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CONSORTS OF GASTROPOD *RAPANA VENOSA* (VALENCIENNES, 1846) IN THE NORTHERN BLACK SEA.
PART V: ANNELIDA (POLYCHAETA)

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The study of Annelida (Polychaeta) taxocene – epibionts of the invasive gastropod *Rapana venosa* – continues the cycle of publications describing the composition of the consortium of the largest gastropod of the Black Sea benthos. *R. venosa* consortium is still a poorly investigated and unaccounted component in the structure of the Black Sea shelf biocenoses. The aim of this work is to study the complex of polychaetes of *R. venosa* consortium. The objectives of this stage are as follows: compiling a list of Annelida (Polychaeta) taxa – rapa whelk epibionts; studying taxocene biogeographic and trophic structure; and analyzing ecological relationships of polychaetes with the consortium core. To study the consort community of rapa whelk, sampling was conducted in seven areas of the northern Black Sea: 1 – Mamaia, Romania; 2 – northwestern Black Sea, Crimea offshore; 3 – Sevastopol; 4 – Alupka; 5 – Yalta – Alushta; 6 – Karadag; 7 – Kerch Strait. In the coastal area down to a depth of 15 m, *R. venosa* was sampled totally using surface-supplied diving equipment; in the deeper-water area (down to 40 m), samples were taken with an “Ocean-50” bottom grab from the board of the RV “Professor Vodyanitsky”. Each rapa whelk specimen (sample) was placed in a separate plastic bag, with the indication of the area, depth, and biotope. In total, 2,411 samples were taken and analyzed: 977 – rock rapa whelks and 1,434 – sand rapa whelks. *R. venosa* shell coverage with epibionts (fouling intensity) was determined as a percentage of the total area of the outer shell surface. Polychaeta taxocene of *R. venosa* consortium includes 31 species representing 31 genera of 15 families of 2 subclasses. Most species (18) belong to Errantia, and half of them are representatives of the families Nereididae and Syllidae. Sedentaria includes 13 species; by the largest number of species (4), the family Serpulidae is represented. Polychaeta taxocene of *R. venosa* consortium is represented by three biogeographic groups: native species of the Mediterranean-Atlantic genesis (84 %), the Black Sea endemics (10 %), and recent invaders of various geographical genesis (6 %). On sand rapa whelk, 31 Polychaeta species were found; on rock rapa whelk, only 5 species were recorded. The indicators of Polychaeta fauna development differ significantly by the depth and research area. The most diverse polychaetes are those in bays of Sevastopol (the area No. 3) at depths of 2–10 m; the maximum depth of Polychaeta finding (40 m) corresponds to the greatest depth of rapa whelk sampling. The area of shell coverage with polychaetes reaches 70 %; occurrence in several areas is up to 95 %. The maximum number of species found at a single rapa whelk specimen is 8; on average, 2–4 Polychaeta species are recorded at *R. venosa* individuals. Taxonomic diversity and abundance of polychaetes determine their significance in *R. venosa* consortium. Due to the invasive predatory mollusc *R. venosa*, polychaetes get additional opportunities for spread on the Black Sea shelf.

Keywords: consortium, Polychaeta, *Rapana venosa*, Black Sea, ecology, epibionts

The study of Annelida (Polychaeta) taxocene – epibionts of the invasive gastropod *Rapana venosa* (Valenciennes, 1846) – is a continuation of a series of works on the description of the consortium of this largest gastropod of the Black Sea. In the previous parts, representatives of six phyla were considered: Cnidaria, Bryozoa, Porifera, Chordata (Bondarev & Revkov, 2017a), Mollusca (Bivalvia, Gastropoda, Polyplacophora) (Bondarev & Revkov, 2017b, 2018), and Arthropoda (Chelicerata: Arachnida; Crustacea: Malacostraca, Hexanauplia) (Bondarev & Bondarenko, 2019). In total, 64 zoobenthos species belonging to those higher taxa were identified in the rapa whelk consortium, and their list continues to broaden with new studies. In the consortium, 65 macroalgae species – rapa whelk foulers were identified; their coverage density can reach 100 % of the shell surface (Bondarev & Milchakova, 2018).

Previous studies have shown that the ecological role of *R. venosa* is not limited to predation (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Emel'yanov et al., 2010 ; Bondarev & Milchakova, 2018 ; Savini et al., 2004). A rather large rapa whelk shell serves as a solid substrate for sedentary animals. On *R. venosa* shell, a complex of organisms of different taxonomic groups can form, related to each other topically and trophically. Such a naturally formed system of heterogeneous organisms, which are in close contact relations and depend either mutually or unilaterally on each other during the whole life cycle or at least at some of its phases, may be defined as a consortium, the core of which is *R. venosa*. Wide distribution and high abundance of rapa whelk in many areas of the northern Black Sea necessitate studying and considering the contribution of its consortia to the overall biodiversity structure of benthal ecosystems (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Emel'yanov et al., 2010 ; Bondarev & Milchakova, 2018).

In 1990s–2000s, there was a significant reduction of the settlements of *Mytilus galloprovincialis* (Lamarck, 1819), one of the main objects in *R. venosa* diet, on the rocks (Boltachova et al., 2015); following it, a considerable decrease in rapa whelk abundance was recorded (Bondarev, 2010, 2014). Most current local populations of *R. venosa* inhabit loose sediments (Bondarev, 2010, 2016). In the biotope of loose sediments, the presence of motile oases of attached forms of zoo- and phytobenthos, formed on mollusc shell surface, is associated with rapa whelk (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Emel'yanov et al., 2010 ; Bondarev & Milchakova, 2018 ; Savini et al., 2004). As established earlier, the greatest species diversity of epibionts and the maximum degrees of their shell coverage are inherent in the rapa whelk inhabiting loose sediments (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Emel'yanov et al., 2010 ; Bondarev & Milchakova, 2018). Therefore, in this work, most attention is paid to the study of this ecological group of *R. venosa*. Rapa whelks are conventionally divided into rock and sand ones according to their affiliation to one of the ecological groups (Savini et al., 2004). We use these definitions for brevity likewise, classifying mollusc individuals, inhabiting other types of loose sediments, as sand rapa whelk as well.

