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# THE ALIEN MOLLUSC *RAPANA VENOSA* (VALENCIENNES, 1846; GASTROPODA, MURICIDAE) IN THE NORTHERN ADRIATIC SEA: POPULATION STRUCTURE AND SHELL MORPHOLOGY

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*Rapana venosa* (Valenciennes, 1846; Gastropoda, Muricidae), 'Rapa whelk', is a predator of bivalves, native to the Japanese seas. It has been reported in the Northern Adriatic Sea since 1973. Recently, its biogeographical distribution has been widening (probably favoured by ship traffic) including the Atlantic coasts of the USA, Argentina and France, where the species colonised transition zones, such as estuaries or lagoons, economically important for shellfish harvesting. This work investigates the population structure of the Rapa whelk (size classes distribution, sex ratio) in Cesenatico (Emilia-Romagna coast), where local fishermen have been recently observing increasing numbers of *Rapana* in their by-catches. During summer 2001, analyses were performed on sexually mature adult specimens obtained from sandy bottoms and artificial rocky breakwaters. Male and female individuals were reported in approximately equal numbers with a minimum shell length of 67.0 and a maximum of 136.7 mm. *Rapana* collected on breakwaters were significantly larger and heavier than *Rapana* from sand substratum (ANOVA, $P < 0.05$). Sand shells and rock (breakwater) shells differed also in colour and epibiont cover. The role of man-made hard structures such as breakwaters in maintaining and promoting a further expansion of *R. venosa* is discussed.

*Keywords*: *Rapana venosa*; Molluscs; Alien species; Population structure; Northern Adriatic Sea

## 1 INTRODUCTION

The Asian whelk *Rapana venosa* (Valenciennes, 1848; Gastropoda, Muricidae) spread out its native biogeographic range – Sea of Japan, Yellow Sea, Bohai Gulf, East China Sea (Tsi *et al.*, 1983; Chung *et al.*, 1993) – colonizing European – Black Sea, North Adriatic Sea, Aegean Sea, Quiberon Bay, NW Atlantic (Cesari and Pellizzato, 1985; Koutsoubas and Voultsiadou-Koukoura, 1991; Zolotarev, 1996; Goulletquer, 2000) – North American – Chesapeake Bay (Harding and Mann, 1999) and South American – Bahia Samborombon (Pastorino *et al.*, 2000) – estuarine and marine environments (salinity > 20 PSU). This voracious predator of bivalves of economic interest (oysters, mussels and clams, Savini *et al.*, 2002) has been credited in the Black Sea with the collapse of the Gudaut oyster bank (Drapkin, 1963).

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*Rapana venosa* is characterised by a strong ecological fitness due to high fertility (Chung *et al.*, 1993), fast growth [*Rapana* sexual maturity is reached after 1–3 years at 50–70 mm size (Ciuhcin, 1984; Harding and Mann, 2001)] and tolerance to low salinity (Mann and Harding, 2000), water pollution and oxygen deficiency (Zolotarev, 1996). Furthermore, long distance dispersal of *Rapana* larvae is assisted by a planktonic phase lasting from a minimum of 14 to a maximum of 80 days allowing accidental transfer throughout the oceans within ship ballast waters (Mann and Harding, 2000). All these factors make the 'Rapa whelk' one of the most unwelcome invaders worldwide.

A resident population of this gastropod has existed in the North Adriatic sea since 1973 (Ghisotti, 1974). From 1973 to 1984 *Rapana* specimens have been found from Trieste (Friuli Venezia Giulia) to the south of Rimini (Emilia-Romagna) on sandy bottoms, and on artificial and natural rocky bottoms (Cesari and Pellizzato, 1985). The aim of the present work is to provide a description of the whelk distribution, abundance, adult population structure, biometry, sex ratio and shell morphology in Cesenatico (Emilia-Romagna), where, recently, local fishermen have been observing an increase in numbers of by-catch of this gastropod. Squid fishermen are particularly disturbed by the presence of the gastropod which utilises nets as spawning substratum crawling inside, occupying all the room available and adding extra load to the draught.

Results of the present study will integrate findings of other international ongoing investigations aimed at a 'risk assessment' concerning *R. venosa* transfer and introduction worldwide.

## 2 MATERIALS AND METHODS

During summer 2001 (13/06–10/07), 302 adult living whelks were caught on sandy bottoms by local fishermen using squid nets deployed on a fishing ground of about 10 $km^2$ (depth: 3–8 m); 244 other adult gastropods were collected weekly (20/06/01–18/07/01) by SCUBA diving on three approximately 15 m long × 3 m high × 4 m wide (available surface for the whelk population: $\sim 115\,m^2$) rocky breakwaters located 300 m off the Cesenatico beach (depth: 2–3 m) (Fig. 1; Tab. I). Moreover, in order to make sure that smaller individuals did not go overlooked by the visual census, clearing of the whole surface of 15 × 15 cm squares of the breakwaters was made on four sampling dates and the collected material was carefully inspected under a dissection microscope to look for *Rapana* juveniles. Finally, breakwaters were again examined (February 2002) to check for the presence of the whelk in wintertime.

The following parameters were measured for each specimen collected:

- size – shell length (SL), shell shoulder width (SSW), shell thickness (ST), aperture height (AH), aperture width (AW) (Magalhaes, 1948);
- weights – total animal wet weight (TW), shell weight (SW), flesh wet weight (BWW), flesh dry weight (DW);
- sex (male: presence of penis and testis; female: presence of ovary and gonopore);
- shell colour;
- shell morphology (presence of shell spines or aperture marginal teeth);
- shell integrity (erosion).

