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Long-term Variations in the Black Sea Population of Smooth Scallop, *Flexopecten glaber* (Linnaeus, 1758) (Bivalvia: Pectinidae): A Review

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Abstract

Data on the presence and characteristics of smooth scallop *Flexopecten glaber* (Linnaeus, 1758) aggregations in various parts of the Black Sea shelf (BSS) have been subjected to a retrospective analysis. The waters of the northern (Crimean coast), eastern (Central and North Caucasian), and Anatolian sectors of BSS can be considered the most favorable habitats for smooth scallop, where massive beds of this species were found in the first half of the 20th century. However, no such data are available for the northwestern and western BSS, where freshwater discharges from the Danube, Dniester, and Dnieper form a permanent zone of lower water salinity. The period of decline in the Black Sea scallop population recorded in the 1970s–1990s generally coincided with the well known ecological crisis due to the anthropogenic eutrophication of the Black Sea in the second half of the 20th century. In the late 2000s and the 2010s, the scallop beds in the Crimean BSS showed a tendency to recover, which may be associated with the general improvement of the ecological condition of the Black Sea basin. A similar recovery of scallop beds is expected to occur in the eastern (North and Central Caucasian) and southern BSS, but has not yet been recorded. The results obtained suggest a possibility of downgrading the conservation status of this species in the Red Data Books of the City of Sevastopol and the Republic of Crimea from the “species declining in abundance” to the “species recovering in abundance and distribution”.

Introduction

Among marine bivalve mollusks of the family Pectinidae Rafinesque, 1815 distributed across the world’s oceans, the genus *Flexopecten* Sacco, 1897 comprises only four known species: *Flexopecten felipponei* (Dall, 1922), *F. flexuosus* (Poli, 1795), *F. glaber* (Linnaeus, 1758), and *F. hyalinus* (Poli, 1795) (WoRMS Editorial Board, 2021). Of them, only the smooth scallop *F. glaber* forms stable aggregations in the Black Sea. According to the latest taxonomic edit history in WoRMS of April 2009, *F. glaber* in the Black Sea is represented by the subspecies *F. glaber ponticus* (MolluscaBase, 2022). However, the subspecies status of *F. glaber ponticus* has not kept up, and its name is currently placed in synonymy with the parent species *F. glaber* (Bondarev, 2018; Slynko et al., 2020). The population of *F. glaber* in the Black Sea is referred to as the Black Sea scallop (Revkov et al., 2021b).

The Black Sea scallop has been found within a depth range from 0 to 40 m with various occurrence frequency and abundance values almost all along the Black Sea coast (Zernov, 1913; Arnol’di, 1949; Kiseleva, 1981; Albayrak, 2003; Fashchuk et al., 2012, etc.). This species is sensitive to oxygen depletion and is a stenohaline form in the Black Sea, occurring in habitats with an optimum salinity range of 16–17‰ (Nevesskaya, 1965). It is large in size, can reach relatively high

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densities in some areas and, therefore, is potentially a target aquaculture species (Revkov et al., 2021b). The feasibility of *F. glaber* cultivation in the Black Sea will depend largely on the stability of its natural broodstock aggregations.

The status of *F. glaber* in the general structure of benthos off the Crimean coast is dynamic and has varied over a century-long history of studies from the entry into the group of dominant forms (Zernov, 1913; Kiseleva & Slavina, 1963, 1964; Nevesskaya, 1965) to becoming a rare member of benthos that requires protection measures (Revkov, 2015, 2018). In the present review, we aimed to carry out a retrospective analysis of the status of the Black Sea *F. glaber* population.

Materials and Methods

No studies on spatial and temporal variations of the *F. glaber* population in the Black Sea have been conducted to date. Therefore, we collected this information for various parts of the sea from published works on macrozoobenthos. Additionally, we used data from the database of the Benthos Ecology Department, A.O. Kovalevsky Institute of Biology of the Southern Seas RAS. This data was obtained by sampling off the Crimea coast in a depth range 0–50 m both during the 70th (2011), 72nd (2013), 84th (2016), 86th (2016), and 96th (2017) research cruises aboard the RV *Professor Vodyanitsky* using an *Okean-50* bottom grab sampler (S=0.25 m²), and also by SCUBA divers during the shore-based expeditions in 1989 and 2017 using a manual grab sampler (S=0.04 m^2).

