been recently reviewed by Kool (1993). *R. venosa* is one of three species of *Rapana* in Chinese waters being native to the Sea of Japan, Yellow Sea, Bohai Sea, and the East China Sea to Taiwan (Tsi et al. 1983; Lai and Pan 1980). *Rapana bezoar* occurs off the southern provinces bordering the South China Sea (Cai and Huang, 1991) and is more widely distributed in the Western Pacific and Indian Ocean. *Rapana rapiformis* occurs in the East and South China Seas.

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 (Figure 1). The columella is broad, smooth, and slightly concave. Small, elongate teeth are present along the edge of the outer lip of the large, ovate aperture. The 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 and atypically blonde, with darker brown dashes on the spiral ribs. The aperture and columella vary from deep orange to yellow or off-white. Spiral, vein-like coloration, varying from black to dark blue, occasionally occurs internally, originating at the individual teeth at

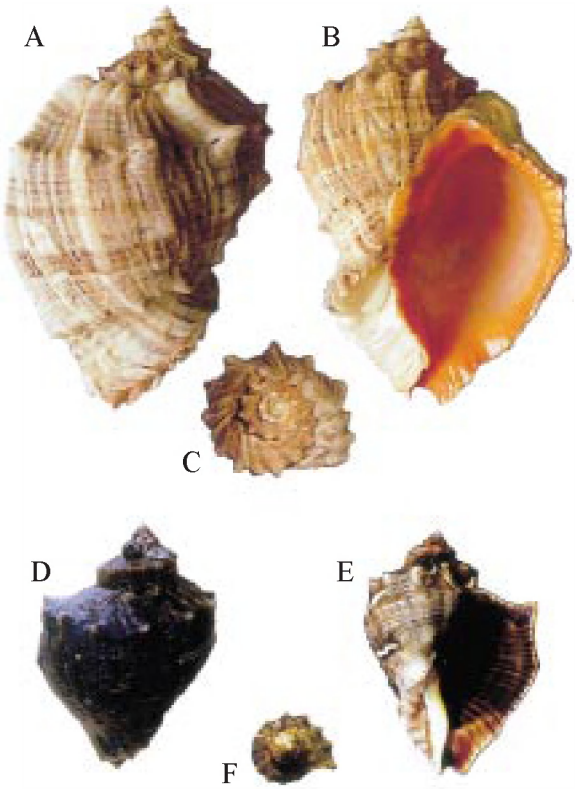

Figure 1. Rapana venosa. A–B. Shell length 165 mm, cleaned of epibionts. Note the deep umbilicus, and the broad, smooth and slightly concave columella. This specimen exhibits the common deep orange internal color. C. Apical view of a same specimen. D–F. *Rapana venosa.* Shell length 68 mm, cleaned of epibionts. Note the color variation compared to A–C, brown internal color with dark blue-brown spiral, vein like coloration originating at the individual teeth at the outer lip of the aperture.

the outer lip of the aperture. Individual specimens can be large. The maximum dimension, hereafter termed shell length (SL), used throughout this contribution and cited from previous work is from the apex of the spire to the tip of the siphonal canal. The largest individual *R. venosa* reported by Chung et al. (1993) is an individual of 168.5 mm SL from Korean waters. A single specimen of 183 mm SL is reported by Hwang et al. (1991) from Taiwan, although we suspect this might be a printing error given the accompanying weight for the specimen.

Adult distribution patterns

A single *R. venosa* was collected in the lower James River, Virginia (lat. 36°57.12′ N, long 76°24.86′ W) in June 1998 in an otter trawl (38 mm stretch mesh body, 6.35 mm mesh cod liner) by the Virginia Institute of Marine Science (hereafter VIMS) Fisheries Trawl Survey (M. Land and P. Geer). Subsequently, adult *R. venosa* were collected from the lower Chesapeake Bay from August 1998 through February 1999 by the authors using an oyster dredge (2.5 cm mesh size) or donated to the VIMS *Rapana* research collection by local citizens (mostly stranded animals on exposed beaches after storms) as well as commercial watermen and seafood processors. The majority of specimens were collected by size-selective fishing gear including crab pots, patent tongs, and crab dredges (6 cm bag ring size). Collection locations for each animal including water depth, bottom type, and geographic location, were documented at the time of donation. SL was measured to the nearest mm for each animal. Each shell was examined for presence of epibionts and external signatures of parasites (such as shell boring) or predators (damaged shell edges).

Collection of egg cases and larval culture

A single mass of *R. venosa* egg cases (approximately 50 individual cases) was collected from the James River, Virginia just north of the Monitor-Merrimac Bridge tunnel on 24 August 1998 (location given on Figure 2). The lemon-yellow egg cases were attached basally to a hydroid mat and were collected using the previously described otter trawl. The entire egg mass was immediately placed in seawater (26 °C, approximately 21 ppt) and was returned to the VIMS laboratory at Gloucester Point, Virginia, on the northern shore of the York River, Chesapeake Bay. In the laboratory, the egg cases were maintained in filtered (5 μm), static sea water with gentle aeration at 24–26 °C and 18–21 ppt under a 14 h light/10 h dark regime. Sea water was changed daily. Four days post-collection, the egg cases began changing color from lemon-yellow towards dark brown or black as larval development proceeded towards hatching. At this time, individual egg cases were carefully dissected from the egg case mat and placed in 2-l glass beakers containing 1-l of filtered seawater at densities of 1–2 individual egg cases per beaker. This color change continued until 7 days post-collection at which time most of the egg cases were completely black and individual veliger larvae were distinguishable through the walls of each egg case. Egg cases began hatching on 31 August 1998 and continued hatching through 21 September 1998. Each egg case

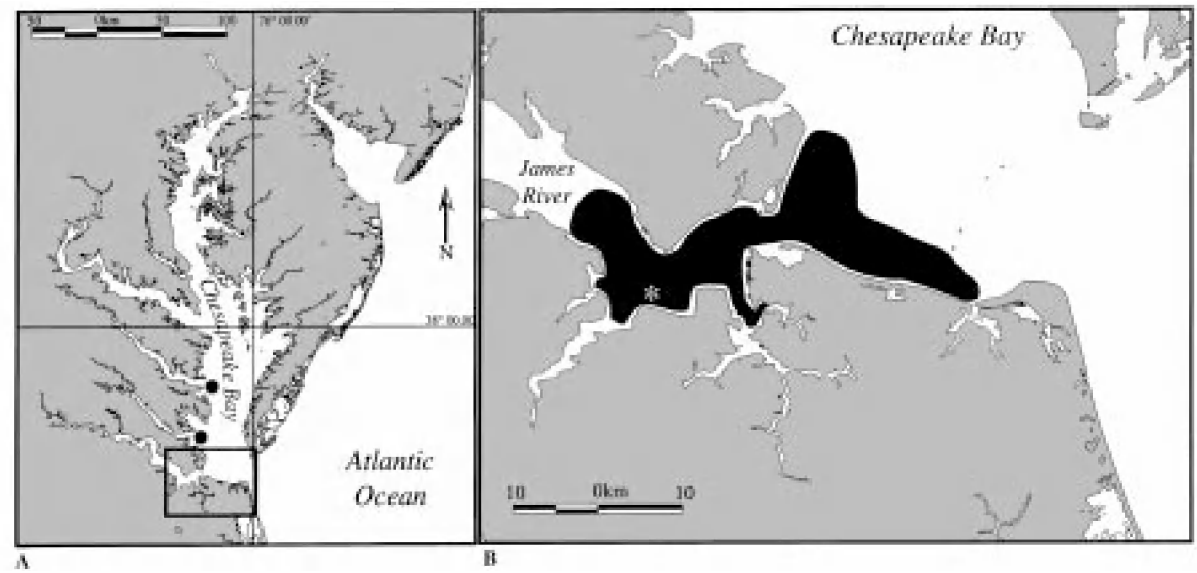

Figure 2. A. Distribution of *Rapana venosa* within the Chesapeake Bay. Figure B is the enlarged region of the lower James River and the southern shore of the Chesapeake Bay. ∗ marks the site of the first collection ((lat 36° 57.12′ N, long 76° 24.86′ W).

contained 300–400 individual veliger larvae. Veliger larvae were filtered from the egg case culture water using 80 µm Nytex sieves and maintained in aerated filter seawater (18–21 ppt) at 24–26 °C at densities of approximately 500 veligers l^{-1}. Veligers were fed a monospecific diet of *Pseudoisochrysis paradoxa* daily and were maintained at 14 h light/10 h dark conditions. Subsequent studies (Harding and Mann 1999 studies in progress, unpublished data) continue to examine mixed diatom and flagellate diets.

