RUNDOWN ON THE RAPA

Introduction

What is a "rapa?" Rapa whelks, also known as veined rapa whelks, are large marine snails (Figure I.1). These snails, or gastropods, may grow as big as a softball or a small head of lettuce and may live for more than 10 years. The scientific name for a rapa whelk is *Rapana venosa*, referring to the distinct black horizontal lines or veins that are obvious on some individual snail's shells

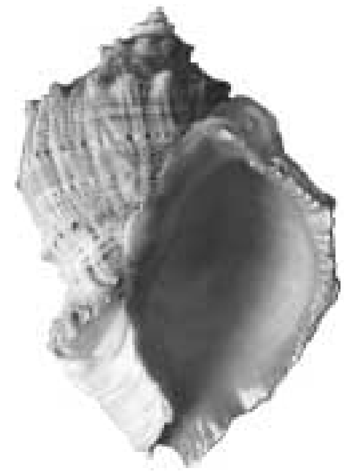
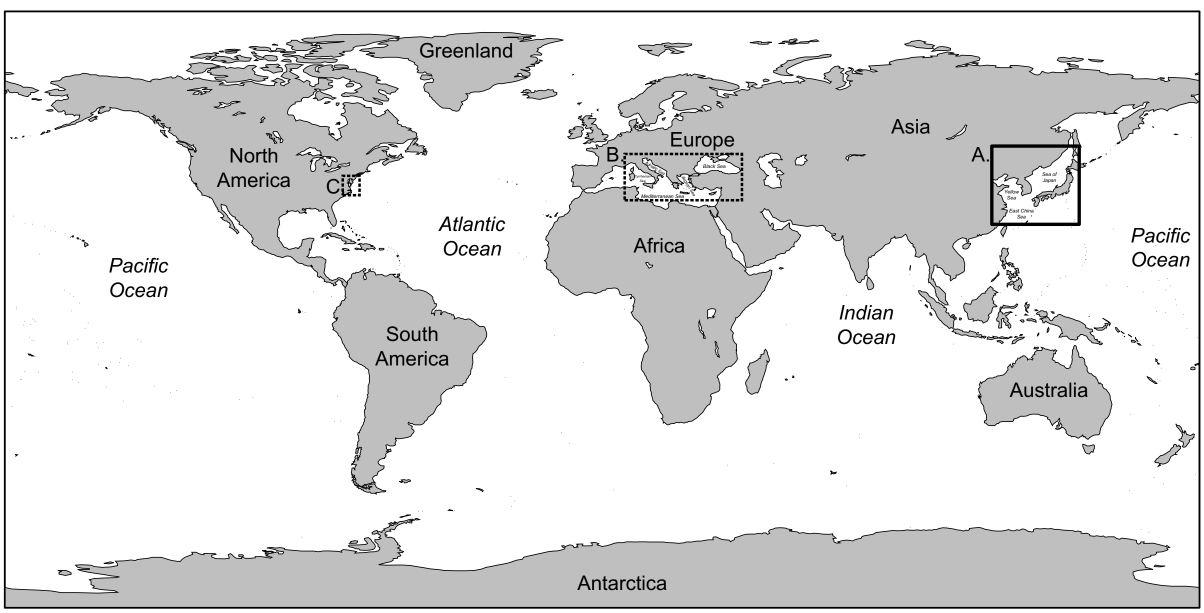


Figure I.1: An adult rapa whelk shell from Chesapeake Bay, USA. This animal was 165 mm long, approximately the size of a small head of lettuce.

Rapa whelks are native to the oceans near Korea and Japan (Figure I.2) They were found in the Black Sea in the mid 1940s after World War II and almost certainly were transported to the Black Sea by humans. The movement of new or non-native species into a habitat by humans is often referred to as an "introduction." Thus the non-native species are often called "alien" or "introduced" species. Rapa whelks were introduced into the Black Sea. Since their introduction to the Black Sea, rapa whelks have spread into the Adriatic, Aegean, and Mediterranean Seas. In 1998, rapa whelks were

Figure I.2: Map the native range of rapa whelks (A.) as well as locations where the animal has been introduced. Non-native populations in order of discovery are the Black Sea and Mediterranean region (B.) and Chesapeake Bay, USA (C.). (World map template is from MapArt (©1995, Cartesia Software, Lambertville, NJ, USA).



Related educational resources:

COMPANION ACTIVITY BOOKLET FOR EDUCATORS:
Harding, J.M., V.P. Clark, and R. Mann. 2002. Rundown on the Rapa: Activity Booklet for Educators. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-02-20, VIMS-ES-52 10/2002.

Harding, J.M., Mann, R., and V.P. Clark. 1999. Oyster Reef Communities in the Chesapeake Bay: A Brief Primer. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-99-05, VIMS-ES-44. 4/1999.

Harding, J.M., Mann, R., and V. P. Clark. 1999. Oyster Reef Communities in the Chesapeake Bay [CD-ROM]. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-99-06, VIMS-ES-45. (see the ORCCB CD website: http://www.vims.edu/mollusc/meeduc.orccb.html for release notes and CD updates). 6/1999.

Harding, J.M., Mann, R., and V.P. Clark. 1999. Shell Games. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-99-13, VIMS-ES-47 11/1999.

Harding, J.M., V.P. Clark, and R. Mann. 2002. Shellfish Stalkers: Threats to an Oyster. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-02-21, VIMS-ES-53. 10/2002.

Harding, J.M., V.P. Clark, and R. Mann. 2002. Shellfish Stalkers: Threats to an Oyster Activity Booklet for Educators. Virginia Institute of Marine Science, Gloucester Point, VA. VSG-02-22, VIMS-ES-54. 10/2002.

The VORTEX (Virginia's Oyster Reef Teaching EXperience) website. http://www.vims.edu/mollusc/meeduc/vortex.html (provides regular updates on VORTEX program activities and resource materials).

The Bridge: An On-Line Ocean Science Resource Center for Teachers. http://www.vims.edu/bridge/ (see "biology" section for a list of links to websites on oysters and other molluscs).

The VIMS Molluscan Ecology Program website. http://www.vims.edu/mollusc (provides a technical overview of ongoing oyster reef research and restoration activities in Virginia).

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www.vims.edu/mollusc/meeduc/vortex.html

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discovered in the Virginia portion of the Chesapeake Bay. The most likely vector or method of introduction for rapa whelks to the Chesapeake Bay is via ballast water carried by large ships.

Very large commercial and military ships often pump water into special ballast tanks to even out the distribution of weight on board the ship, thus avoiding twisting or bending of the ship's hull. In ancient times, rocks were used to counterbalance a ship's cargo or weight but modern vessels rely on large quantitites of ballast water to maintain a ship's structural integrity. Some ships may carry millions of gallons of ballast water in a single cruise! Unfortunately, many of the very small, sometimes microscopic organisms that live in the water called "plankton" also get pumped up into the ship with the ballast water. These very small organisms are carried by the ship to its destination. When the ballast water is pumped overboard into the new harbor, the plankton from the original harbor go too and some may still be alive and able to take up residence in the new harbor.

Rapa whelk babies or veligers are very small, about the size of a pepper grain, and swim with other small animals in the plankton. The adult rapa whelks discovered in the Chesapeake Bay are almost certainly descendants of Black Sea rapa whelks.