The Black Sea shelf (BSS) with scallop habitats within the 0–40 m depth range was divided into five sectors: northwestern (Ukrainian), western (Romanian and Bulgarian), southern (Turkish), eastern (Central and North Caucasian), and northern (Crimean) (Figure 1). A more detailed analysis of the material available was carried out for the Crimean BSS sector. The latter, in turn, was divided into five regions: Karkinit Bay, Yevpatoria–Sevastopol region (with Donuzlav Bay considered separately), the southern Crimea coast region (with the Laspi area considered separately), Feodosia region (Karadag), and the Kerch Strait region (Vodyanickij, 1949). The Kerch Strait was considered separately, along with the Kerch pre-strait zone and the adjacent Caucasian sector.

Results

Northwestern and Western BSS Sectors

The Black Sea scallop was listed on the check list of invertebrates from the northwestern Black Sea covering the periods until 1965 and from 1966 to 2003 (Zaitsev et al., 2006). However, this species does not form own eponymous community and is categorized as a rare and endangered member of the benthos in the region (Alexandrov & Zaitsev, 1998; Zaitsev & Alexandrov, 1998; Zaitsev et al., 2006). In the period 1979–1985,

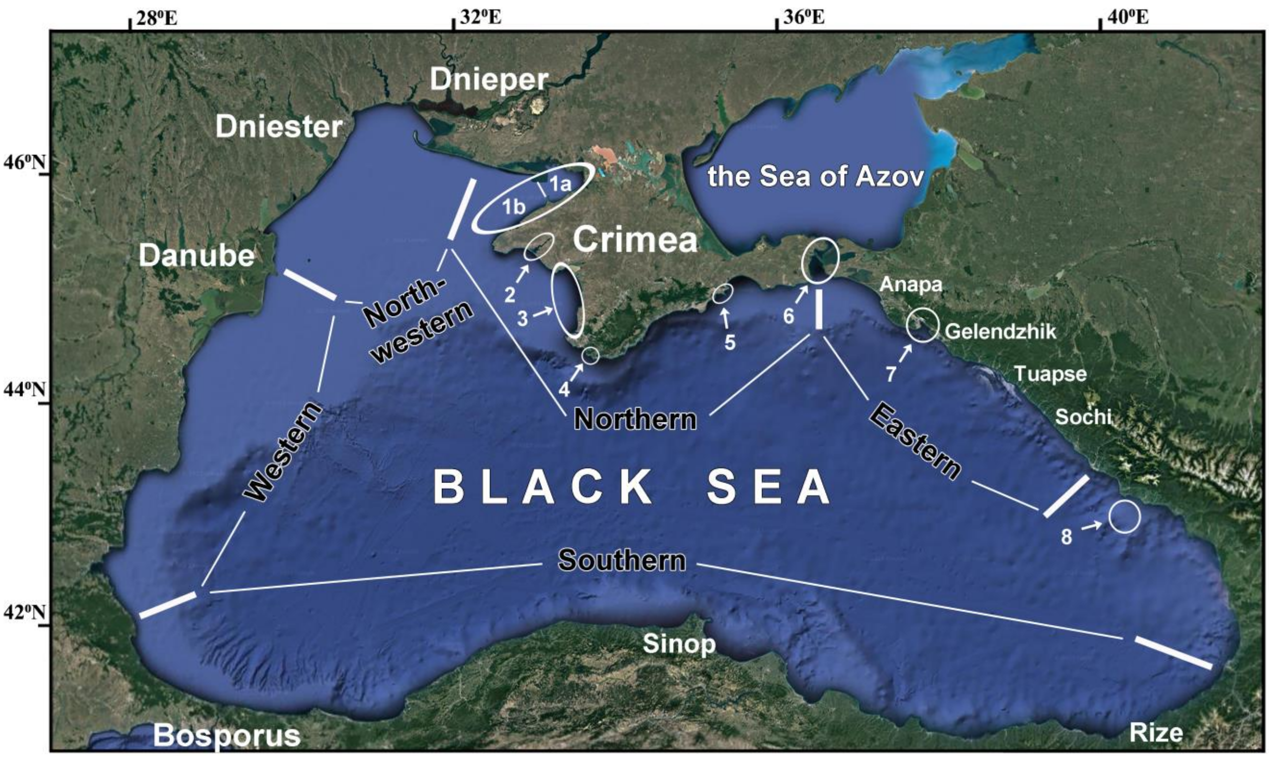

Figure 1. Map of the sectors used in the analysis of dynamics of the *Flexopecten glaber* population in the Black Sea.
The conditional boundaries in the main spatial subdivision of the Black Sea shelf are marked with thick white lines. Separate polygons within the Northern (Crimean) Black Sea shelf are represented by the following designations – Zabakalsky area (1a), Predbakalsky area (1b), Donuzlav Bay (2), Yevpatoria–Sevastopol region (3), Laspi area (4), Feodosia region (5), Kerch Strait region (6), Novorossiysk Bay (7), and Gudauta oyster bed (8).

scallops were recorded only in 1980 from a depth of up to 30 m, where they had an average abundance of 0.1 ind./m^2, a biomass of 0.65 g/m^2, and an occurrence frequency of 2.6% (Samyshev & Zolotarev, 2018).