Larval length-at-age relationships

Beginning on 1 September 1998 (day 0) and continuing through 20 September 1998 (day 20), 4–12 individual veliger larvae were removed daily from larval cultures hatched on 1 September 1998 and were preserved in 10% neutral buffered formalin. Individual veligers were subsequently measured to the nearest micron using an image capture and analysis system (Image Pro v. 2.0) coupled with a compound microscope.

Larval salinity tolerance experiments

Larval cultures designated for particular experiments were maintained at initial experimental salinities for 48 h prior to the initiation of an experiment. One hour before the beginning of an experiment, larval cultures were sieved through an 80 µm mesh to condense the larvae and a 1 ml sub-sample was removed and examined under a dissecting microscope to determine both veliger health (as indicated by the percentage of veligers with velum extended and filtering) and abundance (ml^{-1}). This initial sub-sample was preserved in 10% neutral buffered formalin as an index collection for each experiment.

A series of salinity tolerance experiments at salinities ranging from 7 to 12 (low) and 9 to 15 (high) ppt using veligers from 1- to 6-day-old were completed during a 10-day period from September 7 to 17, 1998. The overall salinity range (7 to 15 ppt) was chosen because it is representative of the salinity conditions in Chesapeake Bay tributaries and subestuaries that are most vulnerable to tidal advection of *R. venosa* veligers from downstream sites. Each salinity tolerance experiment tested a single age of *R. venosa* and incorporated 3 replicates of 8 different salinity levels. Individual boiling tubes were used as experimental chambers and were filled with 20 ml filtered seawater at 24 to 26 °C. *R. venosa* veligers were added to individual boiling tubes to give densities of at least 1 veliger ml^{-1}. Low salinity experiments began at initial salinities of 12 ppt and high range salinity experiments began at initial salinities of 15 ppt. Salinities within individual tubes were decreased at 5 min intervals by the serial addition of 1 ml deionized water (DI). Tube 1 (the control

tube) received no DI water additions and remained at initial salinities (12 or 15 ppt) throughout the experiments. During the experiments, larvae were fed 5 ml of *P. paradoxa* per chamber daily. After 44 h, 1 ml of concentrated neutral red in filtered seawater solution was added to each experimental chamber. Neutral red is a non-toxic vital stain that is absorbed by living tissue; veligers that were alive at 44 h absorbed the stain and were subsequently distinguished from dead veligers by their pink tissue. Experiments were terminated after 48 h by the addition of 5 ml 10% neutral buffered formalin to each tube and were examined under a dissecting microscope to determine the percentage survival of veligers per chamber after 48 h.

Percentage survival data from all salinity experiments satisfied assumptions of homogeneity of variance (per Bartlett's test; Zar 1996) but failed to meet the assumptions of normality regardless of the transformation (arcsin square root, natural logarithm). Two-factor ANOVAs (initial veliger age × salinity) were used to compare percentage survival data within similar salinity ranges i.e., one ANOVA was completed for the low range data and one was completed for the high range salinity data. Fisher's multiple comparison test (Zar 1996) was used for *post-hoc* comparisons when appropriate. All significance levels were established at $P = 0.05$ *a priori*.

Estimation of dispersal range

Estimation of potential range of dispersal and establishment based on temperature and salinity tolerances used monthly summaries for these parameters in the Chesapeake Bay for the years 1989–1991 as given in Rennie and Neilson (1994). For larger geographic scales comparison focused on temperature tolerances. Temperature summaries for selected United States Atlantic coast and Gulf of Maine locations were taken from the World Wide Web site of the National Oceanic Atmospheric Administration National Data Buoy Center (http://www.ndbc.noaa.gov/images/climplot/ and http://www.nws.fsu.edu/B/buoy series). Comparative data for the temperature were taken from Chung et al. (1993) for Korea, Liu (1994) for Hong Kong, and from the www site for Sevastopol (http://www.sevastopol.org/geograpе.htm) and the Black Sea Ecosystem database page (http://www.gis.rnd.runnet.ru/team/mtbase/part1-2-2.html) for the Black Sea and Sea of Azov.

Results

Adult distribution patterns

The known distribution of *R. venosa* in the Chesapeake Bay, based on 650 individuals, extends from the mouth of the Rappahannock River in the north, to the Chesapeake Bay Bridge tunnel in the southeast, to the Elizabeth River (east of Craney Island) and Lafayette Rivers in the south, to just above the State Route 258 James River Bridge in the southwest (Figure 2A). The Rappahannock specimen was collected in October 1998 from Butler's Hole, an oyster reef downstream of the US Route 3 bridge on the north side of the river. To date, this individual is the only specimen collected north of the York River (Figure 2B). The majority of *R. venosa* have been collected from Hampton Roads below the James River Bridge through Buckroe Beach, Ocean View and Little Creek (Figures 2B and 8). The offshore limit of the distribution downstream in the mouth of the James River extends to the Thimble Shoals Channel, the southerly of the two major shipping channels entering the Chesapeake Bay. The bathymetric range occupied within this region is on hard sand bottom in depths ranging from 5 to 20 m at salinities of 18–28 ppt. The majority of the individuals collected are in the size range 120 to 165 mm SL, with a limited number extending as small as 68 mm SL. Determination of age in these individuals was not possible. A comprehensive discussion of population demographics within the described range is given in Harding and Mann (1999).

The methods of collection limit statements concerning the ability of *R. venosa* to occupy hard substrates such as docks and bridge pilings in the above distribution range. Chukhchin (1984) reports that young-of-the-year *R. venosa* eat the barnacle *Balanus improvisus*. A single observation of *R. venosa* egg cases was made in the summer of 1998 at 3–4 m depth during commercial underwater inspections of bridge structures in the collection region shown in Figure 2 using SCUBA (T. Warthen, Collins Engineers Inc., Newport News, Virginia). It remains to be resolved whether these egg cases were deposited by smaller, mature individuals before transition to the infaunal life style, or are indicative of mature individuals remaining on hard substrate, or of mature individuals leaving the soft sediment environment in breeding season.

Examination of shells of local *R. venosa* was effected based on the premise that epifaunal and infaunal

