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ИнБЮМ – IBSS

Морской биологический журнал
Marine Biological Journal
2024, vol. 9, no. 2, pp. 3–18
https://marine-biology.ru

SCIENTIFIC COMMUNICATIONS

UDC 594.329.65-15(262.5.04)

PECULIARITIES OF POPULATION STRUCTURE AND BIOCENOTIC RELATIONSHIPS OF *RAPANA VENOSA* (VALENCIENNES, 1846) (GASTROPODA, MURICIDAE) IN THE DONUZLAV BAY (THE BLACK SEA)

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Received by the Editor 15.10.2021; after reviewing 03.02.2022;
accepted for publication 19.02.2024; published online 20.05.2024.

The Western Pacific gastropod *Rapana venosa* (Valenciennes, 1846) is classified among the hundred most dangerous invasive species of the Black and Mediterranean seas. Moreover, it is recognized as a dangerous invader in a number of coastal water areas on both sides of the Atlantic Ocean that determines the relevance of the study of population characteristics and biocenotic relationships of the rapa whelk in the areas of its invasion. The analysis of a previously unexplored *R. venosa* population in the Donuzlav Bay (the Northwestern Crimea) of the Black Sea in 2020 showed as follows: in the occurrence of an abundant and diverse food base, the rapa whelk does not form mass aggregations and, consequently, does not significantly affect benthic biocenoses. This fact is also confirmed by the ratio of biomass of the predatory mollusc and its prey. *R. venosa* mean biomass in the study area was 3.8 g·m^{-2}, and the mean biomass of its food objects (Bivalvia) was 162.8 g·m^{-2}. The features of the population structure and biocenotic relationships of the rapa whelk in the Donuzlav Bay are considered and discussed for the first time. Direct underwater observations and indirect evidence indicate that the distribution of this invader is controlled by aboriginal predators, crabs. The main species limiting *R. venosa* abundance in the study area is the crab *Carcinus aestuarii* Nardo, 1847.

Keywords: biocenoses, algae, invasive species, crabs, molluscs, predator–prey

A large predatory gastropod *Rapana venosa* (Valenciennes, 1846) entered the Black Sea from the Sea of Japan in the early 1940s and significantly affected bottom biocenoses [Bondarev, 2014; Chukhchin, 1961b, c; Pereladov, 2013; Snigirov et al., 2013] and the sea ecosystem in general [Alien Species Alert, 2004; Chukhchin, 1984; Katsanevakis et al., 2014; Zolotarev, 1996]. *R. venosa* mostly feeds on bivalves [Bondarev, 2010, 2011, 2015a, 2016, 2020; Chukhchin, 1961b, c, 1984; Kosyan, 2013; Savini et al., 2004; Zolotarev, Yevchenko, 2010] whose complex plays an important role of a biofilter in the Black Sea ecosystem [Zenkevich, 1963]. The Black Sea rapa whelk tends to completely exterminate its food objects within the habitat [Chukhchin, 1961b], and this fact was the ground for its inclusion in the top 100 of the most dangerous invasive species of the Black Sea [Feneva, Kosyan, 2018] and Mediterranean Sea [Streftaris, Zenetos, 2006]. In the USA, various methods to control the unwanted invader are being developed, including extensive public education programs and paying a bounty to remove any collected rapa whelk and its egg capsules [Alien Species Alert, 2004].

The success of the Black Sea colonization by *R. venosa* is believed to be related not only to tolerance to abiotic environmental factors, but also to occurrence of a rich food supply along with the absence of trophic competitors and predators [Alien Species Alert, 2004; Chukhchin, 1984; Katsanevakis et al., 2014; Zolotarev, 1996]. The rapa whelk has filled a free niche among second-order heterotrophs [Chukhchin, 1984], and the main factor limiting its development is food [Chukhchin, 1961b]. At the same time, in the most northwestern Black Sea, with numerous food resources (molluscs), *R. venosa* is not abundant [Zolotarev, 1996]. The Donuzlav Bay is one of the areas characterized by the occurrence of a wide range of food items, but the rapa whelk is not widely distributed there.

The first study of the Donuzlav Bay fauna was conducted in 1981, 20 years after a channel was dug, and the bay was connected with the sea. As found, since then, fauna of the formerly hypersaline lake has acquired a benthos composition characteristic of the Black Sea, and biocenoses occurring at appropriate sea depths have been formed there. As revealed, gastropods predominantly inhabit sand and coquina biotopes on algae and sediments, where the rapa whelk was also found [Chukhchin, 1992]. *R. venosa* occurrence in benthic communities of the Donuzlav Bay was established in subsequent investigations as well [Boltacheva et al., 2002; Kosyan, 2013, 2016; Pereladov, 2013]. As noted, the rapa whelk distribution was limited to an area near the strait connecting the Donuzlav Bay with the sea, and its settlement density at the detection site was less than 0.01 ind.·m^{-2}. Importantly, the diversity and quantity of food objects did not limit *R. venosa* distribution throughout the bay [Pereladov, 2013].

Based on observations in an aquarium, one species that possibly could control *R. venosa* distribution is the blue crab *Callinectes sapidus* Rathbun, 1896 [Harding, 2003]. This rather large crab (its carapace width is up to 230 mm) from the western Atlantic is already widespread in the Mediterranean Sea. In the Black Sea, the species was first recorded in 1967 but is still rare [Makarov, 2004]. In the Donuzlav Bay, *C. sapidus* has not been revealed yet. As assumed, a limiting role in the rapa whelk distribution and abundance is played by local species of blue crabs which may consume its juveniles in shallow waters [Pereladov, 2013]. To date, biological methods of controlling *R. venosa* have been poorly investigated [Feneva, Kosyan, 2018].

The study of *R. venosa* structure and biocenotic relationships in local populations, where its development is limited by natural factors, can both contribute to understanding the processes of equilibrium interaction between this invasive species and native fauna and provide insight into possible ways of limiting the mollusc distribution. The aim of this work was to obtain such information on the example of a local population of the rapa whelk in the Donuzlav Bay. Population structure of *R. venosa* was considered: its distribution pattern and size, weight, age, and sex composition in the study area. When analyzing biocenotic relationships, the confinement of the rapa whelk to specific biocenoses was established. Attention was focused on feeding spectrum and relationships with predators.

