

Structure of the macrozoobenthos assemblages in the central part of the northwestern Black Sea shelf (Zernov's Phyllophora field) at the beginning of the 21st century

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Abstract

In the first half of the 20th century, there was an extensive biocoenosis of the unattached red algae *Phyllophora crispa* on the mussel muds of the central section of the Black Sea's northwestern shelf, which is known as Zernov's *Phyllophora* Field (ZPF). At that time, the area of ZPF was approximately 11000 km². More than a century after the description of ZPF, long-term changes in its phyto- and zoobenthos have been noted. A period of ecological crisis of the Black Sea ecosystem during the second half of the 20th century was destructive for the phytobenthos of ZPF, with the complete degradation of unattached *Phyllophora* biocoenosis. In contrast, after a sharp decline in the quantitative development of macrozoobenthos of the soft bottoms in the 1970s, its recovery to pre-crisis levels in the 2010s was noted. Despite the difference in the aforementioned phyto- and zoobenthos dynamics, habitat in the 4025 km² area of the botanical sanctuary of national importance "Zernov's *Phyllophora* Field" was recognised as Critically Endangered (CR) within the European Red List of Habitats. In this context, the goal of the present study is to clarify the applicability of the CR category to the entire benthic complex of ZPF water area and to assess the current biocoenotic structure and habitat ordination of the zoobenthos on soft bottoms of the ZPF water area in the current conditions of Black Sea de-eutrophication. The obtained results indicate the presence of one biocoenotic complex (*Mytilus galloprovincialis*) and three subcomplexes in the zoobenthos of ZPF, where the bivalves *Mytilaster lineatus*, *Modiolula phaseolina*, as well as Polychaeta are the next most important subcomplex-forming taxa. Throughout all studies of ZPF, relative stability in the biocoenotic representation of the bottom fauna—with the dominance of *M. galloprovincialis*—has been observed. Due to the current levels of development in both the soft-bottom macrofauna and assemblages of unattached alga *Phyllophora*, two different habitats were proposed for identification in the water area of the botanical sanctuary. The first habitat – "Aggregations of unattached red algae *Phyllophora* in the central part of the northwestern shelf of the Black Sea" – was degraded and can be classified as a CR habitat. The second one – "Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds, shell deposits, with encrusting corallines and attached foliose sciaphilic macroalgae" – represents the soft-bottom biotope and was associated with the biocoenotic complex *M. galloprovincialis*, proposed for classification as Least Concern. In accordance with three biocoenotic subcomplexes of complex *M. galloprovincialis*, the spatial position of the three subhabitats was determined on the soft-bottom in the water area of ZPF.

Key words: biocoenosis, biocoenotic complex, bottom habitat, EUNIS habitat classification, *Mytilus galloprovincialis*.

Introduction

Zernov's *Phyllophora* Field (ZPF) is a part of the northwestern shelf of the Black Sea (NWBS), with an area of about 11000 km² and a depth of 30–60 m. At the beginning of the 20th century, there were large accumulations of unattached red algae *Phyllophora crispa*. According to various sources, between 5–7 (Zenkevich 1956) and 7–10 million tonnes (Zaitsev & Mamaev 1997) of this algae were discovered by the academician Zernov (1909) and named the "*Phyllophora* Sea" after his proposal. He also identified a separate for the Black Sea biocoenosis of unattached *Phyllophora*, which is located on "mussel muds between 31–32° E and 45–46° N", and made the first description of its qualitative composition (Zernov 1913). In the 1950s, ZPF was the world's largest aggregation of *Phyllophora* algae (Zaitsev & Mamaev 1997), occupying ~10% of the entire Black Sea basin shelf area.

In describing the "*Phyllophora* field biocoenosis", Zernov (1913) noted its "mixed character". According to his perspective, this fact was indicated by "the presence of *Mytilus galloprovincialis* Lk. var. frequens Mil., which is typical for the shallow mussel facies, and the appearance of *Modiola phaseolina* Ph. and numerous specimens of *Trophonopsis breviatus* Jeffr., which indicate the deeper-sea facies of the phaseolina muds" (Zernov 1913). In subsequent studies, the biocoenosis subdivision of the benthos proposed by S.A. Zernov was generally preserved. According to benthic surveys from 1954–1960, the central zone of the northwestern part of the Black Sea (ZPF region) presented the biocoenosis of red algae *Phyllophora* and the biocoenosis of mussel muds (Zakutsky & Vinogradov 1967).

Significant changes occurred in the benthos of the ZPF water area during the environmental instability period of the Black Sea ecosystem in the second half of the 20th century. While the areas occupied by the main biocoenosis *Mytilus galloprovincialis* decreased (Sinegub 2006), the seasonal local development of such biocoenoses as *Nephtys* (spring, summer-autumn 1979), *Nereis* (spring 1979), *Mytilaster lineatus* (summer-autumn 1979) and *Melinna palmata* (summer-autumn 1981) were observed within ZPF from 1979 to 1989, as well as the presence of areas with destroyed biocoenoses and areas with macrobenthos absence (Samyshev & Zolotarev 2018). There was a sharp decrease in the stocks and areas occupied by a biocoenosis of unattached red algae *Phyllophora* (Zaitsev 2006).

In 1991, the zoobenthos of ZPF was represented by a mussel biocoenosis, with a 58–100% mass-share of *M. galloprovincialis* (Mikhailova 2002). Another species, *M. phaseolina*, previously observed in the mixed ZPF biocoenosis, had an average biomass of 2.6 g/m² and an occurrence of 15% during this period. Based on the results of large-scale studies of the region's benthic fauna in 1984–2003, three biocoenoses were described, including *Mytilus galloprovincialis* (in the depth range of 21–45 m), *Melinna palmata* + *Nephtys hombergii* (25–35 m) and *Modiolula phaseolina* (49–54 m) (Sinegub 2006). The biocoenosis of unattached red algae *Phyllophora* on the central part of the NWBS had actually degraded by that time (Milchakova et al. 2013; Gubbay et al. 2016). In order to "protect a large (our correction: previously large) colony of algae from the genus of *Phyllophora*, the revival of flora and fauna of the coastal waters of the Black Sea" over an area of 4025 km², a botanical sanctuary of national importance—"Zernov's *Phyllophora* Field"—was established in 2008 (Nature reserves 2009).

Materials on the fauna of ZPF from previous decades were presented by the results of two benthic surveys performed in 2012 (Kovalishina & Kachalov 2015) and 2010–2013 (Revkov et al. 2018). These works focus on the quantitative parameters of macrozoobenthos development (number of species, abundance, biomass) and their long-term changes. The goals of the present study were 1) to assess the current biocoenotic structure and habitat ordination of the zoobenthos on soft bottoms in the ZPF area under the current conditions of Black Sea de-eutrophication and 2) to clarify the applicability of the Critically Endangered (CR) category (according to the European Red List of Habitats) to the soft-bottom habitat of the ZPF water area.

Material and Methods

The present work was based on benthic surveys conducted in the water area of ZPF during cruises #68 (2010), #70 (2011) and #72 (2013) aboard R/V "Professor Vodyanitsky" (Fig. 1). The method of collection and primary sample processing at 43 stations in ZPF was previously described (Revkov et al. 2018).

To describe the quantitative development of bottom fauna the following equation of functional abundance index (IFA) (Mal'tsev 1990) was used:

$$IFA = N_i^{0.25} \times B_i^{0.75},$$

where N_i and B_i are the abundance (ind./m²) and biomass (g/m²) of "i" taxon, respectively.

In classification constructions using the IFA index, two numerical parameters are considered at a time, which makes it possible to level out the differences between organisms of higher individual mass and those organisms with a lower mass that are often more numerous in the benthos.