Why do we care that veined rapa whelks are in the Chesapeake Bay? Veined rapa whelks are predators; that is, they eat other animals. Rapa whelks eat shellfish including oysters (*Crassostrea virginica*) and hard clams (*Mercenaria mercenaria;* Figure I.3). Unfortunately, rapa whelks are very efficient consumers and have very large appetities! Scientists are concerned about rapa whelks in the Chesapeake Bay for two main reasons:

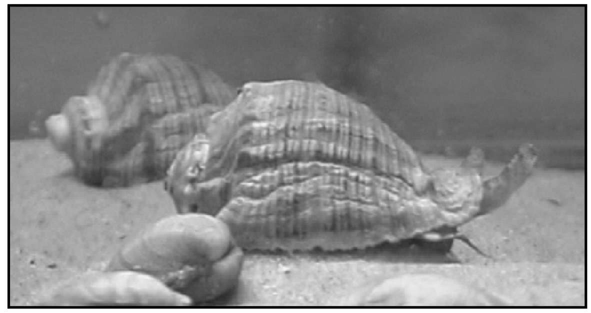


Figure I.3: A live rapa whelk moving across a sandy bottom on the hunt for prey items, possibly hard clams.

1. Veined rapa whelks eat commercially valuable oysters and hard clams.

2. The presence of a new or introduced species disrupts the natural ecological balance in the Chesapeake ecosystem. Because rapa whelks are new to the Chesapeake Bay, they do not have any natural enemies in the Bay. Rapa whelks also compete with the native Chesapeake snails for food and habitat resources.

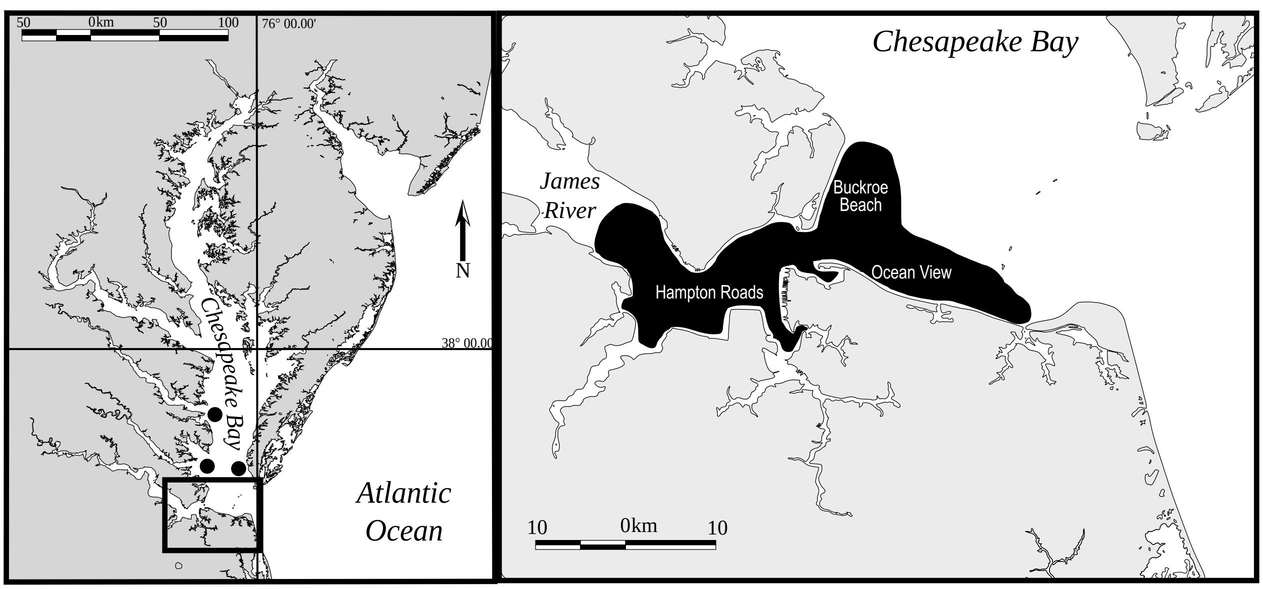
This booklet describes the biology of the veined rapa whelk in comparison to native Chesapeake snail species and discusses why the rapa whelk is so successful in different habitats. The first chapter, ***Aliens Among Us***, describes rapa whelk morphology and color in relation to several similar native or "local" snails: channelled and knobbed whelks. Chapter 2, ***Recipes for Reproduction***, discusses the reproductive strategies or "recipes" of rapa whelks in relation to the same suite of local whelks. The life history traits of rapa whelks that make them such successful invaders are presented in the final chapater, ***Locals by Land, Aliens by Sea***.

Aliens Among Us

One of the first steps in identifying the presence of any invading species be it plant or animal is to develop an estimate of where the invaders are and how many of the invaders are in the habitat. Reliable estimates of distribution and abundance require fairly intensive sampling of an area. In the Chesapeake Bay, scientists at the Virginia Institute of Marine Science (VIMS) are collaborating with local watermen and seafood processors to develop estimates of the rapa whelk's distribution and abundance in Virginia waters.

Between the initial discovery of rapa whelks in the Chesapeake Bay in July 1998 and August 2002, over 4,300 adult rapa whelks have been collected from Virginia waters. Even though the numbers of rapa whelks collected from the Bay are increasing, the geographic distribution of the animal within the Chesapeake is the approximately the same in 2002 as it was in 1998 (Figure 1.1). The known distribution extends from the mouth of the Rappahannock River in the north, through the York River and Mojback Bay to the lower James River and Ocean View to the southeast. Most rapa whelks have been found in the lower part of the James River and in the waters off Ocean View and Buckroe Beach.

It would be relatively easy to map the distribution and count the number of rapa whelks in the Chesapeake, if every large snail that was caught in the Chesapeake Bay was a rapa whelk. Rapa whelks

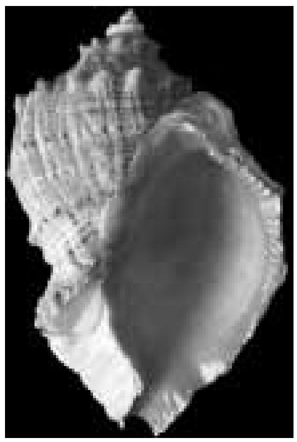
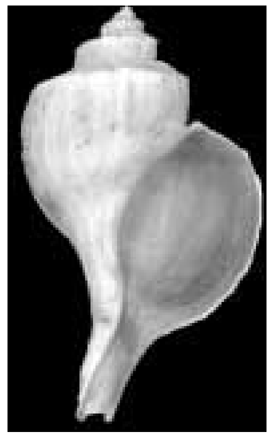
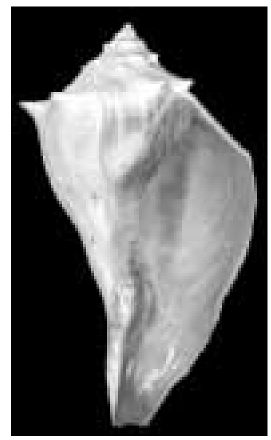


A. B.

Figure 1.1: Map of the known distribution of A) rapa whelks in the Chesapeake Bay as of July 2002 including B) areas where adult rapa whelks are most frequently collected by watermen (after Harding and Mann, 1999).

are not the only large gastropods that live in the Bay. Channelled whelks and knobbed whelks are native to the Chesapeake Bay as well as many coastal habitats up and down the Atlantic coast of North America. Adult channelled, knobbed, and rapa whelks share many similarities including where they live (habitat) and what they eat (diet). Some of the similarities between the three whelk species are described in Table 1.1.