MATERIAL AND METHODS

The Donuzlav Bay is located on the western coast of Crimea (Fig. 1) and borders the Tarkhankut Peninsula from the south. The bay length is about 30 km, and its width averages 5 km. The widest spot (8.5 km) is at the mouth which was originally separated from the Black Sea by a sandy spit.

In 1961, a channel of about 200 m wide was dug, and two sandy spits were formed. The northern part of the former spit is called the Belyaus Spit, while the southern is called the Southern Spit. The salinity of most water area of the modern bay corresponds to the Black Sea salinity (17.5–18.2‰). In summer, the water temperature rises to +24…+25 °C, and in shallows, the value is even higher. In winter, it drops to 0 °C, and the bay is partially or completely covered with ice. Water exchange between the sea and bay occurs practically throughout its entire area and involves the water column from the surface to the bottom [Zuev, Boltachev, 1999].

Fig. 1. Schematic map of the study area with indication of the sampling sites and population abundance (A) of *Rapana venosa* (ind.·m^{-2})

In most areas of the bay, depths of less than 4–5 m prevail; in the central basin, the depth reaches 28 m. Bottom sediments are chiefly represented by multigrain sands silted to varying degrees, while in shallow areas and in the deepest part of the bay, silts predominate. At various depths, along the bay perimeter, coquina occur, as well as rocky outcrops of hard calcareous sandstones in the form of slabs, individual fragments, and stone rubble.

There are eight main biocenoses within the bay: sand with *Venus*, sand with *Chara*, *Chara*, *Zostera* on sandy mud, mussel and mussel–oyster coquina, silty sand, silt with *Abra*, and deep-water mud. It is consistent with the data of the previous study [Chukhchin, 1992].

The distribution of *R. venosa*, its potential prey, and predators was examined visually *in situ* from the bay mouth to the inner area. Benthos was sampled in the summer–autumn period of 2020 (28 June – 28 September); molluscs were collected with scuba diving equipment, totally from the area of 1,000 m^2 at each station. At 7 stations within the bay, 300 specimens of the rapa whelk were sampled. At each station, *R. venosa* settlement density was estimated based on the results of sampling (Fig. 1); in the mollusc aggregations, with a 1 × 1 m frame. To determine the quantitative and taxonomic composition of food items of the rapa whelk in biotopes, macrobenthos was sampled with the 1 × 1 m frame simultaneously from the surface of solid substrate and algae and from the surface layer of loose sediments (5-cm layer). Then, it was washed through a sieve with a mash diameter of 5 mm. One frame sample was taken at each station on a characteristic spot of the water area.

The feeding spectrum of the rapa whelk and crabs was studied by prey items taken directly from feeding individuals. In total, 59 feeding *R. venosa* and 72 feeding crabs were found. During feeding, rapa whelks hold their prey with leg muscles. Crabs feed on their prey while clamping it in the claw. In 20 *R. venosa* individuals, food contents of the gastrointestinal tract were investigated under an MBS-10 stereo microscope.

When analyzing each *R. venosa* specimen, we determined the following parameters: shell height (SH) from the apex to the end of the siphonal canal; wet weight of the mollusc with its shell (total weight, TW); sex (F, female; M, male); and age. In our samples, only mature individuals were taken into account. Sex was determined by the presence/absence of penis and color of gonads, and age was established by spawning marks [Bondarev, 2015b; Chukhchin, 1961a, c]. In parallel, we sampled crabs – potential predators of the rapa whelk; their size was estimated by carapace width (CW). The length of valves (L) of bivalves taken directly from feeding *R. venosa* was measured as well. Since soft tissues of these preys were partially or completely eaten, data on their mass are not representative. The quantitative proportion of each prey species of *R. venosa* (Q_1, %) in the total amount of recorded food objects was estimated. For comparison, according to sampling data, the mean value of the quantitative contribution (Q_2, %) of bivalves on which the rapa whelk feeds was determined in Bivalvia taxocenes of the Donuzlav Bay. The mean biomass of *R. venosa* and bivalves in the study water area was estimated.

Linear sizes of mollusc shells were established, and crab carapaces were measured with a caliper with an accuracy of 0.1 mm. Wet weight of individuals was determined on electronic scale WLM-200 with an accuracy of 0.1 g.

Graphs were plotted, and mean values (M) and standard deviation (σ) were calculated using programs within MS Office Excel, v. 10.

RESULTS

Population structure of *Rapana venosa*. Shell height values of sexually mature rapa whelks in the Donuzlav Bay are characterized by a wide range (32.1–135.0 mm), the same as wet weight values of studied molluscs (4.0–365.2 g). In the sample, males predominate (57.7%), and their size and weight have higher maximum and mean values (Table 1).

Table 1. Size and weight characteristics of *Rapana venosa* in the Donuzlav Bay divided by sex: F, females; M, males; *N*, number of individuals; SH, shell height; TW, individual wet weight; min–max, minimum and maximum values; *M*, mean value; *σ*, standard deviation

Sex	*N* (%)	SH, mm			TW, g		
		Min–max	*M*	*σ*	Min–max	*M*	*σ*
F	127 (42.3)	32.1–126.0	82.8	18.6	4.0–335.1	107.5	76.7
M	173 (57.7)	34.4–135.0	89.7	20.1	6.1–365.2	140.8	96.9
F + M	300 (100)	32.1–135.0	86.6	19.8	4.0–365.2	126.8	90.3

Three components of population structure – size (determined by shell height), age (established by spawning marks), and weight ones – with regard to sex are provided in Fig. 2. In the size group of 30–40 mm, females predominate (90%); in the group of 41–50 mm, the abundance of males and females is equal; and in the larger-size groups, except for that of 61–70 mm (F, 65%; M, 35%), males prevail. As SH increases, the proportion of males rises. In the size group of 130 mm and more (1% of the sample), there are no females (Fig. 2A).