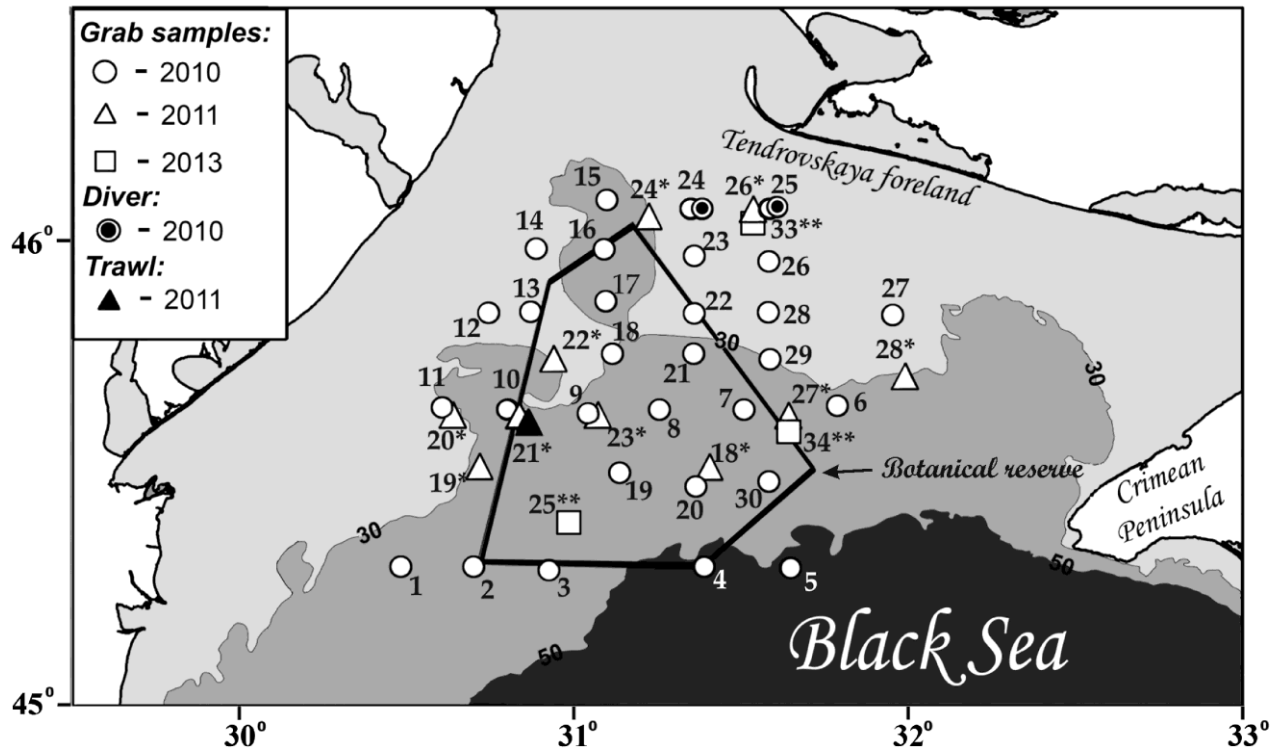


Figure 1. Map (after Revkov et al. 2018 with additions) of the benthic surveys performed in 2010– 2013 aboard R/V "Professor Vodyanitsky" in the Zernov's *Phyllophora* Field water area

In our work, we have used the term "biocoenotic complex". It is similar to the term "biocoenotic grouping", which implies a certain set (complex) of species inhabiting "separate facies within any biotope" (Nikitin 1948), or complex of species formed "under certain conditions" of the biotope (Arnoldy 1949). Each biotope and its facies are represented by a certain set of species, with certain dominant species.

Multivariate statistics algorithms were used to assess the structural organisation of the macrozoobenthos. Data processing was performed using the PRIMER v5 software package (Cluster, MDS, SIMPER analyses) (Clarke 1993; Clarke & Gorley 2001). The selection of biocoenotic complexes (Cluster and MDS analyses) was performed on the basis of a transformed (presence/absence of species) data matrix for each station. The transformed matrix used species with an occurrence of >6% (i.e. found at 3 or more stations), that allowed to obtain the reasonable "stress" values (<0.2) and is acceptable for adequate interpretation of cluster analysis results and reliable arrangement of sampling points on the 2-D ordination plot (Clarke 1993; Clarke & Gorley 2001). The Bray-Curtis statistic (Bray & Curtis 1957) was used as a measure of station similarity. The determination of principal species in the selected spatial groupings of benthos (complexes and subcomplexes) was performed on the basis of their contribution (based on non-transformed IFA index values) to the intra-complex similarity.

This approach differs from the commonly used technique of direct identification of biocoenoses by the biomass-dominated species, as proposed by Vorobiov (1949). In this case, the results of both the direct identification of biocoenotic complexes and identification using the aforementioned methods of

multivariate statistics were compared. The group of characteristic species ("constant" species according to V.P. Vorobiov) is represented by species with occurrences of 50% or more.

Species synonymy was checked using the World Register of Marine Species (WoRMS Editorial Board 2020). The EUNIS (European Nature Information System) habitat classification (Davies et al. 2004) was used for the ordination of selected biocoenotic complexes.

Results and Discussion

Biocoenotic structure of macrozoobenthos. In spite of the performed subdivision of the ZPF polygon into three main groupings of stations (I cluster: 14 stations, II: 24 stations and III: 4 stations) and one marginal station (attributed to the IV cluster), the bottom macrofauna of the water area was rather homogeneous, with the Bray-Curtis similarity of the stations exceeding 30% (Fig. 2). The main complex-forming species in the three main clusters of stations was *M. galloprovincialis*, and its contribution to the intra-complex similarity had absolute superiority over other species (Table 1). In this context, we note the existence of an extensive biocoenotic mussel complex in ZPF, which was present in 42 out of the 43 survey stations. Notably, the marginal station was an exception; here, *M. galloprovincialis* occupied second position (IFA=82.266) in the ranked list of species by its contribution to the average intra-complex similarity, while another mytilid (*M. phaseolina*; IFA=165.902) occupied the top position.

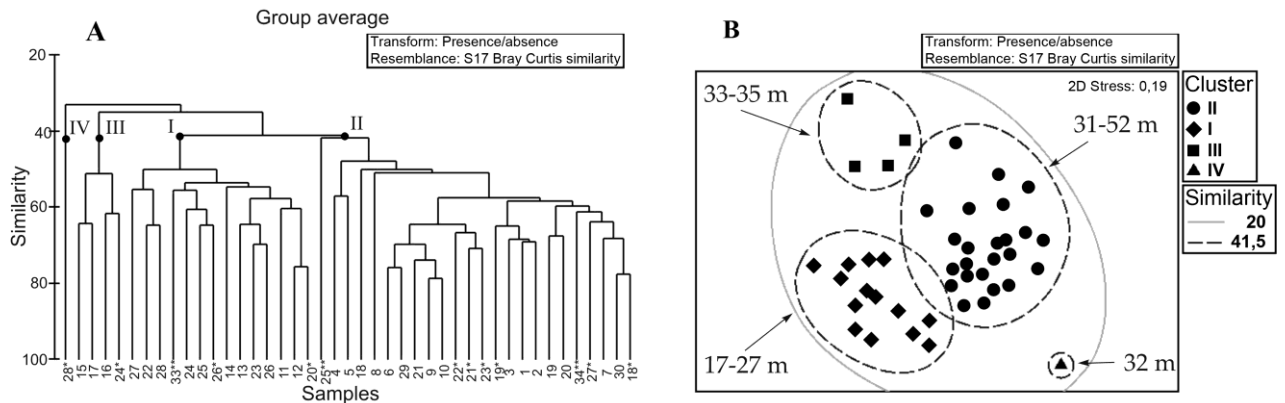


Figure 2. Hierarchical clustering (A) and MDS ordination (B) of survey stations at Zernov's *Phyllophora* Field

The three main clusters of stations can be classified as biocoenotic subcomplexes: *Mytilus galloprovincialis* + *Mytilaster lineatus* (I), *Mytilus galloprovincialis* + *Modiolula phaseolina* (II) and *Mytilus galloprovincialis* + Polychaeta (III). These subcomplexes were based on the contribution of species to the intra-complex similarity (see Table 1). With a decrease in quantitative development by IFA values of the principal species *M. galloprovincialis*, the parity development of several subdominant species of polychaetes was observed in the subcomplex III.

