Veined rapa whelk (*Rapana venosa*) research in North America: Summary of research activity through February 2002.

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INTRODUCTION

Veined rapa whelks (*Rapana venosa*) were first reported from the Chesapeake Bay, U.S.A. during the summer of 1998. The first collections were large adult specimens approximately 140 mm in shell length collected by the Virginia Institute of Marine Science (VIMS) finfish trawl survey and brought to the attention of Dr. Roger Mann, leader of the VIMS Molluscan Ecology program. Shortly after the identification of these animals was confirmed as *Rapana venosa* by malacologists at the Smithsonian Institution’s National Museum of Natural History (Washington, D.C.), the VIMS Molluscan Ecology program instituted a $5 bounty on rapa whelks caught in Chesapeake waters to encourage donation of specimens caught by local watermen and provide data on the distribution and density of the species within the Chesapeake Bay.

The VIMS bounty program continues to the present with over 3800 adult specimens collected to date. Viable egg masses have been collected from Chesapeake waters in 1998, 1999, 2000, and 2001 leaving little doubt that the Chesapeake Bay rapa whelk population is actively reproducing. Using live animals turned in to VIMS through the bounty program, numerous studies examining the biology and ecology of all life history stages of this animal have been initiated and are proceeding under the direction of Drs. Roger Mann and Juliana M. Harding. Details of this research have been and continue to be presented at international and national professional meetings. This booklet contains copies of all of the abstracts describing rapa whelk research done by the Molluscan Ecology Program at the Virginia Institute of Marine Science through February 2002. Additional information regarding the VIMS rapa whelk research program as well as program updates may be found at the VIMS rapa whelk web site: www.vims.edu/mollusc/research/merapven.html.

Two peer-reviewed rapa whelk papers have been published as of this writing (3/15/2002) with several more in preparation. References for the two rapa whelk papers are:


BIOGRAPHICAL SKETCHES OF THE Rapana venosa PRINCIPAL INVESTIGATORS

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Roger Mann is a Professor of Marine Science at the College of William and Mary/Virginia Institute of Marine Science (VIMS). He holds a Ph.D. in Marine Science from the University of Bangor, Wales and a Bachelor’s degree in Biology from the University of East Anglia in the United Kingdom. His graduate work, completed under the direction of the late Dr. Peter Walne of the Shellfish Laboratory at Conwy, Wales, examined the physiological ecology of the Japanese oyster, Crassostrea gigas, following its introduction to the United Kingdom. His programs have focused on a wide variety of issues including mollusc population biology and fisheries of the Chesapeake Bay and Middle Atlantic Bight including shelf species, larval ecology and early life history of molluscs in estuarine environments, restoration ecology, biology of invading species, and the role of ballast water as a vector in biological invasions. He was a 1994 recipient of the Chesapeake Bay Commission Tribute to Excellence for "official recognition of significant contributions to the management and protection of the Chesapeake Bay". He teaches malacology, larval ecology and invasion biology in the graduate program of the School of Marine Science of the College of William and Mary and was the 2001 recipient of the School of Marine Science Outstanding Teacher Award.

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*Rapana venosa* in the Chesapeake Bay: Current status and prospects for range extension based on salinity tolerance of early life history stages

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The Veined Rapa Whelk, *Rapana venosa*, has recently been identified as present in the Hampton Roads region of the Chesapeake Bay. The species is native to the Sea of Japan, but was introduced to the Black Sea in the 1940’s, and has since spread to the Aegean and Adriatic Seas. There is strong evidence that range extension is mediated by transport of early life history stages in ballast water. The current status of knowledge of distribution of *R. venosa* in the Chesapeake Bay is described. There is concern over the potential impact of *Rapana venosa* on local shellfish populations and the industry that they support. Egg cases of *R. venosa* have been collected from the field, and larval forms cultured in the laboratory. Estimates of the salinity tolerance of the larval stages of *Rapana venosa* are described as a precursor to estimating a potential range of distribution of the species within the Chesapeake Bay and its subestuaries. Such estimates are crucial to establishing which shellfish resources are potentially susceptible to predation by local *Rapana venosa* populations.

Key words: *Rapana venosa*, gastropod, Chesapeake Bay, larvae, salinity tolerance, range.