Table 1.1: Summary of similarities between rapa whelks and two other large native gastropods, channelled and knobbed whelks.

	Veined rapa whelk	Channelled whelk	Knobbed whelk
What do they look like?			
What is their scientific name?	*Rapana venosa*	*Busycotypus canaliculatus*	*Busycon carica*
How big are they?	Shell lengths between 4 to 15 cm are common	Shell lengths between 4 to 15 cm are common	Shell lengths between 4 to 15 cm are common
Where do they live?	Sand and mud flats in water with salinities above 15 to 17 ppt; may also be found on rocks or other hard substrate	Sand and mud flats in water with salinities above 15 to 17 ppt	Sand and mud flats in water with salinities above 15 to 17 ppt
What do they eat?	Bivalves including hard clams	Bivalves including hard clams	Bivalves including hard clams
How do they move?	Use a large, muscular foot to walk or burrow	Use a large, muscular foot to walk or burrow	Use a large, muscular foot to walk or burrow

If someone finds a large snail in the Chesapeake Bay or one of its tributaries, how do they tell if it is an alien rapa whelk or a native channelled or knobbed whelk? Although the three kinds of snails share many lifestyle aspects, close examination of the whelks' shells makes identification of the alien rapa whelks easier. The shell features or distinguishing characteristics that are commonly used when identifying marine snails are shown in Figure 1.2 and listed below in Table 1.2.

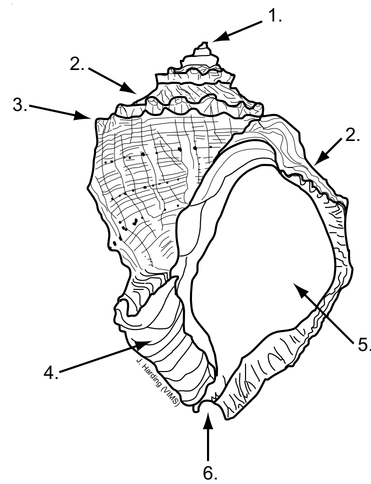


Figure 1.2: Diagnostic features of marine snails as illustrated on a sketch of a veined rapa whelk including 1) shell spire, 2) shell shoulders, 3) knobs, 4) columella, 5) opercular opening, and 6) siphonal canal.

Table 1.2: Identifying characteristics of alien veined rapa whelks in relation to two native whelks commonly found in the Virginia portion of the Chesapeake Bay.

	Veined rapa whelk	Channelled whelk	Knobbed whelk
Exterior color	Pale brown to very dark brown with visible black horizontal stripes or veins	Pale brown often with a velvety greenish or light brown coating	Off-white to pale brown
Length to width relationship	Length and width dimensions are similar	Length greater than width	Length greater than width
General shell shape	Square	Broad top tapering to narrow bottom	Broad top tapering to narrow bottom
Knob morphology	Sharp, pointed knobs visible on shoulders	No knobs on shoulders	Sharp, pointed knobs visible on shoulders
Columella shape	Broad, flat columella; possible to place a finger within columella	Narrow, rounded columella	Narrow, rounded columella
Shape of opercular opening	Boxy, shaped somewhat like a capital letter "D"	Elliptical or tear-drop shaped	Elliptical or tear-drop shaped
Color of opercular opening	In older specimens, bright orange or red; in younger rapa, black veins may be visible	Light brown, if any	Bright orange or red

If you find a large marine snail and identify it, what should you do next? If the animal is a live channelled or knobbed whelk, gently return it to the water where you found it. Our local whelks are part of the Chesapeake Bay's intricate food web. Reduction or removal of a species from the food web affects all of the other species in the habitat in some way. Empty (dead) channelled or knobbed whelk shells are often saved as curios. **Be careful to distinguish between live whelks and empty whelk shells!** A live whelk will retract into its shell when picked up and firmly hold its operculum in place when out of the water.

If the animal is a live rapa whelk, do not put it back into the water. Please keep the snail alive in seawater. If you find a live rapa whelk or even an empty rapa whelk shell, please call the **VIMS Rapa Whelk Reporting Line** at **(804) 684-7361**. VIMS staff will document your collection and come get the whelk or whelk shell from you should you wish to participate in the VIMS effort to map the distribution and abundance of rapa whelks in the Chesapeake Bay.

Why is VIMS paying money to remove the new rapa whelk from the Chesapeake Bay when there were already whelks (channelled and knobbed) living in the Bay? VIMS scientists are concerned enough to put a bounty on the rapa whelk because rapa whelks are efficient predators. Their presence, and apparent success, in the lower Chesapeake Bay places an already challenged ecological community at further risk.

In general, all types of whelks are predators. In the context of a food web or trophic diagram, whelks are secondary consumers (Figure 1.3). Channelled, knobbed, and rapa whelks eat filter feeders (primary consumers) including oysters, hard clams, and mussels. Keep in mind that the relationships between different species in a food web or community have developed gradually over time. Within an undisturbed community, a natural balance between species is usually maintained to some degree through predator-prey relationships.

The addition of a completely new species to a system with developed checks and balances has the potential to throw the entire system out of balance, particularly if the checks and balances that control native species do not apply to the newcomer. Native channelled and knobbed whelks are at risk from predators throughout their lives (Figure 1.3). Young whelks may be eaten by a variety of benthic grazers including blue crabs (*Callinectes sapidus*), and mud crabs (*Eurypanopeus* sp.). Adult channelled and knobbed whelks of all sizes are readily eaten by sea turtles (usually *Caretta caretta*). While young rapa whelks are vulnerable to the same suite of benthic predators that feed on young channelled and knobbed whelks, adult rapa whelks are not vulnerable to sea turtles once they get bigger than a tennis ball.

Sea turtles eat whelks by using their beaks to crack the whelk's shell. To eat a whelk, a turtle must be able to get its mouth around a part of the whelk shell, and crush or crack the shell. Because rapa whelk shells are "boxier" than channelled and knobbed whelk shells (see Table 1.2), it is probably much more difficult for a turtle to get its mouth around a large rapa whelk than it would be to bite a channelled or knobbed whelk of the same shell length. Rapa whelk shells are approximately three times thicker than knobbed whelk shells and six times thicker than channelled whelk shells (Harding and Mann, 1999). Even if a turtle can get its mouth around a rapa whelk, it will take considerably more effort to crack or crush a rapa whelk shell than it will to attack a channelled or knobbed whelk. For these reasons, it is very unlikely that the adult rapa whelk population will be at risk from predation. This means that if a rapa whelk survives beyond the size where it is vulnerable to turtles, there are no other Chesapeake Bay predators that it has to fear during its life time. Thus, the rapa whelk can quietly continue to eat shellfish, lay eggs, and grow until it dies of old age. Rapa whelks may live to be more than 15 years old! As you will see in the next chapter, this longevity translates into considerable repoductive potential and, consequently, invasion success.