In order to compare the two methods of biocoenoses detection, we used the previously obtained results (Table 1) and, within their framework, we highlighted the possible variants of classification by biomass of the dominant species (Table 2). The results indicated that four biocoenoses can be identified within the framework of the three main subcomplexes of ZPF. The main one (located at 39 stations of the polygon) was the biocoenosis of mussels. Three other biocoenoses—*Chamelea gallina* (on st. 12), *Mytilaster lineatus* (st. 25) and *Terebellides stroemi* (st. 5)—were located locally at the margins of ZPF. Notably, only two of these four biocoenoses were previously indicated for ZPF: *M. galloprovincialis* (Zernov 1913; Zakutsky & Vinogradov 1967; Mikhailova 2002) and *M. lineatus* (Samyshev & Zolotarev 2018).

Four biocoenoses that were previously observed on ZPF (*Nephtys*, *Alitta*, *Melinna palmata*, and *Modiolula phaseolina* biocoenoses (Sinogub 2006; Samyshev & Zolotarev 2018)) were not represented in the current classification based on dominant species biomass. However, all of the dominant species of these biocoenoses (except for *Alitta*) were included as subdominant species in biocoenotic subcomplexes *Mytilus galloprovincialis* + *Modiolula phaseolina* and *Mytilus galloprovincialis* + Polychaeta (See Table

1), and were also observed earlier (1979–1989) (Samyshev & Zolotarev 2018) in mussel biocoenosis with an occurrence of over 50% (polychaete *Nephtys hombergii*), 20–50% (the polychaete *Melinna palmata*, mollusc *Mytilaster lineatus*) and 24% (the polychaete *Alitta succinea*).

Table 1. The principal benthic species contributing most to the average similarity within the corresponding grouping.

| Taxa | IFA | β_i | $\beta_i/SD(\beta_i)$ | $\beta_i\%$ | Cum.% |
|----------------------------------------|--------|-----------|-----------------------|-------------|-------|
| Cluster I. Average similarity: 45.82 | | | | | |
| <i>Mytilus galloprovincialis</i> | 248.85 | 38.92 | 1.92 | 84.94 | 84.94 |
| <i>Mytilaster lineatus</i> | 61.88 | 2.57 | 0.38 | 5.60 | 90.54 |
| <i>Prionospio cirrifera</i> | 4.59 | 0.59 | 1.25 | 1.29 | 91.83 |
| <i>Ascidiella aspersa</i> | 9.72 | 0.58 | 0.54 | 1.27 | 93.10 |
| <i>Parvicardium exiguum</i> | 4.98 | 0.50 | 0.76 | 1.09 | 94.19 |
| <i>Amphibalanus improvisus</i> | 2.88 | 0.34 | 0.76 | 0.75 | 94.94 |
| <i>Spio decorata</i> | 2.72 | 0.29 | 0.63 | 0.63 | 95.57 |
| Cluster II. Average similarity: 43.82 | | | | | |
| <i>Mytilus galloprovincialis</i> | 259.82 | 34.48 | 1.49 | 78.69 | 78.69 |
| <i>Modiolula phaseolina</i> | 45.65 | 4.35 | 0.59 | 9.94 | 88.63 |
| <i>Ascidiella aspersa</i> | 12.22 | 1.40 | 0.80 | 3.20 | 91.82 |
| <i>Ciona intestinalis</i> | 12.26 | 0.61 | 0.43 | 1.40 | 93.22 |
| <i>Terebellides stroemii</i> | 3.32 | 0.48 | 0.43 | 1.10 | 94.33 |
| <i>Amphiura stepanovi</i> | 3.60 | 0.38 | 0.59 | 0.86 | 95.18 |
| <i>Papillicardium papillosum</i> | 2.90 | 0.34 | 0.77 | 0.78 | 95.97 |
| Cluster III. Average similarity: 67.93 | | | | | |
| <i>Mytilus galloprovincialis</i> | 65.74 | 66.12 | 4.19 | 97.33 | 97.33 |
| <i>Melinna palmata</i> | 1.51 | 0.53 | 1.55 | 0.78 | 98.11 |
| <i>Nephtys hombergii</i> | 3.76 | 0.38 | 0.87 | 0.56 | 98.67 |
| <i>Dipolydora quadrilobata</i> | 0.35 | 0.16 | 0.74 | 0.24 | 98.91 |
| Nemertea spp. | 0.32 | 0.15 | 0.74 | 0.22 | 99.13 |

Note: IFA – average value of IFA index; β_i – absolute contribution of species “i” to the mean Bray-Curtis similarity within the corresponding groupings; $\beta_i\%$ – relative contribution of species “i” to the mean Bray-Curtis similarity within the corresponding groupings; SD – standard deviation; Cum.% – total relative contribution of species to the mean Bray-Curtis similarity within the corresponding groupings.

Table 2. Biocoenoses of ZPF detected by different methods.

| Method of biocoenosis or biocoenotic complex detection | | | |
|---------------------------------------------------------------|----------------------------------|--------------------|------------------------------------------------|
| Multivariate statistical methods using IFA | Biomass-dominated species method | | |
| Subcomplex | Biocoenosis | Number of stations | Biomass of principal species, g/m ² |
| <i>Mytilus galloprovincialis</i> + <i>Mytilaster lineatus</i> | <i>M. galloprovincialis</i> | 12 | 220.80±41.75 |
| | <i>Chamelea gallina</i> | 1 | 331.28 |
| | <i>M. lineatus</i> | 1 | 232.49 |
| <i>M. galloprovincialis</i> + <i>Modiolula phaseolina</i> | <i>M. galloprovincialis</i> | 23 | 250.39±43.45 |
| | <i>Terebellides stroemi</i> | 1 | 4.8 |
| <i>M. galloprovincialis</i> + Polychaeta | <i>M. galloprovincialis</i> | 4 | 50.526±14.305 |

Note: here and below are the Mean±Std.Err.

The biocoenoses of *Chamelea gallina* and *Terebellides stroemi* can be considered new to ZPF in terms of classification based on biomass-dominated species. The first of the guiding species of these biocoenoses presented in the lists of species at three more stations of subcomplex *Mytilus galloprovincialis* + *Mytilaster lineatus*, and dominated by biomass at station 12. The second one, *T. stroemi*, was a typical species of subcomplex *Mytilus galloprovincialis* + *Modiolula phaseolina*, which was presented in the species lists of 20 more stations of this subcomplex and was dominant by biomass at station 5.

Quantitative representation of macrozoobenthos. The main subcomplexes of ZPF were *Mytilus galloprovincialis* + *Mytilaster lineatus* (I) and *Mytilus galloprovincialis* + *Modiolula phaseolina* (II), which had similarly high levels of quantitative representation (Table 3). In terms of species richness, subcomplexes I and II reached 77 and 81%, respectively, from the total list of 162 species represented in ZPF (Revkov et al. 2016). The bottom macrofauna of the *Mytilus galloprovincialis* + Polychaeta (III) subcomplex was five to six times poorer by abundance and biomass and five times poorer by number of species than that of subcomplexes I and II. This decrease in the quantitative representation of macrozoobenthos in subcomplex III was observed in all basic taxonomic groups (Table 4). The analysis of index values of macrozoobenthos diversity also showed significant differences between subcomplex III and subcomplexes I, II. These differences were especially noticeable in the parameters calculated by biomass. Subcomplex III had a noticeably lower species diversity and evenness, with a higher dominance than that of subcomplexes I and II.