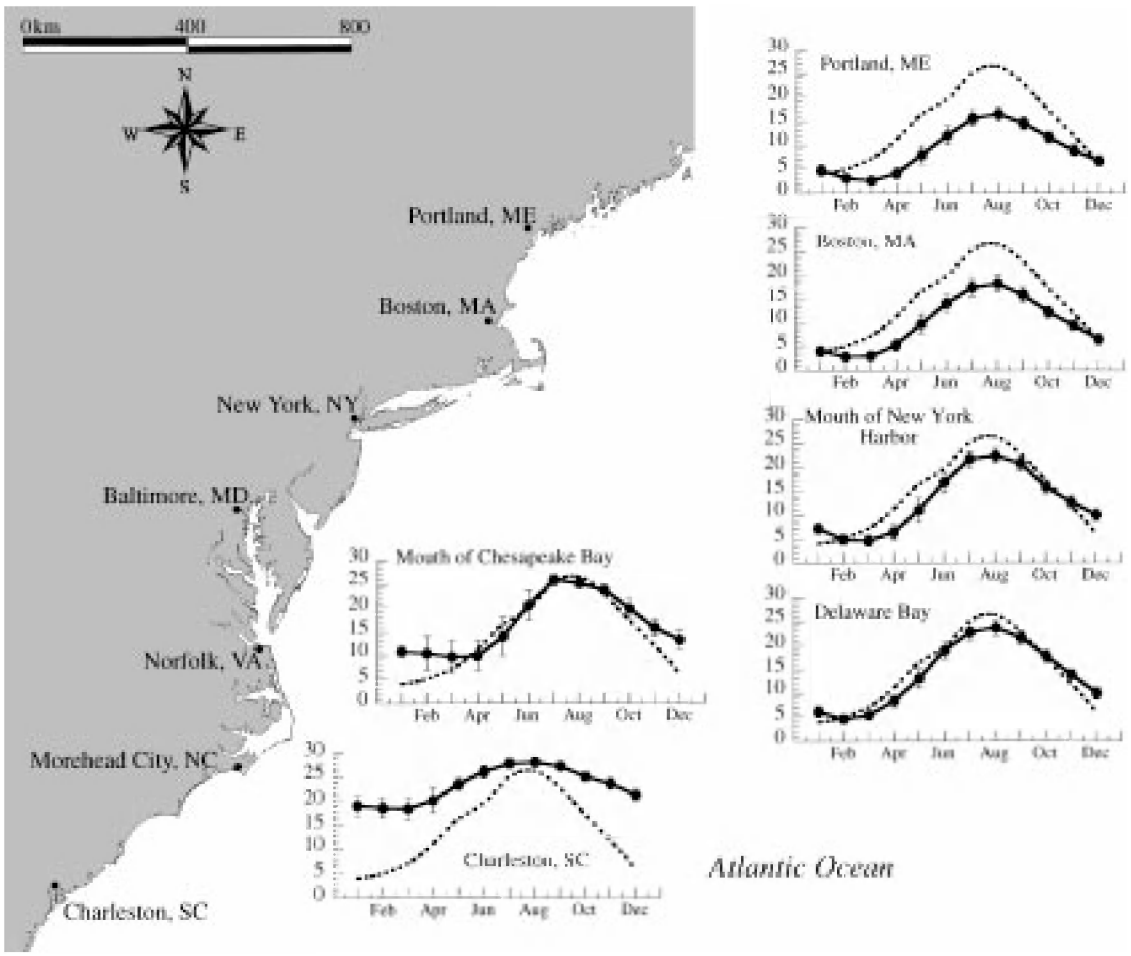

Figure 3. Annual temperature plots (°C monthly mean ± standard deviation for the period 6/78–12/93 versus month) for various United States East coast locations compared to Korean data from Chung et al. (1993). US data from NOAA National Data Buoy Center buoy locations as follows: Portland Harbor, Maine (Buoy number 44007. lat 43°31′53″ N, long 70°8′39″ W), Boston Massachusetts (Buoy number 44013. lat 42°35′ N. long 70°69′ W), Long Island Sound, New York (Buoy number 44025. lat 40°15′1″, long 73°10′0″ W), Delaware Bay mouth (Buoy number 44009. lat 38°27′49″ N, long 74°42′7″ W), Chesapeake Bay mouth (Buoy number 44014. lat 36°34′59″ N, long 74°50′1″ W), Charleston, South Carolina (Buoy number 41004. lat 32°51′ N, long 79°06′ W).

populations of *R. venosa* in the Chesapeake Bay would be subject to differing suites of predators, epibionts, and potential parasites. Frequent, but not universal, boring of the shell in the apical region was observed, corresponding to internal mud blisters characteristic of *Polydora websteri* (see Haigler 1969). Boring was clearly restricted to the early life span of the individual and decreased in prevalence as the diameter of the spire increased. Adult *R. venosa* maintained in laboratory systems burrow completely when provided with sand substrate, only a single siphon is visible. This observation suggests that the size at which the *Polydora* external boring signal disappears may well coincide with a transition size for *R. venosa* to a infaunal existence with increased susceptibility to collection gear reported in this study.

Larval length-at-age and development

Pre-settlement *R. venosa* veligers fed on monospecific diets of *P. paradoxa* exhibited a linear growth relationship (Figure 4; $R = 0.89$) from hatching through attainment of apparent morphological competency. Morphological development is comparable to that described in Chung et al. (1993) with veligers emerging from egg cases with a bilobed velum. A four lobed

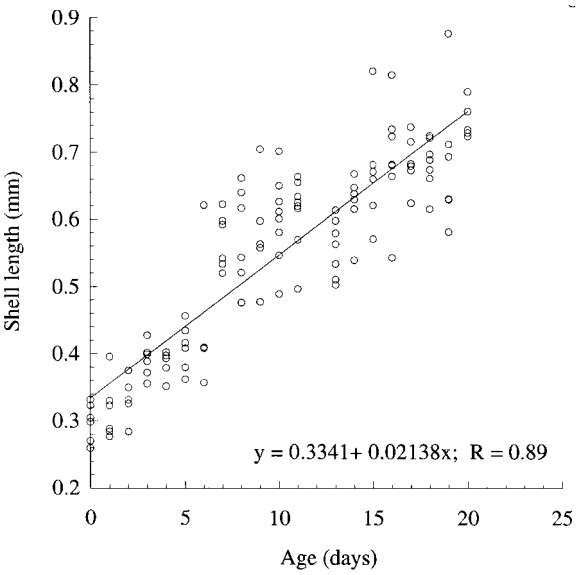

Figure 4. Larval length-at-age relationship for *Rapana venosa* veligers cultured on a diet of *Pseudoisochrysis paradoxa*. The number of individuals (n) is greater than or equal to 4 for each date. No samples were available for day 12.

velum appeared at 4 days post-hatching and a length of approximately 385 µm. Apparent morphological competency was attained at 14–17 days and 623–686 µm SL with development of a distinct foot and eyestalks. Despite the provision of a number of potential settlement substrates, including live encrusting bryozoa and potential prey (oysters), in addition to chemical stimuli (5–50 mM addition of KCl per Pechenik and Heyman 1987), we were unable to induce successful metamorphosis to a crawling juvenile stage from these larval cultures. In continuing work during 1999 (Harding and Mann, unpublished data), *R. venosa* larvae have now been successfully cultured through metamorphosis on a diet of mixed flagellates and diatoms, and local epifaunal species on hard substrates have been demonstrated to stimulate settlement.

Larval salinity tolerance experiments

Veliger age and salinity significantly affected percentage survival of veligers in both high (9–15 ppt) and low (7–12 ppt) salinity ranges (ANOVAs, $P < 0.05$; Table 1). There was a significant interaction between age and salinity observed for both high and low ranges (ANOVAs, $P < 0.05$, Table 1). *R. venosa* veligers older than 4 days seem to be less tolerant

Table 1. Summary of two-factor ANOVAs (initial veliger age × salinity) used to describe salinity tolerances of larval *Rapana venosa* in laboratory salinity tolerance experiments conducted in September 1998.

Salinity range	Source	df	F-value	P-value
Low (7–12 ppt)	Initial veliger age (days)	4	13.4	0.0 *
	Salinity (ppt)	7	12.1	0.0 *
	Initial veliger age * salinity	28	5.3	0.0 *
High (9–15 ppt)	Initial veliger age (days)	3	9.0	0.0 *
	Salinity (ppt)	7	4.9	0.0 *
	Initial veliger age * salinity	21	2.7	0.0 *

Asterisks (*) indicate significance at the $P = 0.05$ level.

of salinity changes than younger (1- to 3-day-old) veligers; 5-day-old veligers showed a sharp decrease in average percentage survival at both salinity ranges (Figures 5 and 6). Six-day-old veligers exposed to low salinities also showed an increase in mortality with decreasing salinity (Figure 5). In the low salinity range, 2-day-old veligers had significantly higher survivorship than 5- and 6-day-old veligers (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$); 3- and 4-day-old veligers at low salinities had significantly higher survivorship than 6-day-old veligers (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). Survival at 7 and 8 ppt was significantly less than at other salinities in the low range (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). One, 2 and 4 day-old veligers in the high salinity range had significantly higher percent survival than 5-day-old veligers (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$). Survival was significantly lower at 9 ppt than at other salinities in the high range (ANOVA, $P < 0.05$; Fisher's test, $P < 0.05$) (Figure 6).

