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Alien Species Alert: *Rapana venosa* (veined whelk)

Prepared by the Working Group on Introductions and Transfers of Marine Organisms

Edited by

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1 Introduction

The large Asian gastropod mollusc *Rapana venosa* Valenciennes 1846 (Neogastropoda, Muricidae) is native to the Sea of Japan, Yellow Sea, Bohai Sea, and the East China Sea to Taiwan. This species has been introduced to the Black Sea with subsequent range expansion to the Adriatic Sea and Aegean Sea, the Chesapeake Bay on the East Coast of the United States, and the Rio de la Plata between Uruguay and Argentina. Reproductive populations are or appear to be present in all three receptor regions.

In addition, there are a limited number of reports of the species from the Brittany coastline of France, Washington State (USA), and two collections from the North Sea and New Zealand. The life history of this species makes it a viable candidate for continuing range expansion and new invasions facilitated by ballast water vectors. This review describes the current status of knowledge of the species in its home range and introduced populations.

2 Identification

Rapana venosa Valenciennes 1846 (English: Rapa whelk, Italian: Cocozza or Bobolone) has also been described with the junior synonyms *Rapana thomasiana* Crosse 1861, and *Rapana thomasiana thomasiana* (Thomas' Rapana venosa). 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).

Class	**Gastropoda**
Subclass	Orthogastropoda
	Apogastropoda Caenogastropoda Neogastropoda
Superfamily	Muricoidea
Family	Muricidae
Subfamily	Rapaninae
Genus	*Rapana*
Species	*venosa*

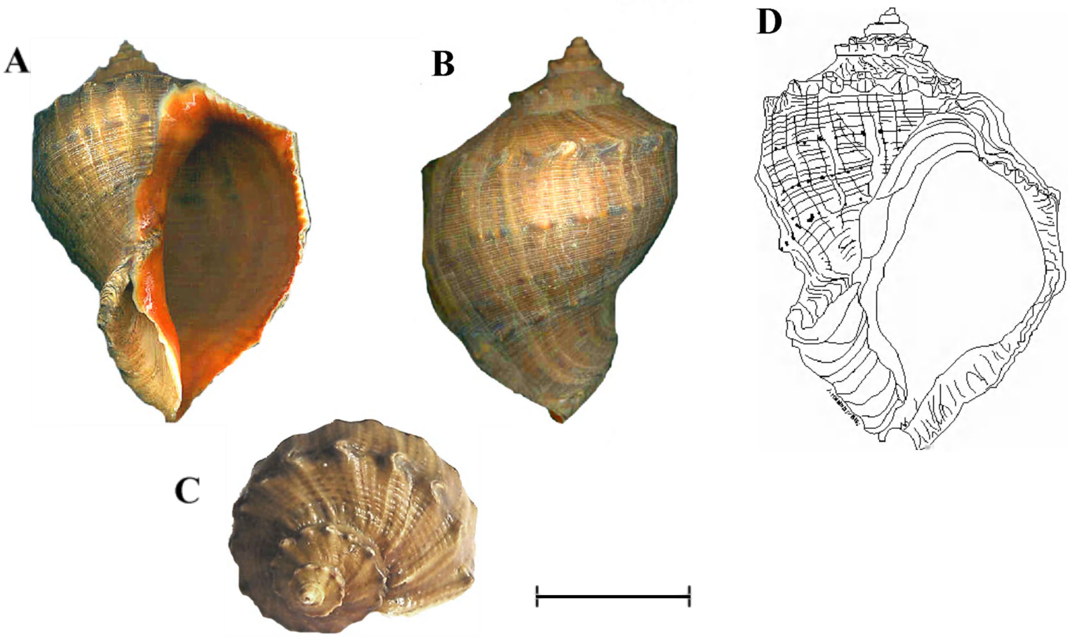


Figure 2.1. An adult *Rapana venosa*, A. opercular view, B. back view, C. Spire view, D. Sketch of an adult rapa whelk (shell length of 165 mm; courtesy of J. Harding, VIMS). Scale bar represents 5 cm.

Rapana venosa has a short-spired, heavy shell with a large inflated body whorl and a deep umbilicus (Figure 2.1). 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 colour 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 colouration, varying from black to dark blue, occasionally occurs internally, originating at the individual teeth at the outer lip of the aperture. Local variation may occur in morphometry and colouration depending on substrate. 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. Individuals of more than 170 mm SL have been collected from Chesapeake Bay, USA.

3 Biology in the Native Range

Rapana venosa is one of three species of *Rapana* in Chinese waters being native to the Sea of Japan, with the northern limit at Vladivostok, the Yellow Sea, Bohai Sea, and the East China Sea to Taiwan (Tsi *et al.*, 1983; Lai and Pan, 1980; Figure 3.1).

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. *R. bezoar* is distinguished by a more scaly sculpture overall and a white aperture. *Rapana rapiformis* occurs in the East and South China Seas. It has a lower spire and lighter shell than *R. venosa.*

3.1 Current status and population demographics

No comprehensive studies of the current populations in the native range were found. Green (2001), as part of a study of comparative morphometrics of populations from Korea, Turkey and the Chesapeake Bay, suggests that the demographics of the Korean population are indicative of intense fishing effort on size frequencies that recruit to the fishing gear.

3.2 Natural history

In its native Korean range, adult *Rapana venosa* demonstrate large annual temperature tolerances (4 °C to 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 *Rapana 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 facilitated by the winter migration into deeper water in these regions (Wu, 1988). No data could be found on salinity tolerance of the species in its native range. In Korea, it is commercially exploited on hard sand bottoms by a mesh pot fishery.

3.3 Growth rate

No data could be found on the growth rate or longevity of *Rapana venosa* in Korea. Wang *et al.* (1997) reported that the snail reached an adult size of 74 mm within thirteen months in Laizhu Bay, China.

3.4 Reproduction

Rapana venosa is dioecious with separate sexes. Size at first maturation has not been examined for female whelks. Chung and Kim (1997) examined the maturation of male *R. venosa* (n = 557, size range 31 mm to 160.2 mm SL) in its native range and observed maturity in 66.7% of individuals from 71 mm to 80 mm SL, and 100% maturity for individuals exceeding 121 mm SL.