The following code was utilised to identify shell morphotypes in rock and sand samples:

- main shell colouration: 0 = dark, 1 = brown, 2 = pale brown;
- shell stripes: 0 = well evident, 1 = scarcely evident;
- shell margin colouration: 0 = white, 1 = dark;
- aperture colouration: 0 = orange; 1 = red; 2 = pink; 3 = dark stripes on a whitish base;

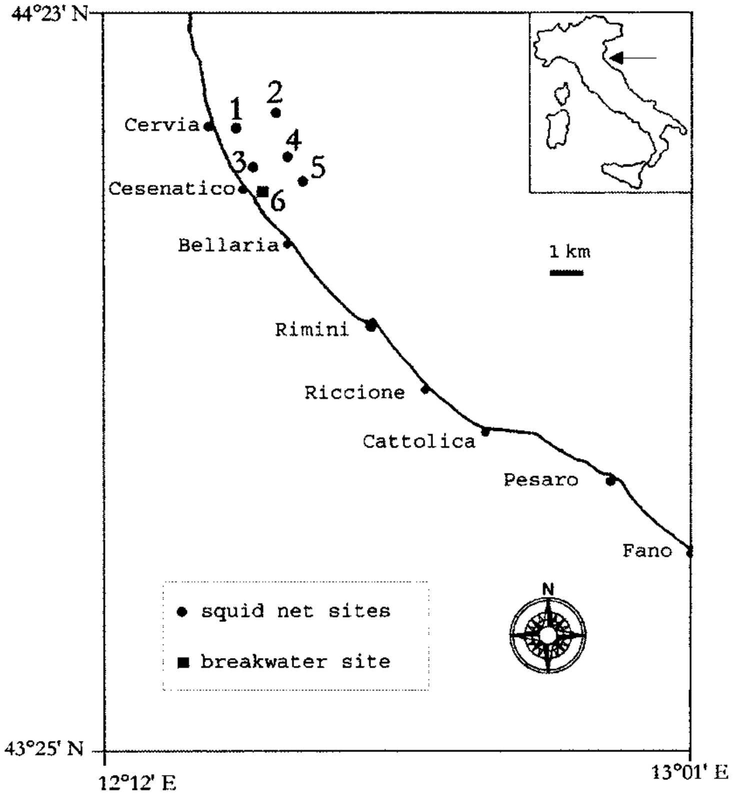

FIGURE 1 Collection sites: 1–5, squid nets; 6, artificial breakwaters.

- shell spines: 0 = short, 1 = long;
- marginal teeth: 0 = not pronounced, 1 = well pronounced.

Dimensions were measured using a calliper (0.1 mm) and weights using a digital scale (0.01 g). For the assessment of sex, SW, BWW and flesh DW samples were boiled 2–3 min in water in order to loosen the columellar muscle and allow an easy extraction of the soft body parts of the mollusc from the shell. Flesh DW was measured after oven-drying the soft body parts of the gastropod for 48 h at 80 °C.

Methods of analysis follow the standard of the Virginia Institute of Marine Sciences (VIMS, Virginia, USA, http://www.vims.edu/mollusc/research/merapven.htm).

TABLE I Sampling details – sampling sites, coordinates, depth, type of substratum, methods of collection and number of adult *Rapana* specimens collected.

| *Sampling sites* | *Cesenatico (from Pinarella to Gatteo Mare)* | *Cesenatico (Eastern beach)* |
|---|---|---|
| Latitude | 44° 13′.4–44° 15′.9 N | 44° 12′.2 N |
| Longitude | 12° 22′.9–12° 26′.6 E | 12° 24′.7 E |
| Method | Squid nets by-catches | Manual collection (SCUBA) |
| Depth | 3–8 m | 2–3 m |
| Substratum | Sand | Rock |
| No of *Rapana* | 302 | 244 |

The main shell epibionts have been identified (presence/absence) and the average epibiont cover has been assessed for comparing shells collected from rock and sand substrata (a higher epibiont cover would indicate a more exposed *lifestyle*).

Statistical analyses were performed using the software Minitab 13.0 for the regression analyses (McKenzie and Goldman, 1999) and the web site http://www.physics.csbsju.edu for the computation of the Kolmogorov–Smirnov test (Conover, 1980).

## 3 RESULTS

### 3.1 Abundance, Biometry, Sex Ratio

Daily by-catches of *R. venosa* ranged from 12 to 74 whelks (average: $38 \pm 22$ whelks) per squid fishing boat. During the fishing season (end of March to end of July; 120 days) fishermen deployed a minimum of 50 squid nets per boat; on average, five squid nets were controlled daily by each boat. Thus, each net was fished every 10 days, about 12 times in all throughout the season. Considering that the Cesenatico squid fishing fleet consists of 17 boats, the average whelk abundance in the study site could be estimated as: 38 (mean daily by-catch) × 50 (number of squid nets × boat) × 12 (net inspection frequency) × 17 (number of boats) $= 387{,}600\,\text{ind.}\ 10\,\text{km}^{-2} = 4\,\text{ind.}\ 100\,\text{m}^{-2}$.