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Habitat and prey preferences of Veined Rapa Whelks (*Rapana venosa*) in the Chesapeake Bay: Direct and indirect trophic consequences

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The recent discovery of Veined Rapa Whelks (*Rapana venosa*) in the lower Chesapeake Bay has ecological consequences beyond the obvious potential for predation on commercially valuable shellfish prey species (e.g., *Crassostrea virginica*, *Mercenaria mercenaria*). In the Black Sea and in their native Sea of Japan, *Rapana* have been reported primarily from hard bottom habitats. Adult Chesapeake Bay *Rapana* have been collected from both hard and soft bottom habitat. Laboratory observations indicate that adult *Rapana* prefer sand bottom and will burrow almost completely into the sand at water temperatures > 20°C (i.e., not overwintering behavior). Burrowing behavior by these large apex predators expands the potential suite of vulnerable prey items to include infaunal shellfish (e.g., *Mya arenaria*, *Ensis directus*, *Cyrtopleura costata*). The presence of large (> 100 mm) empty *Rapana* shells in Chesapeake Bay may enhance growth of the local hermit crab (*Clibanarius vittatus*). Recent collections of *Clibanarius vittatus* from the Hampton Roads area indicate that these animals use empty *Rapana* shells as shelters and are reaching previously unrecorded sizes. The implications of abnormally large crustacean scavengers on Chesapeake Bay benthic epifauna (e.g., oyster spat) are discussed.

Key words: *Rapana venosa*, gastropod, Chesapeake Bay, habitat use, infauna, burrowing, *Clibanarius vittatus*.

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The current status of the Rapa Whelk in the Chesapeake Bay

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The Veined Rapa Whelk, *Rapana venosa*, was identified as present in the Hampton Roads region of the Chesapeake Bay in the summer of 1998. The species is native to the Sea of Japan, was introduced to the Black Sea in the 1940’s, and has since spread to the Aegean and Adriatic Seas. We present evidence that this recent range extension is mediated by transport of early life history stages in ballast water. Our current knowledge of distribution of *R. venosa* in the Chesapeake Bay suggests that the majority of the population is limited to a swath from the James River Bridge, through Hampton Roads and along the shoreline of Willoughby and Oceanview inshore of the Thimble Shoals Channel. A small number of individuals have been recorded from the mouth of the York and Rappahannock Rivers. None have been collected in Maryland waters. Egg cases of *R. venosa* have been collected from Hampton Roads, and larval forms cultured in the laboratory. Estimates of the salinity tolerance of the early larval stages of *R. venosa* will be described as a precursor to estimating a potential range of distribution of the species within the Chesapeake Bay and its subestuaries. These estimates will then be used to examine possible range extension within the Mid Atlantic should a stable, reproducing population become established in the lower Chesapeake Bay.

The presence of *R. venosa* in the lower Chesapeake Bay has ecological consequences beyond the obvious potential for predation on commercially valuable shellfish prey species (e.g., *Crassostrea virginica*, *Mercenaria mercenaria*). In the Black Sea and in their native Sea of Japan, *R. venosa* have been reported primarily from hard bottom habitats. Adult Chesapeake Bay *R. venosa* have been collected from both hard and soft bottom habitat. Laboratory observations indicate that adult *R. venosa* burrow almost completely into the sand at water temperatures > 20 °C (i.e., not overwintering behavior). Burrowing behavior by these large apex predators expands the potential suite of vulnerable prey items to include infaunal shellfish (e.g., *Mya arenaria*, *Ensis directus*, *Cyrtopleura costata*). The presence of large (> 100 mm) empty *R. venosa* shells in Chesapeake Bay may enhance growth of the local hermit crab (*Clibanarius vittatus*). Recent collections of *C. vittatus* from the Hampton Roads area indicate they use empty *R. venosa* shells as shelters and are reaching unusually large sizes. The implications of abnormally large crustacean scavengers on Chesapeake Bay benthic epifauna (e.g., oyster spat) will be examined.

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Rapana venosa in the Chesapeake Bay: Current status and prospects for range expansion based on salinity tolerance of early life history stages

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The Veined Rapa Whelk, *Rapana venosa*, has recently been identified as present in the Hampton Roads region of the Chesapeake Bay. The species is native to the Sea of Japan, but was introduced to the Black Sea in the 1940’s, and has since spread to the Aegean and Adriatic Seas. There is strong evidence that range extension is mediated by transport of early life history stages in ballast water. The current status of knowledge of distribution of *R. venosa* in the Chesapeake Bay is described. There is concern over the potential impact of *Rapana venosa* on local shellfish populations and the industry that they support. Egg cases of *R. venosa* have been collected from the field, and larval forms cultured in the laboratory. Estimates of the salinity tolerance of the larval stages of *Rapana venosa* are described as a precursor to estimating a potential range of distribution of the species within the Chesapeake Bay and its subestuaries. Such estimates are crucial to establishing which shellfish resources are potentially susceptible to predation by local *Rapana venosa* populations.