Seasonal reproductive behaviour of *R. venosa* in Korea is described by Chung *et al.* (1993). Mating occurs over an extended period during the winter and spring preceding egg laying. *Rapana venosa* lays masses of egg cases in April to late July based on gonadal examination; this period corresponds to a temperature range of 13 °C to 26 °C. The egg cases are attached basally to a hard substrate, and may contain as many as 1,000 developing embryos. One female adult can lay multiple egg masses throughout the course of one summer without intervening mating events. Imposex, the development of a male penis by adult females, has been observed (Choi, pers. comm.), although quantitative data are not available.

When laid, the egg cases are white, turning sequentially darker (through lemon to yellow) as the enclosed larvae are first visible as distinct white swimming individuals. The larvae darken and eventually turn black just prior to release, at which time the dorsal tip of the case opens to liberate the swimming larva. Chung *et al.* (1993) report a seventeen-day incubation period between egg laying and first hatching at 18.3 °C to 20.4 °C.

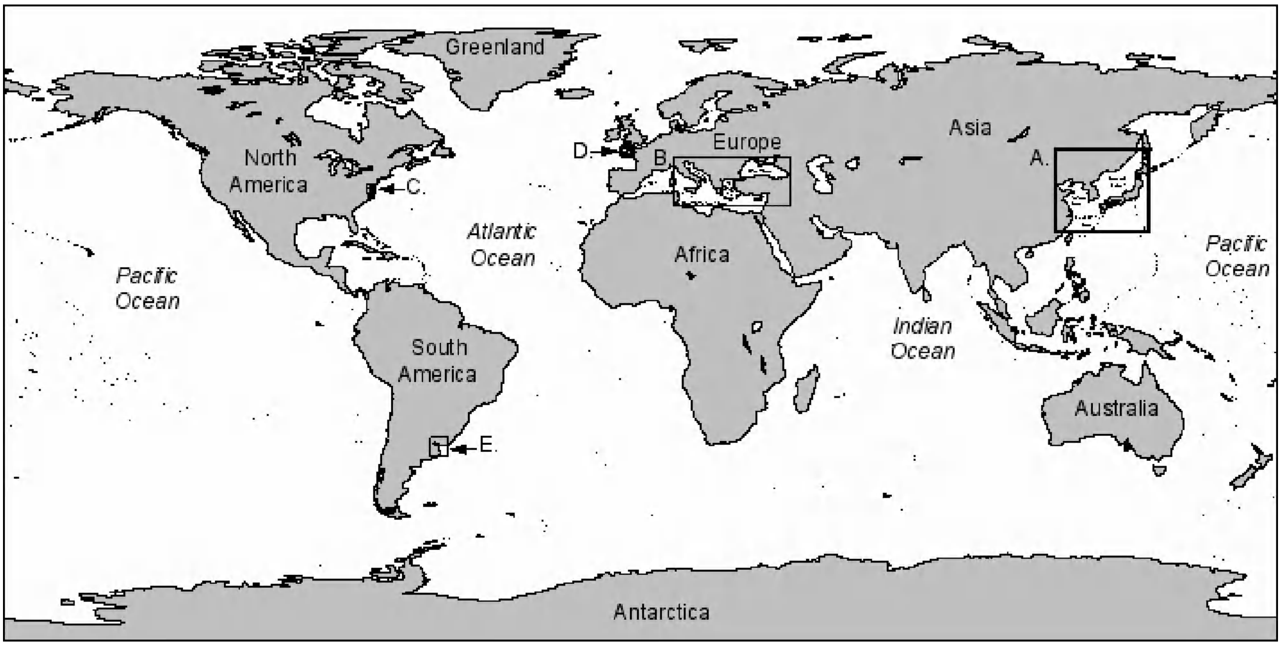


Figure 3.1. Map showing the known global distribution of reproducing rapa whelk populations including the native range in Korean, Japanese, and Chinese waters (A.) as well as locations where the animal has been introduced. Non-native populations in the order of introduction and/or discovery are the Black Sea and Mediterranean region (B.), Chesapeake Bay, USA. (C.), the Brittany coast of France (D.), and the Rio de la Plata, Uruguay and Argentina (E.). Additional information regarding the distribution within habitats, local biology, and abundance estimates for each population is provided in the text and accompanying site-specific figures. (World map template is from MapArt, copyright 1995, Cartesia Software, Lambertville, NJ, USA.).

Upon hatching, the larvae swim with a bilobed velum, and are planktotrophic. A four-lobed velum appears at four days post-hatching and a length of approximately 385 µm. Apparent morphological competency was reported by Chung *et al.* (1993) at fourteen to seventeen days and 623 µm to 686 µm SL with development of a distinct foot and eyestalks. Harding and Mann (manuscript in preparation) have observed significant plasticity in the duration of the planktonic phase, with metamorphosis being observed as late as 80 days after hatching. The variable duration of the planktonic period allows for a variety of dispersal and recruitment strategies by the species, and facilitates invasions.

Chung *et al.* (1993) do not describe post-metamorphic stages. Harding and Mann (manuscript in preparation) have observed spontaneous metamorphosis of competent larvae in the absence of substrates.

4 Non-native distribution

Since the mid-twentieth century, rapa whelks have been successfully introduced to multiple regions worldwide. Currently, there are five known geographic regions containing reproducing populations of rapa whelks that are distinct from the native (Asian) population (Figure 3.1). The modern global economy and associated human vectors for transport across oceans provide continuous means of introduction of this robust animal into new receptor regions. Examination of the biological and ecological effects of this animal on native ecosystems post-introduction will provide valuable insight as to potential control mechanisms and the course of subsequent invasions.