Reference:

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

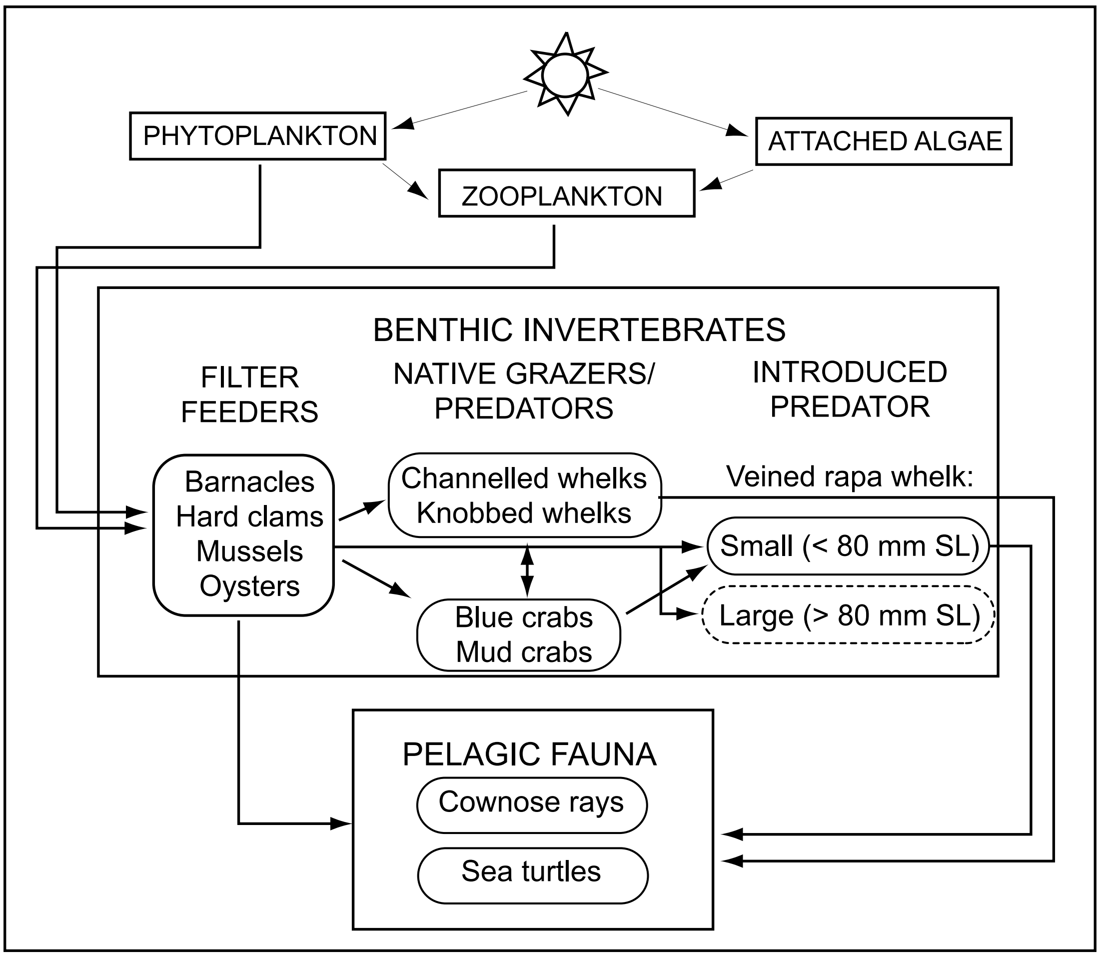


Figure 1.3: A simple food web for Chesapeake Bay benthic communities indicating the main trophic levels but focusing on channelled, knobbed and rapa whelks. The species that are listed for each trophic level are common representatives that are directly relevant to the ecology of all three whelk species. In some cases, there may be many other species within a particular level. Arrows indicate predation events with the arrowhead pointing to the predator. "SL" is the abbreviation for shell length. The dotted border around larger rapa whelks indicates that there is no known predator for them in the Chesapeake Bay ecosystem.

Recipes for Reproduction

Given the efficiency of modern commercial shipping traffic and the mobility of modern recreational boaters it is likely that many alien or non-native species arrive in marine habitats every year. Does the arrival of every non-native species portend a successful invasion of the receptor habitat by that species? No. For an alien species to successfully invade a habitat, individuals must survive and reproduce in the new or receptor habitat. If the aliens are able to reach sexual maturity and successfully produce another generation, it is likely that the second generation will be able to reproduce, creating the potential for a self-sustaining population of aliens in the receptor habitat. Many alien species that arrive in receptor habitats do not survive to successfully reproduce. The alien species that cause the most concern are those like the veined rapa whelk that do survive and are successfully reproducing in receptor habitats.

Because successful reproduction is critical for the success of an invasion, it is important for scientists to examine the reproduction "recipes" or strategies used by veined rapa whelks in comparison with local channelled and knobbed whelks. Veined rapa whelks, channelled whelks, and knobbed whelks have distinct periods in their life cycles that relate directly to reproduction. "Adult" snails are sexually mature and capable of reproduction. All three species of large whelks in the Chesapeake Bay are dioecious or have separate sexes. Some whelks are males and some are females. Fertilization of a female whelk's eggs by a male whelk's sperm takes place inside the female whelk's body. Internal fertilization requires that male and female whelks be in physical contact, thus they must find each other to mate.

For most of the year, adult whelks of all species probably live fairly solitary lives burrowed into the sand or mud bottom by day and emerging to walk around at night. Given the nocturnal nature of these beasts combined with the low visibility in coastal waters of the Chesapeake Bay, how do the whelks find each other? Scientists think that a variety of chemical and physical cues are used by individual whelks to locate other whelks of the same species. The whelks may literally "smell" each other at a distance.

Veined rapa whelks seasonally display an interesting behavior pattern that facilitates successful mating. In the spring, as the water temperature rises, adult veined rapa whelks gather at night and form huge mating piles or aggregations. These piles or groups of whelks may be as big as a kitchen table extending several feet or meters across as well as off the bottom. A mating pile (Figure 2.1) may contain hundreds of individual animals. These mating piles seem to form nightly for several weeks in the spring and then the whelks disperse and move on to other habitats. It is likely that changes in water temperature cue the initiation and termination of these mating aggregations.

Figure 2.1: A rapa whelk mating pile. There are 54 snails in this picture. Can you find all of them?

After a female channelled, knobbed, or rapa whelk has mated with a male and had her eggs fertilized, she places groups of fertilized eggs into protective cases that she makes herself. She leaves groups of these egg cases behind as she moves through the habitat. These egg cases must stay submerged to survive. Over a period of time, the fertilized eggs within the egg cases develop into baby snails which are eventually released from the egg cases and into the habitat.

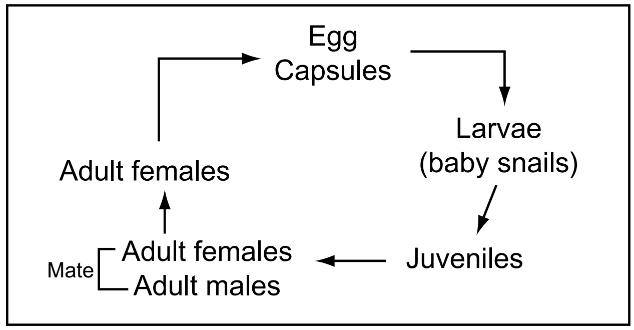


Figure 2.2: Generalized schematic of the life cycle or life history of a channelled, knobbed, or rapa whelk.

Table 2.1: Summary of whelk reproductive strategies observed in Chesapeake Bay. Observations for knobbed whelks are summarized from Castagna and Kraeuter (1994). Channelled whelk information is based on Magahles (1948). Rapa whelk information is from Harding and Mann (1999).