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Habitat and prey preferences of veined rapa whelks (*Rapana venosa*) in the Chesapeake Bay: Direct and indirect trophic consequences

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The recent discovery of Veined Rapa Whelks (*Rapana venosa*) in the lower Chesapeake Bay has ecological consequences beyond the obvious potential for predation on commercially valuable shellfish prey species (e.g., *Crassostrea virginica*, *Mercenaria mercenaria*). In the Black Sea and in their native Sea of Japan, *Rapana* have been reported primarily from hard bottom habitats. Adult Chesapeake Bay *Rapana* have been collected from both hard and soft bottom habitat. Laboratory observations indicate that adult *Rapana* prefer sand bottom and will burrow almost completely into the sand at water temperatures > 20 °C (i.e., not overwintering behavior). Burrowing behavior by these large apex predators expands the potential suite of vulnerable prey items to include infaunal shellfish (e.g., *Mya arenaria*, *Ensis directus*, *Cyrtopleura costata*). The presence of large (>100 mm) empty *Rapana* shells in Chesapeake Bay may enhance growth of the local hermit crab (*Clibanarius vittatus*). Recent collections of *Clibanarius vittatus* from the Hampton Roads area indicate they use empty *Rapana* shells as shelters and are reaching previously unrecorded sizes. The implications of abnormally large crustacean scavengers on Chesapeake Bay benthic epifauna (e.g., oyster spat) are discussed.

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Veined Rapa whelks (*Rapana venosa*) in the Chesapeake Bay: Ecological consequences of a ballast water introduction

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The presence of Veined Rapa whelks in the lower Chesapeake Bay has ecological consequences beyond the obvious potential for predation on commercially valuable shellfish. Although native to the Sea of Japan, *Rapana* were introduced into the Black, Adriatic, and Aegean Seas after World War II and have been responsible for major ecosystem changes. Life histories and life styles of this novel invader will be discussed in comparison to native whelk species and potential ecosystem consequences in the Bay.

Veined Rapa Whelks (*Rapana venosa*) in the Chesapeake Bay: Current status and preliminary reports on larval growth and development

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Since the initial discovery of the Veined Rapa Whelk (*Rapana venosa*) in the Lower Chesapeake Bay in June 1999, over 650 adult specimens have been donated to the Virginia Institute of Marine Science (VIMS) Rapa Whelk research program. Continuing efforts to map the whelk's distribution in the Lower Chesapeake Bay indicate no new range extensions and a relatively constant population in the lower James River, Hampton Bar, and Ocean View/Little Creek regions. During the summer of 1999, VIMS' broodstock animals laid over 500 egg masses with egg laying activity beginning in May and continuing through August. Egg masses and the resulting larvae were successfully cultured through metamorphosis. Recently settled young *Rapana* have a wide range of dietary capabilities and will feed on local fauna including barnacles, oyster spat, mussels, and *Macoma*. Growth post settlement can be quite rapid. The oldest juveniles from the 1999 larval cultures reached total shell lengths in excess of 20 mm within 4 months of metamorphosis and settlement.

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Abundance of small predatory gastropods (*Urosalpinx cinera, Eupleura caudata, Rapana venosa*) in relation to lower Chesapeake Bay oyster (*Crassostrea virginica*) populations

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Oysters in the Virginia portion of the Chesapeake Bay have enjoyed a relative hiatus from oyster drill (*Urosalpinx cinera, Eupleura caudata*) predation since Hurricane Agnes dramatically reduced oyster drill abundance in 1972. In recent years, anecdotal reports have indicated that oyster drill abundance has been increasing in Virginia waters. Increased oyster drill abundance combined with the recent discovery of a third predatory gastropod, Veined Rapa whelk (*Rapana venosa*), in the lower Chesapeake Bay, has potentially significant consequences for the commercial oyster fishery as well as Virginia’s ongoing oyster restoration efforts. Quantitative estimates of the abundance and distribution of small predatory gastropods in relation to existing oyster resources were made during Fall 1999 at > 150 sites in 8 tributaries. Oyster drills were present in < 50% of sites sampled, juvenile *Rapana venosa* were not observed. Both species of oyster drill were more abundant in downriver habitats with salinities ranging from 15 to 25 ppt. Drill abundance ranged from 1 to 4 animals m$^{-2}$.