4.1 Black Sea to Adriatic Sea

4.1.1 Date and mode of arrival, initial population size, and source of introduction

The introduction of *Rapana 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*). The vector of introduction is not certain. Ballast water remains an option, although this is considered unlikely given the combination of distance from home range, typical vessel transit speed at the time of introduction, and limitation of ship passage in the early 1940s from the Orient to the Black Sea because of World War II naval actions. Transport as part of a hull fouling community is a second option. Oyster culture of Japanese oysters (probably *Crassostrea gigas*) was recorded in the region of first observation in the early 1940s, presenting a third option of introduction as an associated species with oyster seed; however, this remains a speculation. 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 (see Figure 4.1.1.1) 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 (Grossu, 1970; Bilecik, 1975; Ciuhcin, 1984; Marinov, 1990; Zolotarev, 1996). Subsequent invasion of the Marmara Sea (Zibrowius, 1991) and the Aegean Sea in 1986 (Koutsoubas and Voultsiadou-Koukoura, 1990), and finally the Adriatic Sea is described by Ghisotti (1971, 1974), Mel (1976), Cucaz (1983), Rinaldi (1985), Bombace *et al.* (1994) and by De Minn and Vio (1997) for the Slovenian coast.

The large population in the Northern Adriatic Sea is generally considered to have had no major detrimental effect. A record from Elba in the Tyrrhenian Sea is provided by Terreni (1980) and by Paolini (1987) near Leghorn. The gradual but sustained nature of this range expansion suggests that *Rapana* has yet to exploit all susceptible locations within the Mediterranean.

4.1.2 Current status and population demographics

In the Black Sea, *Rapana venosa* occurs on sandy and hard-bottom substrates to 40 m depth. The highest abundance occurs in the Kerch Strait at the entrance to the Sea of Azov, near Sevastopol and Yalta (Ukraine), and along the Bulgarian coast. A substantial fishery exists for the species along the Bulgarian and Turkish coasts, with the product being exported to the Orient. The total stock size of *Rapana venosa* along the coast of the former USSR was estimated at 10,000 tonnes in the period 1988–1992 (Serobaba and Chashchin, 1995; Zaitsev and Alexandrov, 1998).

In a comparison of morphometrics of populations from Korea, Turkey, and the Black Sea, Green (2001) demonstrated lower higher rates of allometric growth in Black Sea populations compared to native Korean and Chesapeake Bay populations. Vermeij (1993) states that such intraspecific allometry is indicative of food limitation in gastropods in general. This is in agreement with long-term observations of the Black Sea invasion, with an initial phase of establishment in which *Rapana* depleted many endemic prey species (see *Ecological impacts* section, below), resulting in a subsequent phase of very high densities of invaders affecting intraspecific competition for limited available prey resources. Allometric inferences may be challenged where *n* values are limited; however, one of the strengths of Green's study is the very large *n* value (Korea = 226, Black Sea = 74, and Chesapeake Bay = 107) and the range of sizes examined for all geographic populations.

4.1.3 Natural history in receptor region

In the Black Sea, where winter temperature minima are approximately 7 °C and summer maxima approximately 24 °C, *R. venosa* occupies a salinity range of 25 to 32 (Golikov, 1967). In the Sea of Azov, which is ice covered for two to four 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 salinity value < 12); however, range extension did occur during 1975–1979 when river 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 the present time.

Savini and Occhipinti (unpublished data, manuscript in preparation) examined *Rapana venosa* at the western extreme of its invading range in the Northern Adriatic in 2001. In this location, it is found on both soft bottoms and rock breakwaters that have been installed along 55 km out of 135 km of the Emilia Romagna regional coastline in order to prevent beach erosion. Individuals in this location exhibit the previously mentioned variation in shell spination and colouration. Populations on hard rock substrate have predominantly dark-coloured shells, whereas populations on adjacent sand exhibit a higher frequency of white or pale brown shell.

Information on daily by-catches of *Rapana* from commercial fisheries working on soft bottoms in the North Adriatic was provided by local fishermen and trawlers from five marinas distributed along approximately 130 km of coastline, including the ports of Goro, Porto Garibaldi, Cesenatico, Fano, and Senigallia. A total of 572 *Rapana venosa* were collected from May to October 2001 for biometrical and shell morphology analysis. Shell lengths of the samples ranged from 67.0 mm to 136.7 mm and total weight (shell+body wet weight) from 46.0 g to 553.9 g. Individuals collected on sand substratum were significantly smaller than individuals collected on breakwaters; the size distribution using all the parameters always shows smaller modal values in sand-collected individuals. Most of the individuals (306) were caught by squid fishermen along the coast of Cesenatico marina on sand substrate (Latitude: 44°12.2'–44°24.7' N; Longitude: 12°23.7'–12°26.6' E) from 2 m to 10 m depth. Squid fishermen's daily by-catches ranged from 30 to 80 specimens per boat (4–5 squid-nets) during this period. Focused SCUBA examination of three sections of breakwaters, each section being 15 m long, at a site facing the beach of Cesenatico and located 300 m from the coastline allowed collection of another 245 individual rapa whelks. These hard substrates present valuable, prey-rich resources for rapa whelks, as demonstrated by the rapid invasion of the resource when resident adults are intentionally removed. Individuals in such locations have been observed feeding in temperatures as low as 8° C. A notable feature of the population was the absence of dead individuals and of individuals smaller than 67 mm (Savini and Occhipinti, manuscript in preparation).

Figure 4.1.1.1. Distributional map of *Rapana venosa* in the Black and Mediterranean Seas with the years of the first finding derived from Drapkin, 1963; Grossu, 1970; Bilecik, 1975; Ciuhcin, 1984; Koutsoubas and Voultsiadou-Koukoura, 1990; Zibrowius, 1991, for the Black and Aegean Seas and by Ghisotti, 1974; Mel, 1976; Cucaz, 1983; Rinaldi, 1985; Bombace *et al.*, 1994; De Minn and Vio, 1997; Terreni, 1980; Paolini, 1987, for the Adriatic and Tyrrhenian Seas.

Growth rate

Ciuhcin (1984) estimated that individuals in Sevastopol Bay grow to 20 mm to 40 mm SL in the first year of life, with mean values of 64.6 mm, 79.4 mm, 87.5 mm, 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 ten years based on these observations.