As far as the breakwater rocky habitat is concerned, on average $15 \pm 2$ whelks (average of the number of whelks collected in five diving occasions) were found on a surface of approximately $115\,\text{m}^2$ (15 whelks $115\,\text{m}^{-2}$; $13\,\text{ind.}\ 100\,\text{m}^{-2}$). During the winter dive on the artificial breakwaters, the gastropod was observed actively feeding on natural mussel beds at a water temperature of $8\,^{\circ}\text{C}$ (no counts and no samplings were performed in that occasion).

During summer, whelks collected on sand and rocks were found alive, sexually mature and in spawning activity. Female whelks represented 47% of the sand population and 43% of the rock population. Shell length varied from 67.0 to 136.7 mm and body wet weight (BWW) from 11.1 to 172.2 g. The distribution plots of each biometric variable for rock/sand specimens showed a shift of the mode towards larger individuals in rock specimens (Fig. 2); the Kolmogorov–Smirnov test (KS-test) (Tab. II) confirmed significant differences (KS-test, $P < 0.001$) between rock/sand specimens size–class frequency distributions. Individuals caught on rock appeared slightly but significantly bigger and heavier than individuals caught on sand (ANOVA, $P < 0.05$). Moreover, females appeared significantly smaller and lighter than males (ANOVA, $P < 0.05$), without any significant interaction between habitat and sex (ANOVA, $P > 0.05$) (Tab. III).

Figure 3 shows the results of the regression analyses between SL (as independent variable) and SSW, AH, AW, ST, TW, SW, BWW and flesh DW. In order to normalise and compare the biometric variables, data were $\log_{10}$ transformed (Clarke and Warwick, 1994). All parameters appeared significantly correlated, and regression lines of sand and rock samples showed similar slope values (Tab. IV). Differences were found comparing SL/ST, SL/TW and SL/SW relationships: although the two lines remained parallel showing a similar allometric growth both for sand and rock specimens, they remained separated indicating that for a given value of SL, ST, TW and SW of sand specimens were lower than in rock individuals.

### 3.2 Morphology, Shell Epibionts

Shells showed 60 different combinations of morphological characteristics (morphotypes) (see Methods); 40 represented by sand specimens and 37 by rock specimens.

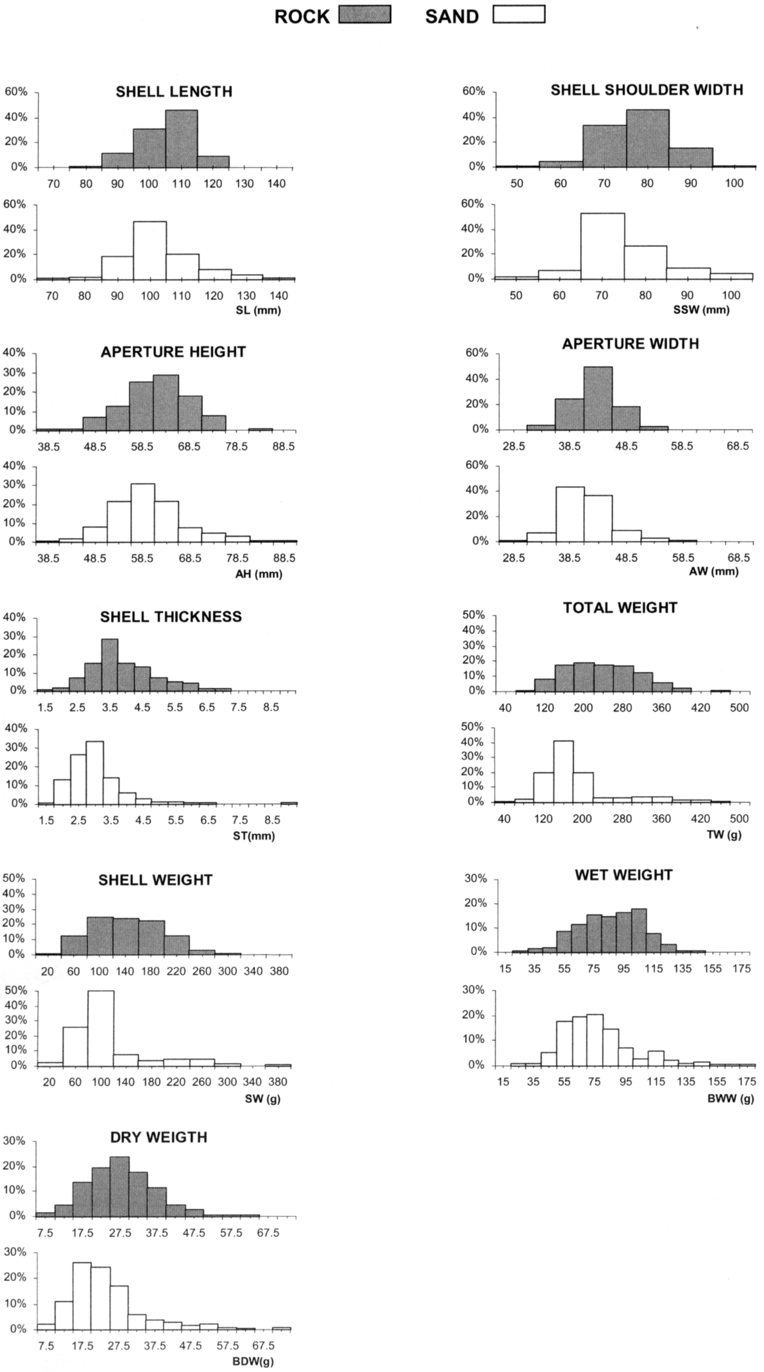

FIGURE 2 Size–class frequency distribution of the biometric variables for the *Rapana* specimens collected on rock (artificial breakwaters) and sand (squid nets) substrata.