Table 3. Main quantitative parameters and ecological indices of macrozoobenthos in the biocoenotic subcomplexes of the ZPF water area.

| Sub-complex | S _{total} | S _{st} | N/B | d | J' | H'(log2) | 1-Lambda' |
|-------------|--------------------|-----------------|-----------------|--------------------|--------------------|--------------------|--------------------|
| I | 125 | 40±2 | <u>3137±285</u> | <u>4.852±0.248</u> | <u>0.645±0.024</u> | <u>3.415±0.136</u> | <u>0.827±0.021</u> |
| | | | 325±49 | 6.992±0.453 | 0.269±0.021 | 1.426±0.122 | 0.441±0.04 |
| II | 132 | 34±2 | <u>2302±185</u> | <u>4.266±0.241</u> | <u>0.663±0.018</u> | <u>3.329±0.107</u> | <u>0.807±0.017</u> |
| | | | 297±47 | 6.230±0.316 | 0.274±0.032 | 1.327±0.134 | 0.408±0.045 |
| III | 25 | 14±1 | <u>503±91</u> | <u>2.019±0.203</u> | <u>0.766±0.042</u> | <u>2.851±0.160</u> | <u>0.786±0.032</u> |
| | | | 58±18 | 3.163±0.226 | 0.167±0.047 | 0.642±0.196 | 0.182±0.064 |
| IV | 23 | 23 | <u>2176</u> | <u>2.863</u> | <u>0.407</u> | <u>1.842</u> | <u>0.479</u> |
| | | | 283 | 3.896 | 0.549 | 2.484 | 0.768 |

Note: S_{total} – total number of species, S_{st} – number of species at station, N – abundance, ind./m², B – biomass, g/m², d – Species richness (Margalef), J' – Pielou's evenness, H'(log2) – Shannon Base 2, 1- Lambda' – Simpson index. The values above the line were calculated by abundance, while values below the line were calculated by wet biomass.

Polychaetes were the dominant group in subcomplex I in terms of abundance, encompassing 59% of the total abundance of macrozoobenthos within the subcomplex, while molluscs rank second at 30%. Molluscs were the dominant group in subcomplexes II and III with abundances of 40 and 60%, respectively, while polychaetes rank second with abundances of 23 and 6%, respectively (Table 4). The very high density of polychaetes in the subcomplex I was primarily caused by the presence of representatives of the Spionidae family (*Prionospio cirrifera*, *Spio decorata*, and *Dipolydora quadrilobata*), which comprised approximately 66% of the abundance of all polychaetes. Notably, polychaetes of this family were detritophages inhabiting the upper layers of the soft bottoms. Many of the spionids—including the aforementioned species—are resistant to organic contamination and are considered as indicators for habitats with high levels of eutrophication (Cinar et al. 2009). In terms of

biomass, molluscs dominated in all three subcomplexes, with abundance of 92 (subcomplex I), 90 (II) and 92% (III) in the total biomass of macrozoobenthos.

Table 4. Quantitative representation of the main macrozoobenthos taxa in terms of abundance (ind./m², above the line) and wet biomass (g/m², below the line) in the biocoenotic subcomplexes of the ZPF water area.

| Taxa | Subcomplex | | |
|------------|-----------------|----------------|---------------|
| | I | II | III |
| Polychaeta | <u>1840±213</u> | <u>718±103</u> | <u>185±30</u> |
| | 9.65±2.03 | 5.41±0.67 | 2.50±1.19 |
| Mollusca | <u>949±155</u> | <u>913±147</u> | <u>301±81</u> |
| | 300.28±47.05 | 265.96±43.11 | 53.46±15.56 |
| Crustacea | <u>154±24</u> | <u>199±30</u> | <u>27±12</u> |
| | 2.18±0.41 | 1.03±0.42 | 0.06±0.02 |
| Ascidiacea | <u>27±10</u> | <u>54±14</u> | <u>0.5</u> |
| | 11.92±6.00 | 21.07±4.55 | 0.98 |

Selected benthic biocoenotic groupings were located in certain areas of the ZPF water area (Fig. 3). All stations of subcomplex II were in the deeper water zone (31–52 m). This subcomplex was bordered by the shallower (17–27 m) stations of subcomplex I on the northwest and northeast areas. The stations of subcomplex III were placed as a narrow belt between two sections of subcomplex I on the northern part of ZPF at a depth 33–35. The only station included in subcomplex IV was located in the direction of the Crimean Shelf at the entrance to the Karkinitzky Gulf. Most likely, the reasons for significantly lower values of zoobenthos development in subcomplex III are due to its location in the zone of the deep corridor, which extends in the ZPF water area from the north to the south on the 30 m isobath, and can serve as a transit zone for the transformed flow of the Danube and Dnieper rivers (Parkhomenko & Rodionova 2011).

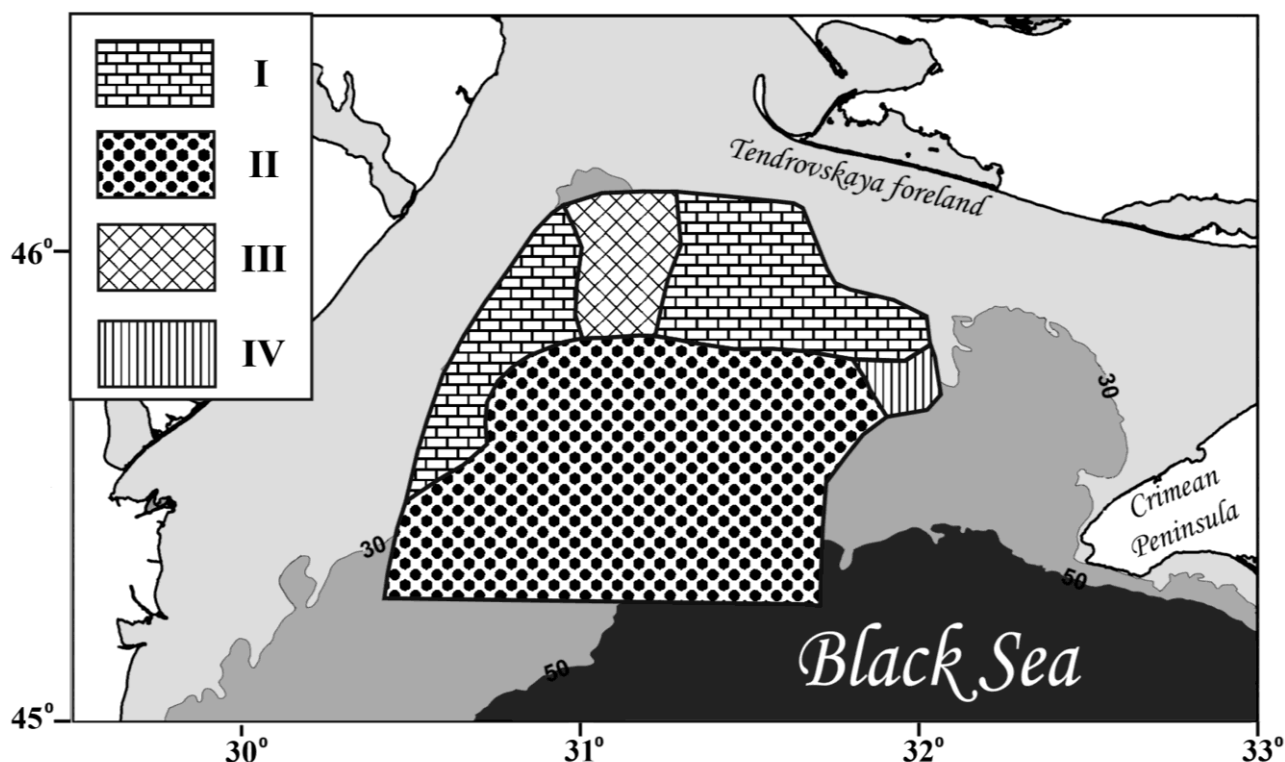


Figure 3. Location of biocoenotic subcomplexes (I–IV) of the bottom macrofauna in the Zernov's *Phyllophora* Field water area.

Bottom habitats of the ZPF water area. To date, a total of 63 habitats (level 4; according to EU28+) have been identified in the Black Sea (including the Marmara Sea). Of these, 1 has the status of Critically Endangered (CR), while 2 are Endangered (EN), 3 are Vulnerable (VU), 1 is Near Threatened (NT), 2 are Least Concern (LC), and 54 are Data Deficient (DD) (Gubbay et al. 2016). The only habitat with CR status is the "Pontic circalittoral biogenic detritic bottoms with encrusting corallines (Phymatolithon, Lithothamnion) and attached foliose sciaphilic macroalgae" (A5.xx), which is located in the ZPF water area.