Reproduction

Ciuhcin (1984) reports that spawning (egg laying) in the Black Sea is marked by a shell thickening and that first spawning occurs in the second year at sizes in the range 35 mm to 78 mm SL, with a mean value of 58 mm SL. Ciuhcin (1984) describes the reproductive period of *R. venosa* in the Black Sea (site not given) as July to September, corresponding to a temperature window of 19 °C to 25 °C. Sahin (1997) reports a spawning period of May to November in the eastern Black Sea.

Savini and Occhipinti (unpublished data) have developed a sequence of five egg-case maturation stages, from deposition to larval release after approximately fourteen days, by parallel daily observations in the field and laboratory. Deposition of egg masses starts at the end of March in the northern Adriatic Sea (when fishermen find the first egg-case clusters laid on squid nets) and ceases in mid-September. Spawning is continuous throughout the reproductive season. High densities of egg laying are observed on hard substrates. For example, Savini and Occhipinti (manuscript in preparation) describe an average 1,340 ± 387 new egg-cases/week laid on a 15-m section of protective breakwater (see earlier commentary). No live young individuals have been found to date at this site; only two young dead individuals of 4 mm and 25 mm length have been found stranded on the adjacent beach after a storm. Rinaldi (1985) also found the shells of small individuals after a storm event. These ranged in size from 12–40 mm SL, with a modal class size of 25–30 mm SL.

Ecological impacts

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 parts of 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.

Establishment of substantial populations of *Rapana* in the Black Sea (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 resident predators, and an abundance of potential prey species.

The ecological impacts in the Black Sea have been severe. Zolotarev (1996) suggests a broad dietary preference for bivalve molluscs including the soft-sediment infaunal mollusc species *Venus gallina*, *Gouldia minima*, and *Pitar rudis*. Marinov (1990) and Rubinshtein and Hiznjak (1988) identify *R. venosa* predation as the prime reason for decline in *Mytilus* *galloprovincialis* in Bulgarian waters, the Kerch Strait and the Caucasian shelf, respectively. Ciuhcin (1984) attributes the near extinction of the native bivalves *Ostrea edulis*, *Pecten ponticus*, and *M. galloprovincialis* on the Gudaut to predation by *R. venosa*.

No records have been found of associated species that may have been introduced to the Black Sea with *Rapana venosa*. The species is subject to attack by a local parasite; Gutu and Marinescu (1979) report the presence of *Polydora ciliata* in the shells of *Rapana venosa* from Romanian waters of the Black Sea. There is no evidence that this parasite can compromise the fitness of *Rapana venosa* in the Black Sea.

Control options

There are no obvious control measures in place to prevent continuing range expansion of *Rapana venosa* westward in the Mediterranean Sea. As described earlier, a substantial fishery for the species now exists in the Black Sea.

Estimates of final range establishment in receptor region

At this time there appears to be no limiting function on the westward movement of *Rapana venosa* in the Mediterranean Sea. The current progression rate is slow, but expected to continue in the future.

4.2 Chesapeake Bay, USA.

4.2.1 Date and mode of arrival, initial population size, and source of introduction

The first record of *Rapana venosa* in the Chesapeake Bay was a single specimen collected in the lower James River, Virginia (latitude 36° 57.12’ N, longitude 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 (Harding and Mann, 1999). Subsequently, adult *Rapana venosa* have been collected from the Lower Chesapeake Bay from August 1998 through March 2002 by the VIMS staff 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), commercial fishermen, and seafood processors. The size of the specimens in the initial collections is large (see below) but the lack of growth rate data for *Rapana venosa* compromises our ability to estimate the date of introduction. Estimates of age given by experienced malacologists, together with extensive anecdotal information from local commercial fishermen, suggest that initial specimens may be on the order of ten years old, indicating an introduction date of as early as 1988. This estimate is subject to revision as the ability to determine the age of individual specimens improves. Current population demographics (see below) suggest a single introduction event, although this cannot be proven conclusively.

There is strong evidence, in the form of vessel transit time from the eastern Mediterranean, a coal export trade to the Mediterranean originating in Hampton Roads and resulting in vessel return in ballast, and the duration of the pelagic phase of early life history, that range extension across oceanic basins is mediated by transport of pelagic early life history stages in ballast water. This evidence has been supported by limited comparisons of both mitochondrial and nuclear DNA from *Rapana venosa* populations in Korea, Turkey, and the Chesapeake Bay (Gensler *et al.*, 2001). While there is strong evidence for a significant founder effect in the Black Sea population compared to the native range, the Chesapeake Bay population appears to exhibit strong similarity to the Black Sea population. This line of investigation is continuing.

4.2.2 Current status and population demographics

The majority of specimens collected to date have been as by-catch of commercial fishing gear including crab pots, patent tongs, and crab dredges (6 cm bag ring size). The fishing gear is size selective so both absolute numbers and population data may reflect only a subsample of the population. Since the initial observation, over 4,000 individuals have been recorded. The majority remain within the range as described by 1999 collections (see Harding and Mann, 1999; Mann and Harding, 2000, Figure 4.2.2.1). The documented range of *Rapana venosa* in the Chesapeake Bay is from the mouth of the Rappahannock River in the north, to the Chesapeake Bay Bridge tunnel in the southeast, to just above the James River Bridge in the southwest, to the Lafayette River in the south (Figure 4.2.2.1). The majority of the individuals collected in 1998–1999 were in the size range 120–160 mm SL, with a smaller proportion < 120 mm SL and a few individuals as large as 170 mm SL. Data for 1998–1999 did not distinguish distinct size classes, but rather a continuous distribution within the size range. By 2001 size class structure was beginning to emerge in the 100–160 mm SL, again with a smaller proportion in the < 100 mm SL range, suggesting > 1 year class and therefore successful local recruitment. A general commentary on the status of the invading population is maintained, with regular updates, on the VIMS website at www.vims.edu/mollusc.

As noted earlier Green (2001), in comparing morphometrics of populations from Korea, Turkey and the Black Sea, demonstrated the lower higher rates of allometric growth in Black Sea populations compared to native Korean and Chesapeake Bay populations.