	Veined rapa whelks	Channelled whelks	Knobbed whelks
Mating season	March - June	June - July	June - July
Egg laying season	May - September	August - November	August - November
Time window when egg capsules hatch	June - September	Mid-March - May	Mid-March - May
Type of egg capsule	Tall, cylindrical case with a flat head	Disc with rounded edges	Disc with square edges
Unit of egg capsules	Carpet-like masses with individual cases like carpet strands	Spiral strings with individual disks joined face to face	Spiral strings with individual disks joined face to face
Location for egg capsule deposition	Base of each case cemented to adjoining cases and a hard surface like rocks, pilings, or other whelk shells	Original end of string buried in the sand and attached to a piece of hard substrate like a shell or rock	Original end of string buried in the sand

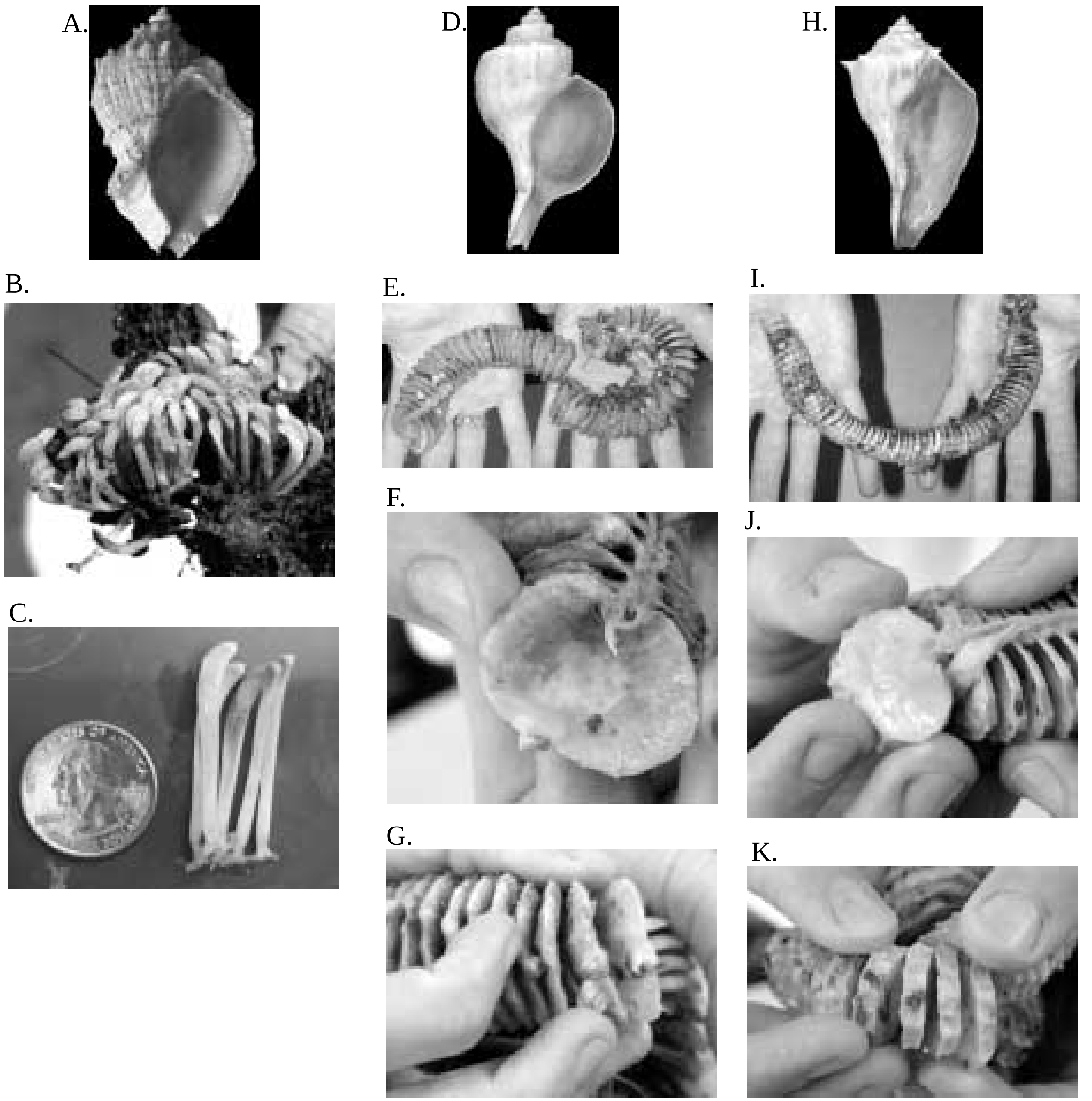


Figure 2.3: Adults, egg masses, and egg capsules from whelks in the Chesapeake Bay including rapa whelk (A) egg masses (B) and individual egg cases (C); channelled whelk (D) egg string (E), and egg disks (F, G); and knobbed whelk (H) egg string (I) and individual egg disks (J,K).

The basics of reproduction (Figure 2.2) are similar between veined rapa whelks, channelled whelks, and knobbed whelks. However, there are major differences in the details of reproduction between rapa whelks and the other two species (Table 2.1). These differences may help explain why the rapa whelk is such a successful invader of new habitats. The most striking differences between reproductive strategies of these three whelk species are 1) the age at which the whelks reach sexual maturity and 2) the radical difference in egg case morphology between the two local species of whelks, channelled whelks and knobbed whelks, and the invading rapa whelks.

Veined rapa whelks are sexually mature and capable of laying viable egg masses within one year of hatching. Channelled and knobbed whelks take much longer to reach sexual maturity than rapa whelks. Knobbed whelks in the Chesapeake Bay do not reach sexual maturity until they are approximately nine years old (Castagna and Kraueter, 1994). It is thought that channelled whelks mature at a rate more similar to knobbed whelks than rapa whelks. In the time it takes a knobbed whelk to reach sexual maturity, a rapa whelk has been reproductively active for eight years. This difference in maturation rate can make a big difference in the rate at which a whelk population, or number of whelks within an area, increases in size.

Veined rapa whelks lay tall, thin cylindrical egg cases that have flattened tops or heads (Figure 2.3). These lemon yellow cases are laid in large carpet-like groups. Female rapa whelks seek hard substrates on which to attach or cement their egg masses. The base of each individual cases is cemented to the neighboring cases on each side and to a hard surface underneath the case. When completed, these egg masses look very similar to a thick, yellow shag carpet with long individual carpet strands (Figure 2.3). An individual rapa whelk egg case may contain as many as 400 eggs (Ware, 2002). An egg mass or group of egg cases may have as many as 500 egg cases within it (Harding, J. and R. Mann, unpublished data). Thus a rapa whelk female may lay as many as 200,000 eggs in a single egg mass. Adult rapa whelk females may lay ten or more egg masses in a single year. In one summer or breeding season, one rapa whelk female may produce as many as TWO MILLION eggs.

Female rapa whelks are not at all particular about where they lay their egg masses provided they can find hard surfaces. Crab fishermen in the lower Chesapeake Bay frequently find rapa egg masses carefully laid on the mesh of their crab pots. SCUBA divers from the Virginia Department of Transportation have observed female rapa whelks carefully depositing egg masses on bridge and dock pilings.