Off the Romania coast, the first reliable record of live Black Sea scallop dates back to 2020, when only three live individuals of this species were found in dredge samples collected at a depth of 25 m near Mangalia (Filimon, 2020). Off the Bulgarian coast, scallop beds have been found extending to a depth of 40 m (Hubenov, 2007). Here, on sands of the subtidal zone, scallop is a relatively rare benthic species whose occurrence frequency value is only about 1% (Marinov, 1990).

Thus, the available data show a historically poor development of scallop beds in the western and northwestern BSS sectors: there is no information that would indicate the ever existence of massive aggregations of this species here.

Southern BSS Sector.

Off the Turkey coast (the southeastern sector of the coast from Sinop to Rize) in 1926–1927, the scallop abundance was as follows: in a fine-grained sand habitat dominated by *Chamelea gallina* (Linnaeus, 1758), at depths between 10 and 16 m, the abundance was 5 ind./m^2; in a habitat with a mixture of fine-grained sand and loose silt dominated by *Spisula subtruncata* (da Costa, 1778), at depths between 20 and 35 m, the abundance was 2 ind./m^2; and in a habitat on dense silty sand with abundant bivalve shell debris dominated by *Mytilus galloprovincialis* Lamarck, 1819, at depths between 35 and 40 m, the abundance reached 25 ind./m^2 (Nikitin, 1948). In the above-mentioned benthic communities, the Black Sea scallop was in the group of characteristic species. Unfortunately, the subsequent information about the structure of the benthos off the Turkey coast, which could be used to judge about the presence of scallop aggregations, is extremely scarce. In 1988–1989, no Black Sea scallops were found at four sampling stations off the Anatolian coast of the Black Sea at a depth of 28–40 m (Mutlu et al., 1993). In 2000–2001, the species had an occurrence frequency of 6.8% in the western (from the Bosporus Strait) sector of the Turkey coast within a polygon of 44 stations arranged at depths of 0.5–60 m (Albayrak, 2003). Thus, as available data shows, the scallop population in the southern BSS sector was well developed in the first half of the 20th century, and there is a lack of sufficiently representative information about the condition of its beds in the second half. In the early 21st century, quite a high frequency of scallop occurrence was recorded, however, only from an area near the Bosporus Strait.

Eastern BSS Sector Including the Kerch Strait.