The suggestion of no food limitation for Chesapeake Bay populations is particularly troubling given the population demographics (see above) and the co-location of the invasion with a native hard clam (*Mercenaria*

mercenaria) population that supports a local fishery worth in excess of $3 million per year dock landing value.

4.2.3 Natural history in receptor region

Growth rate

Harding and Mann report that, once settled onto hard substrates, young *Rapana venosa* are generalist predators and consume large numbers of barnacles, mussels, oyster spat, and small oysters. Recently settled individuals grow at > 1 mm per week, reaching shell lengths of 40–50 mm within five months post-settlement and > 60 mm SL at age 1. These extremely fast growth rates, combined with 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 (see *Ecological impacts* below) that *Rapana venosa* occupies shallow hard-substrate habitats until reaching shell lengths in excess of 70 mm and then migrates into deeper habitats with sand or mud substrates where they forage on infaunal bivalves including soft clams (*Mya* sp.) and hard clams (*Mercenaria mercenaria*).

At this time, we do not have good estimates of growth rate or longevity of *Rapana venosa* in the Chesapeake Bay. Collaborative studies are in progress with Dr Christopher Richardson (Bangor University, Wales) to investigate the use of statolith ring structure in age determination of this species.

Reproduction

Westcott (2001) and Westcott *et al.* (2001) have observed a high incidence of imposex in females collected from upstream regions in the James River, an area formerly subjected to tributyltin (TBT) contamination associated with shipbuilding activity. Extensive investigation of the relationship between imposex in gastropods and TBT exposure has been described by Smith (1971), Gibbs *et al.* (1987, 1988), Ellis and Pattisina (1990), Huggett *et al.* (1992), Bryan *et al.* (1993), Foale (1993), Wilson *et al.* (1993), and Tester and Ellis (1995). This anomaly does not appear to limit reproductive activity in the afflicted female individuals.

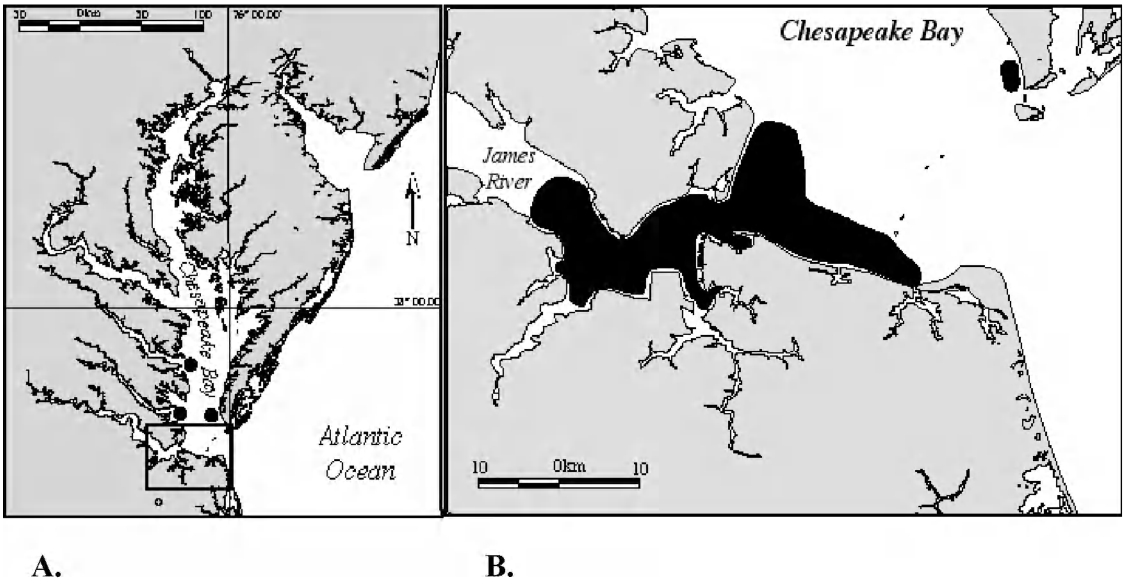
Laboratory populations of animals collected from Chesapeake Bay and maintained at local temperatures and salinities have been observed mating from September through July. Field collections of adult *Rapana venosa* (SL > 80 mm) were made year-round by Westcott (2001) using opportunistic sampling based on commercial fishery by-catch. 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 water temperatures and gametogenesis in animals from Chesapeake Bay is consistent with previously described seasonal reproductive activity in native (Korean) populations, 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 *Rapana venosa* is successfully completing gametogenesis and egg laying throughout the range of collection.

Rapana lays mats of eggs with 50–500 egg cases per mat. Each case may contain 200–1,000 eggs (Ware *et al.*, 2001). The period from egg laying to hatching varies typically between 14 and 21 days, depending on temperature and salinity. As mentioned earlier, *Rapana venosa* veliger larvae display considerable variation in time from hatch to settlement, although they are typically morphologically competent to settle after 21 days at local temperatures and salinities. Veligers grow quickly on mixed algal diets, reaching shell lengths in excess of 0.5 mm at 21 days (Harding and Mann, in prep.). *Rapana venosa* veligers settle successfully on a wide range of locally available attached macrofauna including bryozoans and barnacles, but have also been observed to effect spontaneous metamorphosis with regularity in laboratory cultures.

Ecological impacts

Early work in the VIMS laboratory demonstrated the susceptibility of native hard clams *(Mercenaria)* to *Rapana* predation (Harding and Mann, 1999). Parallel observations of distinctive boring signatures of *Rapana* (chipping or rasping of the shell margin as described by Morton, 1994) on hard clams in the field were made by a number of collaborating commercial fishermen, again underscoring the importance of this interaction in data collection throughout the invasion. Estimated rates of predation and size preference for prey in this relationship were examined by students Dario Savini and Peter Kingsley-Smith (both visiting students from the University of Wales in 2000). Savini *et al.* (2001) demonstrated that whelks with a SL > 101 mm are capable of consuming up to 2.7 grams of clam tissue daily. Smaller whelks (60–100 mm SL) ingest on average 3.6% of their body weight every day, which is more than four times the weight-specific ingestion rates of larger whelks. The limited data set suggests a preference by both size classes of *Rapana venosa* for large hard clams (SL > 71 mm); however, no prey size is immune and predatory signatures have been observed in a wide range of sizes in the field by commercial fishermen. Both Savini and Kingsley-Smith have contributed to an expanding database that we are building of signature predatory scars for a matrix of gastropod predator-bivalve prey organisms over size ranges for both predator and prey. The intent is to provide field biologists and commercial fishermen with a visual aid to identifying gastropod predation and