TABLE II Kolmogorov–Smirnov test.

| *KS test* | *D* | *P value* |
|---|---|---|
| Shell length | 0.23 | $P < 0.001$ |
| Shell shoulder width | 0.25 | $P < 0.001$ |
| Shell thickness | 0.48 | $P < 0.001$ |
| Aperture height | 0.21 | $P < 0.001$ |
| Aperture width | 0.29 | $P < 0.001$ |
| Total weight | 0.39 | $P < 0.001$ |
| Shell weight | 0.43 | $P < 0.001$ |
| Body wet weight | 0.30 | $P < 0.001$ |
| Body dry weight | 0.29 | $P < 0.001$ |

*Note*: *D*, maximum differences between the cumulative distributions of each biometric variables measured for rock and sand *Rapana* specimens, *P*, 99.9% confidence interval.

The dominant morphotype on sand (28% of 302 samples) was '200000': pale brown shell, well evident stripes, white shell margin, orange aperture, short shell spines and nonpronounced marginal teeth. Instead, the dominant morphotype on rock (31% of 244 samples) was '011000': dark shell, scarcely evident stripes, dark shell margin, orange aperture, short shell spines and nonpronounced marginal teeth (Fig. 4, Tab. V).

Whelks caught on rock and on sand showed differences in the external colour of the shell, which was cryptic in relation to the habitat of collection (pale brown shells on sand and dark shell on rock). Whelks were also found to differ in shell integrity. Up to 40% of the rock shells were highly eroded (total erosion of the spines and the apex); 33% partially eroded (partial erosion of the spines and the apex) and only 27% of the shells were complete, whereas up to 60% of the sand shells were complete and only 8% highly eroded. Figure 5 plots shell erosion in function of *Rapana* average SL for rock and sand individuals. In both cases bigger (older) shells show high erosion.

Moreover, 62% of the breakwater shells and 44% of the sand shells were accompanied by a high incidence of bore holes caused by the sponge *Cliona lobata.*

As far as shell epibionts are concerned, the average percentage cover was significantly higher in rock shells than in sand shells (more than 50% in rock samples, less than 20% in sand samples; ANOVA: $F = 403.3$; $P < 0.01$). Epibionts were coelenterates (*Anemonia* sp.), bryozoans, barnacles, serpulids, oyster spats (*Ostrea edulis, Crassostrea gigas*), mussels (*Mytilus galloprovincialis*), the nonindigenous bivalve *Anadara demiri* as well as red encrusting algae and green algal turf. In addition, many shell samples hosted egg-cases of the gastropod *Nassarius reticulatus* and of *R. venosa* itself, and squid eggs (*Sepia officinalis*). Table VI shows the occurrence (% frequency) of the different taxa of epibionts on rock and sand shells. Rock shells were mainly covered by mussels, green algal turf and serpulids, while sand shells by serpulids, oyster spats and by egg-cases of the gastropod *N. reticulatus.*

## 4 DISCUSSION AND CONCLUSIONS

As far as *R. venosa* population is concerned, Gomoiu (1972) found the gastropod distributed on the sea bottom in wintertime and clustered on rocky habitats near the littoral in summer in mating and spawning activities along the Romanian coast. Our observations in summer suggest the presence of a sparsely distributed population (4 ind. 100 $\mathrm{m}^{-2}$) of the gastropod on the sandy bottoms from 300 m to 8 km from the coastline, and of a denser population (13 ind. 100 $\mathrm{m}^{-2}$) clustered on the rocky artificial breakwaters 300 m from the coast, actively

TABLE III Two-ways ANOVA comparison between the average (±SD) values of the biometric variables measured for rock male/female and sand male/female (M,F) *Rapana* specimens.

| | *M* | | *F* | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Rock* | *Sand* | *Rock* | *Sand* | *Habitat* | *Sex* | *Habitat × sex* | *Differences* |
| Shell length (mm) | 106.0 ± 9.2 | 105.7 ± 10.1 | 105.4 ± 8.1 | 101.1 ± 10.5 | $F = 11.8$; $P < 0.05$ | $F = 7.2$; $P < 0.05$ | $F = 1.2$; n.s. | M > F; R > S |
| Shell width (mm) | 78.3 ± 7.6 | 77.3 ± 8.7 | 78.5 ± 7.6 | 73.8 ± 8.6 | $F = 26.9$; $P < 0.05$ | $F = 1.3$; n.s. | $F = 2.6$; n.s. | M = F; R > S |
| Shell thickness (mm) | 4.1 ± 1.0 | 3.5 ± 1.8 | 4.5 ± 3.2 | 3.2 ± 0.7 | $F = 13.4$; $P < 0.05$ | $F = 11.4$; $P < 0.05$ | $F = 0.2$; n.s. | M > F; R > S |
| Aperture height (mm) | 62.9 ± 7.0 | 61.4 ± 7.6 | 60.7 ± 6.1 | 57.6 ± 6.9 | $F = 22.0$; $P < 0.05$ | $F = 13.3$; $P < 0.05$ | $F = 0.1$; n.s. | M > F; R > S |
| Aperture width (mm) | 38.8 ± 4.8 | 37.5 ± 4.3 | 37.4 ± 4.1 | 34.8 ± 4.1 | $F = 77.3$; $P < 0.05$ | $F = 0.1$; n.s. | $F = 3.3$; n.s. | M = F; R > S |
| Shell weight (g) | 144.4 ± 57.0 | 111.6 ± 57.2 | 139.8 ± 45.4 | 104.1 ± 59.3 | $F = 19.9$; $P < 0.05$ | $F = 2.7$; n.s. | $F = 2.6$; n.s. | M = F; R > S |
| Total weight (g) | 235.2 ± 77.0 | 203.9 ± 84.1 | 230.9 ± 69.8 | 169.9 ± 70.7 | | | | |
| Wet weight (g) | 81.5 ± 23.1 | 73.5 ± 25.8 | 72.3 ± 17.5 | 60.2 ± 22.9 | $F = 21.7$; $P < 0.05$ | $F = 17.8$; $P < 0.05$ | $F = 0.53$; n.s. | M > F; R > S |
| Dry weight (g) | 29.17 ± 9.56 | 26.39 ± 10.48 | 26.71 ± 6.80 | 21.46 ± 10.02 | $F = 18.69$; $P < 0.05$ | $F = 8.90$; $P < 0.05$ | $F = 2.13$; n.s. | M > F; R > S |