It is known that the assessment of habitat status for "A5.xx" was based on the state of phytocenosis and long-term dynamics of *Phyllophora* stocks within the ZPF water area boundaries since the beginning of the 20th century (Gubbay et al. 2016). Over the last 50 years, the degradation of the *Phyllophora* biocoenosis and a massive reduction in stocks of at least 100 times was noted—this was the cause for the designation of this habitat as CR. At the beginning of the 21st century, the *Phyllophora* stock within the ZPF water area was less than 6000–100000 tonnes (by wet weight) (Milchakova et al. 2013), while "only a small nucleus of the (phyllophora) habitat survives on the Ukrainian shelf" (Gubbay et al. 2016). The following note was also related to the state of bottom biocoenoses located under the aggregations of unattached *Phyllophora*: "The diversity of associated fauna and flora has also decreased dramatically, although it is now considered to be largely stable" (Gubbay et al. 2016). In this case, the stable depressive state was also recognised for the bottom macrofauna of the ZPF water area. We believe that the opinion on the current depressive state of the bottom macrofauna at ZPF must be corrected.

Destructive changes were also observed in the bottom macrofauna of ZPF. By the late 1970s, the mean biomass and total stock of zoobenthos decreased by seven times at this site (Revkov et al. 2018). However, data from the first decades of the 21st century is a testament to the restoration of the ZPF macrozoobenthos to its pre-crisis level from 1957–1960 based on quantitative representation. Moreover, the current level of macrozoobenthos species richness is the highest (162 species) of all recorded ZPF studies due to the improvement of ecological conditions in the region (Revkov et al. 2018). It seems that the past assessment of the bottom habitat in the water area of ZPF as CR based on the state of biocoenosis of *Phyllophora* does not consider the "good" state of bottom macrofauna at present.

To resolve this contradiction, we propose considering the accumulations of unattached red algae *Phyllophora* as a separate epibenthic biotope with its definition as CR habitat. At the beginning of the 20th century, the unattached *Phyllophora* formed dense aggregations as shafts up to 1 m high on the bottom (Samyshev & Zolotarev 2018). Over 100 species of invertebrates and approximately 40 species of fish were recorded in this *Phyllophora* biotope (Zaitsev 2006). While many agree that the invertebrate fauna in *Phyllophora* biotope is nonspecific in character, its representatives have also been recorded living on the bottom (Samyshev & Zolotarev 2018). However, many of these invertebrates have a characteristic protective "brown-red colour—in full harmony with the colour of the *Phyllophora* itself" (Zernov 1913). In the unattached *Phyllophora* biocoenosis, a higher temperature was registered (up to 4–5°C) in comparison to the surrounding water layers (Vinogradov & Zakutsky 1967), which may be a specific characteristic of this biotope.

In the ZPF water area, *Phyllophora* was represented by attached and unattached ecological forms. The main mass of *Phyllophora* (up to 80%) was represented by the unattached form of *Phyllophora crispa* (= *Ph. nervosa*), localised in the central part of the field and bordered by a belt of the attached form (Vinogradov & Zakutsky 1967; Zaitsev 2006). Factors determining the formation of accumulations or, as defined by Zernov (1913), the "sea" of unattached *Phyllophora*, are recognised as being similar to those involved in the formation of accumulations of brown floating algae in the Sargasso Sea (Zenkevich 1963). That is a rather stable circular cyclonic current that leads to a concentration of algae detached from the substrate in the central part of the NW shelf (Zaitsev 2006) and the presence of an extensive flat shelf with suitable light (for photosynthesis) and relatively stable hydrological conditions. This accumulation of *Phyllophora* was first discovered at the end of the 19th century (Andrusov 1890, cited in Vinogradov & Zakutsky 1967) and it is unknown how long they formed in the past. The rate and extent to which *Phyllophora* will recover from near total degradation under favourable conditions is also an open question. However, it is already clear that in the first decade of the 21st century, the tendency for phytobenthos restoration was noted by a number of researchers (Minicheva et al. 2009; Tkachenko & Tretiak 2015; Berlinsky et al. 2014; Stevens et al. 2019) in the ZPF area after the onset of de-eutrophication in the Black Sea basin (Oguz et al. 2008; Zaika 2011; Yunev et al. 2019), the prohibition of bottom fishing for sprat and dredging for mussels (introduced in Ukraine in the late 1980s), and stricter

control over the use of bottom fishing gear, which stopped the harvesting of *Phyllophora* at ZPF and the creation of a botanical sanctuary in 2008 (Nature reserves 2009). However, Milchakova et al. (2013) believe that this is due to the areal expansion of another *Phyllophora* species—the attached form of *Coccotylus truncatus* (= *Ph. brodiaei*).

Considering the aforementioned information, we propose the identification of two basic habitats at the bottom of the ZPF water area according to the EUNIS habitat classification. The first is degraded, which tends to restore the biotope – “Aggregations of unattached *Phyllophora* in the central part of the northwestern shelf of the Black Sea” that can now be classified as CR habitat (A5.xx according to (Gubbay et al. 2016)). The second is “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds, shell deposits, with encrusting corallines (Phymatolithon, Lithothamnion) and attached foliose sciaphilic macroalgae” (Fig. 4). The name proposed by (Gubbay et al. 2016) would be retained; however, it is not associated with the biocoenosis of degraded red algae *Phyllophora*, but rather biocoenotic complex *Mytilus galloprovincialis*. Since the main task of the present study was habitat ordination of the selected faunistic complexes, we will provide a more detailed description of the second selected habitat.

Habitat of *Mytilus galloprovincialis* biocoenotic complex. The proposed code designation is A5.62x. It is located offshore in an area with water depths of 17–52 m, where the wave impact on bottom landscapes is slight. In the ZPF water area, the bottom sediments are mixed (shells, sand, and alevrit muds), with a predominance of mussel shells (Samyshev & Zolotarev 2018).



Figure 4. “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds, shell deposits, with encrusting corallines and attached foliose sciaphilic macroalgae” habitat in the Zernov's *Phyllophora* Field water area. The photo was taken by scuba diver Taras Getman at st. 26 (2010).

This habitat can currently be classified as LC due to the recovery of the bottom macrofauna of ZPF after the ecological crisis of the Black Sea ecosystem in the second part of the 20th century (Revkov et al. 2018). In addition to the main complex-forming species (*Mytilus galloprovincialis*), the characteristic species include the polychaetes – 8, the bivalves – 3, the crustaceans – 2 species, by one species of bryozoan, ascidian and amphiuroid (Table 5).

In accordance with subdivision of the mussel biocoenotic complex into three subcomplexes, we identified three subhabitats corresponding to these subcomplexes: A5.62x1 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Mytilaster lineatus*”, A5.62x2 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Modiolula phaseolina*” and A5.62x3 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with Polychaeta”.

Biocoenotic subcomplex *Mytilus galloprovincialis* + *Mytilaster lineatus*. Proposed code designation of subhabitat – A5.62x1 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Mytilaster lineatus*”. This subcomplex is located in the northwestern and north-eastern parts of ZPF at a depth of 17–27 m. According to Mikhailova (2002), the bottom substrate is represented by silted shells with a silt cover of up to 20–30 mm. The share of the sand fraction in the bottom sediment is 0.06–4%, while that of the silts is 0.6–5% (Samyshev & Zolotarev 2018). In addition to the main complex-

forming species, *Mytilus galloprovincialis* and *Mytilaster lineatus*, the characteristic species include the polychaetes – 15, the bivalves – 3, the crustaceans – 4, the bryozoan – 2, the ascidian – 1 species (Table 6, Fig. 5). Most of these are warm-water species.