Figure 4.2.2.1. Distributional map: Chesapeake Bay region, U.S.A. A) Known distribution of rapa whelks (*Rapana venosa*) in Chesapeake Bay, U.S.A. as of March 2002 (after Harding and Mann, 1999), B) Enlarged view of the lower James River and Chesapeake Bay where a majority of collections have been reported (after Harding and Mann, 1999).



discriminating between the predators in the absence of direct collection of the latter. The distribution and employment of such tools have a profound effect on the collective ability of the benthic ecologists and commercial fishermen alike to track any expansion in range of an invader, like *Rapana*, in near real time and where direct observations may be limited by low predator densities.

In addition to the initial focus of *Rapana* predation on hard clams, Harding and Mann (unpublished data) have presented both field-collected adults and post-metamorphic juveniles from laboratory cultures with a variety of local bivalves including oysters (*Crassostrea virginica*), mussels (*Mytilus edulis*), and soft-shell clams (*Mya arenaria*). All prey are consumed with ease by the invader. Indeed, the combination of these broad dietary capabilities with broad salinity tolerance suggests that no substantial extant bivalve resources in the lower Chesapeake Bay are in a spatial refuge from predation. Further, the possibility remains that the native oyster drill, *Urosalpinx cinerea*, will suffer from direct competition with *Rapana venosa*. *Urosalpinx* populations were once extensive and abundant within the bay, but the freshets associated with Hurricane Agnes in 1972 decimated their populations. Post-Agnes survival was limited to a region near the bay mouth; essentially all oyster beds in the sub-estuaries of the bay were purged of *Urosalpinx* by this single event. Unlike *Rapana, Urosalpinx* has no pelagic larval stage. Juveniles hatch and crawl away from the substrate-attached egg masses. *Urosalpinx* has literally been recolonizing its former bay habitat over the past three decades by crawling up the bay bottom over "islands" of suitable substrate. In the absence of an invader, the temporary displacement of *Urosalpinx* is but a minor perturbation in evolutionary time; however, the introduction of *Rapana* adds a new component to this re-establishment process. There now exists a race to reoccupy this temporarily vacated niche between the crawling native and the invader with the pelagic larvae.

Rapana shells provide shelter for the expanded range of the striped hermit crab, *Clibanarius vittatus,* which has demonstrated an ability to eat significant numbers of oyster spat when they reach sizes commensurate with their newly found "import size" shelters.

There are no observations of predation on *Rapana venosa* by native species in the field. In laboratory experiments, the native blue crab, *Callinectes sapidus,* has been shown to be a voracious predator on small, post-metamorphic stages (Harding, unpublished data). In the field, it is suggested that *Rapana venosa* reaches a predator refuge size at several years of age in part due to its shell morphology. Rapa whelk shells are thicker and very broad with respect to SL when compared to large native gastropods such as *Busycon* and *Busycotypus.* Given that predation by seasonally migrating large predators (turtles) is related to mouth gape size, the wide aspect ratio of the shell of *Rapana venosa* makes it less susceptible, for a given length, than native gastropods (see Harding and Mann, 1999). Once this predator refuge size is attained, it is suggested that *Rapana venosa* may remain as an unchallenged predator for up to a decade.

No records were found of associated species that may have been introduced with *Rapana venosa.* The whelk is, like the Black Sea populations, subject to attack by a local species of *Polydora*. Examination of shells of local *Rapana venosa* was affected in 1998–1999 (Mann and Harding, 2000) based on the premise that epifaunal and infaunal populations of the whelk 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 *Rapana* 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 an infaunal existence that is more typical of predatory muricids (see comments in Morton, 1994).

Control options

No widely effective control options to eliminate the species are available at this time. An extensive public education programme and a joint effort with local commercial fishermen (110 collaborating fishermen as of 2002) pays a bounty to remove any *Rapana venosa* collected in local waters and delivered to the Virginia Institute of Marine Science. In addition, the programme has widely distributed descriptions of egg cases with guidance to destroy such egg cases when found. While successful in stimulating collections to date, this programme does not address early post-settlement stages that are below the size selectivity of typical commercial fishing gear. Efforts are under way to develop specialized local markets for the species to provide economic stimulus for continued collection by commercial fishermen in the event that either the bounty programme is terminated or the resources of that programme are unable to keep pace with the annually increasing numbers of adult specimens collected.

Estimates of final range establishment in receptor region

Potential distribution limits of adult *R. venosa* in the Chesapeake Bay bottom can be inferred using Chesapeake Bay 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. A projected range of adult *Rapana* survival in the Chesapeake Bay extends across the entire Bay to a northern limit at the mouth of the Rappahannock River. Marginal limits of this range encroach several km into all major Virginia sub-estuaries. 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 sub-estuaries that typify the Chesapeake Bay. The demonstrated low salinity tolerance of at least the early post-hatch larval stages (see Figures 4 and 5 in Mann and Harding, 2000) and the relative position of winter bottom and summer surface isohalines (Figures 6A and 6C in Mann and Harding, 2000) suggest survival of larvae transported into the major sub-estuaries in the summer to positions upstream of the currently documented or estimated limits for benthic adult *R. venosa*. Surface circulation within the Chesapeake Bay, combined with the duration of the pelagic larval phase, suggests that extant adult populations can support recruitment to projected benthic populations if larvae can locate and successfully metamorphose on suitable substrates. Local population centres of adult *R. venosa* are concurrent with those of the hard clam (*Mercenaria mercenaria*) (see Figure 7 in 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*, populations which are currently limited to lower salinity habitats by endemic diseases.