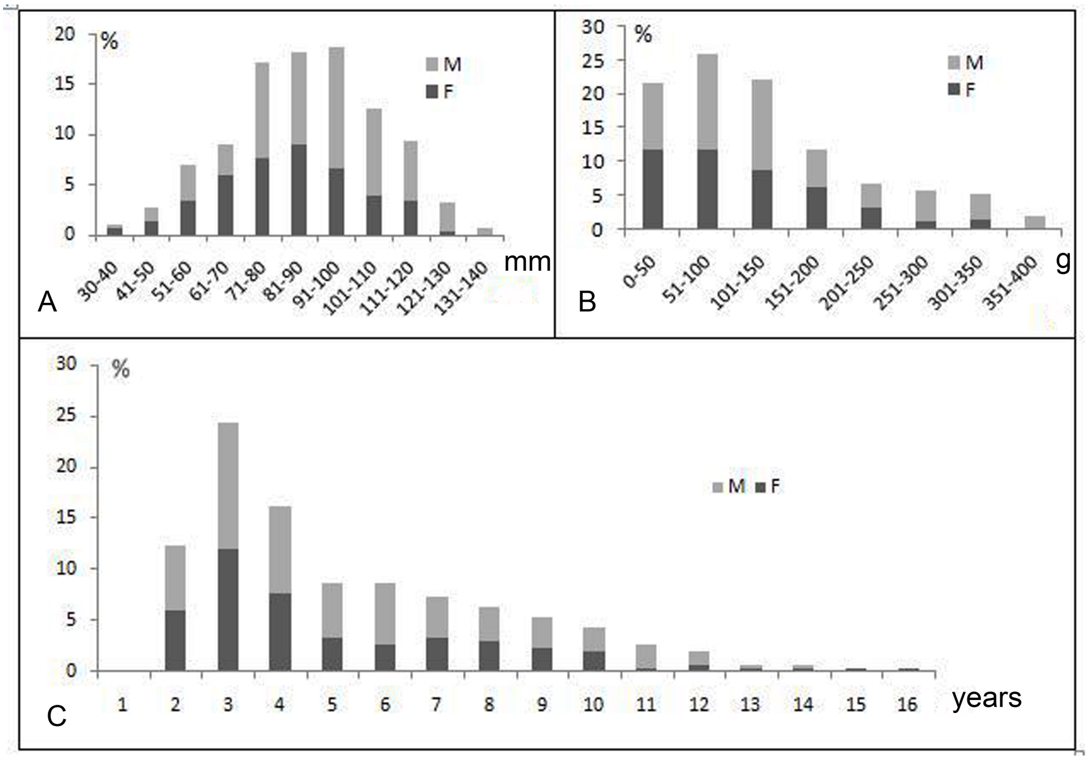

Fig. 2. Population structure of *Rapana venosa* in the Donuzlav Bay divided by sex (F, females, M, males): A, size; B, weight; C, age

In the group with individual weight up to 50 g, females predominate (54%); in all other ones, males prevail. In the group with the highest TW (> 350 g; 1.7% of the sample), there are no females (Fig. 2B), the same as in the group with the maximum SH. The mean biomass of the rapa whelk in the study area was 3.8 $g \cdot m^{-2}$.

In the age groups of 2 to 12 years, males predominate (56%); in the groups of 2 to 4 years, sex ratio is close to parity (F, 49%; M, 51%). As the age increases, the proportion of males rises. Notably, in the groups of 13 and 14 years (1.4% of the sample), the proportions of males and females are equal. Out of rapa whelks at the age of 15 and 16 years (0.35% of the sample each), only females are revealed.

Biocenotic relationships of *Rapana venosa*. In the Donuzlav Bay, the mollusc was found in a depth range of 1.0–5.0 m in biocenoses of sand with *Venus*, sand with *Chara*, coquina, *Chara*, and *Zostera*. Rapa whelks were observed copulating, forming egg capsules, feeding, and moving on the substrate.

The mollusc distribution is irregularly patchy. Its maximum concentrations in June–September are related to spawning; therefore, most *R. venosa* were sampled in areas with hard substrates (rocky outcrops or individual stones) where females attach egg capsules. Sometimes, other rapa whelks, algae, or objects of anthropogenic origin serve as a substrate for attaching egg capsules.

The rapa whelk and its egg capsules were not found in the inner area of the bay despite the abundance and diversity of potential Bivalvia food items (oysters, mussels, scallops, *Venus*, *Cardium*, and *Anadara*) and the occurrence of rocky substrate. The highest density of *R. venosa* is characteristic of the bay spots with patchy combination of different biocenoses: it provides an opportunity for the species development at all stages of ontogenesis after larvae settling on the substrate. Individuals of all sizes are found there, and the distribution density is maximum, up to 0.1 ind.·m^{-2} (Fig. 1). When both copulating and feeding, *R. venosa* can form groups of several individuals (up to 10 ind.·m^{-2}).

Feeding spectrum. We found 43 *R. venosa* individuals feeding on Bivalvia (14.3% of the total abundance). The food objects of the mollusc identified for the study area are listed in Table 2.

Table 2. Species list of molluscs – food objects of *Rapana venosa* in the Donuzlav Bay, their size (L), proportion as prey (Q_1), and mean value of their quantitative input to the Bivalvia taxocene (Q_2)

Taxon	L, mm	Q_1, %	L, mm	Q_2, %
Cerastoderma glaucum (Bruguière, 1789)	28.0–40.2	4.7	6.1–42.6	3.9
Chamelea gallina (Linnaeus, 1758)	11.6–27.8	34.8	5.0–27.6	20.4
Flexopecten glaber (Linnaeus, 1758)	37.7	2.3	9.1–60.2	5.1
Gastrana fragilis (Linnaeus, 1758)	26.3	2.3	12.2–26.8	0.1
Gouldia minima (Montagu, 1803)	7.2	2.3	5.5–10.6	2.0
Irus irus (Linnaeus, 1758)	14.4	2.3	10.2–15.2	0.2
Lucinella divaricata (Linnaeus, 1758)	5.2–6.7	4.7	5.0–7.9	4.0
Modiolus adriaticus Lamarck, 1819	25.2–38.0	25.5	6.5–35.2	10.2
Mytilaster lineatus (Gmelin, 1791)	15.0–23.7	4.7	5.0–24.1	22.1
Parvicardium exiguum (Gmelin, 1791)	12.0–12.5	4.7	5.0–14.1	17.7
Pitar rudis (Poli, 1795)	12.0	2.3	5.5–12.7	3.3
Polititapes aureus (Gmelin, 1791)	14.5–25.0	9.4	6.0–27.0	5.1
Other Bivalvia	–	–	5.4–84.2	5.9