Environmental tolerances of adult Rapana venosa

In its native Korean range, adult *R. venosa* demonstrate large annual temperature tolerances (4–27 °C for the location described by Chung et al. 1993). The upper thermal tolerance of the species occurs between 27 °C and the summer maximum for Hong Kong (35 °C; Liu 1994) where *R. venosa* is displaced by *Rapana bezoar* (Tsi et al. 1983; see also Morton 1994). The ability to exploit estuarine regions with warm summer temperatures but possible surface freezing in winter is

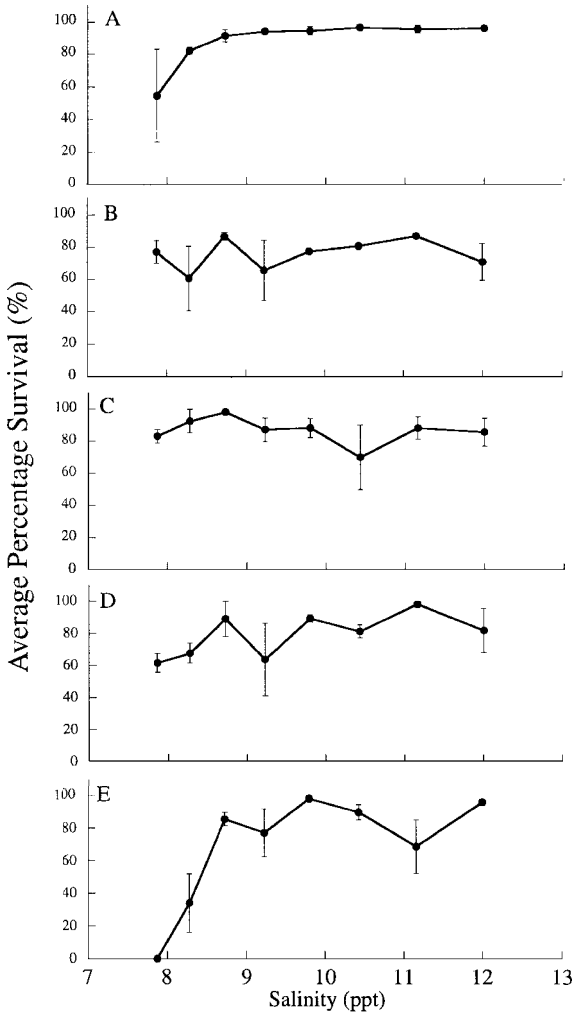

Figure 5. Composite summary for low (7–12 ppt) range salinity tolerance experiments with *Rapana venosa* larvae: A = 2-day-old, B = 3-day-old, C = 4-day-old, D = 5-day-old, E = 6-day-old (see text).

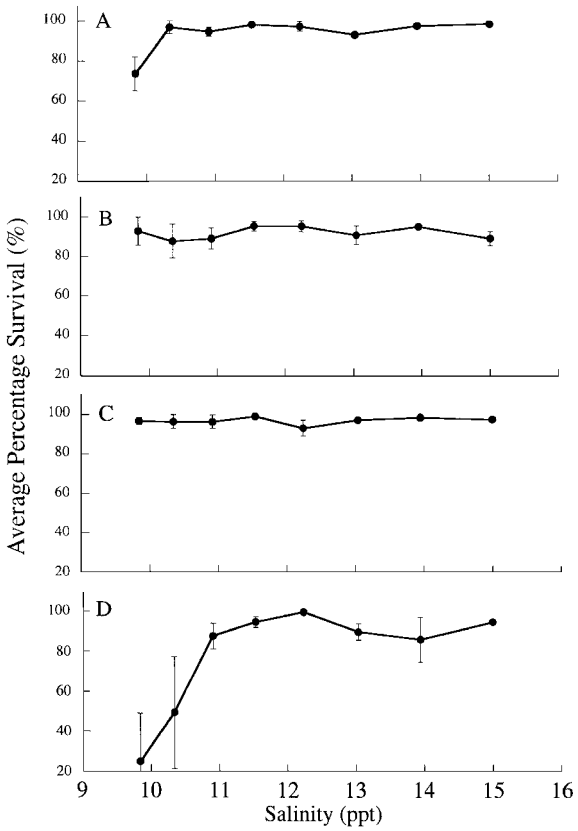

Figure 6. Composite summary for high (9–15 ppt) range salinity tolerance experiments with *Rapana venosa* larvae: A = 1-day-old, B = 2-day-old, C = 4-day-old, D = 5-day-old (see text).

facilitated by the winter migration into deeper water in these regions (Wu 1988). We can find no data on salinity tolerance of the species in its native range. In the Black Sea, where winter temperature minima are approximately 7 °C and summer maxima approximately 24 °C, *R. venosa* occupies a salinity range 25–32 ppt (Golikov 1967). In the Sea of Azov, which is ice covered for 2–4 months per year, *R. venosa* was restricted to the southernmost region adjoining the Kerch Strait by low persistent salinity in the remaining water body (mean annual value < 12 ppt); however, range extension did occur during 1975–1979 when riverine discharge into the Sea of Azov was markedly reduced by water diversion projects. These projects were discontinued in 1990 and the fresher environment again persists. The status of *R. venosa* in the main body of the Sea of Azov and its precise distribution with respect to prevailing salinity is unclear at this time.

Figure 7A and B illustrate, respectively, mean surface and bottom salinity and temperature values for the Chesapeake Bay for the month of January. Figure 7C and D illustrate comparable data for July. Temperature data for all collection sites in this study are within the thermal tolerances described by Chung et al. (1993). The collection site of the single specimen from the Rappahannock River experiences the lowest salinity with bottom winter and summer values of approximately 16 ppt (compare Figure 2 with 7). Collection sites near the State Route 258 James River Bridge, the current upstream limit in the James River, approach this low value during the winter.

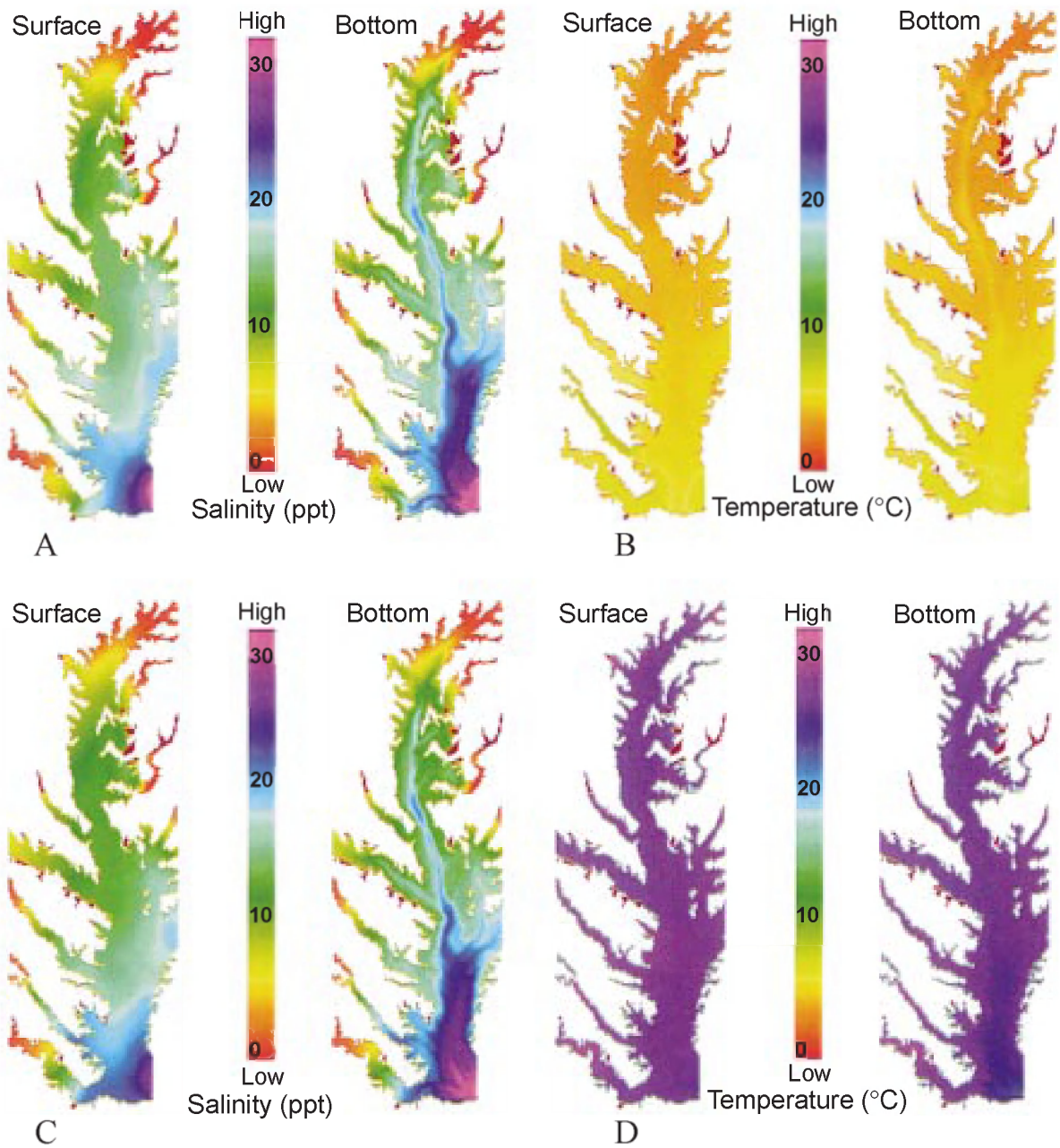

Figure 7. Mean January surface and bottom salinity (A) and temperature (B) values for the Chesapeake Bay as well as comparable data for July salinity (C) and temperature (D). All summaries are based on data for 1989–1991 from Rennie and Neilson (1994).