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Variability in larval development of Veined Rapa Whelk *Rapana venosa* from Chesapeake Bay, USA: Implications for ecological success in local habitats

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The apparent success of the introduced Veined Rapa Whelk, *Rapana venosa*, in the lower Chesapeake Bay is facilitated by the observed flexibility of larval forms. Within an individual egg mass, egg case incubation time ranges from 14 to > 45 days. Veliger larvae display considerable variation in time from hatch to settlement although they are morphologically competent to settle after 21 days. On identical mixed diets, settlement time ranged from 28 days to > 70 days post hatch. The high variability in pelagic larval duration combined with the Chesapeake Bay's semi diurnal tidal regime, offers a viable dispersal mechanism for local range extension of these animals. Settling Rapa Whelks did not display substrate-specificity and settled in the absence of added chemical inducers (e.g., MgCl, extract from cultures of local fouling organisms). Juvenile (post settlement) Rapa Whelks grazing on local bryozoa and small barnacles at ambient salinities (12-18 ppt) and temperatures (15 - 28°C) grow at approximately a mm per week. At shell lengths (SL) > 10 mm, juvenile snails can open small mussels as well as barnacles and begin drilling oyster spat. Bryozoa, barnacles, mussels, and oyster spat are locally abundant on both natural and artificial substrates ranging from oyster shell to bridge pilings and tunnels. In the absence of larval Rapa Whelk substrate and/or prey specificity during settlement, the lower Chesapeake Bay offers considerable potential habitat for these animals.

Larval ecology of the Veined Rapa Whelk *Rapana venosa* from Chesapeake Bay, USA

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Since the discovery of adult Veined Rapa Whelks *Rapana venosa* in the lower Chesapeake Bay, USA in June, 1998, the Virginia Institute of Marine Science (VIMS) has maintained an active research program focusing on the biology, ecology, and local distribution of Rapa Whelks. From May through August, 1999, VIMS' broodstock animals laid over 500 egg masses that were subsequently cultured through hatching. Egg mass size ranged from 25 to > 500 egg cases per egg mass. The resulting larval snails were cultured through settlement. Diet, growth, and development of these juvenile (post-settlement) snails continue to be monitored weekly. Optimal growth of Rapa Whelk veligers was observed on a mixed diet of algae and diatoms. Time to settlement ranged from 28 to > 70 days post-hatch. Settlement occurred in the absence of added chemical inducers (e.g., MgCl, extract from cultures of local fouling organisms). Mortality post settlement is low in laboratory cultures (< 10%). On progressive diets of local benthic macrofauna (bryozoa, barnacles, mussels, oyster spat), juvenile rapa whelks grow up to a mm per week in shell length (SL) at water temperatures above 15°C. Rapa Whelk juveniles drill round holes in small oysters but open mussels with no visible predation signature. In laboratory cultures, juvenile Rapa Whelks may attain shell lengths in excess of 30 mm within 10 months of hatching.

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Coming soon to a restoration site near you: The invading, predatory oriental gastropod *Rapana venosa*

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*Rapana venosa* Valenciennes 1846 (Neogastropoda, formerly Muricidae, currently Thaididae) is a predatory gastropod native to the Sea of Japan, Yellow Sea, East China Sea, Bohai Sea, and Taiwan. The species has been introduced to the Black Sea, Adriatic Sea, and Aegean Sea, where it is generally considered to be responsible for decimation of local commercially valuable mollusc species. It was first reported in the Chesapeake Bay in 1998. Ballast water transport of larval stages from the eastern Mediterranean or Black Sea is the suspected vector of introduction. To date over 1200 specimens of adult *Rapana* have been collected from Hampton Roads and a limited region of the Southern Chesapeake Bay. Population demographics, records of *Rapana* egg cases in the field and our ability to culture early life history stages at prevailing temperature and salinity strongly suggest active breeding in this receptor location. Temperature and salinity tolerance data for *Rapana* suggest that it can both invade the higher salinity regions of most East Coast estuaries and survive on exposed shorelines from Cape Cod, MA to Charleston, SC. Dispersal is facilitated by pelagic development, and may be exacerbated by ballast water transport of larval stages originating in Hampton Roads. Hard substrate habitat, typical of many current shellfish restoration efforts, appears optimal for post settlement stages, but larger adults may invade soft sediments. Predation has been demonstrated on a range of commercially valuable shellfish species including *Mercenaria mercenaria, Crassostrea virginica, Mya arenaria* and *Mytilus edulis.*

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Salinity tolerance of larval *Rapana venosa*: Implications for dispersal and establishment range on the U.S. East coast