The established feeding spectrum of the rapa whelk in the study area covers 12 Bivalvia species, and their sizes (L) vary from 5.2 mm (*Lucinella divaricata*) to 40.2 mm (*Cerastoderma glaucum*). Among *R. venosa* preys, *Chamelea gallina* prevailed: it was found in 34.8% of individuals feeding on Bivalvia. *Modiolus adriaticus* ranked second in frequency of capture by the rapa whelk (25.5%). It was followed by *Polititapes aureus* (9.4%). Remaining species were registered as *R. venosa* preys once (2.3%) or twice (4.7%) each (Table 2).

In the area of the rapa whelk habitat, the mean biomass of Bivalvia on which it feeds is 162.8 g·m^{-2}.

In the Donuzlav Bay, in addition to bivalves, *R. venosa* feeds on the green alga *Chara* sp. (Fig. 3). Its fragments were recorded in esophagus and stomach of 16 molluscs, and this number exceeded the number of the rapa whelk feeding on *Ch. gallina*. Thus, the proportion of feeding *R. venosa* in the bay was about 20% of the total sample.

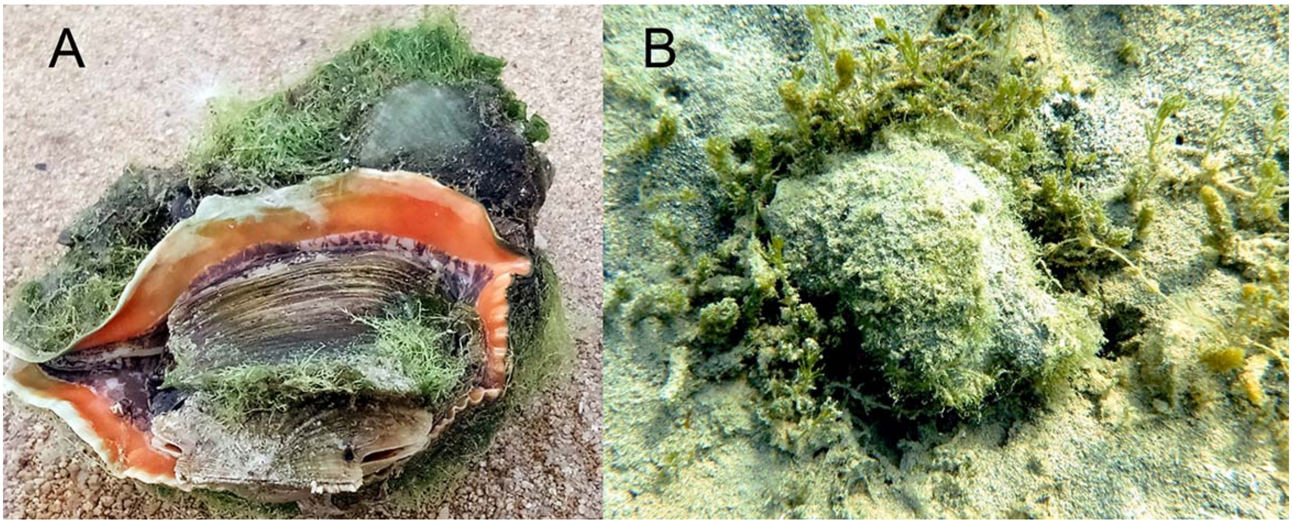

Fig. 3. *Rapana venosa* feeding on the bivalve *Flexopecten glaber* (A) and the green alga *Chara* sp. (B)

Predator–prey. According to *in situ* observations, the Mediterranean green crab *Carcinus aestuarii* Nardo, 1847 (Fig. 4A) feeds on the rapa whelk. In accordance with our data, in the Donuzlav Bay, males of this crab reach a weight of 168 g with a carapace width (CW) of 86.2 mm. The distribution density of *C. aestuarii* by visual assessment during daylight averages 0.05 ind.·m^{-2}.

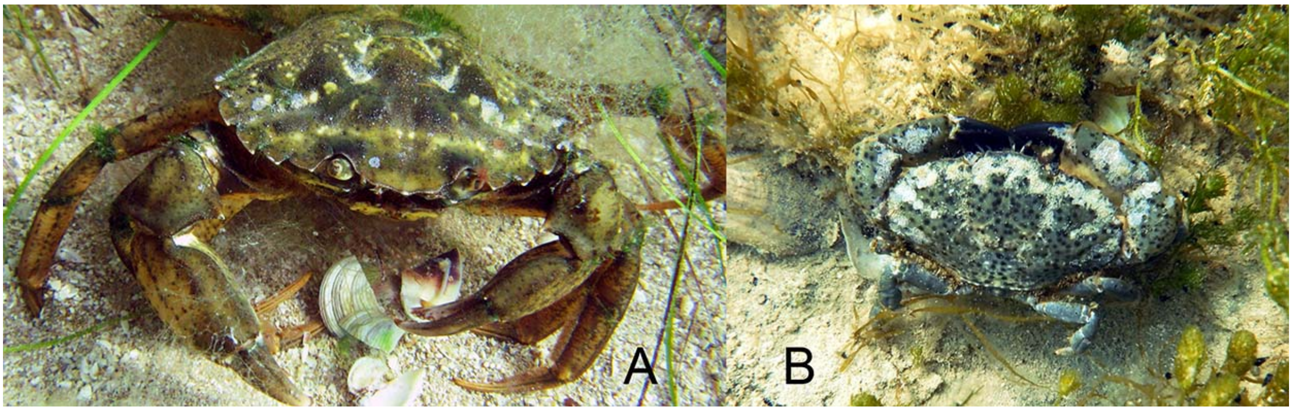

Fig. 4. Crabs – predators of the rapa whelk: A, *Carcinus aestuarii* (CW of 78.2 mm) broke *Chamelea gallina* shell and feeds on its meat, the Donuzlav Bay, depth of 2.8 m; B, *Xantho poressa* (CW of 46 mm) feeds on *Mytilaster lineatus*