Discussion

Although there is an extensive record of the introduction of *Rapana* to the Black Sea and its subsequent range expansion throughout the eastern Mediterranean, the current record is arguably, the first documentation of transoceanic transport of this predatory gastropod. The introduction of *R. venosa* into the Black Sea is suspected to have occurred some time in the 1940s with the first record of observation being for

Novorossiysky Bay (Drapkin 1963; who originally misidentified the species as *R. bezoar*). Once established in a founder location, the Black Sea invasion could have been facilitated by planktonic larval dispersal alone without the need to invoke other vectors. Range extension occurred along the Caucasian and Crimean coasts and to the Sea of Azov within a decade of the first report, and subsequently to the Northwest Black Sea, where populations are reported as 'stable' and not 'numerous' according to Zolotarev (1996), and the coastlines of Romania, Bulgaria, and Turkey (Chukchin 1984; Marinov 1990; Zolotarev 1996). Subsequent invasion of the Aegean Sea in 1986, and finally the Adriatic Sea is described by Ghisotti (1971, 1974), Mel (1976), Cucaz (1983), Rinaldi (1985), Koutsoubas and Voultsiadou-Koukoura (1990), and Bombace et al. (1994). A record from Elba in the Tyrrhenian Sea is provided by Terreni (1980). The gradual but sustained nature of this range expansion suggests that *Rapana* has yet to exploit all susceptible locations within the eastern Mediterranean. Indeed, the demonstrated ability to sustain such a range expansion provides cause for concern for a similar sustained range expansion along the Atlantic American coast.

Isolated reports of occurrence of *R. venosa* beyond its native range have also been made for the North Sea, approximately 30 km south of the Dogger Bank (London Times, 26 August 1992), in shallow waters off the coast of Brittany, France (Dr Philippe Goulletquer, IFREMER, La Tremblade, France, personal communication, 1999), although these do not appear to be substantial populations and do not present evidence of active breeding or presence of multiple year classes. A report of occurrence in New Zealand (Powell 1979, p. 172) is for shells only and implicates disposal of non native species from ships galleys as the probable vector.

The Chesapeake Bay, the site of the current introduction, is the largest estuary on the North Atlantic seaboard of the United States and home to the ports of Hampton Road, Virginia and Baltimore, Maryland, respectively the first and third largest coal exporting terminals in the world, in addition to significant international trade in oil and container traffic. A brief review of invasions of marine and estuarine habitats has recently been compiled (Ruiz et al. 1997) as part of the National Ballast Water Information Clearinghouse (see World Wide Web site at http://www.serc.si.edu/invasions/ballast.htm) and emphasizes the role of ballast water in facilitating invasions. A coal trade involving export from Chesapeake Bay ports to the eastern Mediterranean and Black Sea, with the return of vessels in ballast, has existed for over 40 years. Ruiz (Smithsonian Estuarine Research Center, Edgewater, Maryland; personal communication) estimates that forty percent of the ballast water entering Hampton Roads originates from this source. We suspect this to be the route of entry of *R. venosa* into the Chesapeake Bay.

The potential role of ballast water should not, however, preclude examination of alternate vectors. *Rapana* supports significant fisheries in both its native Korean and introduced ranges in Bulgaria and Turkey. International trade in live seafood for direct consumption has been implicated in previous marine invasions. We believe this to be unlikely in the current instance in that local and regional seafood industries illustrate a minimal demand for gastropod (conch) products. Indeed, these industries support an extensive national and international export trade in conch meat based on fisheries for native *Busycon* and *Busycotypus* species. Invasions based on disposal of non native species from ships galleys have also been documented (Powell 1979); however, both the number and size range of individual *Rapana* collected to date in the current study argues against this vector in this location, unless the disposal events were large in number and involved gravid animals.

Carlton (1999) describes the emerging role of sea chests in ships hulls as facilitators of transoceanic passage of molluscs. Could this have been a vector mechanism by which *Rapana* arrived on the Atlantic coast? Richards (1990) elegantly describes the transport of the tropical muricid *Thais blandfordii* Melvill, 1983 in the sea chest of a cargo vessel over extended periods from tropical to northern latitudes and back again. *T. blandfordii* emerges from the egg capsule as a crawling juvenile. There is no dispersing pelagic phase. The initial introduction of individuals into the sea chest must have been as adult animals. Once established and feeding on fouling barnacles within the confines of the sea chest the population of snails could be maintained. Although the possibility exists that small *Rapana* could have been drawn into sea chest on floating debris, their transition to a preferred infaunal habit with an associated change in dietary preference with increasing size (see below), maturation at a large size and production of pelagic larvae, not crawling young, suggests that facilitated dispersal by this vector would be less successful than for *T. blandfordii*.

The ability to determine the age of *R. venosa* from the lower Chesapeake Bay would allow statements concerning the timing of the arrival of this invading species in this new location. Unfortunately, there is only a modest body of literature describing age versus size in the genus *Rapana* in its native range. Chukhchin (1984) estimates that individuals in Sevastopol Bay grow to 20–40 mm SL in the first year of life, with mean values of 64.6, 79.4, 87.5 and 92.1 mm SL in years two through six respectively. This terminal size is smaller than the maximum of 120.1 mm SL reported by Smagowicz (1989) for a specimen in a collection from Bulgaria and Georgia; the exact location of collection of the largest specimen is not reported. Black Sea specimens would appear to live in excess of 10 years based on these observations, and given the larger terminal size of Chesapeake Bay specimens, a reasonable estimate of the time since first introduction may well exceed ten years.

Chukhchin (1984) reports that spawning is marked by a shell thickening and that first spawning occurs in the second year at sizes in the range 35–78 mm SL with a mean value of 58 mm SL. Chung and Kim (1997) examined maturation of male *R. venosa* ($n = 557$, size range 31–160.2 mm SL) in its native range and observed maturity in 66.7% of individuals from 71–80 mm SL, and 100% maturity for individuals exceeding 121 mm SL, but offered no comment on related changes in shell morphology. External growth lines were present on the shells of the majority of specimens collected in this study; however, these could not be definitively ascribed to spawning, seasonal, or annual events. The wide spacing of early growth lines suggests rapid growth which, in combination with the thick shell of *R. venosa* , confers an ability to reach a size refuge from potential local crab and fish predators at a young age (see Harding and Mann (1999) for a discussion of potential *Rapana* predators in Chesapeake Bay). Numerous *R. venosa* specimens demonstrated a substantial ability to repair shell growth edges.

The observed range of sizes suggests either significant variability in growth rates within a single cohort of introduced individuals, multiple introductions, or active and successful breeding of the older cohorts. Subsumed within this question is the important, but as yet undocumented, size at first maturation of *R. venosa* in the Chesapeake Bay. The apparent absence of juvenile individuals in collections to date further confuses the discussion of number of possible cohorts within the population. All commercial fishery collection techniques reported herein are size selective for larger individuals and focus on target species in sand, mud, or shell substrates. Thus, absence of very small individuals from collections should not be viewed as definitive evidence of absence in the field. Further, no data are yet available on either occurrence of *R. venosa* in regions of the southern Chesapeake Bay not subject to commercial fisheries targeting other species, or on hard substrates, which we suggest later in the text may be important in early post-settlement stages. We argue in this report that larval distribution within the Chesapeake Bay from egg case hatching in the Hampton Roads region is tractable. Thus resolution of the multiple cohort option from local breeding remains a goal for continuing study.