*Note*: independent variables: habitat (rock, sand) and sex; dependent variables: biometric variables. *F*, test value; *P*, 95% confidence interval; n.s., nonsignificant differences.

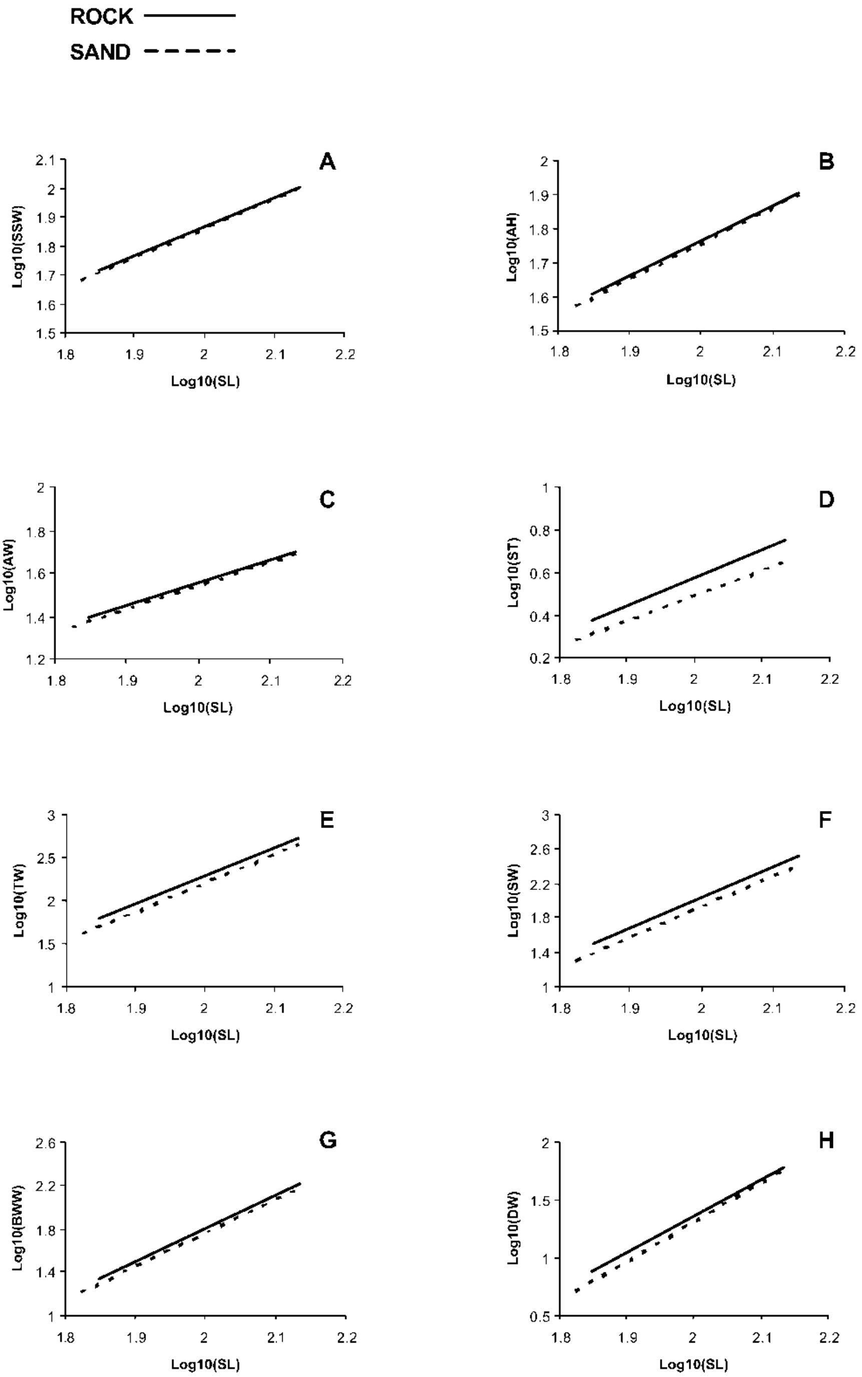

FIGURE 3 Linear relationships (data $\log_{10}$ transformed) between shell length (independent variable) and the other biometric variables (dependent variables) measured for rock and sand samples of *R. venosa.* (A) Shell shoulder width/shell length; (B) aperture height/shell length; (C) aperture width/shell length; (D) shell thickness/shell length; (E) total weight/shell length; (F) shell weight/shell length; (G) body wet weight/shell length; (H) body dry weight/shell length.