Invasive range estimates for the Atlantic coast employ comparative temperature data from susceptible and known ranges of *Rapana*. Mann and Harding (2000) presented 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, with an inclusion of the temperature data from Chung *et al.* (1993) for the native Korean range. 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 of supporting larval development (21 days at 24 °C to 26 °C and salinities > 18 to 21 (Mann and Harding, 2000), and similar periods at 18.3 °C to 20.4 °C (Chung *et al.*, 1993) for Korean waters and 20–22 °C (Ciuhcin, 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 where, as mentioned earlier, *Rapana venosa* is displaced by *Rapana bezoar* (Tsi *et al.*, 1983; see also Morton, 1994, species separation confirmed by mitochondrial and nuclear DNA markers by Gensler *et al.*, 2001). While both Charleston and Hong Kong 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 *Rapana venosa*. Further, based upon the statements of broad dietary preferences of *R. venosa* as reported earlier, there appears to be ample potential prey species for *R. venosa* throughout the Cape Cod to Charleston region. The dispersal rate 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.

4.3 Rio de la Plata, Uruguay and Argentina

A single published report describes collection of *Rapana venosa* in the north of the Bahia Samborombon on Rio de la Plata in 1999 (Pastorino *et al.,* 2000). A single female specimen of 97.1 mm SL and egg capsules were found at approximately latitude 35.3 °S longitude 55.4 °W in 13 m depth of water. An independent collection of *Rapana venosa* by scientists from Uruguay was made in the same year (Scarabino, 2000). Local populations of mussels (*Mytilus edulis platensis*) and oysters (*Ostrea puelchana*) are probable prey items. The current status of the South American population is that *Rapana* is now widely distributed on the Uruguayan (northern) coast (Montevideo-Punta del Este) of the estuary of the Rio de la Plata (the junction of the Parana and Uruguay Rivers with the Atlantic), but not on the Argentinean (southern) coast (personal communications to Roger Mann from Fabrizio Scarabino and Guido Pastorino, respectively, March 2002). It is restricted to the estuarine salinities. In summer months reproductive activity is evident with egg cases often being abundant on some beaches after strong winds. No data are available for this invasion concerning ecological impacts or the potential extent of establishment over time. No control measures are being attempted.

4.4 Brittany coast of France

The date of first introduction of *Rapana venosa* into the Brittany coast of France has not been firmly established, although the first confirmed sighting was in 1997. In the 1999 report of the ICES Working Group on Introductions and Transfers of Marine Organisms (WGITMO), the collection of three large individuals in a subtidal area of the Bay of Quiberon in June 1998 is described, together with the sighting of others in the summer of 1997. Patrick Camus (J.P. Joly and P. Goulletquer, IFREMER, La Trinité Sur Mer, France, personal communication to Roger Mann, 1999) indicated that up to ten large individuals (average SL of 140 mm) were collected from the Bay of Quiberon in southern Brittany by local and coastal fishermen using gillnets. No specific location and depth records are available. Philippe Goulletquer (IFREMER, La Tremblade, France, personal communication to Roger Mann, 1999, J.P. Joly, IFREMER, La Trinité Sur Mer, France, personal communication) also reported that adults had been collected in Brittany, although there did not appear to be substantial populations and they did not present evidence of active breeding or the presence of multiple year classes. Two individuals were collected in 1997, followed by three, two, four, and two from 1998 to 2001. Since the first sighting, a total of eleven individuals was observed in 2000 and an intense effort was made to search for other specimens with the intent of eradication (J.P. Joly, IFREMER, La Trinité Sur Mer, France, personal communication, ICES WGITMO Report 2001). The vector for introduction of these animals remained in question until 2001, when two more whelks were collected (National Report for France, ICES WGITMO Report 2002). *Rapana* were apparently used to ballast clam culture bags of *Tapes philippinarum*, that were transferred from the Adriatic, where *Rapana* is now established (see earlier section on Black Sea through Adriatic invasion), and meanwhile were likely imported for shell collectors (P. Goulletquer, IFREMER, La Trinité Sur Mer, France, personal communication). No size information is available on the 2000 or 2001 *Rapana* collections. The National Report for France for 2001 to ICES WGITMO states that one individual was collected in the “same area and depth” as previous capture (3–5 m depth range, sandy bottom), with a second individual on settlement substrate for flat oysters. The oyster substrate is an off-bottom structure made of metal and mussel shells. Ten egg cases, each 25 mm long, were found on the same structure approximately 30 cm off the bottom. This is considered to be the first evidence of reproductive success of *Rapana* in Brittany. The egg cases were collected, maintained in the laboratory, and subsequently released larvae which grew until metamorphosed. These observations are troubling given that annual water temperature ranges in Brittany are arguably marginal for the establishment of *Rapana venosa* based on comparison with previously described native and invaded ranges. However, in the Bay of Quiberon the temperature range is 18–22 °C and salinity ranges from 33 to 34, enabling a successful development of larvae. The juveniles are being maintained for research purposes in quarantined systems. Following only one mating, 742 egg cases were obtained in four spawnings lasting from early July to August 2001. In total, thirteen adult individuals have been collected until now, mainly in the “Anse du Pô” location, with only one individual in Crach river (Bay of Quiberon) (P. Goulletquer, IFREMER, La Trinité Sur Mer, France, personal communication). Both a renewed eradication programme using nets and dredges, and a public education programme are under way at the time of preparation of this report. Control measures to prevent continued introduction in association with commercial clam shipments are strongly endorsed.

5 Limited records, not suggestive of established introductions

5.1 North Sea

A single report of occurrence of *Rapana venosa* was made for the North Sea, approximately 30 km south of the Dogger Bank (London Times, 26 August, 1992). This may have been associated with disposal from a ship’s galley. No other specimens have been collected from this location. ICES (WGITMO Report 1993) suggests that the specimen was misidentified. The collected specimen has not been examined by the authors, so definitive confirmation of the species is not possible for this record.