Egg cases were collected within a temperature window (see Figure 8) comparable to that reported by Chung et al. (1993) for spawning periodicity of *R. venosa* in its native Korean waters (April to late July based on gonadal examination, corresponding to a temperature range of 13–26 °C). Chukhchin (1984) describes the reproductive period of *R. venosa* in the Black Sea (site not given) as July to September, this corresponding to a temperature window of 19–25 °C. Sahin (1997) reports a spawning period of May to November in the eastern Black Sea. Of considerable

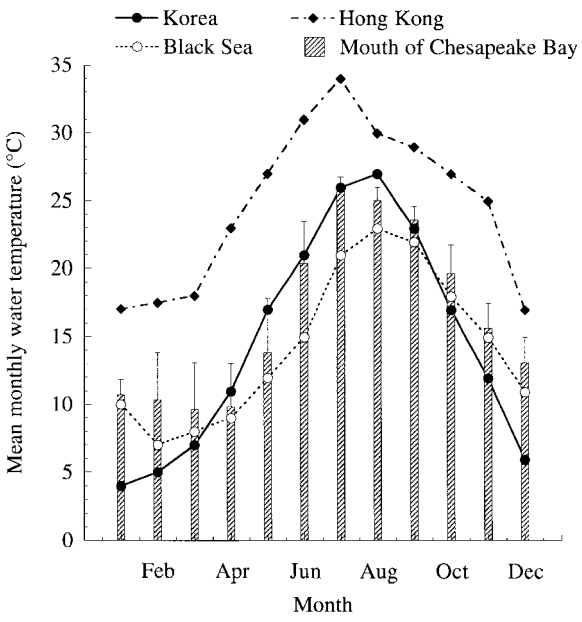

Figure 8. Annual temperature plots for the mouth of the Chesapeake Bay (Buoy number 44014 as in Figure 3) Korean native range (Chung et al. 1993), Hong Kong (Liu 1994), and Sevastopol (Black Sea).

interest in the present study is the observed asynchrony in egg capsule hatching within a single egg mass that is presumed to have been laid by one female adult. The date of egg deposition could not be determined from the collected material. Egg cases began hatching 7 days post-collection. Chung et al. (1993) report a 17 d incubation period between egg laying and first hatching at 18.3–20.4 °C, whereas Chukhchin (1984) reports a period of 26 days at 20–22 °C for Black Sea populations. Both of these reports are at lower water temperatures than the 24–26 °C used in this study; however, the latter range corresponds to that at the end of the spawning season in the native Korean range and the maximum observed at Sevastopol (24 °C) on the Black Sea during the July to September period when *Rapana* larvae are observed in local waters (temperature range 20–24 °C from www.sevastopol.org, larval data from Chukhchin 1984). Hatching over a 21-day period, as observed in the current study, is an exhibition of considerable phenotypic plasticity in veliger development within a single mass. Such plasticity within an egg mass suggests ability of *R. venosa* to exploit optimal hatching conditions within a variable environment, thus improving its ability to exploit and invade new environments.

Growth rate of *R. venosa* larvae to apparent metamorphic competency on a monospecific diet in our laboratory studies were comparable to those reported by Chung et al. (1993) and Chukhchin (1984), and argue for strong consideration of successful local breeding. Larvae did not respond to 5–50 mM addition of KCl (per Pechenik and Heyman 1987; see also Pechenik and Gee 1993; Yool et al. 1986) as a metamorphic inducer. Gastropod larvae have been shown to respond to highly specific metamorphic inducers related to their eventual benthic habitat (e.g., Morse 1992). Local bryozoans were offered as potential settlement and metamorphic substrates in the 1998 studies, but proved inadequate to trigger metamorphosis. The option that dietary limitation to one food species during larval development may have been adequate for larval growth but inadequate to sustain metamorphosis was not examined for *R. venosa* in 1998 studies, but is suggested by the general improvement in percentage metamorphosis observed in larval culture of other muricids with multi-species feeding regimes in larval culture (Aldana-Aranda and Suarez 1998). In continuing work during 1999 (Harding and Mann, unpublished data), *R. venosa* larvae have now been successfully cultured through metamorphosis on a diet of mixed flagellates and diatoms, and local epifaunal species on hard substrates have been demonstrated to stimulate settlement. Furthermore, post-settlement juveniles have now been cultured to sizes in excess of 25 mm SL on varied diets of epifaunal species and local molluscs (Harding and Mann, unpublished data). Collectively, these data support the prospect of successful breeding of the invading population.

Native parasites can be effective in limiting the success of invading populations. The observation of holes made by the boring polychaete *Polydora websteri* in *R. venosa* shells in the current collections strongly suggests a post-metamorphic period with juveniles occupying hard substrates such that their shells are exposed and susceptible to attack by shell borers. Large regions of natural rock outcrops are essentially absent from the shorelines of the Chesapeake Bay and Mid Atlantic region of the United States, although there is an abundance of man-made hard substrates in the form of concrete and stone retaining structures and bridge pillars, in addition to wooden structures. The fouling communities on these structures would form a rich food resource for juvenile *R. venosa* until such time as they migrate to the sediment and adopt the infaunal lifestyle that is more typical of predatory muricids (see comments in Morton 1994). The signature boring of *Polydora* in local populations is much less prevalent above a size equivalent to the 2-year-old animals of Chukhchin (1984) or at the approximate size of first maturity of Black Sea populations. As noted earlier, no data are currently available for first size at maturity of local populations, but the transition to a richer infaunal food resource at the onset of breeding activity would appear tenable. Effective burial of the shell with adoption of the infaunal life style results in both the elimination of further recruitment of borers to the shell and gradual mortality of those borers that recruited during the prior epifaunal existence. The long term susceptibility of invading *R. venosa* to and possible control by endemic parasites such as *Polydora* species is worthy of further investigation in that Gutu and Marinescu (1979) report the presence of the *Polydora ciliata* in shells of *R. venosa* from Romanian waters of the Black Sea. It is notable that in recent quarantine experiments with the Pacific oyster, *Crassostrea gigas* (Thunberg), at our Gloucester Point laboratory by one of the authors (R.M.), this non-native species also exhibited high susceptibility to the native *P websteri.*

The extensive native range of *R. venosa*, and established range in the Black Sea and eastern

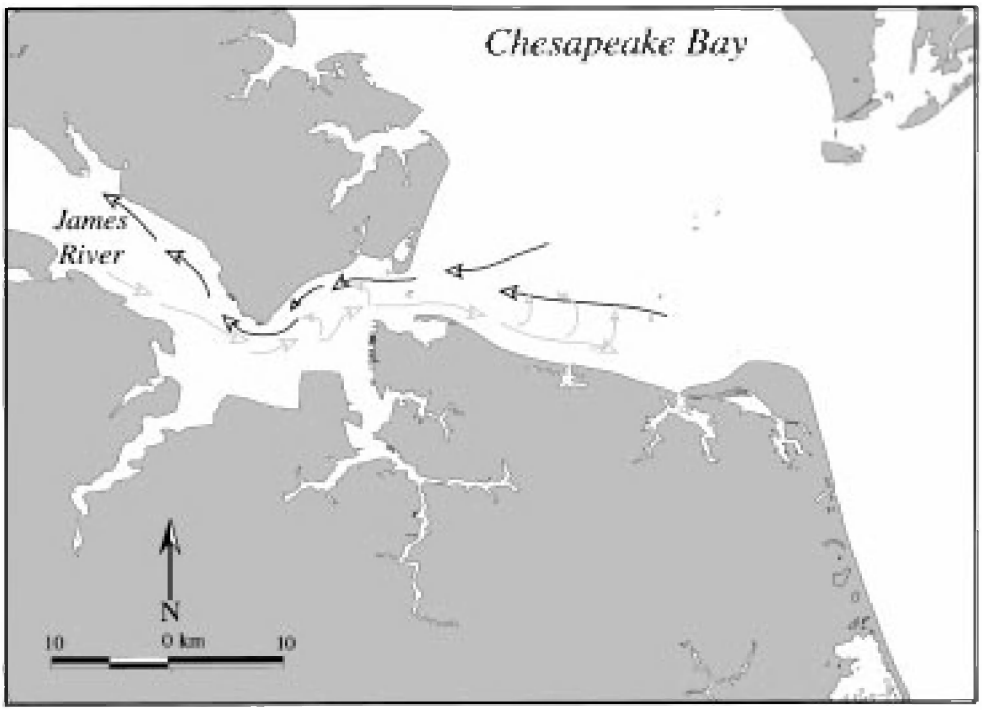

Figure 9. Local circulation in the lower James River and southern shore of the Chesapeake Bay. Darker arrows indicate prevailing inflowing current. Lighter arrows indicate prevailing outflowing current.