On mollusc shell surface, the presence of polychaetes as a significant fouling component was noted long ago (Zernov, 1913). The presence of polychaetes on rapa whelk shells has been reported for both the Mediterranean Sea (Savini et al., 2004) and the Black Sea (Emel'yanov et al., 2010); however, in all cases, there were sedentary forms only, which build a calcareous tube. The technique of sampling in zipper plastic bags applied by us made it possible to more fully record sedentary forms and, for the first time, detect errant forms, which predominate in terms of the number of species.

R. venosa consortium is still a poorly investigated component in the structure of the Black Sea shelf biocenoses, and its research continues. The aim of this work was to study Annelida (Polychaeta) complex of *R. venosa* consortium. The objectives of the stage are compiling a list of Polychaeta taxa – rapa whelk epibionts, as well as studying the biogeographic and trophic structure of the taxocene, distribution by areas and depths, and ecological relationships of polychaetes with the consortium core.

MATERIAL AND METHODS

Sampling and field studies of epibionts of *R. venosa* shells were carried out in 2007–2018, June to November, in seven areas of the northern Black Sea (Fig. 1, Table 1).

Fig. 1. Sampling map: 1 – Mamaia Beach (Romania); 2 – northwestern Black Sea, Crimea offshore; 3 – Sevastopol; 4 – Alupka; 5 – Yalta – Alushta; 6 – Karadag; 7 – Kerch Strait

Table 1. Research areas in the northern Black Sea and indicators of *R. venosa* shell surface total coverage with zooconsorts, % (min.–max. / mean value)

No.	Area	Number of samples	Depth, m	Month, year	Bottom ground	Shell coverage, % of the surface
1	Mamaia Beach	12	0–1.5	XI, 2008	sand	2–35 / 5
2	Northwestern Black Sea	11	19.5–25.0	X–XI, 2010	silt and shell	0–5 / 2
3	Sevastopol	1,250	2–10	VI–IX, 2015, 2018	sand	0–100 / 35
		130	1.5–4	VI–IX, 2015, 2018	rock	0–60 / 25
4	Alupka	125	0.5–5.5	IX, 2016, 2018	rock	0–30 / 10
5	Yalta — Alushta	2	34; 40	X–XI, 2010	silt	20; 25
6	Karadag	722	3–10	VI–VII, 2007, 2009	rock	0–70 / 30
		14	21.8–23	X–XI, 2010	sandy silt	5–85 / 30
7	Kerch Strait	145	0.5–15	VII, 2012, 2018	sand	5–90 / 20

At depths of down to 15 m, *R. venosa* specimens were sampled totally by hand and using surface-supplied diving equipment. Each rapa whelk specimen with epibionts (sample) was placed in a separate plastic bag, with the indication of the depth and biotope. In the deeper-water area, samples were taken with an "Ocean-50" bottom grab from the board of the RV "Professor Vodyanitsky" (cruise No. 68, 2010). In total, 2,411 *R. venosa* specimens were sampled and analyzed, of which 977 were rock rapa whelks and 1,434 were rapa whelks of loose sediments. The size of the studied *R. venosa* individuals varied 31.3 to 110.8 mm (on average 54.4 mm); the age varied 1 to 12 years (on average 4 years). Rapa whelk shell coverage with epibionts (fouling intensity) was determined as a percentage of the total area of the outer shell surface (Bondarev & Revkov, 2017a).

The generalized characteristic of the taxa occurrence in a summary table (see Table 2) is given according to the following scale: "–" – no taxon was found in a mollusc sample; "+" – rare species (up to 1 % of a sample); "++" – uncommon (2–10 %); "+++" – common (11–30 %); "++++" – very common (> 30 %). *R. venosa* linear dimensions were measured with a caliper with an accuracy of 0.1 mm; Polychaeta ones – under an MBS-10 microscope. Weighing of the objects studied (wet weight) was carried out on a WLM-200 laboratory analytical balance: rapa whelk specimens – with an accuracy of 0.1 g; polychaetes – with an accuracy of 0.0001 g. The trophic specialization of polychaetes is given according to (Kiseleva, 2004 ; Khlebovich, 1996 ; Giangrande et al., 2004 ; Serrano et al., 2006).

RESULTS AND DISCUSSION

The list of Polychaeta taxa of *R. venosa* consortium includes 31 species representing 31 genera of 15 families. Most species (18) belong to Errantia; half of them are representatives of the families Nereididae and Syllidae. Out of Sedentaria (13 species), the largest number (4 species) represents the family Serpulidae (Table 2).