Off the Caucasian coast in the 1930s, the Black Sea scallop, along with *Ostrea edulis* Linnaeus, 1758, *M. galloprovincialis*, *Modiolus adriaticus* Lamarck, 1819, *Pitar rudis* (Poli, 1795), and *C. gallina*, was categorized as a common member of benthos with an occurrence frequency value of 75% (Nikitin, 1934). In the 1950s–1960s, in addition to oyster beds, scallop was a member of the *M. galloprovincialis* community at a depth of 20 m (Kiseleva, 1981). In 1958–1963, off the western shore of Novorossiysk Bay, where the bottom substrate was composed of coarse shell debris, scallops formed a bed with a density lower than 5 ind./m^2 at a depth of 12 m (Milovidova, 1966). During this period, the abundance of large-sized mollusks in the bay, including scallops, was observed to decrease, which was associated with the predation of veined rapa whelk, *Rapana venosa* (Valenciennes, 1846). In 1958, Black Sea scallop was a member of the *P. rudis* community. But by 1963, as a result of changes in species dominance, it got in the *Gouldia minima* (Montagu, 1803) community with an occurrence frequency value of more than 50%. At almost the same time (in 1965), scallops were not found during a survey of other areas of the North and Central Caucasus regions (the waters off Anapa, Gelendzhik, Tuapse, and Sochi) at 54 stations in a depth range of 5–25 m (bays and adjacent waters), and also in the Anapa area and at 0.5 and 32 m (Milovidova, 1967). After 10 years (1975–1979), scallops appeared at a 3% occurrence frequency in the Anapa area (Milovidova & Kirjukhina, 1985). Despite the above-mentioned absence of scallop from quite an extensive part of the Caucasian coast in 1965, this species was permanently present in Novorossiysk Bay with minor fluctuations at a relatively low occurrence frequency value, from 1 to 5%, in 1958–1979 (Milovidova & Kirjukhina, 1985).

In 1980, in the Kerch pre-strait area, the average abundance, biomass, and occurrence frequency values for scallops in the *C. gallina* community (13–20 m) were, respectively, 1 ind./m^2, 0.91 g/m^2, and 25%; in the *M. galloprovincialis* community (25–35 m), the values were, respectively, 0.8 ind./m^2, 1.57 g/m^2, and 20%; in the *Mod. adriaticus* community (18–34 m), respectively, 1.4 ind./m^2, 2.23 g/m^2, and 35% (Nikolaenko & Povchun, 1993). In the following years, 1986–1990, scallops in the Kerch pre-strait area were recorded from the *Mod. adriaticus* community and categorized as a rare species with an average abundance of 0.77 ± 0.47 ind./m^2 and a biomass of 3.5 ± 2.4 g/m^2 (Terentyev, 2008). Although, scallops were not found in the Gudauta oyster bed in 1990 (Zolotarev & Terentyev, 2012), they reappeared here in small numbers in the *M. galloprovincialis* community in 1994 (Varshanidze & Guchmanidze, 2004). The following record of scallops from the benthos of the North Caucasian sector took place in 2006. A scallop bed was found during a bottom trawling in the Gelendzhik area (Golubaya Bay) at a depth of 38–39 m (Mokievsky, 2006). According to the data published in literature, it was the last record of the Black Sea scallop population off the Caucasian coast. No Black Sea scallops were found both in the northeastern BSS sector (Dzhubga–Kudepsta) at depths of 13–29 m in

2010 (Zagorskaya, 2014) and in the waters of the Utrish State Nature Reserve in 2016. Furthermore, the scallop is even absent from the annotated list of species of the Reserve (Kolyuchkina et al., 2017).

Within the Kerch Strait, a rapid depopulation of the Black Sea scallop was observed in the 1980s–2000s. In 1986, it was a co-leading species in the *C. gallina–F. glaber* and *F. glaber–O. edulis* communities in the central and southwestern parts of the strait, and also in the *Mod. adriaticus* community in the southeastern part (Fashchuk et al., 2012). Already in 1989, its abundance was found to decrease due to both the bottom siltation and the rapa whelk predation (Ivanov & Sinegub, 2008). In 2009–2010, it completely vanished from the strait (Alemov & Tikhonova, 2012; Fashchuk et al., 2012).

Thus, in the eastern BSS sector, including the Kerch pre-strait area and immediately within the strait, there has been only a decrease in the scallop bed dynamics so far, up to the complete lack of records of this species in the last decade, which began as early as in the 1960s. The specific pattern of the benthos dynamics in the region under consideration is associated generally with the effect of the highly trophic Sea of Azov water and with the anthropogenic transformation of benthic communities due to the siltation of vast bottom areas and the rapa whelk predation (Ivanov & Sinegub, 2008; Nabozhenko, 2011; Fashchuk et al., 2012; Zolotarev & Terentyev, 2012; Terentyev, 2013).