Mediterranean Sea prompts consideration of the potential time frame for and possible latitudinal range of invasion of the Atlantic coast of North America. We suggest that the current localized population is a product of local circulation in relation to prospective sites of larval release in deballasting operations. The partial gyre like circulation in the lower James River and southern shore of the Chesapeake Bay (Figure 9) may serve to retain larval *R. venosa* in this location. The period of transit of bulk carriers from the Black Sea or eastern Mediterranean to Hampton Roads is commensurate with the duration of larval development as described earlier. Thus, early post-hatching stages collected in ballasting operations at the point of passage origin would be approaching metamorphic competency on arrival in the southern Chesapeake Bay. Inbound bulk carriers with ballast entering the port of Hampton Roads typically moor and partially deballast on the southern shore of the Thimble Shoals channel within the immediate vicinity of *Rapana* collection sites off Little Creek and Ocean View. Bulk carriers then typically move to the coal loading facility at Newport News Point where deballasting proceeds as coal is loaded. Under such a scenario, release of larval *R. venosa* would occur at one or both 'ends' of the gyre-like circulation in this region. Dispersal to collection sites in the mouths of the York and Rappahannock Rivers would be possible within a few days of release at the Thimble Shoals channel site by transport in deeper inflowing currents that extend to and beyond these locations.

Potential distribution limits of adult *R. venosa* in the Chesapeake Bay bottom can be inferred using local salinity and temperature data (Rennie and Neilson 1994), data from Chung et al. (1993), Golikov (1967), and the observation of a single adult specimen in a location where winter salinities may reach 16 ppt. A projected range of adult *Rapana* survival in the Chesapeake Bay extends across the entire Bay mainstem to a northern limit at the mouth of the Rappahannock River. Marginal limits of this range encroach several km into all major Virginia subestuaries. Summer values of surface salinity and temperature can be used to infer distribution limits of pelagic *R. venosa* larvae, making the assumption that larval forms depth regulate at or near the surface in stratified subestuaries that typify the Chesapeake Bay. The demonstrated low salinity

tolerance of at least the early post-hatch larval stages (Figures 5 and 6) and the relative position of winter bottom and summer surface isohalines (Figure 7A and C) suggests survival of larvae transported into the major subestuaries in the summer to positions upstream of the currently documented or estimated limits for benthic adult *R. venosa*. Surface circulation within the Chesapeake Bay mainstem combined with the duration of the pelagic larval phase suggest that extant adult populations can support recruitment to projected benthic populations if larvae can locate and successfully metamorphose on suitable substrates. Local population centers of adult *R. venosa* are concurrent with that of the hard clam (*Mercenaria mercenaria* L.). In laboratory studies, adult *R. venosa* have demonstrated high predation rates on *M. mercenaria* (Harding and Mann 1999). The projected establishment range for *R. venosa* in the Chesapeake Bay suggests continued predation pressure on *M. mercenaria* populations, but less on the native oyster, *Crassostrea virginica* (Gmelin), populations which are currently limited to lower salinity habitats by endemic diseases. Indeed, no *Rapana* specimens to date have been collected from currently exploited oyster beds.

Invasive range estimates for the Atlantic coast employ comparative temperature data from susceptible and known ranges of *Rapana*. Figure 3 presents a summary of temperature data from a number of sites on the eastern seaboard of the United States extending from Charleston, South Carolina to Portland, Maine (monthly mean ± standard deviation for the 1978–1993 period) with an inclusion of the temperature data from Chung et al. (1993) for the native Korean range. Typical summer temperatures from the mouth of the Chesapeake Bay in the south to at least New York in the north in typical (mean temperature value) years appear capable supporting larval development (21 days at 24–26 °C and salinities >18–21 ppt (this study), and similar periods at 18.3–20.4 °C (Chung et al. 1993) for Korean waters and 20–22 °C (Chukhchin 1984) for Black Sea populations). Boston, Massachusetts, may encounter amenable temperatures for larval survival in atypically warm years. Given the common zoogeographic boundary of Boreal molluscs with temperate species at Cape Cod (see Franz and Merrill 1980), a northern limit of potential distribution at Cape Cod appears tenable. A potential boundary to the south of the Chesapeake Bay mouth may occur at Cape Hatteras, another distinct zoogeographic boundary described by Franz and Merrill (1980), or towards Charleston, South Carolina. The critical temperature comparison is that of Charleston with Hong Kong (compare Figures 3 and 8) where, as mentioned earlier, *R. venosa* is displaced by *Rapana bezoar* (Tsi et al. 1983; see also Morton 1994). While both locations share a similar annual temperature minimum (approximately 17 °C) the mean summer maximum in Charleston (28 °C) is considerably less than that in Hong Kong (35 °C) suggesting that the Charleston coastline may be susceptible to invasion by *R. venosa*. Further, based upon the statements of broad dietary preferences of *R. venosa* in the Black Sea as reported earlier, there appears to be ample potential prey species for *R. venosa* throughout the Cape Cod to Charleston region.

Factors other than environmental tolerances can be important in developing predictions of potential establishment and impact on non-native species. In addition, both the time frame within which such invasions could occur and the subsequent stability of the invading population are difficult to estimate. For example, despite the passage of decades since the original introduction there is evidence that the Black Sea population of *Rapana* has yet to reach a stable equilibrium in this environment. Zolotarev (1996) comments that *R. thomasiana* is "very fertile and is tolerant of low salinities, water pollution, and to oxygen deficiency", yet he further comments that *Rapana* is not numerous in the northwestern Black Sea despite the fact that food resources (molluscs) are abundant and levels of water contamination are lower than in some other sites where *Rapana* is very common. Despite a considerable database on its ecology and physiology *Rapana* remains a good example of our poor ability to synthesize such data and develop good predictions of the eventual success or failure of biological invasions.

Limited ability to predict the temporal or spatial success of an expanding invasion should not preclude a examination of the associated ecological impacts, especially so in the case of *R. venosa* where documented impacts in the Black Sea have been severe. Zolotarev (1996) suggests a broad dietary preference on bivalve molluscs including the soft sediment infaunal mollusc species *Venus gallina*, *Gouldia minima*, and *Pitar rudus*. Marinov (1990) and Rubinshtein and Hiznjak (1988) identify predation by *R. venosa* as the prime reason for decline in *Mytilus galloprovincialis* in Bulgarian waters, the Kerch Strait and the Caucasian shelf, respectively. Chukhchin (1984) attributes the near extinction of the native bivalves *Ostrea edulis*, *Pecten ponticus*, and *M. galloprovincialis* on the Gudaut to

predation by *R. venosa*. Further, establishment of substantial populations of *Rapana* (Marinov 1990; Zolotarev 1996; Alpbaz and Temelli 1997) appears to have been facilitated by the general lack of competition from other predatory gastropods, a lack of direct predation on *Rapana* by other predators, and an abundance of potential prey species.

There is clear cause for concern for the long term ecological impact of *R. venosa* on the Atlantic coast of North America. The local collection of egg cases which produce viable pelagic larvae, its demonstrated ability as a predator on local species (*M. mercenaria* see Harding and Mann 1999), and apparently rapid rate of growth to a refuge size all suggest continuing expansion of the current invasion. Dispersal may be enhanced in that Hampton Roads, Virginia serves as a major container port for shipping along the Atlantic coast and in trade with Europe and Asian ports, and is the location of Norfolk Naval Base, the largest naval installation in the western hemisphere. Elimination or eradication options for this animal are limited at this time. Local *Rapana* population centers are concurrent with that of commercially exploited hard clam (*M. mercenaria*) populations. Large scale attempts to remove or reduce *Rapana* populations in these regions to functionally non-reproductive densities could cause major disturbance of hard clam habitat and have impact on long term management of this fishery resource. The consequences of not attempting to eliminate local *Rapana* populations are, however, much less predictable and potentially much more serious.