Table 2. List of Polychaeta taxa of *R. venosa* consortium and their trophic specialization, T (C – carnivores; D – detritivores; F – filter feeders; H – herbivores; and O – omnivores); occurrence at shells of molluscs inhabiting loose (1) and rocky (2) bottom ground by depths and research areas according to Fig. 1

Taxon	T	Occurrence		Depth, m	Areas
		1	2		
Errantia					
Phyllodocidae Örsted, 1843					
Mysta picta (Quatrefages, 1865)	C	+	–	2.0–5.0	3
Eulalia viridis (Linnaeus, 1767)	C	+	–	2.5–8.0	3
Genetyllis tuberculata (Bobretzky, 1868)	C	+	–	2.0–6.0	3
Polynoidae Kinberg, 1856					
Harmothoe imbricata (Linnaeus, 1767)	C, O	+	–	2.5–6.0	3
Pholoidae Kinberg, 1858					
Pholoe inornata Johnston, 1839	O	+	–	3.0–10.0	3
Nereididae Blainville, 1818					
Alitta succinea (Leuckart, 1847)	D, O	+	–	3.0–6.0	3

Continue on the next page…

Taxon	T	Occurrence		Depth, m	Areas
		1	2		
Hediste diversicolor (O. F. Müller, 1776)	O, H	+	–	3.0–10,0	3, 7
Nereis zonata Malmgren, 1867	D, H	+	–	3.0–6.0	3
Perinereis cultrifera (Grube, 1840)	H, D	++	–	2.5–10	3
Platynereis dumerilii (Audouin & Milne Edwards, 1833)	H, O	+++	–	2.0–10	3, 6, 7
Syllidae Grube, 1850					
Exogone naidina Örsted, 1845	H	+	–	4.5	3
Salvatoria clavata (Claparède, 1863)	O	+	–	2.0–6.0	3
Syllis gracilis Grube, 1840	O	+	–	3.0; 6.0	3
Trypanosyllis zebra (Grube, 1860)	D	+	–	4.0	3
Pilargidae Saint-Joseph, 1899					
Sigambra tentaculata (Treadwell, 1941)	C, D	+	–	5.5	3
Eunicidae Berthold, 1827					
Eunice vittata (Delle Chiaje, 1828)	C	+	–	2.5–7.0	3
Lysidice ninetta Audouin & H. Milne Edwards, 1833	D	+	–	2.5–6.0	3
Dorvilleidae Chamberlin, 1919					
Protodorvillea kefersteini (McIntosh, 1869)	O	+	–	4.5	3
Sedentaria					
Orbiniidae Hartman, 1942					
Naineris laevigata (Grube, 1855)	D	+	–	4.0	3
Spionidae Grube, 1850					
Polydora sp.	D	++	+	0.5–12.0	3, 5, 6, 7
Prionospio cirrifera Wirén, 1883	D	+	–	6.0	3
Spio decorata Bobretzky, 1870	D	+	–	4.5	3
Opheliidae Malmgren, 1867					
Polyophthalmus pictus (Dujardin, 1839)	D	++	+	2.0–5.0	3, 6, 7
Capitellidae Grube, 1862					
Capitella capitata (Fabricius, 1780)	D	+	–	5.0	3
Sabellariidae Johnston, 1865					
Sabellaria taurica (Rathke, 1837)	F	+	–	4.0–8.0	3, 7
Terebellidae Johnston, 1846					
Amphitritides gracilis (Grube, 1860)	D	+	–	4.5	3
Polycirrus jubatus Bobretzky, 1869	D	+	–	4.0	3
Serpulidae Rafinesque, 1815					
Hydroides dianthus (Verrill, 1873)	F	++	–	2.0–8.0	3, 7
Spirobranchus triqueter (Linnaeus, 1758)	F	++++	+++	0.5–40.0	1, 2, 3, 4, 5, 6, 7
Spirorbinae Chamberlin, 1919					
Janua heterostropha (Montagu, 1803)	F	++++	++++	0.5–23.0	1, 2, 3, 4, 5, 6, 7
Pileolaria militaris Claparède, 1870	F	+++	+++	1.0–8.0	3, 4, 6, 7

In *R. venosa* consortium, 64 zoobenthos species were recorded earlier representing six phyla: Cnidaria, Bryozoa, Porifera, Chordata, Mollusca, and Arthropoda (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019). With the largest number of taxa, the phylum Arthropoda was represented (27 species) (Bondarev & Bondarenko, 2019). According to our data, the class Polychaeta, which includes 31 species, is taxonomically the most diverse group of rapa whelk zooconsorts.

In the previous studies of rapa whelk consorts in the Black Sea (Emel'yanov et al., 2010), only two Polychaeta species were identified – *Spirobranchus triqueter* and *Janua heterostropha*. Of polychaetes, the list of epibionts of rock and sand rapa whelks of the Adriatic Sea contains only serpulids as well, without specifying their species (Savini et al., 2004). Shell-boring polychaetes *Polydora ciliata* (Johnston, 1838) and *Polydora websteri* Hartman in Loosanoff & Engle, 1943 were previously recorded in the shells of oyster *Magallana gigas* (Thunberg, 1793) grown on mariculture farms in the Black Sea (Gaevskaya & Lebedovskaya, 2010 ; Lisitskaya et al., 2010); however, representatives of this genus were not registered in *R. venosa* shells earlier. Thus, our studies significantly enhance the understanding of the biodiversity of Polychaeta taxocene consorting to *R. venosa*.

The taxocene biogeographic characteristics. The fauna of polychaetes of *R. venosa* consortium consists of three biogeographic groups: native species of Mediterranean-Atlantic genesis, the Black Sea endemics, and recent invaders of various geographical genesis. Polychaeta taxocene of the consortium is predominantly (25 species, ~ 84 %) represented by the species of Mediterranean-Atlantic genesis. These species, which have become permanent faunal components, have a status of native in the Black Sea basin.

Three species (~ 10 % of the total number of species) are the Black Sea endemics: *Genetyllis tuberculata* (Fig. 2A), *Sabellaria taurica*, and *Polycirrus jubatus*.