Since rapa whelk egg cases are usually cemented to hard surfaces that are part of a larger structure like a bridge or a rock jetty below the low tide line, it is unlikely that the egg cases will be exposed to the air and the risk of dessication is very low. Because female rapa whelks do a very good job of cementing their egg cases, the risk of egg cases being dislodged from the original attachment site by tidal currents is very low. In fact, tidal currents and constant movement of water around the egg mass and between the egg cases may help keep the egg mass healthy. It is very likely that a rapa whelk egg mass will stay where the female whelk placed it from the time it is laid through when it hatches. Most rapa whelk egg masses hatch within one month of being laid. Warm summer water temperatures facilitate this relatively short development time.

In contrast, channelled and knobbed whelks lay long strings of egg capsules that resemble the spiral coils of rotini pasta (Figures 2.3). The individual egg capsules are flattened disks that resemble checkers or tiny hockey pucks (Figure 2.3). Each egg disk is attached to its neighbor by a single strand of connective membrane (Figure 2.3). Knobbed whelk egg capsules or disks may each contain 10 to 50 eggs per disk (Magahlaes, 1948; Castagna and Kraeuter, 1994). There are usually between 40 and 120 egg disks per knobbed whelk string (Castagna and Kraeuter, 1994). Thus a single knobbed whelk female may lay as many as 6000 eggs per egg string. If a knobbed whelk lays three egg strings per fall or breeding season, she will lay 18,000 eggs.

Both channelled and knobbed whelks bury one end of their egg string into the sand or mud on the bottom. However, channelled whelks may cement the first disk in their egg string to a piece of hard substrate like a shell or a rock, giving the egg string more of an anchor.

Channelled and knobbed whelks lay their egg masses in shallow water usually on sand or mud tidal flats. On these tidal flats, the egg strings risk being exposed to the air for at least part of the day as well as being dislodged from the bottom by tidal current. Once an egg string is uprooted from where the female whelk buried it, it is likely that the egg string will be rolled along the bottom and perhaps even carried onto the beach by the waves and tidal currents. Since channelled and knobbed whelk egg strings are laid in the fall and develop over the winter, they must survive wind and waves from winter storms for approximately seven months. During transport by the waves, the egg string may be damaged and broken into smaller segments. If the egg string is carried onto the beach, it is likely that the eggs or developing baby whelks will die from exposure to the air, the sun, or colder winter temperatures.

As you can see, there are major differences in the reproductive or life history strategies employed by knobbed and rapa whelks. Ecologists usually describe life history strategies using a concept called *r*/*K* selection. This concept is based on a mathematical model commonly used to describe population growth called the logistic growth model. The equation describing this model uses the variable *r* to describe a species' ability to reproduce and the variable *K* to describe the carrying capacity of a population. "Carrying capacity" refers to the density where the birth rate equals the death rate in a population. The application of this population model assumes that certain habitats favor either *r*- or *K*- selected species. Generally, an *r*- selected population lives in a habitat that is unpredictable in time while a *K*-selected species lives in a habitat that is constant or predictably seasonal. Certain life history or reproductive strategies favor survival and reproductive success in each habitat (Table 2.2). Realize that the concept of *r*- and *K*- selection is a model that ecologists use to describe the relationship of a species with its habitat and community. In reality, species may have traits from both models but may favor one model more than the other. This is the case with knobbed and rapa whelks. Knobbed whelk life history is more similar to the *K*-selected model while rapa whelk life history is suited to the *r*-selected model in *most aspects*. Not surprisingly, the *r*-selected model has been historically used to describe species that are good at rapidly colonizing new habitats. Thus, life history and reproductive patterns suited to the *r*-selected model might be expected in species that successfully invade new habitats.

The differences in egg capsule morphology and deposition sites between the alien rapa whelk and the local channelled and knobbed whelks may al-

Table 2.2: Summary of life history and reproductive characteristics associated with *r*- and *K*-selected species or populations.

Life history trait	*r*-selected model	*K*-selected model
Relative size of adult	Smaller	Larger
Time to sexual maturity	Mature early in life span	Mature later in life span
Allocation of energy to reproduction	Large energy allocation	Small energy allocation
Relative size of offspring	Smaller	Larger
Number of offspring	Many	Few

low more rapa whelk egg capsules to successfully hatch. Does a greater number of successfully hatching baby rapa whelks translate into a greater number of juvenile or adult rapa whelks? Not necessarily. Successful development within an egg case is just one part of the life cycle of a whelk. Many other factors influence the success or failure of a baby whelk once it emerges from the egg capsule. Some of these factors and their implications are described in the next chapter.

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Locals by Land, Aliens by Sea

In the opening days of the American Revolutionary War, the midnight ride of Paul Revere was cued by the placement of lanterns in the Old North Church in downtown Boston. One lantern indicated a British invasion by land, two lanterns warned of an invasion by sea. If the same signalling system were used to describe the invasion of the Chesapeake Bay by veined rapa whelks, two lanterns would be required. Unlike local whelk species, rapa whelks have a swimming or planktonic life history stage. These swimming baby rapa whelks are central to the rapa whelk's ability to invade new habitats and expand its range once in a new area.

Life as a larvae

As discussed in the previous chapter, adult veined rapa whelks, channelled whelks, and knobbed whelks all lay clusters of egg capsules (Figure 3.1). The crucial difference in life histories between the alien rapa whelk and the native channelled and knobbed whelks is obvious when the egg cases or capsules hatch and release baby snails. Channelled and knobbed whelks emerge from their egg strings as miniature replicas of their parents right down to the presence of a relatively large muscular foot. This foot, used for crawling and burrowing, is the baby channelled and knobbed whelks' only means of locomotion. Thus, these little snails can only move as far as they can crawl. Knobbed and channelled whelks are approximately 4 mm long when they hatch and these very small snails do not move very quickly.

In contrast, baby rapa whelks swim out of their egg cases and live in the water column for at least four to five weeks after they hatch. When a larval or baby rapa whelk hatches, it has a special organ called a velum (Figure 3.2). The larval rapa whelk (also called a veliger) uses the velum as a swimming as well as feeding organ. The rapa whelk veliger uses long hair-like structures called cilia on its velum to stroke through the water. By moving the cilia through the water, the veliger swims much like a human uses arms to move through a swimming pool. As the cilia move through the water, these hair-like projections trap particles that they encounter in the water. Suitable food particles are moved toward the rapa whelk veliger's mouth and ingested.

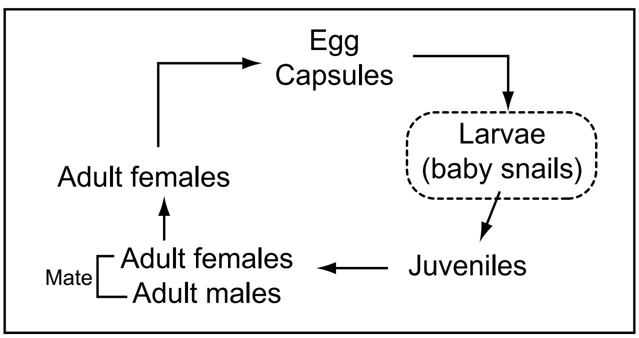

Figure 3.1: Generalized schematic of the life cycle or life history of a channelled,knobbed, or rapa whelk. Larval snails (enclosed with a dashed line) will be highlighted in this chapter.