Scallop Aggregations off the Crimean Coast

Here, Black Sea scallops form beds, extending almost from shore to a 40 m depth, in silty, sandy, shell debris, pebbly bottoms habitats and their various combinations (Zernov, 1913; Arnol'di, 1949; Kiseleva & Slavina, 1964; Nevesskaya, 1965; Petukhov et al., 1991; Revkov et al., 2021a).

In Karkinit Bay in the 1930s, scallops were a common species of benthos, including even shallow-water silty habitats with *Zostera* L. and *Lamprothamnium* J. Groves, 1916, where they “adapted to live on plants, attached to their tops, as is characteristic of *Parvicardium* (=*Cardium*) *exiguum* (Gmelin, 1791)” (Arnol’di, 1949). In our opinion, the scallops’ migration up thalli of macrophytes, reported by Arnol’di, is an adaptation aimed to temporary escape low-oxygen conditions that arise in the near-bottom water layer on shallow-water silty sediments during the summer warming.

Unfortunately, there is a gap of data on the zoobenthos of this region for the subsequent long time interval. The existence of adult scallop beds in the Predbakalsky and Zabakalsky areas was confirmed only in 2008–2019 (Table 1). In 2008, scallops were present in the *Mytilaster lineatus* (Gmelin, 1791) community and dominated in biomass at the stations located north of the Lebyazhy Islands (Revkov et al., 2010). In the present study, both a higher occurrence frequency and a greater quantitative representation of scallops in Karkinit Bay were recorded in the 2000s–2010s, as compared to the data of the 1930s.

The data from Donuzlav Bay turned out to be quite illustrative. There is a pontization process the enrichment of the fauna of the bay in species began in 1961 after the construction of the canal connecting it to the sea. The first record of a scallop in the bay dates back only to 2007 (Pereladov, 2016). The process of colonization of these waters by scallops was confirmed in 2017 and 2019 (Alyomov et al., 2020; Revkov et al., 2021a) (Table 1). Apparently, the long-term absence of the necessary pool of larvae in the waters adjacent to Donuzlav in the 1960s–1990s explains the fact that no scallops were found in the bay during the benthic surveys conducted here in 1981, 1990, and 1997.

Off the Karadag coast, the Black Sea scallop was a common benthic species only in the 1930s–1950s. In the subsequent years, this species either was not recorded or had a low abundance. After a 30-year absence, it reappeared here in 2020. According to the personal communication of S.V. Alyokhin, a senior inspector of the Karadag Nature State Reserve, scallops with a shell length of up to 3 cm were found during a visual inspection of a shallow-water (2.5–3.5 m) sandy area from the Kuzmichev stone to the Ivan Razboinik rock in July and August 2020.

In the Sevastopol region, scallops were found in abundance from the early 20th century to the 1950s. In the 1970s, the Black Sea scallop disappeared from the check lists of benthic species and then, for about 43 years, remained a rare member of the fauna in the region. In 2016–2018, a recovery of Black Sea scallop beds was observed in Kazachya and Kalamita bays (Table 2).

A pattern of dynamics of scallop aggregations similar to that in the Sevastopol region was also observed in the Laspi Bay area (Table 2). Scallops ceased to occur here in the late 1980s and were recorded in abundance only in 2017 and 2020 (Revkov & Boltachova, 2022).

Discussion

When considering the Black Sea scallop population, we highlight two key points of interest. The first is the existence of regions with historically poor development of scallop beds. These are the western and northwestern BSS sectors. On the other hand, there are regions with clearly similar long-term dynamics in the development of scallop population: from being a common member of benthos in the first half and middle of the 20th century to single findings and complete absence of scallops in the second half. These are the areas of the southern, eastern (Central and North Caucasus), and northern (Crimea) BSS. Such large-scale spatial and temporal heterogeneities in the Black Sea scallop population should apparently be caused by effects of similar in scale factors in the ecosystem of the Black Sea basin.