TABLE IV Equations and significance level (ANOVA) of the linear regressions between the biometric variables measured for rock and sand *Rapana* specimens.

| | *Regression equation, $R^2$* | *ANOVA* |
|---|---|---|
| $\log_{10}$SL/$\log_{10}$SSW | | |
| Rock (244) | $\log_{10}\mathrm{SWW} = -0.131 + 1.00\ \log_{10}\mathrm{SL}$;<br>$R^2 = 74.4\%$ | $F = 703.41$; $P < 0.01$ |
| Sand (302) | $\log_{10}\mathrm{SWW} = -0.209 + 1.04\ \log_{10}\mathrm{SL}$;<br>$R^2 = 81.9\%$ | $F = 1358.12$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$AH | | |
| Rock (240) | $\log_{10}\mathrm{AH} = -0.345 + 1.05\ \log_{10}\mathrm{SL}$;<br>$R^2 = 67.5\%$ | $F = 493.28$; $P < 0.01$ |
| Sand (301) | $\log_{10}\mathrm{AH} = -0.377 + 1.07\ \log_{10}\mathrm{SL}$;<br>$R^2 = 74.2\%$ | $F = 836.75$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$AW | | |
| Rock (240) | $\log_{10}\mathrm{AW} = -0.545 + 1.05\ \log_{10}\mathrm{SL}$;<br>$R^2 = 62.0\%$ | $F = 387.70$; $P < 0.01$ |
| Sand (301) | $\log_{10}\mathrm{AW} = -0.642 + 1.09\ \log_{10}\mathrm{SL}$;<br>$R^2 = 84.1\%$ | $F = 1576.16$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$ST | | |
| Rock (233) | $\log_{10}\mathrm{ST} = -2.08 + 1.33\ \log_{10}\mathrm{SL}$;<br>$R^2 = 25.0\%$ | $F = 77.8$; $P < 0.01$ |
| Sand (301) | $\log_{10}\mathrm{ST} = -1.88 + 1.18\ \log_{10}\mathrm{SL}$;<br>$R^2 = 32.1\%$ | $F = 141.08$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$TW | | |
| Rock (204) | $\log_{10}\mathrm{TW} = -4.13 + 3.21\ \log_{10}\mathrm{SL}$;<br>$R^2 = 71.7\%$ | $F = 510.53$; $P < 0.01$ |
| Sand (302) | $\log_{10}\mathrm{TW} = -4.55 + 3.37\ \log_{10}\mathrm{SL}$;<br>$R^2 = 86.2\%$ | $F = 1880.84$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$SW | | |
| Rock (114) | $\log_{10}\mathrm{SW} = -5.04 + 3.54\ \log_{10}\mathrm{SL}$;<br>$R^2 = 69.8\%$ | $F = 259.29$; $P < 0.01$ |
| Sand (147) | $\log_{10}\mathrm{SW} = -5.33 + 3.63\ \log_{10}\mathrm{SL}$;<br>$R^2 = 79.2\%$ | $F = 552.88$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$BWW | | |
| Rock (211) | $\log_{10}\mathrm{BWW} = -4.31 + 3.05\ \log_{10}\mathrm{SL}$;<br>$R^2 = 67.1\%$ | $F = 426.83$; $P < 0.01$ |
| Sand (298) | $\log_{10}\mathrm{BWW} = -4.54 + 3.15\ \log_{10}\mathrm{SL}$;<br>$R^2 = 77.1\%$ | $F = 998.66$; $P < 0.01$ |
| $\log_{10}$SL/$\log_{10}$DW | | |
| Rock (211) | $\log_{10}\mathrm{DW} = -4.99 + 3.17\ \log_{10}\mathrm{SL}$;<br>$R^2 = 64.5\%$ | $F = 379.02$; $P < 0.01$ |
| Sand (298) | $\log_{10}\mathrm{DW} = -5.52 + 3.41\ \log_{10}\mathrm{SL}$;<br>$R^2 = 70.6\%$ | $F = 710.00$; $P < 0.01$ |

*Note*: $R^2$, regression coefficient; $F$, test value, $P$, 99% confidence interval; SL, shell length; SSW, shell shoulder width; AH, aperture height; AW, aperture width; ST, shell thickness; TW, total weight; SW, shell weight; BWW, body wet weight; DW, body dry weight.

mating and spawning. Contrary to the observations of Gomoiu (1972) in the Black Sea, in winter *Rapana* was still foraging on the breakwaters, suggesting that part of the introduced population is resident all year round on this type of substratum.