Two species (~ 6 %) are recent invaders: *Sigambra tentaculata* and *Hydroides dianthus*. The only representative of the family Pilargidae and the genus *Sigambra* Müller, 1858 in the Black Sea, *S. tentaculata*, was first recorded for the coasts of Crimea and Caucasus at a depth of 5–40 m on shell and on silt and shell sediments in 1964 (Kiseleva, 2004). The typical habitat of this species is the Atlantic coast of North America (New England); however, it was found in the seas of the Mediterranean basin, off the coast of Europe (Giangrande et al., 2004). In our samples, *S. tentaculata* (length of 7.0 mm, weight of 0.002 g) was recorded once in the Golubaya Bay (Sevastopol, Crimea) at a depth of 6 m on sand rapa whelk.

Serpulid *H. dianthus* is classified as a dangerous invasive species, which is currently actively spreading to various areas of the World Ocean (Sun et al., 2017). Originally, the species was described for the Atlantic coast of North America; later, it was found in the Gulf of Mexico, off the coast of Europe and West Africa, and in the Mediterranean Sea; then, it was recorded off the coast of South America, Japan, and China (Çinar et al., 2014 ; World Polychaeta database, 2019 ; Sun et al., 2017). Some researchers considered *H. dianthus* an invader in the Mediterranean Sea, while others considered it a cryptogenic species (Streftaris & Zenetos, 2006). In the Black Sea, this species was first discovered in 2009 on oysters *Magallana gigas*, grown in the Kazachya Bay (Sevastopol), and later – in the fouling of stones and mussel collectors in the Sevastopol Bay (Boltachova et al., 2011). Detailed genetic studies of *H. dianthus* from various areas of the World Ocean have shown that Black Sea specimens are closest to ones from the Gulf of Mexico (Texas, USA) and were introduced into the Black Sea directly from the American population (Sun et al., 2017). We have found *H. dianthus* in the largest abundance in the Kazachya Bay (the area No. 3).

In general, Polychaeta taxocene of *R. venosa* consortium, in terms of biogeographic division, coincides with the structure of Polychaeta fauna in the Black Sea. To a certain extent, the presence of rapa whelk contributes to preservation and spread of endemic polychaetes and invasive species.