The explanation for the historically poor development of scallop beds in the western and northwestern BSS can be the effect of some strong regional ecological factors negative for the Black Sea scallop. In this regard, we should note the fact that these areas of the shelf are located actually in a zone of permanently decreased water salinity (Ivanov & Belokopytov, 2011), i.e. beyond the optimum of 16–17‰ for scallops in the Black Sea (Nevesskaya, 1965). No live scallops have been found to date in even fresher waters of limans in the northwestern BSS and in the Sea of Azov with their salinities below 13–14‰ (Zaitsev et al., 2006; Anistratenko et al., 2011).

We consider anthropogenic organic pollution as the most influential of the factors that could be responsible for similar patterns of long-term variations in scallop aggregations over the major part of the Black Sea (the Crimean, Central and North Caucasian, and Turkish sectors). It was considered as one of the most serious threats to pelagic and benthic ecosystems of the Black Sea basin in the second half of the 20th century (NATO, 1997; Zaitsev & Alexandrov, 1998; BSC, 2008). The river runoff with excess levels of organic matter and nutrients led to a disequilibrium in the production–destruction balance in the Black Sea ecosystem towards accumulation of organic matter with the peak of eutrophication of the basin recorded in the late 1980s to the early 1990s (Alexandrov & Zaitsev, 1998; Zaitsev & Mamaev, 1997; Zaitsev & Alexandrov, 1998; Yunev et al., 2019). However, the organic matter in the water column alone is not a factor that causes mandatorily negative pressure on a benthic ecosystem, since it is utilized as food by seston filter-feeders (including scallops) and other detritus feeding benthic species. The excess organic matter in the near-bottom layers and on the bottom in combination with the deficiency of oxygen for its degradation poses a serious threat to benthic fauna, especially for its oxyphilic species such as scallop.

Table 1. Characteristics of the Black Sea scallop (*Flexopecten glaber*) beds off the Karadag coast, in Donuzlav Bay, and in Karkinit Bay (Crimean coast, Black Sea)

Region	Year	Habitat / Depth / Number of sampling stations	Occurrence frequency, %	Abundance (ind./m^2) / biomass (g/m^2)	References
Karkinit Bay	1934–1938	Predbakalsky area, silty sand and sandy shell debris / 10–22 m / no data	7	0.7 / 0.6	Arnol'di, 1949
		Zabakalsky area, sandy silt with shell debris / <10 m / no data	20	1.5 / 4.51	
		silt of shallow-water coves with *Zostera* sp., *Lamprothamnus* sp. / ~0.8 m / no data	10	1 / 0.20	
	2008–2009	sandy silt with shell debris / 0.2–9 m / 53	19	6 / 49.24	Revkov et al., 2010
	2011	Predbakalsky area, silted shell debris / 12–36 m / 8	13	0.5 / 1.9	Our data (cruise #70 of R/V *Professor Vodyanitsky*)
		Zabakalsky area, silted shell debris / 9–11 m / 5	60	9.2 / 1.38	
	2016, 2017	Predbakalsky area, silted shell debris / 15–38 m / 23	22	2.2 / 10.22	Our data (cruises ##84, 86, and 96 of R/V *Professor Vodyanitsky*)
Donuzlav Bay	1981, 1990, 1997	sand, silted sand, shell debris / 1.5–15 m / 144, 40, 29 (in different years)	No		Boltacheva et al., 2002
	2007	“waters of Donuzlav Lagoon”	Live specimens recorded for the first time from a qualitative sample		Pereladov, 2016
	2017, 2019	northwestern part of the region, near-shore sand / 0.5–2 m / 3	Recorded as commonly present	Visual estimation in 2019, up to 0.5 / no data	Alyomov et al., 2020; Revkov et al., 2021a
Karadag coast	1938–1939	pure coarse sand and gravel / 3–20 m / 13	40	2.8 / 5.59	Bekman, 1952
		shell debris / 14–32 m / 6	60	1.7 / 0.72	
	1956–1957	shell debris / 18–35 m / no data	20	10 / 32.61	Losovskaya, 1960
	1976	fine sand, silty sand, coarse sand, mussel silt / 7–40 m / 10	No		Milovidova, Kirjukhina, 1985
		shell debris off Cape Kapsel and off the Krymskoe Primorye Sanatorium	Large scallops were found in dredge samples		Milovidova, 1979
	1981	sand with admixture of pebbles, gravel, and shell debris / 5–15 m / 12	“Single individuals were found only in qualitative samples from some stations”		Kiseleva et al., 1984
	1990	sand / 3–23 m / 26	4	0.6 / 12.308	Revkov et al., 2004
	2008	silted sand, pebbles, shell debris / 5–15 m / 11	No		Mazlumyan et al., 2009
	2020	sand / 2.5–3.5 m	Presence recorded	Visual estimation	Personal communication of S.V. Alyokhin