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The lack of quantitative data on environmental tolerances of early life history stages hinders estimation of both dispersal rates and establishment ranges for invading species in receptor environments. This is particularly evident in consideration of invading species with pelagic larval life history phases where the pelagic stage effects most if not all of the dispersal at the time frame of a single generation. We present salinity tolerance data for all stages of the ontogenetic larval development of the invading predatory gastropod *Rapana venosa*. We propose that salinity tolerance is the dominant response controlling potential dispersal (= invasion) range of the species into the estuaries of the Atlantic coast of the United States. Salinity tolerance is then examined in conjunction with temperature, which dictates both periodicity of adult egg laying and larval development rate, and extant nearshore and estuarine current data, to estimate rates of dispersal and range expansion from the current invading epicenter in the southern Chesapeake Bay. All larval stages exhibit 48 hr tolerance to salinities as low as 15 ppt with minimal mortality. Below this value survival grades to no survival at less than 10 ppt. This tolerance is greater than of the adults of the large native predatory gastropods of the genera *Busycon* and *Busycotypus* with which, we predict, *Rapana* will compete directly for space and prey, notably infaunal pelecypods. We predict that counter clockwise, gyre-like circulation within the Chesapeake Bay will initially distribute larvae northward along the bay side of the DelMarVa peninsula, and eventually to the lower sections of all the major subestuaries of the western shore of the bay. The discovery in summer 2000 of small (80 mm as opposed to adult specimens of >160 mm maximum dimension) *Rapana* at the along the northerly leg of this gyre adds weight to the predicted dispersal route. Dispersal onto and along the coastal shelf outside of the bay mouth may be influenced by both northward and southward flowing residual current depending on depth, wind conditions, and time within the known egg laying period of the invader in the southern Chesapeake Bay. Establishment over a period of decades from Cape Cod to Cape Hatteras by natural dispersal is considered a high probability. This time frame may, however, be considerably reduced by passive dispersal of larval forms in ballast water during intra-coastal maritime trade.

Key words: *Rapana venosa*, salinity, temperature, dispersal, establishment

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Growth rates of larval and juvenile rapa whelks *Rapana venosa* from Chesapeake Bay, U.S.A.: From hatch through Age 1

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The apparent success of the introduced veined rapa whelk, *Rapana venosa*, in the lower Chesapeake Bay, U.S.A. is facilitated by general habitat and food requirements resulting in rapid growth rates of larval and juvenile snails. Rapa whelk veliger larvae display considerable variation in time from hatch to settlement although they are morphologically competent to settle after 21 days. Veligers grow quickly on mixed algal diets reaching shell lengths in excess of 0.5 mm at 21 days. Rapa whelk veligers display little substrate specificity at settlement and settle successfully on a wide range of locally available attached macrofauna including bryozoans and barnacles. Once settled onto hard substrates, young rapa whelks are generalist predators and consume large numbers of barnacles, mussels, oyster spat, and small oysters. Recently settled rapa whelks grow at > 1 mm per week reaching shell lengths of 40-50 mm within 5 months post-settlement and > 60 mm SL at Age 1. These extremely fast growth rates combined with the rapa whelk's cryptic coloration, nocturnal habits, and preference for oysters as both food and habitat offer serious cause for concern particularly in light of ongoing oyster restoration efforts in the lower Chesapeake. Evidence suggests that rapa whelks occupy shallow hard substrate habitats until reaching shell lengths in excess of 70 mm and then migrate into deeper habitats with sand or mud substrates where they forage on infaunal bivalves including soft clams (*Mya* sp.) and hard clams (*Mercenaria mercenaria*).

Key words: Veined rapa whelk, *Rapana venosa*, oyster, hard clam, generalist predator

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Reproductive biology of Chesapeake Bay, U.S.A. veined rapa whelks *Rapana venosa*

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Successful introduction of a species requires the establishment of a viable reproductive population in the receptor environment. In the event that animals become established post-introduction, there will be temporal and spatial variation within the population in the ability to successfully reproduce resulting in foci of reproductive activity or a functional reproductive range of the invader. This study describes temporal and spatial variability in gametogenesis in veined rapa whelks, *Rapana venosa*, as a surrogate for egg laying along an environmental and spatial gradient. Laboratory populations of animals collected from Chesapeake Bay and maintained at local temperatures and salinities have been observed mating from October through July. Field collections of adult rapa whelks (shell length > 80 mm) were made year-round using opportunistic sampling based on commercial fisheries where this animal is bycatch. Representative individuals were sampled from the extreme ends of the environmental and spatial gradient of the observed population distribution. Individual animals were sacrificed and examined for gross external morphology as an indicator of sex ratio and incidence of imposex. Histological analyses were used to describe progression of gametogenesis in individual animals. The observed relationship between gametogenesis and water temperatures in animals from Chesapeake Bay is consistent with a.) previously described seasonal reproductive activity in native (Korean) populations and b.) laboratory observations of egg laying from mid-May through mid-August and field collections of egg masses in Chesapeake Bay. Collectively, these data sets indicate that the Chesapeake Bay population of rapa whelks is successfully completing gametogenesis and egg laying throughout the range of collection. These data describing reproductive capability are integrated with available demographic data from the same source to develop spatial estimates of highest reproductive output or reproductive foci within Chesapeake Bay.

Key words: *Rapana venosa*, Chesapeake Bay, gametogenesis, imposex, sex ratios

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Temporal and spatial variation in egg cases of *Rapana venosa* from the Chesapeake Bay, U.S.A.