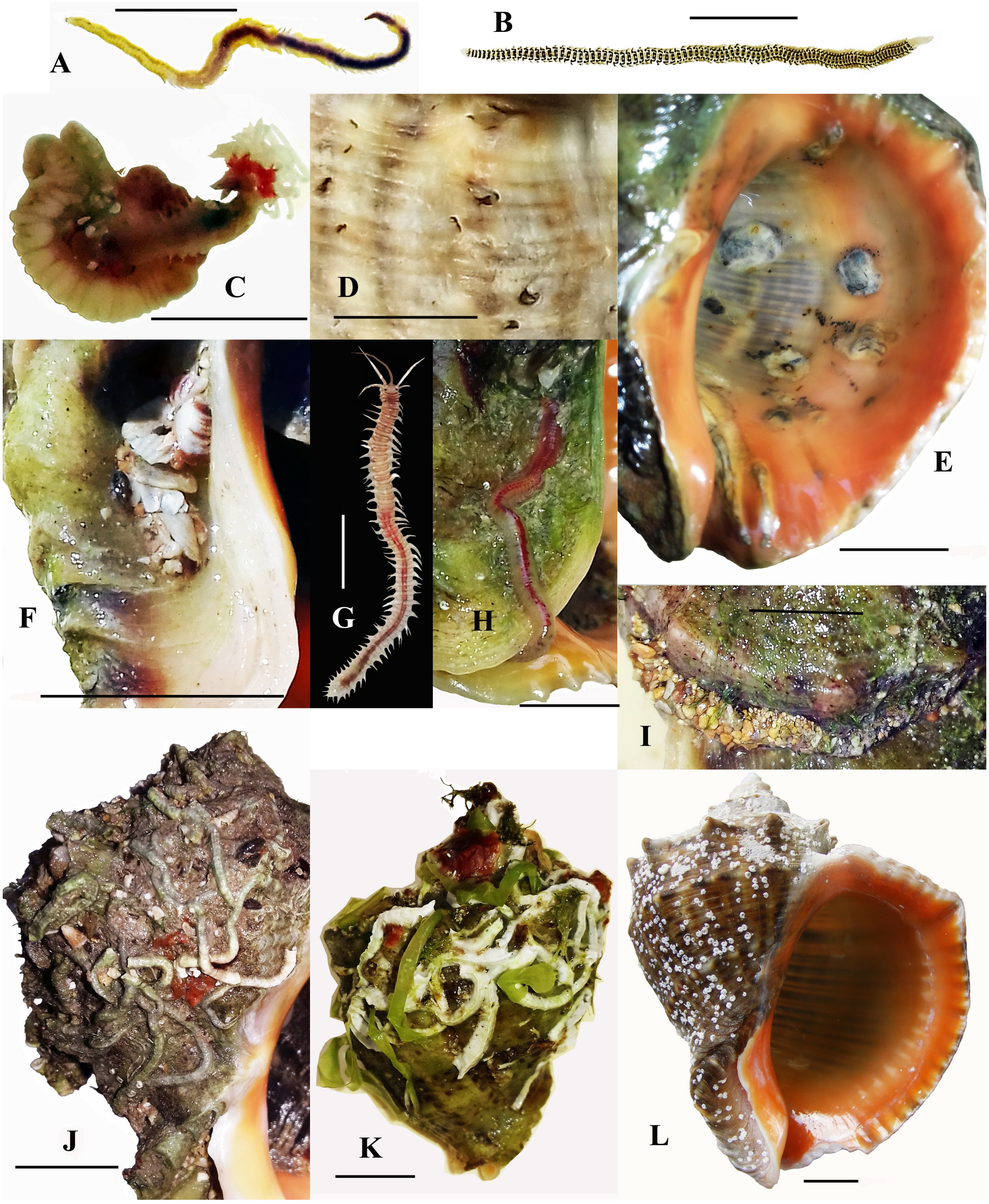

Fig. 2. Polychaetes of *R. venosa* consortium: A – *Genetyllis tuberculata*; B – *Mysta picta*; C – *Amphitritides gracilis*; D – *Polydora* sp. boring on a shell surface cleaned from fouling; E – blisters at the shell mouth blocking *Polydora* sp. passages; F – leathery tube encrusted with mollusc shell fragments, protruding from the umbilical cavity of the rapa whelk shell; G – *Eunice vittata*; H – *E. vittata* crawled out of the umbilical cavity of the rapa whelk shell; I – *Sabellaria taurica* sand tube located on the whorl suture of the rapa whelk shell; J–L – calcareous tubes of serpulids on the rapa whelk shell surface (J – *Hydroides dianthus*; K – *Spirobranchus triqueter*; L – *Janua heterostropha*). Scale bars – 1 cm

Indicators of the taxocene development by biotopes and areas. On sand rapa whelk, we found 31 species, on rock rapa whelk – only 5 species representing Sedentaria (Table 2). The situation is similar for other indicators of Polychaeta assemblages development – occurrence and abundance. In general, according to our data, those are higher for sand rapa whelk, although they can vary significantly across the research areas. The maximum shell coverage (70 %) with polychaetes and their occurrence (up to 95 %) were recorded in sand rapa whelk (the area No. 3), but the minimum values of these indicators (up to 5 %) were also registered in rapa whelk inhabiting loose sediments (the areas No. 1 and 2).

The highest values are typical for bays of Sevastopol (the area No. 3), where all Polychaeta species of the consortium were recorded; this may partly be due to the fact that more samples were taken in this area than in other ones. Nevertheless, the main reason is obviously the favorable conditions in the bays: moderate water dynamics does not prevent the development of the complex of rapa whelk epibionts.

In general, the highest Polychaeta occurrence was recorded for spirorbins *J. heterostropha* and *P. militaris* (in the Kazachya Bay, it reached 90 %). The second place in terms of occurrence (in some areas, up to 75 %) was occupied by serpulid *S. triqueter*, and in the Kazachya Bay – by the invasive species *H. dianthus*. Both of these species can be present together on one rapa whelk specimen (the areas No. 3 and 7). The next most common species (Sedentaria representatives, *Polydora* sp. and *P. pictus*) were much less common (2–10 % of rapa whelks). It should be noted that at a depth of 0.5–2.0 m in the Kerch area (the area No. 7), up to 90 % of *R. venosa* individuals are damaged by *Polydora* sp.

Out of Errantia, the most common species are *P. dumerilii* and *P. cultrifera*; their occurrence in the Kazachya Bay is 30 and 10 %, respectively. Several species were found in the consortium singularly (1–5 specimens over the entire research period): *A. gracilis*, *C. capitata*, *M. picta*, *N. laevigata*, *N. zonata*, *P. jubatus*, *P. cirrifera*, *P. kefersteini*, *S. decorata*, and *T. zebra*. In amount of 6–10 specimens each, *E. viridis*, *H. imbricata*, *L. ninetta*, and *S. gracilis* were found. In general, the number of Polychaeta species, whose occurrence does not exceed 1 %, is 23 (74 % of the total number).

The abundance of polychaetes on a single rapa whelk specimen, even within one area, varies over a very wide range (1 to 132 specimens) in the case of the presence of serpulids and especially spirorbins. The maximum Polychaeta abundance was recorded on 4-year-old rapa whelk (height of 71.5 mm) from the area No. 3; on older individuals (up to 12 years) in the same area, a significantly smaller abundance of polychaetes was registered (12–48 individuals). In the areas No. 1 and 2, the values of the indicators of Polychaeta fauna development in rapa whelks of all ages and sizes are minimal. Since the overwhelming majority of polychaetes of *R. venosa* consortium live for about a year, their competitive capabilities are lower than those of perennial species capable of expanding their presence for a long time. When serpulid larvae settle, free space and formation of several external conditions for development are of great importance, since serpulids are massive sedentary forms. These conditions include the peculiarities of hydrophysics and lithodynamics in the area, their interannual and seasonal changes, competitive struggle with other epibionts, devouring by predators, *etc*. Such multifactorial nature and peculiarities of biology lead to the fact that the natural tendency for the presence of ephibionts to increase as a shell surface area increases during rapa whelk growth (Bondarev & Revkov, 2017a, b ; Bondarev & Bondarenko, 2019 ; Bondarev & Milchakova, 2018) is not traceable for polychaetes.

The maximum number of species found on a single rapa whelk specimen is 8. Usually, *R. venosa* specimens contain 2–4 Polychaeta species. The size of polychaetes in the consortium varied 0.5 mm (juveniles of *J. heterostropha* and *P. militaris*) to 61.5 mm (*A. gracilis*) (on average 6.2 mm), and the weight varied 0.0001 to 0.017 g (on average 0.0012 g). The area of rapa whelk shell coverage with polychaetes can reach 70 %, and the weight of polychaetes is 0.021 g, which is no more than 0.03 % of the weight of the mollusc – the consortium core. The weight of other rapa whelk epibionts, *e. g.* Bivalvia, can be comparable to the weight of the mollusc itself (Bondarev & Revkov, 2017b). Therefore, contribution of polychaetes to the biomass of *R. venosa* consortium is insignificant.