In the Donuzlav Bay, the Mediterranean green crab is the object of active amateur fishing; however, it maintains high abundance due to a rich food base including bivalves and gastropods, *inter alia* the rapa whelk. *In situ* observations (5 cases) showed as follows: *C. aestuarii* feeds on *R. venosa* juveniles (SH up to 22 mm) first crushing a shell with its claws. It is not the only mollusc among the crab food items. With its strong claws, *C. aestuarii* is capable of crushing both a relatively thin-walled shell of *M. adriaticus* (3 observations) and a thicker-walled shell of *Ch. gallina* (14 observations) (Fig. 4A). These two Bivalvia species, the same as the rapa whelk, are food objects of the Mediterranean green crab.

Relatively small (SH up to 65 mm) *R. venosa* individuals were repeatedly (6 observations) attacked by *C. aestuarii*, with the crab not releasing its prey and dragging it along the bottom even in case of alarm (a close approach of a diver). Larger rapa whelks of the Donuzlav Bay often have traces of crab attacks – characteristic traces of damage to basal and palatal edges of the mouth (Fig. 5) [Bondarev, 2013]. The height of the largest damaged shell at the time of injury was 122 mm, which means that even large *R. venosa* can be attacked by crabs. More than a half (52%) of the mollusc individuals in the study area have at least one scar on the shell from damage by crab claws in different places, from its top to its last whorl.

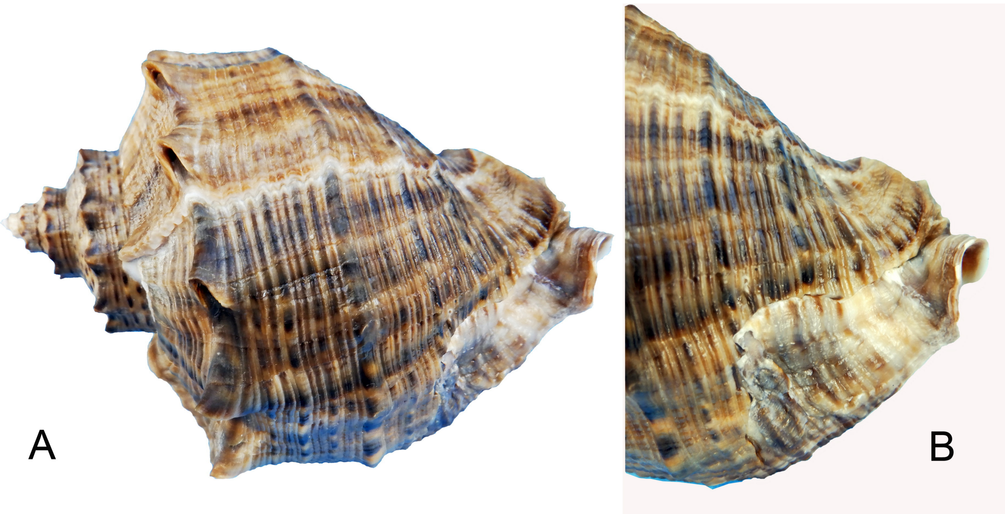

Fig. 5. A, dorsal side of *Rapana venosa* shell (SH of 90.0 mm) with a regenerated area; B, the basal part of the shell (×1.5)

In general, the feeding spectrum of *C. aestuarii* is close to that of *R. venosa*, as it includes all Bivalvia species on which the rapa whelk feeds. Also, it includes fish, algae, and *R. venosa* itself.

Apparently, a potential predator for the rapa whelk juveniles is the jaguar round crab *Xantho poressa* (Olivi, 1792) (Fig. 4B). This small crab with a carapace width (CW) up to 42.3 mm [Kobyakova, Dolgopolskaya, 1969], and possibly up to 47 mm [Makarov, 2004], has relatively large claws and is capable of crushing shells of *Mytilaster lineatus* (Gmelin, 1791) (Fig. 4B) and *R. venosa* juveniles. The largest specimen of this crab for the study area (Fig. 4B), with CW of 46 mm and weight of 24.7 g, was found on rocks among *Chara* sp. thickets. In the Donuzlav Bay, this species is often encountered among stones, on mussel beds, and among algae.

Single and copulating individuals of the grey swimming crab *Liocarcinus vernalis* (Risso, 1827) were noted in the bay water area on sandy sediments. This small (CW up to 39 mm) crab [Makarov, 2004] is inferior in abundance and size to two above-mentioned species, and there is no direct evidence that it feeds on the rapa whelk. However, considering the size of its claws, *L. vernalis* is capable of crushing shells of *R. venosa* juveniles.

DISCUSSION

In material of the first study of the Donuzlav Bay benthos carried out in 1981 [Chukhchin, 1992], the size of found rapa whelks is not specified. In 2007, the mean SH of single individuals was 86 mm; absence of *R. venosa* egg capsules, juveniles, and empty shells was reported [Pereladov, 2013]. In 2009–2012 in the Donuzlav Bay on sandy sediments, 60 *R. venosa* (SH of 30–79.9 mm; age of 3–5 years) were sampled [Kosyan, 2013, 2016]. The mean size of the rapa whelk shells in our sample (SH of 86.6 mm) is close to that of individuals recorded in 2007 by M. Pereladov [2013]. Since noticeably smaller and larger rapa whelks were not registered in a sample of 2007, it can be assumed that the above mean size does not differ significantly from the extreme values.

In the mature part of *R. venosa* population in the Donuzlav Bay, there are individuals with a wide range of SH – from 32.1 to 135.0 mm. Quite a high abundance of young, 2–3-year-old, rapa whelks (52.8%) and the occurrence of 14–16-year-old ones (1.4%) (Fig. 2) indicate the sufficiency of food resources for the species.