Table 5. Quantitative representation of the characteristic species in terms of abundance (N, ind./m²), wet biomass (B, g/m²) and occurrence (F, %) in *Mytilus galloprovincialis* biocoenotic complex.

| Taxa | N | B | F |
|----------------------------------|--------|--------------|-----|
| <i>Mytilus galloprovincialis</i> | 427±57 | 205.47±28.19 | 100 |
| <i>Parvicardium exiguum</i> | 23±6 | 1.14±0.33 | 67 |
| <i>Papillicardium papillosum</i> | 17±4 | 1.09±0.28 | 67 |
| <i>Modiolula phaseolina</i> | 278±80 | 13.97±3.73 | 65 |
| <i>Prionospio cirrifera</i> | 444±84 | 0.422±0.095 | 95 |
| <i>Heteromastus filiformis</i> | 77±17 | 0.14±0.05 | 93 |
| <i>Nephtys hombergii</i> | 22±5 | 1.22±0.24 | 79 |
| <i>Dipolydora quadrilobata</i> | 147±44 | 0.29±0.09 | 67 |
| <i>Pholoe inornata</i> | 41±12 | 0.03±0.01 | 65 |
| <i>Spirobranchus triqueter</i> | 12±3 | 0.06±0.02 | 63 |
| <i>Harmothoe reticulata</i> | 14±4 | 0.08±0.02 | 60 |
| <i>Terebellides stroemii</i> | 18±4 | 1.39±0.42 | 58 |
| <i>Phtisica marina</i> | 30±6 | 0.02±0.01 | 74 |
| <i>Amphibalanus improvisus</i> | 17±5 | 0.52±0.14 | 58 |
| <i>Cryptosula pallasiana</i> | 52±20 | 0.54±0.21 | 79 |
| <i>Asciella aspersa</i> | 17±4 | 10.04±2.23 | 74 |
| <i>Amphiura stapanovi</i> | 74±19 | 0.72±0.22 | 51 |
| Porifera | 20±5 | 0.47±0.13 | 53 |
| Nemertea | 33±5 | 0.14±0.02 | 93 |

Biocoenotic subcomplex *Mytilus galloprovincialis* + *Modiolula phaseolina*. Proposed code designation of subhabitat – A5.62x2 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Modiolula phaseolina*”. This subcomplex is located in the southern section of the ZPF water area at a depth of 31–52 m. The sediments are represented by sand with shells and a layer of grey mud located on the bottom surface (Mikhailova 2002). There is from 10 to 20% of mud fraction in the sediments, reaching up to 78% in the southernmost section of the ZPF water area (Kovalishina & Kachalov 2015). Along with the main complex-forming species, *Mytilus galloprovincialis* and *Modiolula phaseolina*, the characteristic species include the polychaetes – 10, the bivalves – 3, the crustaceans – 6, the ascidian – 2 species and by one species of the bryozoan and the amphiuroid (Table 6, Fig. 5).

Biocoenotic subcomplex *Mytilus galloprovincialis* + Polychaeta. Proposed code designation of subhabitat – A5.62x3 “Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with Polychaeta”. This subcomplex is located in the northern part of the ZPF water area at a depth of 33–35 m. The content of mud fraction in the mixed sediment averages 10–20% here (Kovalishina & Kachalov 2015). Along with the main complex-forming species, *Mytilus galloprovincialis*, which is characterised by an abundance, biomass and occurrence of 185±57 ind./m², 50.53±14.31 g/m² and 100%, respectively, there are another 16 characteristic species of the subcomplex. These include the polychaetes *Melinna palmata* (43±25, 0.51±0.38, 100), *Nephtys hombergii* (47±43, 1.62±1.37, 75), *Dipolydora quadrilobata* (27±19, 0.08±0.04, 75), *Prionospio cirrifera* (18±1, 0.02±0.01, 100), *Heteromastus filiformis* (19±6, 0.03±0.01, 100), *Harmothoe reticulata* (11±8, 0.13±0.12, 50), *Harmothoe imbricata* (8±5, 0.07±0.04, 50) and *Phyllodoce mucosa* (9±5, 0.04±0.03, 50), Nemertea (12±4, 0.11±0.06, 75), the crustaceans *Phtisica marina* (20±12, 0.03±0.02, 50) and *Amphibalanus improvisus* (3±2, 0.03±0.02, 50), the bivalves *Parvicardium exiguum* (14±9, 0.05±0.04, 50), *Papillicardium papillosum* (9±8, 0.24±0.22, 50) and *Abra alba* (6±4, 0.005±0.004, 50), the bryozoan *Conopeum seurati* (2±1, 0.005±0.004, 50) and the phoronid *Phoronis psammophila* (32±17, 0.40±0.39, 75). This represents a significantly depleted subcomplex in the quantity and quality of subcomplex *Mytilus galloprovincialis* + *Modiolula phaseolina*.

Table 6. Quantitative representation of the characteristic species in terms of abundance (N, ind./m²), wet biomass (B, g/m²) and occurrence (F, %) in *Mytilus galloprovincialis* + *Mytilaster lineatus* (I) and *Mytilus galloprovincialis* + *Modiolula phaseolina* (II) biocoenotic subcomplexes.

| Taxa | Subcomplex | | | | | |
|----------------------------------|------------|--------------|-----|---------|--------------|-----|
| | I | | | II | | |
| | N | B | F | N | B | F |
| <i>Mytilus galloprovincialis</i> | 609±103 | 198.19±39.26 | 100 | 377±73 | 239.96±42.89 | 100 |
| <i>Modiolula phaseolina</i> | | | | 433±119 | 21.75±5.37 | 96 |
| <i>Mytilaster lineatus</i> | 175±63 | 45.84±22.48 | 86 | | | |
| <i>Parvicardium exiguum</i> | 50±15 | 2.56±0.83 | 100 | 10±3 | 0.52±0.2 | 58 |
| <i>Papillicardium papillosum</i> | | | | 25±7 | 1.63±0.44 | 83 |
| <i>Pitar rudis</i> | 7±2 | 1.72±1.1 | 71 | | | |
| <i>Anadara kagoshimensis</i> | 6±3 | 3.42±1.79 | 50 | | | |
| <i>Abra alba</i> | | | | 13±5 | 0.51±0.21 | 50 |
| <i>Prionospio cirrifera</i> | 914±191 | 0.83±0.23 | 100 | 260±46 | 0.27±0.07 | 96 |
| <i>Heteromastus filiformis</i> | 172±38 | 0.32±0.07 | 100 | 33±8 | 0.06±0.02 | 88 |
| <i>Pholoe inornata</i> | 87±30 | 0.066±0.02 | 100 | 21±7 | 0.02±0.01 | 54 |
| <i>Harmothoe imbricata</i> | 78±20 | 0.49±0.14 | 93 | | | |
| <i>H. reticulata</i> | 26±10 | 0.15±0.04 | 86 | | | |
| <i>Spirobranchus triqueter</i> | | | | 20±5 | 0.10±0.03 | 88 |
| <i>Spio decorata</i> | 182±51 | 0.68±0.23 | 93 | | | |
| <i>Lagis neapolitana</i> | 37±21 | 2.81±1.58 | 86 | | | |
| <i>Nephtys hombergii</i> | 12±5 | 0.93±0.3 | 64 | 24±5 | 1.29±0.34 | 88 |
| <i>Terebellides stroemii</i> | | | | 29±6 | 1.77±0.46 | 88 |
| <i>Dipolydora quadrilobata</i> | 112±61 | 0.29±0.14 | 64 | 193±70 | 0.38±0.13 | 71 |
| <i>Eumida sanguinea</i> | | | | 16±4 | 0.07±0.02 | 71 |
| <i>Pionosyllis pulligera</i> | 26±10 | 0.004±0.002 | 64 | | | |
| <i>Platynereis dumerilii</i> | 32±11 | 0.42±0.18 | 64 | | | |
| <i>Phyllodoce mucosa</i> | | | | 16±5 | 0.22±0.11 | 63 |
| <i>Capitella capitata</i> | 47±31 | 0.028±0.012 | 57 | | | |
| <i>Alitta succinea</i> | 15±7 | 0.35±0.17 | 57 | | | |
| <i>Aonides paucibranchiata</i> | 4±1 | 0.017±0.002 | 50 | 36±15 | 0.08±0.04 | 54 |
| <i>Clymenura clypeata</i> | 11±6 | 0.18±0.12 | 50 | | | |
| <i>Amphibalanus improvisus</i> | 39±12 | 1.28±0.35 | 93 | | | |
| <i>Phtisica marina</i> | 23±8 | 0.008±0.005 | 64 | 37±9 | 0.02±0.01 | 83 |
| <i>Caprella acanthifera</i> | | | | 50±14 | 0.03±0.02 | 79 |
| <i>Apherusa bispinosa</i> | | | | 17±5 | 0,006±0.002 | 63 |
| <i>Microdeutopus gryllotalpa</i> | 19±10 | 0.012±0.008 | 57 | | | |
| <i>M. versiculatus</i> | | | | 8±2 | 0.002±0.001 | 54 |
| <i>Athanas nitescens</i> | 15±6 | 0.11±0.05 | 57 | | | |
| <i>Stenosoma capito</i> | | | | 13±3 | 0,14±0.04 | 54 |
| <i>Orchomene humilis</i> | | | | 11±3 | 0.02±0.01 | 50 |
| <i>Cryptosula pallasiana</i> | 47±24 | 0.5±0.26 | 86 | 65±33 | 0.67±0.35 | 92 |
| <i>Conopeum seurati</i> | 10±6 | 0.024±0.015 | 57 | | | |
| <i>Asciidiella aspersa</i> | 16±7 | 10.4±5.5 | 71 | 20±5 | 11.17±2.38 | 83 |
| <i>Ciona intestinalis</i> | | | | 30±11 | 9.83±3.14 | 67 |
| <i>Amphiura stepanovi</i> | | | | 123±30 | 1.14±0.35 | 83 |
| Porifera | | | | 33±8 | 0.71±0.18 | 83 |
| Nemertea | 29±6 | 0.14±0.04 | 100 | 39±7 | 0.14±0.02 | 96 |
| Oligochaeta | 48±17 | 0.011±0.004 | 57 | | | |