Table 2 shows as follows: the number of Polychaeta species of *R. venosa* consortium differs significantly depending on the biotope which the rapa whelk (the consortium core) inhabits, and this is similar to the presence of other epibionts on rapa whelk. The number of species, occurrence, abundance, and biomass of epibionts of other taxonomic groups on sand rapa whelk in most research areas are higher than the same indicators for rock rapa whelk (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Bondarev & Milchakova, 2018). However, the indicators of Polychaeta fauna development differ significantly by areas: for sand rapa whelk, we recorded both minimum and maximum values (Table 2).

Based on research *prior* to our study, the indicators of the development of *R. venosa* epibionts depend rather on the area rapa whelk inhabits than on its affiliation to the rock or sand form. Two Serpulidae species were found; on sand rapa whelk, their occurrence was minimal (0–2 %), and on rock *R. venosa*, maximum values (up to 99 %) were registered (Emel'yanov et al., 2010). According to the studies of *R. venosa* consorts from the Adriatic Sea, the frequency of occurrence of serpulids on rock rapa whelk is significantly higher than on sand one (93 % *vs.* 13 %) (Savini et al., 2004). These data on sand rapa whelk only partially correspond to ours.

Unfortunately, the comparison can be made based on the occurrence of serpulids alone. Other Polychaeta species in the rapa whelk consortium have not been registered either in the Black Sea or in the Adriatic Sea. Therefore, our data are the basis for further studies of Polychaeta taxocene of *R. venosa* consortium.

Relation with the consortium core. Errantia representatives and several Sedentaria species move freely over rapa whelk shell surface, hiding among algal fouling. Sometimes, they can be found among egg capsules of rapa whelk, laid on a shell or between zoobenthos individuals (mainly Bivalvia) fouling *R. venosa* shell. Predatory polychaetes of the family Phyllodocidae – *E. viridis*, *G. tuberculata*, and *M. picta* (Fig. 2B) – can hide in coiled thalli of green algae *Ulva* spp. This these polychaetes themselves are likely to create temporary shelters from algae thalli.

Both in the presence and absence of fouling, polychaetes prefer to hide in natural grooves and cavities of a shell. Such grooves are the whorl suture of the rapa whelk shell and the umbilical cavity, which is formed when the whorls are wound around the column. The depth of the umbilical cavity canal depends on the size of rapa whelk shell; it may exceed the length of the largest Polychaeta from our sample. Terebellidae specimen, *A. gracilis* (Fig. 2C) 60.5 mm long, was found in the umbilical cavity of 102-mm rapa whelk shell from the Kruglaya Bay (the area No. 3). This specimen left the shelter when irritated with a long needle, but it is often impossible or only partially possible to get a Polychaeta out of a narrow umbilical cavity.

Grooves and cavities on the surface of rapa whelk shell and in it may result from sponge *Pione vastifica* (Hancock, 1849) boring (Bondarev & Revkov, 2017a). In the passages formed by *P. vastifica*, *L. ninetta* were found, which, apparently, widen the passages, since they are capable of boring mollusc shells (Vinogradov, 1949). Polydorins are shell borers as well. For the Black Sea, two species of the genus Polydora, having this capability, are known: the native species *P. ciliata* and the recent invader *P. websteri* (Gaevskaya & Lebedovskaya, 2010). The number of *Polydora* sp. found by us in the shells of live rapa whelk reached 26 ind. *per* 1 specimen. On the outer shell surface, the passages formed by worms have holes (Fig. 2D), which allow *Polydora* sp. to feed by collecting detritus and to get rid of waste products. Molluscs, protecting themselves from the irritating effect of polychaetes, form blisters in the spots of their penetration into the inner shell layer (Fig. 2E). Previously, it was shown as follows: *P. ciliata* prefers inhabiting the shells of the Black Sea *Tritia reticulata* (Linnaeus, 1758) occupied by hermit crabs; in the Mediterranean Sea, *Dipolydora armata* (Langerhans, 1880) predominantly bores either empty shells of the gastropod *Stramonita haemastoma* (Linnaeus, 1767) (Muricidae) or shells of this species occupied by hermit crabs (Vinogradov & Losovskaya, 1968 ; Bick, 2006).

Several worm species were registered in leathery tubes often encrusted with sand grains and tiny fragments of mollusc shells (Fig. 2F): *E. vittata* (Fig. 2G, H), *L. ninetta*, *P. cultrifera*, and *P. dumerilii*. Most often, leathery tubes with polychaetes are located in the aforementioned grooves and cavities, and their parts located on rapa whelk shell surface are encrusted with debris (Fig. 2F). *P. dumerilii* was found in most of these tubes. *S. taurica* builds durable sand tubes on the outer shell surface (Fig. 2I). The most common are the calcareous tubes of serpulids (Fig. 2J–L), which can cover up to 70 % of *R. venosa* shell surface.

It is of interest whether the relation of polychaetes with the consortium core is accidental or ecologically determined. For many Sedentaria, a close relation with rapa whelk is determined by the use of a shell as a substrate for penetration (*Polydora* sp.) or the attachment of durable tubes (Sabellariidae, Serpulidae). For Errantia, this relation is much less obvious and requires additional consideration.