The formation of suffocation zones and the events of mass mortality of benthos over vast areas of the northwestern BSS were associated with the excess levels of unprocessed organic matter under low oxygen conditions in the near-bottom layer. The latter is described in sufficient detail in a number of works (Zaitsev, 1992; Alexandrov & Zaitsev, 1998; Zaitsev & Alexandrov, 1998; Zaitsev et al., 2006; Revkov et al., 2018). No similar events of extensive benthos mortality have been observed in the northern, eastern, and southern BSS sectors. The consequences of eutrophication in the Crimean sector became clearly evident in the first half of the 1990s. Along open coasts, there was a shift of the most productive belt of benthos toward shallower depths and a peak of benthic biomass due to the significant increase in the abundance of bivalve mollusks from the group of seston filter-feeders, with a pronounced dominance of *C. gallina* (Revkov, 2011).

In contrast to the vast suffocation zones of the northwestern Black Sea, there was a compensatory increase in consumers of the emerging excess of available organic matter in conditions of better aeration of the near-bottom layer recorded along the Crimean coast of the Black Sea. However, it did not completely rule out the probability of low oxygen conditions to form in the near-bottom layer: the oxygen degradation of excess organic matter near the bottom could cause oxygen depletion to a threshold value, thus, limiting the possibility of existence of oxyphilic species. Unfortunately, we do not have available data on long-term variations in the oxygen content of the near-bottom layer which includes a narrow zone of the filtration activity of bivalves. Nevertheless, we assume that the depopulation of the Black Sea scallop in the 1970s–1990s, which coincided in time with the anthropogenic eutrophication of the Black Sea basin, could be associated with the probable near-bottom

Table 2. Characteristics of the Black Sea scallop (*Flexopecten glaber*) beds in the Yevpatoria–Sevastopol region and in the Laspi Bay area (Crimean coast, Black Sea)

Year	Habitat / Depth / Number of sampling stations	Occurrence frequency, %	Abundance (ind./m²) / biomass (g/m²)	References
		Yevpatoria–Sevastopol region		
Early 20th century	Sevastopol Bay, Sevastopol coast / oyster beds and deeper layers of near-shore sand / no data	Common species		Zernov, 1913
1928–1929	Sevastopol Bay / silty sediments, to 18 m / 175	< 10	no data	Chigirin, 1938
1953–1956	Sevastopol Bay	Larvae present		Murina et al., 1999
1957	Tarkhankut Peninsula, off Cape Uret / *Gouldia* community, shell debris with sand and a slight admixture of silt, 10–25 m / 39	5	10 / 13.1	Kiseleva, Slavina, 1964
1989	Kalamita Bay / silted sand, pebbles, shell debris, 7–25 m / 27	3.7	0.01 / 0.13	Our data (shore-based expedition)
1987–1997	Sevastopol Bay	No larvae in plankton		Murina et al., 1999
1973–2009	waters of the Sevastopol region / soft bottom, 3–20 m / (monitoring surveys 1 time every 3 years; one survey covers ~58 stations)	No		Milovidova, Kirjukhina, 1985 Mironov et al., 2003, 2009, 2018
2013	Tarkhankut Peninsula to Cape Lukkul / silted sand with shell debris, 12–38 m / 7			Our data (cruise #72 of R/V *Professor Vodyanitsky*)
2016–2017	Tarkhankut Peninsula to Cape Lukkul / silted sand with coarse shell debris, 17–40 m / 6	50	2.5 / 6.1	Our data (cruises ##84, 86, and 96 of R/V *Professor Vodyanitsky*)
2017–2018	Eastern branch of Kazachya Cove / in *Zostera noltei* beds, on sand–shell debris sediments, 1–6 m / visual estimation	throughout the area	1–10 / no data	Bondarev, 2019
		Laspi Bay area		
1983, 1984	Laspi Bay / sand, silted sand, 20, 22, 25 m / 33	9	1.5 / 1.929	Petukhov et al., 1991, our data
1989	Laspi Bay / sand, sand with shell debris / 3–21 m / 30	No		Our data (shore-based expedition)
1991	Balaklava to Cape Aya area (Zolotoi Beach) / soft bottom, 5–25 m / 15			Revkov et al., 2001
1996	Laspi Bay / sand, silted sand, 5–32 m / 29			Revkov, Nikolaenko, 2002
2017	Laspi Bay / subtidal sandy sediment, 4–37 m / 21	14	5 / 2.7	Our data (shore-based expedition)
2020	Mechty Cove / slightly silted *Amphioxus* sand with shell debris, 13–34 m / 4	75	81 / 169	Revkov, Boltachova, 2022