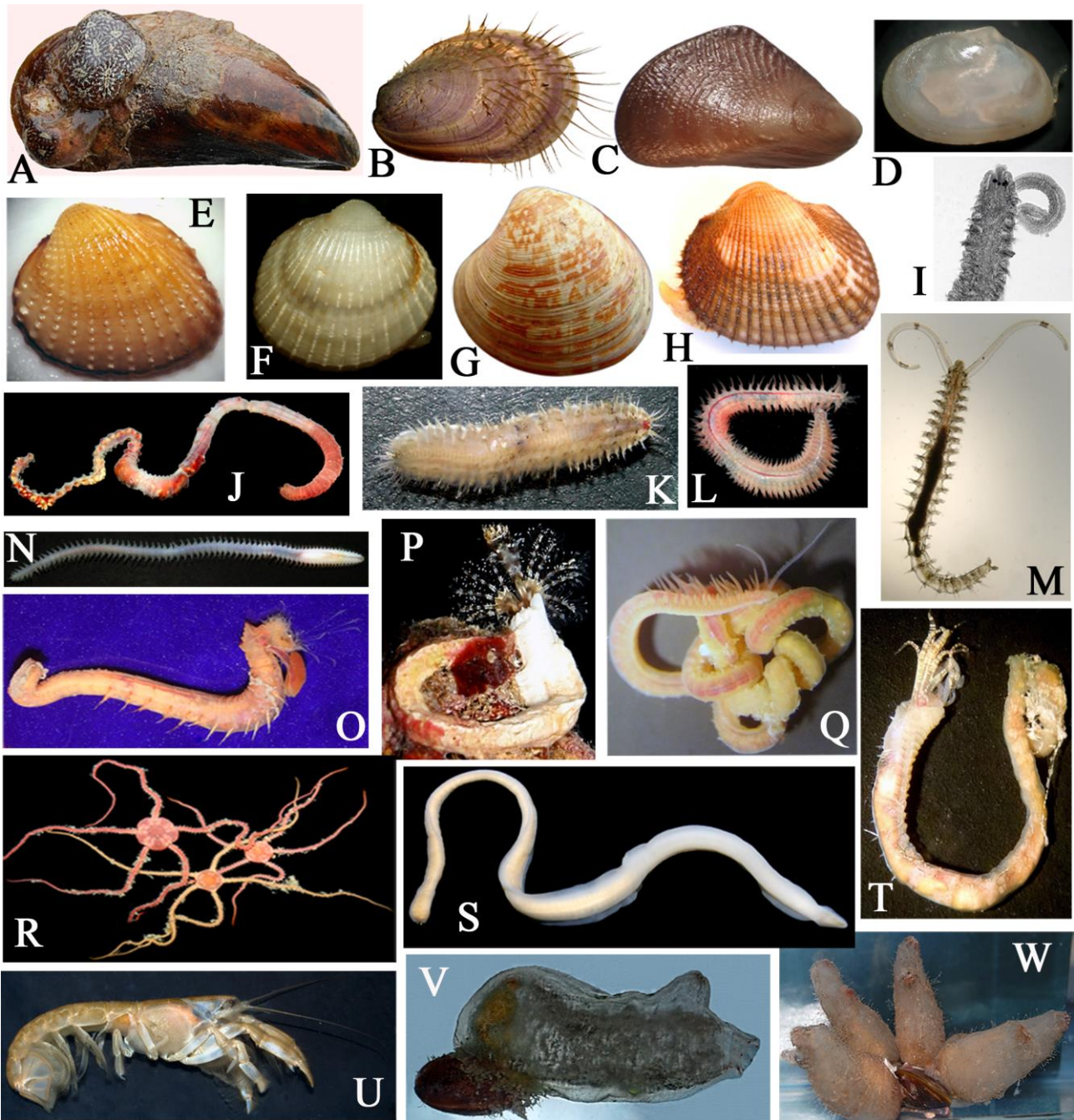


Figure 5. Some characteristic species in *Mytilus galloprovincialis* biocoenotic complex at the Zernov's *Phyllophora* Field. A – *Mytilus galloprovincialis* with a colony of *Botryllus schlosseri* on the shell; B – *Modiolula phaseolina*; C – *Mytilaster lineatus*; D – *Abra alba*; E – *Papillicardium papillosum*; F – *Parvicardium exiguum*; G – *Pitar rudis*; H – *Anadara kagoshimensis*; I – *Dipolydora quadrilobata*, anterior end; J – *Heteromastus filiformis*; K – *Harmothoe imbricata*; L – *Alitta succinea*; M – *Spio decorata*; N – *Nephtys hombergii*; O – *Terebellides stroemii*; P – *Spirobranchus triqueter*; Q – *Aonides paucibranchiata*; R – *Amphiura stepanovi*; S – Nemertea; T – *Melinna palmata*; U – *Upogebia pusilla*; V – *Ciona intestinalis*; W – *Ascidiella aspersa*; (photos A. Nadolny and N. Revkov).

Peculiarities of distribution of some principal species on ZPF. The recent alien species in the Black Sea, such as the molluscs *Anadara kagoshimensis* and *Rapana venosa* and the polychaetes *Polydora cornuta* and *Dipolydora quadrilobata* were recorded on the soft bottoms of the ZPF water area. Of these, the most developed settlements were formed by *D. quadrilobata*, which is one of the characteristic species of the three biocoenotic subcomplexes with the highest abundance values (up to 1184 ind./m²) in the southwestern part of ZPF water area at a depth of 37 m. The highest occurrence and abundance of *Dipolydora* was registered in the *Mytilus galloprovincialis* + *Modiolula phaseolina* subcomplex.

Dipolydora quadrilobata is an Arctic-Boreal species known from the Atlantic coast of Europe and North America (Fauvel 1927; Blake 1971), the Pacific coast of Asia and North America (Radashevsky 1993; Blake 1996) and the Adriatic Sea (Castelli et al. 1995). In the Black Sea, it was first detected in Bulgarian waters in 2003 (Todorova and Panayotova 2006, cited in Surugiu, 2009), then observed off the coast of Romania (Surugiu 2009, 2012), near the mouth of the Danube River (Bondarenko 2012; Surugiu 2012) and on the Crimean shelf up to the Kerch Peninsula (Boltachova & Lisitskaya 2014). *D. quadrilobata* is one of the characteristic species in the *M. phaseolina* community, with a maximum density of 2600 ind./m² on the Romanian coast (Surugiu 2012). Notably, two different ecological forms have been encountered in this species (Blake 1969, 1971). Both forms reproduce in winter but differ in their optimal temperature for larvae development (6–10 and 10–15°C, respectively) (Blake 1969). This creates prerequisites for the development of *D. quadrilobata* settlements both in the zones of moderately warm water (lower infralittoral zone, biocoenosis of mussel muds) and cold water (circalittoral zone, biocoenosis of *M. phaseolina* silts) on the Black Sea shelf.