Some Nereididae are known to build tubes. *Nicon moniloceras* (Hartman, 1940) inhabits smooth parchment tubes; the parchment tubes of *Simplisetia erythraeensis* (Fauvel, 1918) are encrusted with sand grains and rusty silt particles (Khlebovich, 1996). *P. dumerilii* and *Platynereis bicanaliculata* (Baird, 1863) inhabit translucent tubes attached to algae, stones, or shells (Khlebovich, 1996). We found both Nereididae (*P. dumerilii* and *P. cultrifera*) and Eunicidae (*E. vittata* and *L. ninetta*) on *R. venosa* shells in leathery tubes, often encrusted with shell fragments and sand grains. Polychaetes use the morphological elements of *R. venosa* shell, primarily its umbilicus, for shelter. Thus, several errant Polychaeta species have a close relationship with the consortium core, using rapa whelk shell as a substrate.

Probably, mobile Polychaeta species can hide from predators in algae and among sedentary animals on *R. venosa* shell; some species seem to find food there. This primarily applies to herbivores, such as *P. dumerilii* and *P. cultrifera*, which can be attracted by algal fouling of rapa whelks, but also applies to species feeding on the fauna, which accompanies algae, such as *P. pictus*. It is known that Nereididae form large aggregations on mussel banks; the reason is the ability to feed on mollusc pseudofeces, which has been confirmed experimentally (Khlebovich, 1996). On the Black Sea rapa whelk, mytilides are one of the most common foulers (Bondarev & Revkov, 2017b); accordingly, they can provide food for some Polychaeta species. Moreover, rapa whelk itself, actively feeding, produces feces every day for most of the year. There were no direct observations of polychaetes feeding with these fecal masses, but such a trophic relationship is not excluded.

The pedal glands of rapa whelk abundantly secrete mucus, which serves to protect the shell from external effects and to lubricate the sliding surface of the foot sole when crawling. The outer covering of rapa whelk secretes mucus, which is a mixture of acidic and neutral mucopolysaccharides or mucoproteins. In addition to mucus, the outer covering of rapa whelk secretes protein. When rapa whelk attacks bivalve, the hypobranchial mucus in large quantities penetrates into the victim's shell (Chukhchin, 1970). We observed a feeding rapa whelk attracting carnivore molluscs *T. reticulata*, which surrounded the predator along the shell perimeter. It can be assumed that while grinding the victim with a radula of the rapa whelk, some pieces of food fall into the water, attracting benthos carnivores. These remains, as well as the listed rapa whelk secretions, can probably serve as food for polychaetes.

Thus, *R. venosa* is not only a substrate for many polychaetes; it also attracts species of various nutrition types, which results in the formation of the trophic chains of rapa whelk elementary biocenosis.

Trophic structure. The trophic affiliation of Polychaeta species of *R. venosa* consortium is presented in Table 2. For species of a mixed nutrition type, the sequence of letter indices is given according to the predominance or type characteristic of adults. Most species of the taxocene (12 species, 39 %) are detritivores. Next in decreasing order are carnivores (6 species, 19 %), filter feeders and omnivores (5 species each, 16 %), and herbivores (3 species, 10 %).

In terms of Polychaeta abundance, the trophic structure of the taxocene is significantly different. More than 90 % of polychaetes of the rapa whelk consortium are filter feeders, mainly serpulids. The second place in terms of abundance (5.5 %) is occupied by herbivores or predominantly herbivores. At the same time, about 70 % of their abundance falls on *P. dumerilii*, whose adults are omnivores with a predominance of herbivorousness (Kiseleva, 2004). Detritivores are the third in abundance (2.5 %); they are followed by carnivores (1.5 %) and polyphages (0.5 %). The abundance of carnivores and polyphages is insignificant, which probably reflects their less connection with the consortium core.

As known, most of the Black Sea polychaetes are detritivores (Kiseleva, 2004). A considerable part of the species of Polychaeta taxocene of the rapa whelk consortium are also detritivores. However, in terms of Polychaeta abundance, the trophic structure of the taxocene is different: detritivores occupy only the third place, significantly inferior to filter feeders.

For filter feeders, that require a solid substrate, rapa whelk is almost the only natural opportunity to expand their presence in the biotope of loose sediments. The penetration of herbivores or predominantly herbivores, as well as Polychaeta species, which feed on animals inhabiting macrophytes, into the development zone of loose sediments is also associated with *R. venosa* – a favorable substrate for the development of algae (Bondarev & Milchakova, 2018).

Distribution by depths. Most of polychaetes of the consortium are confined to depths of 2–10 m. Spirorbines *J. heterostropha* were found on a depth of 0.5 down to 23 m, and only serpulids *S. triqueter* were present on rapa whelk from a depth of 0.5 m down to a maximum sampling depth of 40 m (Table 2).

The most diverse species composition of polychaetes in the Black Sea was observed at a depth of 10–50 m (Kiseleva, 2004). Most of Polychaeta species of *R. venosa* consortium were registered at depths of 2–3 down to 6–10 m (Table 2). It was shown earlier that the abundance of algae and invertebrates along the depth gradient is largely determined by the dynamic characteristics of the aquatic environment (Bondarev & Revkov, 2017a, b, 2018 ; Bondarev & Bondarenko, 2019 ; Kiseleva, 2004 ; Bondarev & Milchakova, 2018). On coastal rocks, water dynamics prevents the development of algae and mobile forms of benthos. At depths of down to 2 m, sandy sediments are highly mobile and have an inhibiting effect on epibenthos development. This fully applies to polychaetes of the consortium, especially to the species related to algae topically and trophically. Thus, *P. dumerilii* and *N. zonata* are recorded 0 down to 30 m, but in large numbers they inhabit macrophytes growing at a depth of 3–15 m (Kiseleva, 2004). At depths of 2–10 m, the photic conditions for the development of algae are the most favorable. Water dynamics, especially in the bays, at these depths does not prevent the larvae settling and the vital activity of juveniles and adults on rapa whelk shell surface. An equally important circumstance is that aggregations of *R. venosa*, the consortium core, are confined to this depth range. In summer, when rapa whelk spawn and actively feed, it migrates to shallow water and forms aggregations there (Bondarev, 2014).