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Invading species face a number of challenges in receptor environments if they are to become established members of the new ecosystem. Distribution data of adult life history stages reflect presence of available prey (in the case of invading predators) within the physical tolerance of the invading species; however, the functional reproductive range of the invader may be only a subset of the range occupied. It is critical to identify the functional reproductive range early in an invasion if control measures are to be effective in limiting range expansion or, preferably, eliminating the invader. The invading predatory marine gastropod *Rapana venosa* was first described from the Chesapeake Bay in 1998. Over 1200 adult specimens have been collected since that time, with the vast majority limited to a small section of the southern Chesapeake Bay. Evidence of reproduction in this receptor environment includes collection of egg masses from the field, population demographics consistent with multiple year classes, and successful culture of larval forms through metamorphosis at local temperatures and salinities from egg masses originating from field collected adults. *Rapana* lays mats of eggs with 50-300 egg cases per mat. Each case may contain 200-400 eggs. As a surrogate for determining reproductive potential in the field, adult populations from five locations in the Chesapeake Bay have been maintained and successfully bred in the laboratory during both 1999 and 2000. The five locations of origin represent a spatial cline of environmental gradients of substrate type, salinity and other physical factors. Morphological variations in the egg cases of *R. venosa* suggesting a response to this environmental cline were observed in 1999. Extensive studies of egg mass morphometrics, egg number per egg case, and viability of eggs within each case, were effected for both temporal (May through August, 1999 and 2000) and spatial (5 collection locations) clines within the known adult population in order to examine the option that successful reproduction was limited to a subset of the area from which adults have been collected. This analysis was then supplemented with spatial data describing density of breeding adults to estimate the spatial limitation of functional breeding in the lower Chesapeake Bay.

Key words: Veined rapa whelk, *Rapana venosa*, Chesapeake Bay, morphological variation, reproductive success

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Morphological variation between three populations of the veined rapa whelk, *Rapana venosa*, a recent gastropod invader of the Chesapeake Bay, Virginia, U.S.A.

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The gastropod form, such as that of *Rapana venosa*, is restricted by its unique molluscan phylogeny, yet gastropods show remarkable diversity both on the interspecific and intraspecific levels. Since the phenotypic traits of the gastropod shell are under genetic and environmental controls, bioinvasions yield an opportunity to investigate the impact of novel environments on a single species. The initial introduction of *R. venosa* from the Bohai Sea, Yellow Sea, and Sea of Japan system of Northern Asia to the Black Sea and Mediterranean Sea systems of Europe occurred during the 1940s. Subsequently, *R. venosa* was introduced from presumably the European population to the Chesapeake Bay, Virginia, U.S.A. in the 1990s. This invasion allows for the comparison of three populations of whelks in environments that differ in their present day and historical ecologies. For this study, *R. venosa* were collected from the Yellow Sea, Korean Straits, Black Sea, and Chesapeake Bay, U.S.A. Additional specimens were obtained from the historical collection within the Smithsonian Institute's Museum of Natural History. Using computer based image analysis, characteristic measurements were made. These measurements were then compared using both multivariate and bivariate methods. The majority of the variance was due to size and allometric differences. The observed shell form variation in *Rapana venosa* most likely results from ecological as opposed to genetic controls. This study examines potential ecological causes and impacts to shell form between the Yellow Sea, Korean Straits, Black Sea, and Chesapeake Bay populations of the invasive gastropod, *Rapana venosa*.

Key Words: *Rapana venosa*, Veined rapa whelk, Chesapeake Bay, gastropod, morphometrics

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The genetics of invasion: A study of the Asian veined rapa whelk, *Rapana venosa*

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Molecular techniques have proven useful in assessments of patterns of invasion and colonization. Here, we use DNA sequencing of a 732 bp portion of the mitochondrial cytochrome b gene to investigate genetic relationships among native and introduced populations of *Rapana venosa*, a large predatory neogastropod. *Rapana venosa* is native to temperate Asian waters and has been to be a successful invader in the 20th century. *Rapana venosa* was introduced into the Black Sea in the late 1940s, probably through the unintentional transport of the bivalve predator in overland shipments of aquaculturally important Asian oysters. Since then, *R. venosa* has spread through European waters, and has become established in Uruguay (1999), and Chesapeake Bay, USA (1998). These latter introductions are believed to be mediated via ballast water transport of pelagic larvae. Larval propagules could be from single or multiple introductory events, and the source population could be either the native Asian populations or the colonial European populations.

As samples of both native and non-native populations are available for study, this work examines the relationship between genetic variability and colonization efficacy, and tests the hypothesis that colonial populations are less genetically diverse than the original parent population. Also, as we believe the newly discovered Chesapeake Bay population is the result of a relatively recent invasion, this study offers the opportunity to establish a genetic baseline, from which we can document changes in genetic variation over time.