oxygen deficiency in the zone of filtration activity of the species. During this period, scallops either were not found in benthos samples or had a low abundance.

In the late 2000s and the 2010s, recovery processes occurred in the Crimean population of scallop, and the species began to reappear in abundance in various parts of the open coast and in bays. Following the logic of our analysis, the observed recovery of scallop beds off the Crimean coast resulted from the de-eutrophication of the Black Sea basin from 1993/1994 to the early 2000s and the overall improvement of its ecological status (Zaika, 2003, 2011; Yunev et al., 2019). Similar recovery processes were also reported for populations of some other species of benthic fauna (Abaza et al., 2018; Revkov et al., 2019). Due to the lack of recent data on the zoobenthos in the eastern and southern BSS sectors, we cannot yet state that there exists a general tendency for the entire Black Sea scallop population to recover, but we assume it.

Along with the above-noted factors responsible for the spatial and temporal variations in the Black Sea scallop population, there were undoubtedly other factors that also had their effects during the century-long observation period. As the researchers studying benthos indicate, these include the anthropogenic siltation of bottom substrate, the rapa whelk predation, and the pollution of waters (Milovidova, 1967; Ivanov & Sinegub, 2008; Terentyev, 2008; Fashchuk et al., 2012). Similarly to the stress factors that caused the depopulation of the European flat oyster *O. edulis*, their general list for scallop can be extended by adding diseases and the direct destruction of scallop beds by bottom trawling operations during commercial seafood harvesting that were actively conducted, e.g., off the Crimean coast from the mid-1970s to the late 1980s. According to our data, most scallop beds in 2008–2009 in the Karkinit Bay were affected by the shell disease caused by the red boring sponge *Pione vastifica* (Hancock, 1849). Nevertheless, in this review we tend to focus on a key problem of the second half of the 20th century: anthropogenic eutrophication of the Black Sea basin, whose effect could only be amplified by other, local-scale stress factors.

Conclusion

The data collected for the Black Sea scallop extend our understanding of the general and regional specific responses of various species in conditions of the ecological crisis of the Black Sea ecosystem associated with the eutrophication of the basin in the second half of the 20th century.

Our analysis of long-term variations in the Black Sea population of the smooth scallop *F. glaber* allows us to categorize the northern (Crimean coast), eastern (Central and North Caucasian) and Anatolian sectors of the Black Sea shelf as the areas with the most favorable conditions for the existence of scallop beds. The results obtained suggest a possibility of downgrading the conservation status of this species in the Red Data Books of the city of Sevastopol and the Republic of Crimea from the “species declining in abundance” to the “species recovering in abundance and distribution”.

Ethical Statement

This study does not require an ethics committee report.

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Author Contribution

Contributed substantially to the conception and design of the study, the acquisition of data, or the analysis and interpretation – Nikolai Revkov, Tatiana Revkova.

Drafted or provided critical revision of the article - Tatiana Revkova.

Provided final approval of the version to publish – Nikolai Revkov.

Agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved - Nikolai Revkov, Tatiana Revkova.

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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