During the whole experimental period juveniles of *Rapana* have never been observed in the wild. Smaller individuals were never found when clearing of the whole surface of squares of 15 × 15 cm of the breakwaters, on four sampling dates. Only two small dead specimens (4 and 25 mm, respectively) were found stranded on the beach after a big storm in November 2001 (pers. observation). Rinaldi (1985) found hundreds of small whelks (size: 12–30 mm) stranded on the shore of Rimini (Emilia-Romagna, Italy) after a big storm, but since then no other information have been made available to us. The question of the paucity of juvenile specimens is an open question also in other localities where *R. venosa* has been introduced: Mann and Harding (2000) did not report *Rapana* juveniles in

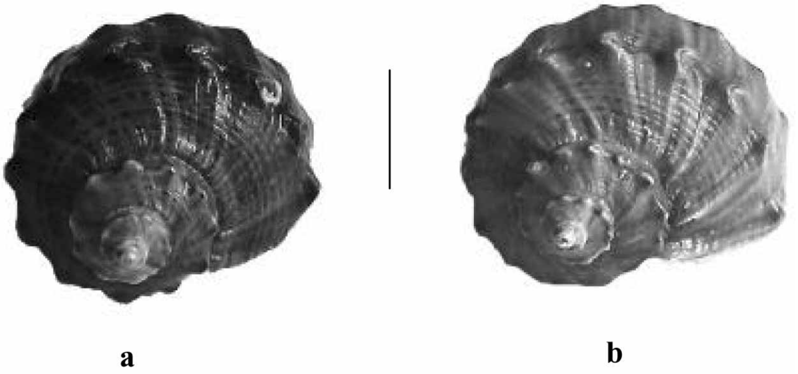

FIGURE 4 Photograph of the two dominant shell morphotypes of *R. venosa*: *a* = rock dominant morph '011000', *b* = sand dominant morph '200000'. Scale bar: 5 cm.

Chesapeake Bay either in stranded animals on exposed beaches after storms, or in oyster dredge, crab pots, patent tongs and crab dredge samples; however, they stated that the absence of very small individuals from collections should not be viewed as definitive evidence of their absence in the field as the collection methods utilised are size selective. Also, Gomoiu (1972) reports small specimens were collected on the Romanian shore after a storm, but no observations in the wild. Juveniles could be living in a peculiar habitat that has not been identified yet.

The adult individuals collected on Cesenatico breakwaters statistically differ from individuals collected from sand localities in biometry, shell colour and epibionts cover (Tab. VII). These differences and our field observations suggest a relatively sedentary behaviour of the whelks living on breakwaters, that are probably living for long periods on the rocky environment. The possible influence of the environmental variables on the observed characteristics of *R. venosa* shells is briefly discussed below.

*Rapana* dominant shell morphotypes appear cryptic with regards to the substratum, indicating the possibility of a selective predation. Predation has been reported by Parsonage and Hughes (2002) as the agent responsible for selection of colour morphs for *Littoraria* (Gastropoda, Littorinidae). In fact, high densities and richness of crabs such as *Pachygrapsus marmoratus, Eriphia verrucosa* and *Pilumnus hirtellus* have been observed on artificial breakwaters (Savini, unpublished data). It is also known from laboratory observations by Mann *et al.* (2002) in Chesapeake Bay that crabs (*Callinectes sapidus*) are voracious predators of small *Rapana.*

TABLE V Frequencies of the main shell morphotypes in rock and sand *Rapana* samples. The category 'others' includes 32 and 34 morphs for rock and sand specimens, respectively (each morph with a frequency <2%).

| *Morph code* | *Percentage frequency on rock specimens (n = 244)* | *Percentage frequency on sand specimens (n = 302)* |
|---|---|---|
| 110000 | 31 | 17 |
| 200000 | 5 | 28 |
| 101000 | 6 | 6 |
| 111000 | 9 | 0 |
| 210000 | 4 | 6 |
| 010000 | 7 | 4 |
| 001000 | 3 | 8 |
| Others (<2% each) | 35 | 31 |