Collections have been obtained from native (Korea, n=80) and non-native (Black Sea, n=40, and Chesapeake Bay, n=80) locations. A portion of the cytochrome b gene, generated through PCR amplification using primers designed by Collins et al (1996), will be sequenced. Haplotype frequencies and percent sequence divergence will be calculated. Estimates of genetic variation and genetic divergence within and among native and non-native populations will be assessed using phenetic and cladistic methods.

Key words: *Rapana venosa*, genetic variation, bioinvasion, DNA, cytochrome b


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Experimental evaluation of *Rapana venosa* feeding rates preying on the bivalve *Mercenaria mercenaria* in the lower Chesapeake Bay, U.S.A.

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The recent discovery of adult veined rapa whelks *Rapana venosa* (Valenciennes, 1848) in the Lower Chesapeake Bay, U.S.A. offers cause for both ecological and economic concern. Adult rapa whelks are large predatory gastropods that consume bivalves including commercially valuable species such as hard clams, *Mercenaria mercenaria*. Laboratory feeding experiments were used to evaluate daily consumption rates of two sizes of adult rapa whelks feeding on two size classes of hard clams. Empty clam shells were removed from experimental tanks and replaced with similar sized live clams daily. Hard clam shell width - tissue wet weight relationships were used to estimate the amount of flesh wet weight (g) consumed by each snail. Large rapa whelks (shell length, SL > 101 mm) are capable of consuming up to 2.7 grams of tissue daily. Smaller rapa whelks (60 - 100 mm SL) ingest in average 3.6% of their body weight every day, which is more than four times the ingestion rates of bigger *Rapana* (0.8%). Ivlev's index of preference shows that both size classes of rapa whelks preferentially consume large hard clams (shell width > 71 mm). The voracious and selective consumption of large hard clams by rapa whelks presents an economic threat to the local hard clam industry as well as an ecological threat to the Lower Chesapeake Bay in that consumption of large filter feeding bivalves affects not only hard clam stocks and reproductive potential but local benthic-pelagic coupling dynamics as well.

Key words: Rapa whelk, *Rapana venosa*, *Mercenaria mercenaria*, consumption rates, Chesapeake Bay

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Estimation of dispersal and establishment range for the predatory marine gastropod *Rapana venosa* on the U.S. East Coast.

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The lack of quantitative data on environmental tolerances of early life history stages complicates estimation of both dispersal rates and establishment ranges for invading species in receptor environments. This is particularly evident in review of species with pelagic larval life history phases which effect most, if not all, of the dispersal at the time frame of a single generation. We present tolerance data for all stages of the ontogenetic larval development of the invading predatory gastropod *Rapana venosa* with respect to salinity - a physical variable which, we argue, dominates potential dispersal (= invasion) range of the species into the estuaries of the Atlantic coast of the United States. Salinity tolerance is then examined in conjunction with temperature, which dictates both periodicity of adult egg laying and larval development rate, and extant nearshore and estuarine current data, to estimate rates of dispersal and range expansion from the current invading epicenter in the southern Chesapeake Bay. All larval stages exhibit 48 hr tolerance to salinities as low as 15 ppt with minimal mortality. Below this value survival grades to no survival at less than 10 ppt. This tolerance is greater than of the adults of the large native predatory gastropods of the genera *Busycon* and *Busycotypus* with which, we predict, *Rapana* will compete directly for space and prey. Counter clockwise, gyre-like circulation within the Chesapeake Bay will, we predict, distribute larvae northward along the bay side of the DelMarVa peninsula, and eventually to the lower sections of all the major subestuaries of the western shore of the bay. The discovery in summer 2000 of small (60 mm as opposed to adult specimens of >160 mm maximum dimension) *Rapana* along the northerly leg of this gyre adds weight to the predicted dispersal route. Dispersal onto and along the coastal shelf outside of the bay mouth may be influenced by both northward and southward flowing residual current depending on depth, wind conditions, and time within the known egg laying period of the invader in the southern Chesapeake Bay. Establishment over a period of decades from Cape Cod to Cape Hatteras by natural dispersal is considered a high probability. This time frame may, however, be considerably reduced by passive dispersal of larval forms in ballast water during intra-coastal maritime trade.