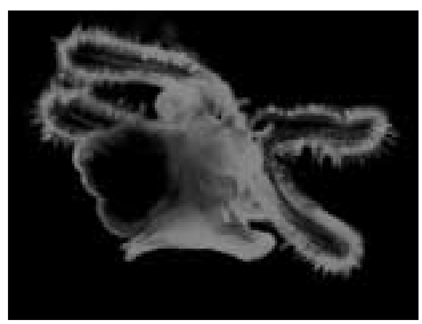

Figure 3.2: A 30 day old rapa whelk veliger. This animal is approximately 1 mm long.

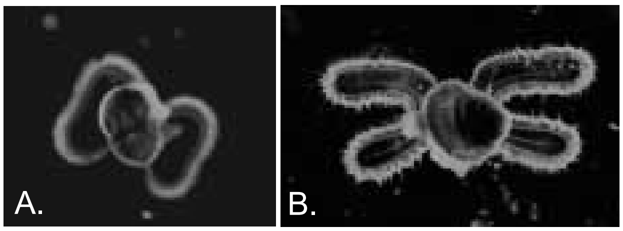

Figure 3.3: A three day old rapa whelk veliger (A) with a bi-lobed velum and a 36 day old rapa veliger (B) with a four lobed velum. The 3 day old whelk is approximately 0.3 mm long while the 36 day old whelk is almost 1 mm long.

As the rapa whelk veliger grows, its velum gets bigger and grows from a structure with two lobes (bi-lobed) to a more complicated structure containing four lobes (Figure 3.3). By growing from two lobes to four lobes, the velum increases in surface area and effectiveness as both a swimming and feeding structure.

Rapa whelk veligers are approximately 300 microns or 0.3 mm long when they hatch from their egg cases. These very small filter feeders rely on algae and photosynthetic diatoms for food. In estuaries like the Chesapeake Bay, the highest concentrations of algae and other photosynthetic organisms are found in the upper meter of the water column close to the sunlight. Rapa whelk veligers spend much of their time near the surface in the same vicinity as their food.

Even though rapa whelk veligers can swim, because they are so small they move along with the water that immediately surrounds them. Tidal currents are a major source of water motion in the lower Chesapeake Bay. A planktonic animal will be carried upriver on the incoming tide and downriver on the ebbing tide twice a day. Depending upon the strength of the tidal currents, planktonic animals like rapa whelk veligers may have a net movement of several kilometers up or down a river within a span of a few days. Over the course of several weeks, rapa whelk veligers potentially

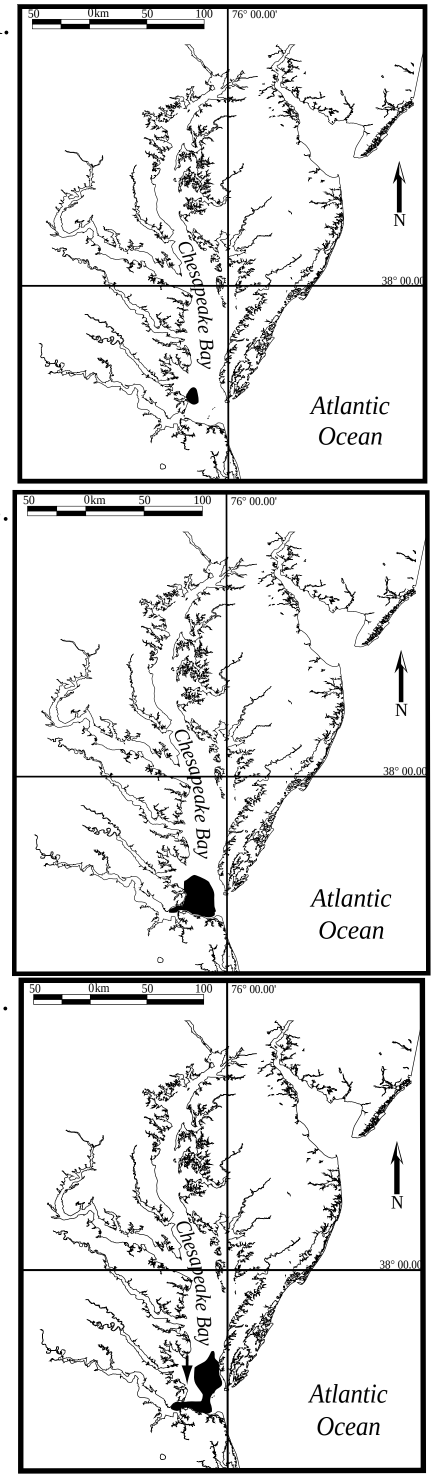

Figure 3.4: Maps showing the predicted distribution of veliger larvae carried by tidal currents 1 day (A), 10 days (B) and 20 days (C) after hatching near the mouth of the Back River (arrow in C). Predictions are derived from the VIMS Physical Sciences HTM 3D Hydrographic model (1998).

could move quite a distance from the geographic location at which they hatched simply by riding the tidal currents (Figure 3.4).

When a rapa whelk veliger reaches the end of its planktonic phase, the baby snail descends to the bottom and sheds its velum. In the absence of this swimming organ, the little rapa whelk must remain on the bottom and rely exclusively on its muscular foot for locomotion. Since the velum is also a feeding organ, the little whelk must begin to use its tongue or radula to graze on animals and plants that are attached to hard surfaces. Without a velum, the rapa whelk can no longer filter particles out of the water. The transition from planktonic (swimming) to benthic (bottom-dwelling) existence is a major event. Once a rapa whelk sheds its velum, the young whelk is a minature replica of its parents (Figure 3.5). Recently settled rapa whelks are approximately 1 mm long.

At any given moment during the summer months, there are probably MILLIONS of tiny rapa whelk veligers swimming around in the waters of the lower Chesapeake Bay while gently being transported around the region. Because these snails are no bigger than black pepper grains, they are easy to overlook.

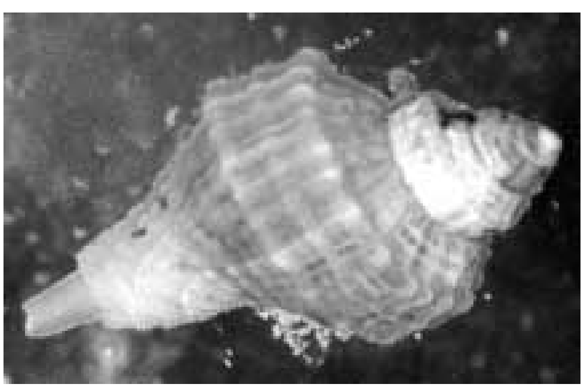

Figure 3.5: A 60 day old rapa whelk. This animal has been settled on the bottom for 30 days and is approximately 8 mm long..

Imagine for a moment that millions of gallons of water are pumped from the surface of the Chesapeake Bay and placed into a very large tank on a ship. The ship then slowly sails across the Atlantic Ocean bound for a European port. Because the volume of water in the ship's tank is so large and the rapa whelk veligers that were pumped into the tank with the Bay water are so small, the fact that the Bay water is confined to the tank makes little functional difference to the whelks. The rapa veligers can still swim around and eat the algae and diatoms that were pumped into the ship's tank with them.

It usually takes modern commercial ships less than two weeks to sail from Norfolk, Virginia to any one of many European ports. Remember that rapa whelk veligers swim in the plankton for at least a month after they hatch. When the Virginia ship arrives in the European port and begins to pump the water in its tank overboard into the European harbor, many of the rapa whelk veligers that sailed across the Atlantic Ocean in the tank on the ship are being pumped overboard with the water.