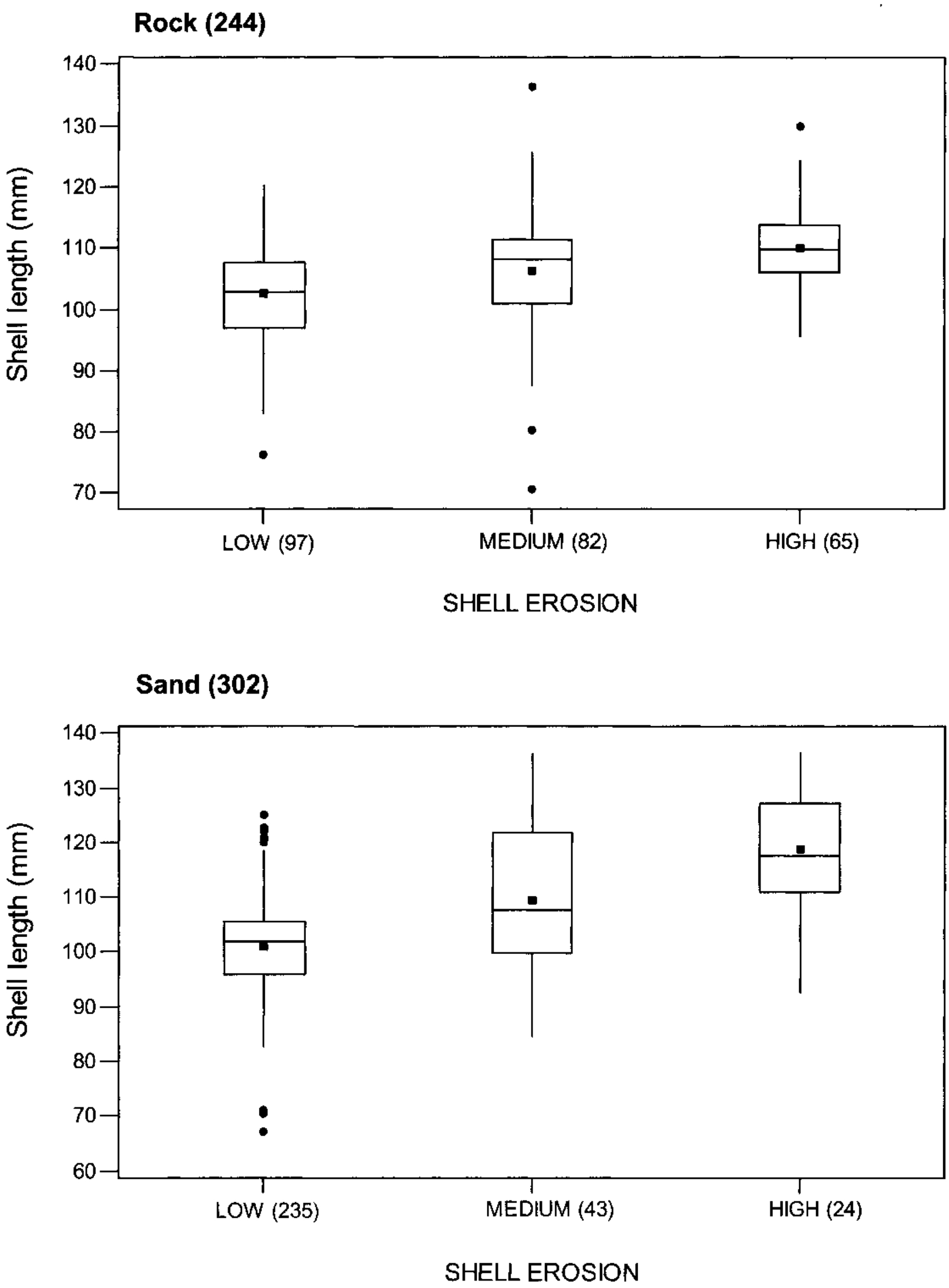

FIGURE 5 The distributions of shell length in function of low, medium and high shell erosion in sand and rock *Rapana* specimens are described by means of box-and-whiskers plot, in which minimum and maximum values (the 'whiskers' extremities), the out-layer values (the black circles), the 25th and the 75th percentiles (the 'box' bottom and top, respectively), the mean (the black square) and the median (the 'box' intermediate line) are shown.

TABLE VI Frequencies of the main epibionts found on rock and sand *Rapana* specimens.

| *Epibionts* | *Percentage frequency on rock specimens (n = 244)* | *Percentage frequency on sand specimens (n = 302)* |
|---|---|---|
| *Anadara demiri* | 3 | 0 |
| Anemones | 24 | 5 |
| Barnacles | 48 | 7 |
| Bryozoans | 35 | 5 |
| Encrusting red algae | 16 | 0 |
| Green algae turf | 69 | 2 |
| *Mytilus galloprovincialis* | 78 | 4 |
| *Nassarius reticulatus* egg cases | 3 | 6 |
| Oysters | 49 | 8 |
| Serpulids | 93 | 13 |

Furthermore, predator pressure could act as a selective agent toward the development of thicker shells. This phenomenon has been shown by Vermeij (1992) for marine snails of the genus *Littorina* and *Nucella.*

Bigger dimensions and thicker shells of *Rapana* specimens on breakwaters could also be a consequence of the large availability of food resources present in this habitat. In gastropods $CaCO_3$ deposition is determined by the environmental availability of $Ca^{2+}$ and by the metabolic production of $CO_2$ (Nicol, 1967). Since environmental availability of calcium carbonate is not limiting in estuarine and marine environments, and breakwaters are extremely rich in potential preys for *Rapana*, high food availability would drive increasing metabolic production of $CO_2$, which can be used to build up a thicker shell. Both visual observations and the amount/type of epibionts present on the shell of breakwater samples (encrusting red algae and green algal turf) give an indication of an exposed lifestyle. Thus, contrary to sand specimens that spend most of the day burrowed into the sand (Harding and Mann, 1999), rock specimens probably spend much time in feeding and growing quicker.

Rock shells appeared more eroded than sand shells. Shell erosion is a consequence of wave action, sand abrasion, epibionts cover and drilling parasites (Day *et al.*, 2000). Many shells were found drilled by the clionid *C. lobata*, an Atlantic ubiquitous species never observed in the Mediterranean Sea (Bavestrello, pers. comm.). At the moment, there are no explanations of how the clionid reached the North Adriatic. It would be of great interest to examine *Rapana* shells from the native areas and from other areas of introduction with the purpose of understanding if *R. venosa* could be the vector responsible for the introduction of the clionid, or if *C. lobata* reached the Adriatic Sea by other means.

In conclusion, this investigation points out how breakwaters could represent preferential sites for the maintenance of *R. venosa* populations in the Northern Adriatic Sea as they

TABLE VII Main differences between *Rapana* specimens collected on rock and sand substrata.

| *Rocky habitat* | *Sandy habitat* |
|---|---|
| >average dimensions | <average dimensions |
| >average weight | <average weight |
| >average shell thickness | <average shell thickness |
| Dark shells with scarcely evident stripes and dark shell margins | Pale brown shells with evident stripes and white shell margins |
| Consistent epibionts cover | Scarce epibionts cover |
| High shell erosion | Scarce shell erosion |
| High incidence of bore holes | Scarce incidence of bore holes |

are utilised as spawning and feeding grounds, and raises a series of open questions on how the features of the habitat of introduction could influence population structure, biometry and morphology of a nonindigenous species such as the 'Rapa whelk' promoting or controlling its population status and distribution.

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