5.2 Willapa Bay, Washington State, USA

Hanna (1966, page 47) provides a picture of *Rapana thomasiana* and the following text: "The first specimen of this species which was made available to me for illustration was furnished by Dr D.B. Quayle of the Fisheries Research Board of Canada. The shell does not appear to be fully grown. It measures 22.4 mm in length and 16.9 mm in diameter. Locality information is not available. A much larger specimen (length 100 mm, diameter 73.4 mm) was given to Mrs Eleanor Duggan by Professor Kincaid. It, along with others, was collected in Willapa Bay, Washington, a locality from which Burch (1952, p. 16) (reference lacking) recorded it." The citation to Burch is apparently a notation in the minutes of the Conchological Club of Southern California for August 1952. The original material is not available to the authors.

The shell of a single specimen exists in collections maintained by Washington State Department of Fisheries, this having been collected in Willapa Bay (Brett Dumbault, personal communication to Roger Mann, 2001, date and specific location information not given). This specimen is considered to have been introduced with historical seed oyster shipments from Japan, and was probably collected in a similar time frame to the Willapa Bay specimens described above. Oyster seed shipments were discontinued several decades ago. Summer water temperature in Willapa Bay is too low to support reproduction of *Rapana venosa*.

5.3 New Zealand

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.

6 Prospects for further invasions

The emergence of ballast water as a major vector in marine introductions over the past half century, combined with the imposing volumes of water moved as part of commercial ship traffic, suggest that continued dispersal of *Rapana venosa* will occur within the native and established introduced ranges as well as in new regions. The Black Sea through the western Mediterranean invasion has progressed for approximately 60 years and appears to be still expanding. The Chesapeake Bay invasion appears on the verge of expansion, given increasing numbers of individuals collected and recent demographic changes within the population. The limited data on the Rio de la Plata invasion must also be viewed as threatening. In all of these locations, there are one or more major ports which may, through ballast water vectors, serve as potential donor locations to support new introductions.

The possibility of attached fouling as a vector for introductions of *Rapana* was discussed earlier with respect to the initial introduction into the Black Sea. Modern hull anti-fouling treatments reduce, though do not eliminate, the viability of this vector in potential future introductions. To this point, we have not addressed the potential role of transport in ships' sea chests as a vector mechanism for further introductions of *Rapana venosa*. Richards (1990) elegantly describes the transport of the tropical muricid *Thais blandfordii* 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 and 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 be drawn into a sea chest on floating debris, their possible transition to a preferred infaunal habitat with an associated change in dietary preference with increasing size, maturation at a large size and production of pelagic larvae, suggest that facilitated dispersal by this vector would be less successful than for *T. blandfordii.*

The introduction of *Rapana* together with oysters or clams transferred for aquaculture purposes is another suggested vector of introduction that has been raised for the Black Sea and Brittany (France).

The native range of the species shows comparable temperatures (low single digit-values to mid- to high 20s °C) and salinities (a broad range from mid-estuarine (approximately 15) through oceanic values) to those encountered in established invasions. If the temperature remains above 20 °C for extended periods, then egg case deposition, hatching, and larval development may occur. Plasticity in the duration of the pelagic larval phase, the absence of specific larval settlement cues, broad dietary options in the early post-settlement stage, rapid growth to possible predation refuge, relatively early onset of sexual maturity, high fecundity, considerable longevity, and tolerance of challenging environments with respect to anthropogenic stressors make *Rapana venosa* a formidable invasion threat to regions that are both served by the identified vectors and within the broad niche descriptors. It may be possible to predict further areas to which it may expand given a better understanding of likely vectors of further transmission.

7 Prospects for control or management where introductions occur

As with many introductions, the probability of observing the initial introduction event is minimal. The cryptic nature of *Rapana venosa* contributes to the improbability of observing invading individuals until they are large and imposing members of either the benthic community or a fishery catch. Given that the larval stage is considered a probable candidate for introduction via ballast water vectors, any observation of large adults in a receptor site will occur only after considerable time delay during which accompanying invading individuals will have dispersed and, if they survive, established elsewhere. Further, if the invaders have survived in sufficient densities and to sufficient size, recalling the relatively modest size at first maturity, then the probability of mating and egg laying in the receptor location before first record is high. Prospects for control or eradication of an invading population are bleak when physical conditions and potential prey concentrations are amenable to establishment. The complex life cycle of the species involves minimally a pelagic dispersal phase and a benthic adult. The latter optionally, indeed probably, involves a size-dependent transition from an epifaunal to an infaunal habit common to large predatory muricid gastropods. Further, seasonal aggregation for mating and subsequent egg mass deposition on hard substrates contribute to a complex pattern of resource utilization by the species over its life cycle. Attempts to target the species for control or eradication must choose the most susceptible stage or stages for practical control measures. Unfortunately, any such strategy has notable weaknesses. Egg case mats, although visible and often concentrated, may be spread over vast areas, and, given the large numbers of developing embryos per case, represent considerable propagule pressure when present even in small numbers. Larval forms are too dispersed to be considered tractable targets when free swimming in receptor environments. Identification and collection of post-settlement forms on hard substrates is difficult in complex community structures, given that the probability of confusion with other gastropods is high, while total community destruction is untenable. While large epifaunal individuals are identified with comparative ease, their selective collection represents an enormous investment of diver time. Collection of infaunal individuals is tractable with commercial dredges or pots/traps designed for target infauna. Extensive dredging for disparate populations of the invader would precipitate unacceptable levels of environmental destruction with accompanying debilitation of native species. In summary, there are no proven methods currently available for control or eradication of this species should it become established in a receptor environment. Investigations are in progress to examine the use of such techniques as side-scan sonar to identify significant mating aggregations on open sand substrate regions in the lower Chesapeake Bay. These may prove useful in guiding removal of those aggregations with reduction in propagule pressure, but they are not universally applicable and will not result in complete removal of reproductively capable or active individuals. As such, this is a possible control but not eradication option, and becomes less attractive should the observed range begin to expand rapidly.

Commercial fisheries still represent, by far, the most significant avenue for the collection of *Rapana venosa* in numbers to implement control. While the development for a fishery can be argued to support maintenance of the population for economic reasons, public education can and must be supported to underscore the potential damaging effects of this species on native species of commercial and/or ecological importance. As such, the argument for a temporary focused fishery, even a subsidized effort, is worthy of consideration.

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