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References

Aldana-Aranda D and Suarez VP (1998) Overview of diets used in larviculture of three Caribbean Conchs: Queen Conch *Strombus gigas*, Milk Conch *Strombus costatus* and Fighting Conch *Strombus pugilis*. Aquaculture 167: 163–178

Alpbaz A and Temelli B (1997) A review of the molluscan fisheries of Turkey. NOAA Technical Report NMFS 129, pp 227–232 (Abstract)

Bombace G, Fabi G, Fiorentini L and Speranza S (1994). Analysis of the efficacy of artificial reefs located in five different areas of the Adriatic Sea. Bulletin of Marine Science 55(2–3): 559–580

Cai RX and Huang WH (eds) (1991). Fauna of Zhejiang, China (Mollusca). Zhejiang: Zhejiang Science and Technology Publishing House

Carlton JT (1999) Molluscan invasions in marine and estuarine communities. Malacologia 41(2): 439–454

Chukchin V (1984) Ecology of the Gastropod Molluscs of the Black Sea. Academy of Sciences, USSR, Kiev Naukova Dumka, 175 pp [in Russian]

Chung EY and Kim S-Y (1997) Cytological studies on testicular maturation and cyclic changes in the epithelial cells of the seminal vesicle of the male purple shell *Rapana venosa* (Gastropoda: Muricidae). Malacological Review 30: 25–38

Chung EY, Kim SY, and Kim YG (1993) Reproductive ecology of the purple shell, *Rapana venosa* (Gastropoda: Muricidae), with special reference to the reproductive cycle, deposition of egg capsules and hatching of larvae. Korean Journal Malacology 9(2): 1–15

Cucaz M (1983) *Rapana venosa* (Valenciennes, 1846) vivente nel Golfo di Trieste. Boll. Malacologico, Milano 19(9–12): 261–262

Drapkin E (1963) Effect of *Rapana bezoar* Linne' (Mollusca, Muricidae) on the Black Sea fauna. SRR, Doklady Akademii Nauk 151(3): 700–703

Franz DR and Merrill AS (1980) The origins and determinants of distribution of molluscan faunal groups on the shallow continental shelf of the Northwest Atlantic. Malacologia 19(2): 227–248.

Ghisotti F (1971) *Rapana thomasiana* Crosse, 1861 (Gastropoda, Muricidae) nel Mar Nero. Conchiglie, Milano 7(3–4): 55–58

Ghisotti F (1974) *Rapana venosa* (Valenciennes), nuova ospite Adriatica? Conchiglie, Milano 10(5–6): 125–126

Golikov AN (1967) Gastropoda: In: Animals and Plants of Peter the Great Bay, pp 79–91. Leningrad, Nauka

Gutu M and Marinescu A (1979) *Polydora ciliata* Polychaeta perforates the gastropod *Rapana thomasiana* of the Black Sea. Travaux du Museum d'Histoire Naturelle 'Grigore Antipa' 20(1): 35–42

Haigler SA (1969) Boring mechanism of *Polydora websteri* inhabiting *Crassostrea virginica*. American Zoologist 9: 821–828

Harding JM and Mann R (1999) Observations on the biology of the veined rapa whelk, *Rapana venosa* (Valenciennes, 1846) in the Chesapeake Bay. Journal of Shellfish Research 18(1): 9–17

Hwang DF, Lu SC and Jeng SS (1991) Occurrence of tetrodotoxin in the gastropods *Rapana rapiformis* and *R. venosa venosa*. Marine Biology 111(1): 65–69

Kool S (1993) Phylogenetic Analysis of the Rapaninae (Neogastropoda: Muricidae). Malacologia 35(2): 155–259

Koutsoubas D and Voultsiadou-Koukoura E (1990) The occurrence of *Rapana venosa* (Valenciennes, 1846) (Gastropoda, Thaididae) in the Aegean Sea. Boll. Malacologico, Milano 26(10–12): 201–204

Lai KY and Pan CW (1980) The *Rapana* shells of Taiwan. Bulletin of Malacology, Republic of China 7: 27–32

Liu JH (1994) The Ecology of the Hong Kong Limpets *Cellana grata* (Gould 1859) and *Patelloida pygmaea* (Dunker 1860): Reproductive Biology. Journal Molluscan Study 60: 97–111

Marinov TM (1990) The Zoobenthos from the Bulgarian Sector of the Black Sea. Sofia, Bulg. Acad. Sci. Publ., 195 pp

Mel P (1976) Sulla presenza di *Rapana venosa* (Valenciennes) e di Charonia variegate sequenzae (AR & BEN.) nell'Alto Adriatico. Conchiglie, Milano 12(5–6): 129–132

Morse DE (1992) Molecular mechanisms controlling metamorphosis and recruitment in abalone larvae. In: Shepherd SA, Tegner MJ and Guzman del Proo SA (eds) Abalone of the World: Biology, Fisheries and Culture, Chapter 10, pp 107–119. London, Fishing News Books, 608 pp

Morton B (1994) Prey preference and method of attack by *Rapana bezoar* (Gastropoda: Muricidae) from Hong Kong. In: Morton B (ed) The Malacofauna of Hong Kong and Southern China III, pp 309–325. Hong Kong University Press

Pechenik JA and Gee CC (1993) Onset of metamorphic competence in larvae of the gastropod *Crepidula fornicata* (L), judged by a natural and an artificial cue. Journal of Experimental Marine Biology and Ecology 167: 59–72

Pechenik JA and Heyman WD (1987) Using KCl to determine size at competence for larvae of the marine gastropod *Crepidula fornicata* (L.). Journal of Experimental Marine Biology Ecology 112: 27–38

Powell AWB (1979) New Zealand Mollusca: Marine Land and Freshwater Shells. Auckland, Sydney and London, Collins

Rennie S and Neilson B (1994) Chesapeake Bay Atlas. Virginia Institute of Marine Science, Gloucester Point, Virginia

Richards A (1990) Muricids: a hazard to navigation? Hawaiian Shell News 35(8): 10

Rinaldi E (1985) *Rapana venosa* (Valenciennes) spiaggiata in notevole quantita sufla spiaggia di Rimini (Fo). Boll. Malac-ologico, Milano 21(10–12): 318

Rubinshtein IG and Hiznjak VI (1988) Stocks of *Rapana thomasiana* in the Kerch Strait. Rybnoye Khoz (Moscow) 1: 39–41 [in Russian]

Ruiz GM, Carlton JT, Grosholz ED, and Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent and consequences. American Zoology 37: 619–630

Sahin T (1997) Investigations on some biological characteristics of sea snail *Rapana venosa* (Valenciennes 1846) population in the Eastern Black Sea. Turkish Journal of Zoology 21(4): 461–466

Smagowicz K (1989) Polymorphism and anomalous shells in juveniles of *Rapana thomassiana* Crosse, 1861 (Gastropoda: Prosobranchia: Neogastropoda) from the Black Sea. Folia Malcologca (Krakow) 3: 149–161

Terreni G (1980) Molluschi poco conosciuti dell'Arcipelago Toscano: 1 – Gasteropodi. Boll. Malacologico, Milano 16(1–2): 9–17

Tsi CY, Ma XT, Lou ZK and Zhang FS (1983) Illustrations of the Fauna of China (Mollusca), Vol 2, pp 1–150; plates I–IV. Beijing, Science Press

Wu Y (1988) Distribution and shell height-weight relation of *Rapana venosa* Valenciennes in the Laizhou Bay. Marine Science/Haiyang Kexue 6: 39–40

Yool AJ, Grau SM, Hadfield MG, Jensen RA, Markell DA and Morse DE (1986) Excess potassium induces larval metamorphosis in four marine invertebrate species. Biology Bulletin 170: 255–266

Zar JH (1996) Biostatistical Analysis, 3rd edn. New Jersey, Prentice Hall

Zolotarev V (1996) The Black Sea Ecosystem Changes Related to the Introduction of New Mollusc Species. Ecology 17(1–3): 227–236