Anadara kagoshimensis was first recorded in the Black Sea in 1968 near the shores of the Caucasus (Kiseleva 1992). By the early 2000s, it had become one of the mass cenozo-forming species on the soft bottoms, found at depths of up to 40 m (Revkov 2016) due to its wide ecological valence (eurhythermism, euryhalinity, resistance to hypoxic environmental conditions) (Soldatov et al. 2018). To date, *Anadara* remains one of the characteristic species of the biocoenotic subcomplex *Mytilus galloprovincialis* + *Mytilaster lineatus* in ZPF. Moreover, the polychaete *P. cornuta* (an invader to the Black Sea basin since 1962 (Losovskaya & Nesterova 1964)) and the predatory gastropod *R. venosa* (an invader to the Black Sea basin since 1947 (Drapkin 1953)) are less numerous. These species were recorded at 3 and 2 stations, respectively, in subcomplex *Mytilus galloprovincialis* + *Mytilaster lineatus* only.

The wide distribution and dominance of *M. galloprovincialis* seemed to be logical for the ZPF water area due to the main zone of mussel settlements in the Black Sea being located at a depth of 20–50 m, with a peak of biomass concentration around 35–40 m (Zaika et al. 1990). The lower boundary of mussel settlements is determined by a summer thermocline deepening on the Black Sea shelf that can reach 60 m (Revkov & Shaliapin 1999). The aforementioned depths for the lower boundary of the summer thermocline coincide with the lower boundary (up to 52 m) of the mussel biocoenotic complex (habitat A5.62x) distribution. Deeper, there is phaseolina silt in the zone of influence of the cold intermediate layer of the Black Sea, where the temperature does not exceed 8–9°C (Puzina & Mizyuk 2016). Therefore, the lower relatively deep section of the ZPF water area is located in the contact zone of two biomes (deeper cold water and shallow warm-water biomes). Even insignificant interannual vertical fluctuation of the lower boundary of the thermocline here can lead to a significant horizontal displacement of its projection to the bottom. In this regard, mixed or transitional communities may form in the contact zone between these two biomes of the shelf, which are capable of surviving the temperature "waves" caused by a possible interannual shift in the lower boundary of the summer thermocline. From our perspective, the biocoenotic subcomplex *Mytilus galloprovincialis* + *Modiolula phaseolina* is the result of such penetration of the deep-water fauna of the low circalittoral zone with a dominance of *M. phaseolina* into the mussel mud of upper circalittoral zone due to the formation of peculiar transition temperature zones in benthic habitat.

Modiolula phaseolina is one of the principal species in this subcomplex and was found across all its depths (31–52 m). Here, its settlement was represented by various sizes of molluscs with a shell length of up to 14.8 mm. Continuation of the deep-water complex penetration is further traced in biocoenotic subcomplex *Mytilus galloprovincialis* + *Mytilaster lineatus*, where we found single juvenile specimens of *M. phaseolina* with lengths of 1.8–2.7 mm (at 26, 25 and 20 m depths) and 6.9 mm (26 m) in this subcomplex.

The depth of *M. phaseolina* penetration into relatively shallow areas (up to 20 m) noted by our team is less than that previously reported for the ZPF water area: 35–45 m (Samyshev & Zolotarev 2018), 42 m (Kovalishina & Kachalov 2015) and 49 m (Sinegub 2006). In general, the presence of *M. phaseolina* in the marginal zone of mussel biocoenosis in the northwestern part of the Black Sea should be recognised as common, with an occurrence of 10–20% in 1979–1989; here, it was a second order dominant species with a biomass of 3.2–20.7 g/m² in 1979–1980 (Samyshev & Zolotarev 2018).

In connection with the aforementioned peculiarities of penetrating the elements of the deep-water complex into the overlying neighbouring areas of the shelf, we note the following. The reasons

determining the upper boundary of the *M. phaseolina* community in the Black Sea remain rather unclear. The assumption the *M. phaseolina* respond to "some abiotic factors changing in the transition zone" between the belts of the *M. galloprovincialis* and *M. phaseolina* communities that prevents the expansion *M. phaseolina* to shallower depths remains relevant (Zaika et al. 1990). Nevertheless, although *M. phaseolina* forms stable settlements in the Black Sea at depths of more than 40–50 m (Kiseleva 1981; Zaika et al. 1990), its penetration into relatively shallow areas of the Black Sea shelf is not exceptional. There is information in the database of the Department of Benthos Ecology of A.O. Kovalevsky Institute of Biology of the Southern Seas of RAS regarding the registration of single *M. phaseolina* specimens in different areas of the Crimean shelf of the Black Sea at shallow depths: at a depth of 4–10 m in northwestern Crimea – Karkinitzky Bay, in western Crimea – Uchkuevka coastal zone, in southern Crimea – Yalta coastal zone (wet mass of specimens 0.0001–0.041 g); at a depth of 11–20 m in southeastern Crimea – Karadag region, in western Crimea – Kalamitsky Bay (wet mass of specimens 0.001–0.032 g) and in southern coast of Crimea – Laspi Bay (wet mass of specimens 0.298 g). According to these averages, adult molluscs of 6–7 mm length can be found even at depths of up to 10 m. These data correspond to the results obtained in the first half of the 20th century by Pauli (1927) *in vitro*. It was demonstrated that adult *M. phaseolina* can live in the surface waters of the Black Sea throughout the year.

Conclusions

The results of the present study indicate the existence of the biocoenotic complex *Mytilus galloprovincialis* in the bottom macrofauna of the ZPF water area. This complex is subdivided into three subcomplexes, where *Mytilaster lineatus* (17–27 m deep), *Modiolula phaseolina* (31–52 m) and Polychaeta (33–35 m) were the next most important subcomplex-forming taxa after *Mytilus galloprovincialis*. In terms of abundance, biomass and number of species, a depressive state of the macrozoobenthos was observed in the northern part of ZPF in the area of subcomplex *M. galloprovincialis* + Polychaeta. Throughout the ZPF water area, a pattern of molluscs domination by biomass (up to 92% of the total macrozoobenthos wet biomass) typical for the Black Sea was noted.

Historically, there was relative stability in the biocoenotic organisation of the bottom macrofauna of the ZPF water area. Regardless of the biocoenosis identification methods (based on biomass-dominated species per station or by means of multivariate statistics), mussels were the main biocoenosis-forming species in the study area. However, both during the period of ecological instability of the Black Sea ecosystem in the second half of the 20th century and at the present stage, there remains the possibility of transition dominance (by biomass) to species from the sub-dominants, or from characteristic species of corresponding biocoenoses, complexes (or subcomplexes). For example, these organisms included the bivalves *Modiolula phaseolina* and *Mytilaster lineatus* and the pelophile polychaetes *Nephtys hombergii*, *Melinna palmata* and *Terebellides stroemi*.

Two habitats are proposed for designation under the EUNIS habitat classification at the bottom of the ZPF water area. The first one is degraded and tending to restore the biotope "Zernov's *Phyllophora* Field – aggregations of unattached *Phyllophora* in the central part of the northwestern shelf of the Black Sea" (A5.xx) that can now be classified as CR habitat. The second one is "Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds, shell deposits, with encrusting corallines (Phymatolithon, Lithothamnion) and attached foliose sciaphilic macroalgae" (A5.62x), representing the biotope of the soft bottoms with a mussel biocoenotic complex. According to the data presented here on the macrozoobenthos state and of its long-term changes, A5.62x habitat can currently be classified as LC. Due to biocoenotic ordination, it is subdivided into three subhabitats: "Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Mytilaster lineatus*" (A5.62x1), "Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with *Modiolula phaseolina*" (A5.62x2) and "Pontic circalittoral biogenic detritic bottoms with dead or alive mussel beds with Polychaeta" (A5.62x3).

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