To date, *R. venosa* with SH of 40–90 mm is most common off the Crimean coast, but this parameter can differ significantly in various populations. Most of recent rapa whelk populations off the Crimean coast consist of "dwarf" individuals – with the size (SH) at mature and old age not exceeding 50–60 mm [Bondarev, 2010, 2011, 2016]. A decline in growth rates and a clear tendency to the mollusc size drop in the Black Sea, as compared to those at the initial stage of its introduction, were recorded already in the late 1950s, and this was associated with a decrease in food base [Chukhchin, 1961b, c]. In the Kerch region, until the early 1990s, the modal size (SH) of *R. venosa* was 90–110 mm; in 1990–1994, it was 80–100 mm; in 1997–2000, SH was 55–85 mm; and in 2001–2006, it was 50–90 mm [Evchenko, 2010]. According to data of a study of 1,581 *R. venosa* in the southeastern Black Sea off the coast of Turkey in January–August 2000, the maximum size of individuals (SH) was 90.0 mm, and the mean one was (53.82 ± 0.410) mm [Sağlam, Düzgüneş, 2014].

A wide range of size and weight indicators of *R. venosa* is maintained in the Donuzlav Bay. Feeding on the alga *Chara* sp. provides additional opportunities for the rapa whelk survival by expanding its food base. Apparently, such an addition to the mollusc feeding spectrum in the bay contributes to the formation of large shells (SH up to 135 mm) and survival of old (16 years) individuals against the backdrop of the general opposite trend observed in the Black Sea. The established occurrence of mature *R. venosa* with SH of 30–50 mm corresponds to previously reported facts of coexistence of individuals differing significantly in size within local Black Sea populations [Bondarev, 2010, 2011; Pereladov, 2013].

Sex ratio F : M = 1 : 1.36 (F, 42.3%; M, 57.7%) in the studied population also indicates rather favorable conditions of its existence. In an "ideal" population, sex ratio is 1 : 1; such a ratio was recorded for the rapa whelk in the Sevastopol Bay in the late 1950s [Chukhchin, 1961a]. In modern populations of *R. venosa* in the Black and Mediterranean seas, the proportion of males usually exceeds that of females [Bondarev, 2010, 2011, 2014, 2016; Sağlam et al., 2009; Savini et al., 2004]. On average, F : M for coastal populations of the Crimean Peninsula is 1 : 1.85 (F, 35%; M, 65%); sometimes, it is 1 : 4.5 (F, 18%; M, 82%) (in 2002 in the Kerch region) [Bondarev, 2011]. F : M = 1 : 1.6 disproportion is reported for the rapa whelk of the Turkish coast of the Black Sea [Sağlam et al., 2009]. Sex ratios similar to our data are provided for *R. venosa* of the Adriatic Sea: females account for 47% of the population on sandy sediments and 43% on rocky sediments [Savini et al., 2004].

The predominance of males in *R. venosa* populations seems to be due to the fact that females incur increased energy costs for reproduction forming a cluster of capsules filled with eggs [Chukhchin, 1970]. Compensation of such energy costs is possible only if there is a sufficient food base. Deficiency in feeding results in increased mortality among females of predominantly older age, and this leads to the observed disproportion of sex ratio in *R. venosa* populations [Bondarev, 2010, 2016]. Features of the Donuzlav Bay are the parity of sexes among 13- and 14-year-old rapa whelks and the occurrence of only females in the oldest age groups, 15 and 16 years. One of the factors contributing to the survival of older females seems to be their smaller size which means that the mollusc does not require a large amount of food to sustain life.

Biocenotic relationships of *Rapana venosa*. During the first survey of the Donuzlav Bay benthos in 1981, it was noted that the mollusc is often found in its southern area in the biocenosis of coquina and is not recorded within other biocoenoses [Chukhchin, 1992]. Our studies confirmed the occurrence of the rapa whelk aggregations on coquina which are predominantly formed around rocky sediments. *R. venosa* confinement to this biocenosis in the summer–autumn period is related to the occurrence of substrate for attaching egg capsules and abundance of potential preys which mostly inhabit sandy sediments surrounding rocky outcrops. For *R. venosa*, widely distributed in the Black Sea food objects are as follows: *Ch. gallina*, *C. glaucum*, *Gastrana fragilis*, *Gouldia minima*, *L. divaricata*, *Parvicardium exiguum*, *P. aureus*, and *Pitar rudis*. Those are typical representatives of infauna of loose sediments. *Flexopecten glaber*, *M. adriaticus*, *M. lineatus*, and *P. exiguum* occur both on loose sediments and solid substrates (coquina and rocks) and on algae. According to our data, the highest density and abundance of the rapa whelk are characteristic of the Donuzlav Bay areas with coexisting different biocenoses: their patchiness provides conditions for the development of all stages of the mollusc ontogenesis from the moment of larvae settling on the bottom. On solid substrate and algae, *R. venosa* attaches egg capsules; in algae, juveniles take shelter and find food; and on loose sediments, most of the rapa whelk finds its prey.

In the summer of 2007 in the Donuzlav Bay water area, *R. venosa* was sporadically recorded at a site about 2 km from the open sea. There, the species settlement density was less than 0.01 ind.$\cdot$m^{-2}. On a spot about 4 km from the open sea, the rapa whelk was not noted at all, despite a pretty high abundance of mussel banks, live relict oysters, and scallop aggregations. In the center and in the inner area of the Donuzlav Bay, *R. venosa* was also not registered. According to local divers, it is found in significant quantities only in the water area adjacent to the channel which connects the bay with the open sea [Pereladov, 2013]. In 2009–2012, the mollusc was sampled in a sand biotope at depths of 5–8 m [Kosyan, 2013, 2016].

According to our data, in the Donuzlav Bay, the rapa whelk was encountered in a depth range of 1–5 m in biocenoses of sand with *Venus*, sand with *Chara*, coquina, *Chara*, and *Zostera*. The settlement density at most stations was < 0.01 ind.$\cdot$m^{-2}. At some sites, it increased by an order of magnitude – up to 0.1 ind.$\cdot$m^{-2} (Fig. 1); sometimes, the value reached 10 ind.$\cdot$m^{-2}.