Sedentary species, for which the presence or absence of a solid substrate is the main limiting factor, were found in a wide depth range. Spirorbins *J. heterostropha* were recorded on a depth of 0.5 down to 23 m, and only serpulids *S. triqueter* were present on rapa whelk down to a maximum sampling depth of 40 m, with a minimum depth of 0.5 m (Table 2).

Conclusion. In *R. venosa* consortium, representatives of the class Polychaeta are taxonomically the most diverse group of benthos invertebrates: 9 orders, 15 families, 31 species.

Polychaeta taxocene consorting to rapa whelk represents 3 biogeographic groups: native species of the Mediterranean-Atlantic genesis, the Black Sea endemics, and recent invaders of various geographical genesis. The first group predominates (84 %), but the contribution of the other two ones is quite significant (10 and 6 %, respectively).

Polychaetes are related to the rapa whelk consortium topically and trophically; they are an important component in the consortium. They rank first among taxonomic groups in terms of occurrence and abundance in *R. venosa* consortium.

Polychaeta are present in the consortium throughout the entire depth range of *R. venosa* habitat, but most of the species are found at depths of 2–10 m, to which rapa whelk aggregations are confined and where the most favorable conditions are formed for the development of algal fouling on its surface.

In total, 31 species were found on sand rapa whelk, and 5 species were recorded on rock rapa whelk. The occurrence and abundance of polychaetes on sand rapa whelk in most research areas are also higher than these indicators for rock rapa whelk.

In *R. venosa* consortium, many Polychaeta species find favorable conditions for living and get additional opportunities for spread on the Black Sea shelf.

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КОНСОРТЫ БРЮХОНОГОГО МОЛЛЮСКА *RAPANA VENOSA* (VALENCIENNES, 1846) В СЕВЕРНОЙ ЧАСТИ ЧЁРНОГО МОРЯ. ЧАСТЬ V: ANNELIDA (POLYCHAETA)

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Изучение таксоцена Annelida (Polychaeta), эпибионтов брюхоногого моллюска — вселенца *Rapana venosa*, продолжает цикл по описанию состава консорции самого крупного брюхоногого моллюска черноморского бентоса. Консорция *R. venosa* до сих пор является мало исследованной и неучтённой компонентой в структуре биоценозов шельфа Чёрного моря. Цель данной работы — изучить комплекс полихет консорции *R. venosa*. Задачи этого этапа: составление списка таксонов Annelida (Polychaeta) — эпибионтов рапаны; изучение биогеографической и трофической структуры таксоцена; исследование экологических связей полихет с ядром консорции. Для изучения консортного сообщества рапаны были осуществлены сборы в семи районах северной части Чёрного моря: 1 — Мамайя, Румыния; 2 — северо-западная часть Чёрного моря, Крымский сектор; 3 — Севастополь; 4 — Алупка; 5 — Ялта — Алушта; 6 — Карадаг; 7 — Керченский пролив. Сбор *R. venosa* в прибрежной зоне до глубины 15 м проводили тотально с использованием легководолазного оборудования, в более глубоководной зоне (до 40 м) — дночерпателем «Океан-50» с борта НИС «Профессор Водяницкий». Каждый экземпляр (пробу) рапаны помещали в отдельный пластиковый пакет с указанием района, глубины и биотопа. Всего отобрано и проанализировано 2411 проб, из них 977 — скальной рапаны и 1434 — песчаной. Покрытие эпибионтами раковины *R. venosa* (интенсивность обрастания) оценивали в процентах от общей площади внешней поверхности раковины. Таксоцен Polychaeta консорции *R. venosa* включает 31 вид, представляющий 31 род 15 семейств 2 подклассов. Бóльшая часть видов (18) относится к Errantia, половину из них составляют представители семейств Nereididae и Syllidae. К Sedentaria относятся 13 видов; наибольшее их количество (4) принадлежит семейству Serpulidae. Таксоцен Polychaeta консорции рапаны представлен тремя биогеографическими группами: аборигенные виды средиземноморско-атлантического генезиса (84 %), эндемики

Чёрного моря (10 %) и современные виды-вселенцы различного географического генезиса (6 %). На песчаной рапане обнаружен 31 вид полихет, а на скальной — только 5. Показатели развития фауны полихет значительно различаются по глубинам и районам исследований. Наиболее разнообразны полихеты в бухтах г. Севастополя (район № 3) на глубинах 2–10 м; максимальная глубина обнаружения полихет (40 м) соответствует наибольшей глубине отбора рапаны. Площадь покрытия раковины рапаны полихетами достигает 70 %, встречаемость в отдельных районах составляет до 95 %. Максимальное число видов, обнаруженных на отдельном экземпляре рапаны, — 8; в среднем на особях *R. venosa* отмечено 2–4 вида полихет. Таксономическое разнообразие и обилие Polychaeta определяют их значимость в консорции *R. venosa*. Благодаря инвазионному хищному моллюску *R. venosa* полихеты получают дополнительные возможности для распространения на шельфе Чёрного моря.

Ключевые слова: консорция, Polychaeta, *Rapana venosa*, Чёрное море, экология, эпибионты