Rapa whelks were almost certainly introduced to the Chesapeake Bay as ships from the Black Sea drained their ballast tanks in preparation for taking on coal at Newport News Point in the lower James River. The Black Sea was invaded by rapa whelks shortly after World War II and currently has a large resident rapa whelk population. The Black Sea region is a major consumer of coal. Coal is carried to the region on ships leaving from Norfolk. These ships return to the Chesapeake Bay carrying ballast water which must be discharged before the ship can take on cargo.

Now that veined rapa whelks have been introduced to the Chesapeake Bay and are successfully reproducing within the Bay, the combination of a planktonic life history stage with local habitat conditions has implications for the potential distribution of rapa whelks within the Bay. As described in Figure 3.4, the Bay's tidal regime facilitates the dispersal of rapa whelk veligers from their hatching location. Is there anything that will keep rapa whelks from finding and settling in every corner of the Chesapeake Bay? Yes. The potential distribution of rapa whelks in the Chesapeake Bay will probably be limited by ecological and environmental conditions.

Ecological limits to rapa whelk success

From an ecological perspective, when rapa whelk veligers are planktonic, they are very vulnerable to a diverse suite of predators that feed exclusively on plankton. Possible predators on planktonic rapa whelks include sea nettles, ctenophores and larval fishes as well as adult filter feeding fishes like Atlantic menhaden (*Brevoortia tyrannus*). Many of these predators are most abundant in the lower Chesapeake Bay during the same months that rapa whelk veligers are hatching and entering the plankton.

While these plankton predators certainly do not eat all of the rapa whelk veligers, they probably reduce rapa whelk veliger abundance by a noticeable amount. From the rapa whelk veliger's perspective, it pays to grow quickly in the plankton and get ready to settle to the bottom as quickly as possible. Once settled, the rapa whelks completely avoid predation by the plankton predators. However, after the rapa whelks take up residence on the bottom, they face the same suite of predators that the young channelled and knobbed whelks face from the very beginning. Possible benthic predators for recently settled rapa whelks include mud crabs (*Eurypanopeus* sp. and *Panopeus* sp.) and blue crabs (*Callinectes sapidus*). Ongoing studies by scientists at the Virginia Institute of Marine Science indicate that blue crabs are voracious consumers of young rapa whelks (J. Harding and R. Mann, unpublished data).

Environmental limits to rapa whelk success

Environmentally speaking, areas that do not meet the habitat requirements necessary for rapa whelk survival are not likely to host rapa whelk populations. Salinity as well as substrate and food availability are factors that will influence rapa whelk success in the Chesapeake Bay.

Rapa whelk veliger survival at salinities of less than 10 ppt is very low. This vulnerability to salinities less than 10 ppt is likely to prevent the establishment of rapa whelk populations in the upper reaches of all Virginia rivers as well as all Maryland waters of the Chesapeake Bay (Figure 3.6).

Within the regions that have salinities above 10 ppt, areas without available hard substrates such as rocks or shells are not likely to be colonized by rapa whelks. Rapa whelk veligers require hard substrate to settle on when they descend from the plankton to the benthos. For the first few months of their lives young rapa whelks crawl around on hard substrates grazing on the attached bryozoans, barnacles, mussels and oyster spat. Eventually juvenile rapa whelks leave the hard substrates and begin to burrow into soft sand and mud sediments. Once they reach maturity, rapa whelks venture onto hard substrates only during mating and egg laying seasons. Hard substrates are required by adult rapa whelks as attachment sites for their egg mats.

Finding hard substrates to settle onto and graze on is only the beginning of a young rapa whelk's quest for suitable food. As the rapa whelk grows, its diet will change from mussels and barnacles to oysters (*Crassostrea virginica*) and hard clams (*Mercenaria mercenaria*). By the time a rapa whelk moves off hard substrates and begins to burrow into soft sand and mud, it is capable of eating burrowing bivalves such as hard clams. As the whelk gets larger, the size of its bivalve prey also increases. The only bivalves in the lower Chesapeake that are similar in size to a large rapa whelk are hard clams. Since rapa whelks must eat to survive, they will live in proximity to their prey (Figure 3.6).

Scientists can say with certainty that rapa whelks cannot inhabit regions with unsuitable environmental conditions. However, the ecological ramifications of this large predator within suitable habitats of the lower Chesapeake Bay are in the initial stages of discovery and description. Indeed, the invasion of the Chesapeake Bay by the veined rapa whelk is still in progress and the story of the rapa whelk in the Chesapeake Bay is really just beginning.

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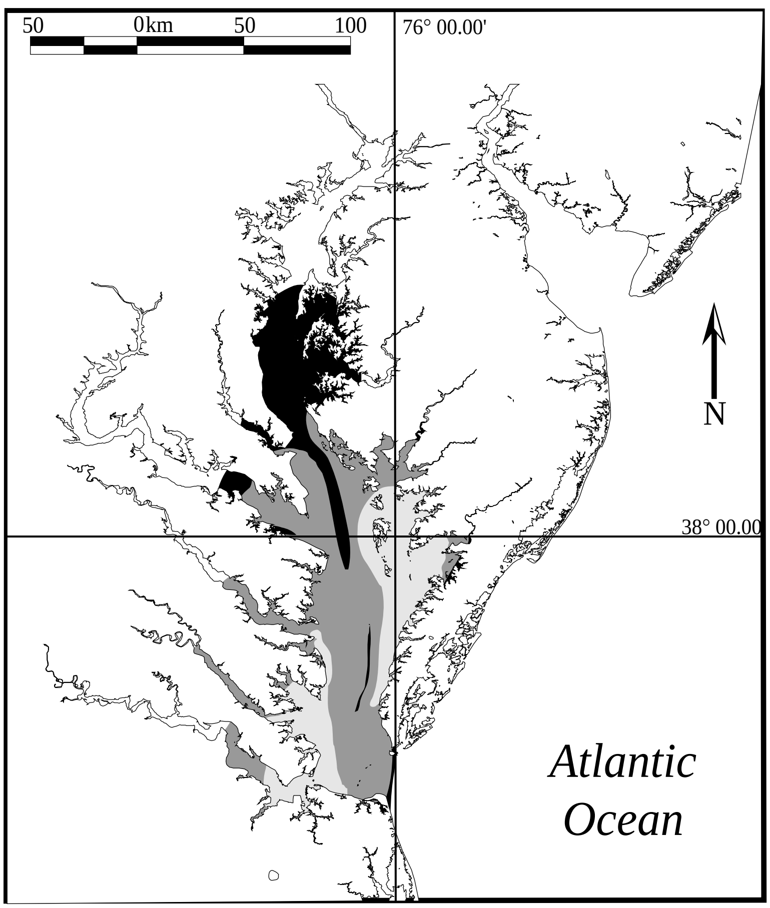

Figure 3.6: Map of the Chesapeake Bay showing the probable limits of rapa whelk distribution based on salinity (black), the presence of hard sand substrate (dark grey) and the distribution of hard clams (light grey), a prey item for rapa whelks. Salinity data are average summer surface values after Shroup and Lynn (1963). Substrate and hard clam distribution are after Roegner and Mann (1991).

VORTEX

Virginia's Oyster Reef Teaching EXperience

An Educational Program for Virginia Science Educators

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