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**Early life history tactics of veined rapa whelks** (*Rapana venosa*) **in Chesapeake Bay:**
*Blueprint for a successful bioinvasion by stealth*

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Veined rapa whelks (*Rapana venosa*), predatory gastropods reaching shell lengths in excess of 150 mm shell length, were discovered in the Chesapeake Bay in 1998. Adult rapa whelks are voracious consumers of commercially valuable shellfish including oysters and hard clams. Rapa whelks larger than 100 mm shell length are regularly reported as by-catch by commercial fishermen in the lower Chesapeake, are more than 2 years of age, and are reproductively active. The most probable method for introduction of this species into the Chesapeake is via ballast water transport of planktonic larval forms much as zebra mussels (*Dreissena polymorpha*) were introduced into the Great Lakes in the early 1990s. However, little is known about the biology, ecology, and impacts of rapa whelk early life history stages on local benthic communities. Ongoing culture and laboratory experiments with rapa whelk veliger larvae and recently settled juveniles indicate that there is considerable plasticity in development time of egg masses and duration of the planktonic larval stage. Rapa whelk veligers display little substrate specificity at settlement and settle successfully on a wide range of locally available attached macrofauna including bryozoans and barnacles. Once settled onto hard substrates, young rapa whelks are generalist predators and consume large numbers of barnacles, mussels, oyster spat, and small oysters with whelks reaching shell lengths in excess of 40 mm within 6 months post-settlement. These extremely fast growth rates combined with the rapa whelk's cryptic coloration, nocturnal habits, and preference for oysters as both food and habitat offer serious cause for concern particularly in light of ongoing oyster restoration efforts in the lower Chesapeake. Evidence suggests that rapa whelks occupy shallow hard substrate habitats until reaching shell lengths in excess of 70 mm and then migrate into deeper habitats with sand or mud substrates where they forage on infaunal bivalves including soft clams (*Mya* sp.) and hard clams (*Mercenaria mercenaria*). By the time whelks are large enough to appear as by-catch in the commercial clam or crab dredge fisheries, they have been reproductively active for at least one season and have consumed oysters, soft clams, and hard clams.

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Identification of spatial breeding limitations in effecting invasions: local variation in egg capsule morphology and larval viability in the invading predatory marine gastropod *Rapana venosa*

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Invading species face a number of challenges in receptor environments if they are to become established members of the new ecosystem. Distribution data of adult life history stages reflect presence of available prey (in the case of invading predators) within the physical tolerance of the invading species; however, the functional reproductive range of the invader may be only a subset of the range occupied. It is critical to identify the functional reproductive range early in an invasion if control measures are to be effective in limiting range expansion or preferably eliminating the invader. The invading predatory marine gastropod *Rapana venosa* was first described from the Chesapeake Bay in 1998. Over 1200 adult specimens have been collected since that time, with the vast majority limited to a small section of the southern Chesapeake Bay. Evidence of reproduction in this receptor environment includes collection of egg masses from the field, population demographics consistent with multiple year classes, and successful culture of larval forms through metamorphosis at local temperatures and salinities from egg masses originating from field collected adults. *Rapana* lays mats of eggs with 50-300 egg cases per mat. Each case may contain 200-400 eggs. Extensive studies of egg mass morphometrics, egg number per egg case, and viability of eggs within each case, were effected for both temporal and spatial clines within the known adult population in order to examine the option that successful reproduction was limited to a subset of the area from which adults have been collected. This analysis was then supplemented with spatial data describing density of breeding adults to estimate the spatial limitation of functional breeding in the lower Chesapeake Bay.

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Current status and potential establishment range for the predatory marine gastropod Rapana venosa on the U.S. East Coast

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The Asian gastropod Rapana venosa Valenciennes was first reported in 1998 for eastern North America in the lower Chesapeake Bay and James River, Virginia, U.S.A. This represents a trans-oceanic range expansion for this species, which had previously been introduced to the Black, Adriatic, and Aegean Seas. Ballast water transport of larval stages from the eastern Mediterranean or Black Sea is the suspected vector of introduction into the Chesapeake Bay. Since 1998 over 2000 specimens have been collected from hard sand, shell and mud bottom types in depths ranging from 5 to 20 m and at salinities of 18 to 28 ppt. Successful reproduction of R. venosa in the Chesapeake Bay is supported by the presence of multiple size classes in extant populations, collection of egg cases from the field, and successful culture of larval stages through metamorphosis in the laboratory under prevailing local conditions of temperature and salinity. Both laboratory and field data indicate the ability of the invader to prey on local species. Salinity tolerance of pelagic larval stages was examined in conjunction with temperature and extant nearshore and estuarine current data, to estimate rates of dispersal and range expansion from the current invading epicenter. Counter clockwise, gyre-like circulation within the Chesapeake Bay will, we predict, distribute larvae northward along the bay side of the DelMarVa peninsula, and eventually to the lower sections of all the major subestuaries of the western shore of the bay. Dispersal onto and along the coastal shelf outside of the bay mouth may be influenced by both northward and southward flowing residual current depending on depth, and wind conditions. Establishment over a period of decades from Cape Cod to Cape Hatteras by natural dispersal is considered a high probability.

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