Our finding of a wider *R. venosa* distribution and areas with a higher settlement density, as compared to those in previous studies, is explained by the nature of its distribution (aggregation and patchiness) and targeted search for the object. In the inner area of the Donuslav Bay, we also did not find the rapa whelk despite the occurrence of coquina and rocky sediments with live molluscs. Several bivalve species included in *R. venosa* feeding spectrum inhabit sand, *inter alia* mussel which occurs on rocks as well (up to 20 ind.$\cdot$m^{-2}). On rocky sediments, the density of oysters alone reaches 5 ind.$\cdot$m^{-2} on some spots [Pereladov, 2016]. Apparently, *R. venosa* distribution towards the inner area of the Donuzlav Bay is hindered by mass development of the Mediterranean green crab.

Feeding spectrum. The rapa whelk is obviously selective regarding food items (Table 2). The preference for *Ch. gallina* is especially evident; this species accounts for 20.4% of the total Bivalvia abundance in the study area and 34.8% of *R. venosa* preys. Specimens sampled in the Donuzlav Bay in 2012 on sandy sediments also predominantly fed on *Ch. gallina* [Kosyan, 2013, 2016].

The rapa whelk prefers this mollusc to other species in modern populations of loose sediments biotopes in most Black Sea areas [Bondarev, 2016, 2020; Kosyan, 2016; Zolotarev, Yevchenko, 2010]. In the northeastern Black Sea from Chauda Cape (the Crimea) to Batumi, only bivalves were recorded in *R. venosa* feeding spectrum, and out of them, *Ch. gallina* accounted for 80% [Zolotarev, Yevchenko, 2010]. Predominant feeding on this species is characteristic of the rapa whelk inhabiting sandy sediments in the bays of Sevastopol [Bondarev, 2016]. In the mollusc feeding spectrum in the Kazachya Bay (Sevastopol, the Crimea), *Ch. gallina* accounted for 80% of preys; *M. adriaticus*, 5%; *P. rudis*, 5%; *P. exiguum*, 4%; *P. aureus*, 3%; *C. glaucum*, 2%; and *G. minima*, 1% [Bondarev, 2020].

Such a group of molluscs with a similar proportion of most prey species is also characteristic of our sample from the Donuzlav Bay. The main differences are a smaller proportion of *Ch. gallina* (34.8%) and significantly higher contribution of *M. adriaticus* (25.5%) – the species accounting on average for 10.2% of the total Bivalvia abundance in the bay biocenoses (Table 2). *P. aureus* is also more frequently recorded among *R. venosa* preys (9.4% *vs.* 5.1% in biocenoses), while *M. lineatus* and *P. exiguum* are noticeably more abundant in biocenoses (22.1% and 17.7%, respectively) than among the rapa whelk preys (4.7% each). One of the factors of the revealed selectivity seems to be the size of Bivalvia individuals (Table 2). Earlier, the correspondence between the size characteristics of *R. venosa* and its preys was evaluated [Bondarev, 2016; Kosyan, 2013; Sağlam, Düzgüneş, 2014]; as shown, since the Donuzlav Bay is inhabited by quite a lot of large rapa whelks, small-sized Bivalvia species are less frequently selected as preys.

Notably, large Bivalvia representatives which were previously considered as the main food objects of *R. venosa* (*Mytilus galloprovincialis* Lamarck, 1819 and *Ostrea edulis* Linnaeus, 1758) were not registered as its preys in the study area, although both species occur in the Donuzlav Bay benthos. Moreover, feeding on the scallop *F. glaber* which forms aggregations in some bay areas with a settlement density of more than 10 ind.$\cdot$m^{-2} was recorded only once. In the immediate vicinity of numerous scallop individuals, we repeatedly registered the rapa whelk feeding on *Ch. gallina* and *M. adriaticus*.

This situation seems to be due to the fact that the largest (SH > 110 mm) *R. venosa* individuals were copulating at that time and did not feed until late September (the month to which the research season was limited). As known, during the degradation of the Gudauta Bank biocenoses and the disappearance of mussels and oysters, out of large Bivalvia, only the scallop remained. It is assumed that large bivalves were destroyed by *R. venosa*, and the scallop survived due to its ability to swim away from predators [Chukhchin, 1961b]. According to our survey, *F. glaber* reacts to the approach of a potential predator (a diver) by closing its valves without changing the position, and the rapa whelk shows no active food interest in this scallop either in natural or in laboratory conditions. In an aquarium, food reaction of *R. venosa* to *O. edulis* was weak, or there was no reaction at all [Pereladov, 2013]. Apparently, the contribution of the rapa whelk to extermination of the Black Sea oysters and scallop is overestimated. As already noted, the issue of its fatal effect on oyster settlements in the Black Sea remains debatable [Pereladov, 2013].

The mean biomass of the mollusc in the study area was 3.8 g·m^{-2}, and the mean biomass of its food objects, Bivalvia, was 162.8 g·m^{-2}. It indicates a sufficient food supply and the lack of a significant negative effect of the predator.

Fragments of the alga *Chara* sp. were found in the esophagus and stomach of large *R. venosa* (SH > 90 mm). Previously, feeding of its juveniles (SH of 12–31 mm) on periphyton formed on the walls of the aquarium was established [Pereladov, 2013]. Actually, the difference in the feeding mechanism of herbivorous gastropods is that those scrape food with their radula, while the rapa whelk uses its radula to bite off pieces of the prey meat [Chukhchin, 1970] and, as it turned out, algae fragments. Algae in *R. venosa* digestive tract are also partially grinded with this anatomical structure. Notably, the species is able to bore shells of not only juveniles but also aged molluscs with its radula [Kosyan, 2016], and this is confirmed by our data. Maybe, the rapa whelk is not an obligate predator, and this expands its adaptive potential. However, this issue requires further research.

Crabs and smaller carnivorous crustaceans (hermit crabs and shrimps) feeding on *Chara* sp. were also recorded in the study area. These algae are known to be a source of food for waterfowl which mainly feed on oospores filled with starch and fat droplets. Due to the high abundance of lime in them, *Chara* algae are applied as fertilizer for heavy soils [Gollerbakh, 1977]. Obviously, the complex of the above important components of *Chara* sp. is actively used by many carnivorous invertebrates.

Predator–prey. Damage to *R. venosa* shells by crabs was previously described for the individuals of the bays of Sevastopol [Bondarev, 2013], where, in addition to *C. aestuarii*, *Eriphia verrucosa* (Forskål, 1775) occurs – the warty crab inhabiting the Black Sea but not found in the Donuzlav Bay. This crab is the largest of the native species and has the strongest first pair of pereopods. The warty crab was repeatedly registered by the author *in situ* with adult rapa whelk in its claws. Crushing of a small *R. venosa* shell (SH of 25 mm) with a wall thickness of about 1.0 mm by the warty crab in an aquarium was recorded as well [Bondarev, 2013].

C. aestuarii is the most common and abundant crab in the Black Sea occurring down to a depth of 70 m. This species usually forms large aggregations in the littoral and sublittoral zone and in lagoons. It inhabits sandy sediments or coquina, lives among algae or, less frequently, on gravel or under rocks. In the XX century (especially before the 1970s), the Mediterranean green crab was most common in the northwestern Black Sea [Makarov, 2004], and this circumstance can explain the previously observed paradoxically low abundance of the rapa whelk in this area against the backdrop of significant amounts of bivalves [Zolotarev, 1996]. To date, as a result of habitat destruction and excessive recreational fishing on some spots, the frequency of *C. aestuarii* occurrence noticeably dropped, and the species is listed in the regional Red Data Book [Krasnaya kniga goroda Sevastopolya, 2018].

The Donuzlav Bay, with its abundant food base including *R. venosa*, is obviously a comfort zone for the development of *C. aestuarii* population; therefore, there are individuals with sizes exceeding the previously known maximum ones. In accordance with literature data, in the Black Sea, the maximum carapace width (CW) of the Mediterranean green crab is 80 mm with a length of 63 mm [Kobyakova, Dolgopolskaya, 1969]. In the Donuzlav Bay, *C. aestuarii* with CW > 80 mm is not rare, and the maximum CW, according to our data, is 86.2 mm. In the Mediterranean Sea population and in other newly formed populations (those of Japan, Australia, New Zealand, and North America), the Mediterranean green crab has significantly smaller CW – up to 65 mm [Yamada, Hauck, 2001]. The large size of *C. aestuarii* in the Black Sea and Donuzlav Bay allows it to hunt not only rather large Bivalvia and *R. venosa* juveniles, but also mature individuals. According to our data, the Mediterranean green crab has a feeding spectrum similar to that of *R. venosa*, with a predominance of bivalves. Thus, for *R. venosa*, *C. aestuarii* is both a trophic competitor and predator.

Importantly, after settling on sediments, the rapa whelk suffers the greatest losses from benthic predators during the early stages of its growth. Right after settling, its juveniles are about 1 mm in size; in two weeks, those grow to 1.5 mm; and in another 6 days, those grow to 2 mm [Chukhchin, 1970]. Therefore, even small-sized crab species can significantly affect *R. venosa* abundance. So, the effect of these crabs on the rapa whelk population should not be underestimated. Although adult large mollusc is also attacked by large-sized crabs, it is much less likely to become prey; moreover, it is capable of regenerating damaged and even lost shell fragments (Fig. 5) [Bondarev, 2013]. Apparently, crab cultivating can contribute to regulating *R. venosa* abundance and limiting its expansion.

Conclusion. There is a stable population of *Rapana venosa* in the Donuzlav Bay – with a complete structure, actively reproducing, and provided with a variety of food items.

With the occurrence of potential food objects throughout the bay, the rapa whelk distribution is limited to the central and southwestern Donuzlav Bay. There, its density ranges from < 0.01 to 0.1 ind.·m^{-2}.

R. venosa food competitors and predators are native Black Sea crabs limiting the abundance and, probably, distribution of this invasive gastropod.

Revealing of the alga *Chara* sp. in the rapa whelk stomachs indicates an expansion of its feeding spectrum and requires further study: it may evidence for the fact that this species has a greater adaptive potential than previously known.

This work was carried out within the framework of IBSS state research assignment "Biodiversity as the basis for the sustainable functioning of marine ecosystems, criteria and scientific principles for its conservation" (No. 124022400148-4).

Acknowledgment. The author is grateful to the anonymous reviewers for their comments and recommendations following which improved the quality of the work.

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ОСОБЕННОСТИ ПОПУЛЯЦИОННОЙ СТРУКТУРЫ И БИОЦЕНОТИЧЕСКИХ СВЯЗЕЙ *RAPANA VENOSA* (VALENCIENNES, 1846) (GASTROPODA, MURICIDAE) В ЗАЛИВЕ ДОНУЗЛАВ ЧЁРНОГО МОРЯ

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Западно-тихоокеанский брюхоногий моллюск *Rapana venosa* (Valenciennes, 1846) отнесён к 100 наиболее опасным инвазионным видам Чёрного и Средиземного морей, а также признан опасным вселенцем в ряде районов прибрежных вод по обе стороны Атлантического океана. Это обстоятельство определяет актуальность изучения популяционных особенностей и биоценотических связей рапаны в районах вселения. Исследования ранее не проанализированной локальной популяции *R. venosa* в заливе Донузлав (Северо-Западный Крым) Чёрного моря в 2020 г. показали, что при наличии обильной и разнообразной пищевой базы рапана не формирует массовых скоплений и, следовательно, не оказывает существенного влияния на донные биоценозы. Этот вывод подтверждается и соотношением биомассы хищного моллюска и его жертв. Средняя биомасса *R. venosa* в обследованном районе составляла 3,8 $г \cdot м^{-2}$, а средняя биомасса объектов её питания (Bivalvia) — 162,8 $г \cdot м^{-2}$. Особенности популяционной структуры и биоценотические связи рапаны в заливе Донузлав рассмотрены и обсуждены впервые. Прямые и косвенные данные свидетельствуют, что распространение вида-вселенца *R. venosa* контролируется аборигенными хищниками — крабами. Основным видом, ограничивающим численность рапаны в исследованном районе, является краб *Carcinus aestuarii* Nardo, 1847.

Ключевые слова: биоценозы, водоросли, инвазионный вид, крабы, моллюски, хищник — жертва