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ФИЦ «Институт биологии южных морей
имени А. О. Ковалевского РАН».
Пр. Нахимова, 2, Севастополь, 299011, РФ.
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Адрес соиздателя:

Зоологический институт РАН.
Университетская наб., 1, Санкт-Петербург, 199034, РФ.

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A. O. Kovalevsky Institute of Biology of the Southern Seas
of Russian Academy of Sciences.
2 Nakhimov ave., Sevastopol, 299011, Russia.
Tel.: +7 8692 54-41-10. E-mail: *mbj@imbr-ras.ru*.
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ICHTHYOFAUNA OF THE BLACK SEA COASTAL ZONE IN THE LASPI BAY AREA (CRIMEA)

E. R. Abliazov[1], **A. R. Boltachev**[1], **E. P. Karpova**[1], **A. N. Pashkov**[2], **and O. N. Danilyuk**[1]

[1]A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
[2]Azov – Black Sea branch of the FSBSI "Russian Federal Research Institute of Fisheries and Oceanography" ("AzNIIRKh"), Krasnodar department, Krasnodar, Russian Federation
E-mail: *e_ablyazov@mail.ru*

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The ongoing processes of the Black Sea salinization and fluctuations in mean annual temperature have already caused the natural dispersal of various representatives of the Mediterranean Basin and Indian Ocean fauna and led to a change in species composition and structure of fish communities, inhabiting the coastal zone of the Crimean Peninsula. As a result, it became necessary to study modern composition of fish fauna and indicators of its species richness and diversity. The Laspi Bay was chosen as a model polygon for the following reasons: relatively low level of anthropogenic load; the fact that its part belongs to the specially protected natural areas, as well as the absence of fishing activity with coastal fixed fishing gear; constant free entry of pelagic fish species; biotopes diversity; and smooth change in depth. These peculiarities of the Laspi Bay allow assessing the presence of fish from different ecological groups and provide conditions for monitoring. The study was carried out in the spring-autumn periods of 1990–1994 and 2017–2018. The material was sampled with net fishing gear, hook tackle, and traps. The nets were set at various depths both perpendicular and parallel to the shoreline during the day (10:00 to 18:00) and at nighttime (18:00 to 06:00). Visual observations were also carried out. In total, 70 fish species were registered. Out of them, 14 species were previously not recorded for this area; 5 of them [salema *Sarpa salpa* (Linnaeus, 1758), red-mouthed goby *Gobius cruentatus* Gmelin, 1789, Bath's goby *Pomatoschistus bathi* Miller, 1982, mystery blenny *Parablennius incognitus* (Bath, 1968), and chestnut goby *Chromogobius quadrivittatus* (Steindachner, 1863)] are recent invaders, actively spreading in the Black Sea over the past 15–20 years only. Most of the analyzed species (64) are marine euryhaline fish. The brackish-water group is represented by three species, indigenous to the Black Sea: mushroom goby *Ponticola eurycephalus* (Kessler, 1874), round goby *Neogobius melanostomus* (Pallas, 1814), and knout goby *Mesogobius batrachocephalus* (Pallas, 1814). Out of anadromous fish, starry sturgeon *Acipenser stellatus* Pallas, 1771 is registered, as well as two Clupeidae species: Black Sea shad *Alosa tanaica* (Grimm, 1901) and Pontic shad *Alosa immaculata* Bennett, 1835. As established, the observed seasonal dynamics of species diversity indices within the studied water area is associated with fluctuations in the abundance of horse mackerel *Trachurus mediterraneus* (Steindachner, 1868). In April – May, when this species headed to shallow water for feeding and breeding, the indices have the lowest values; in August, when the abundance of horse mackerel decreases, the maximum values are observed.

Keywords: Black Sea, Laspi Bay, fish fauna, composition, abundance, species richness, diversity, invaders

The Black Sea ichthyofauna is actively investigated (Boltachev & Karpova, 2017 ; Vasil'eva, 2007 ; Zuev et al., 2018). Out of these studies, the analysis of fish communities in the coastal zone stands out, characterized by a higher biological diversity than that of the open sea.

V. A. Vodyanitsky, relying on the distribution of macrozoobenthos, algae, and fish in the coastline and taking into account the peculiarities of separate water areas, identified several zones along the Crimean coast, which were noticeably different from each other (Vodyanitsky, 1949). Later, another zoning of the Crimean coast was proposed – with the allocation of the Sevastopol region, the southern boundary of which is the Laspi Bay (Boltachev & Karpova, 2012).

In the 1980s, A. O. Kovalevsky Institute of Biology of the Southern Seas organized a biological station in the Laspi Bay, which marked the beginning of a comprehensive study of this sea area: its hydrological and hydrochemical conditions, flora, and fauna. The first ichthyological studies in the Laspi area, carried out in 1981–1985 (Salekhova et al., 1987), covered the entire coastal zone up to Sevastopol. As a result, 84 fish species were recorded in the Laspi Bay; the authors noted the ongoing process of the invasion of fish from the East Atlantic complex into the Black Sea, which has been identified in previous works (Oven & Salekhova, 1969 ; Puzanov, 1967, 1965).

In 2005–2011, underwater visual ichthyological observations were carried out (Get'man, 2014); as a result, 23 fish species were recorded, inhabiting the Laspi Bay rocky biotopes. The families Blenniidae and Labridae were represented by the largest number of species.

Part of the bay water area is included in the natural landscape reserve "Cape Aya" and the hydrological nature monument of regional significance "Coastal aquatic complex at Cape Sarych", which determines the high conservation value of ichthyofauna studying in this area.

The Black Sea is characterized by a weak external water exchange and a two-layer hydrological structure of waters, which is a consequence of its inland position. The processes of salinization and fluctuations in mean annual temperature are currently registered (Kazmin et al., 2010 ; Shaltout & Omstedt, 2014).

Salinity in the Black Sea increases by an average of 0.0038 ‰ per 10 years (Belokopytov, 2017), mainly due to a constant influx of the Sea of Marmara water and a reduction in fresh runoff from the mainland. Mean annual water temperature in the Black Sea, based on observations of 1982–2015, increases every decade by an average of 0.64 °C (Sakalli & Basusta, 2018). These processes contribute to natural dispersal of representatives of the Mediterranean Basin fauna (bogue *Boops boops* (Linnaeus, 1758), red-mouthed goby *Gobius cruentatus* Gmelin, 1789, *etc.*) and the Indian Ocean fauna (silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin, 1789), which has entered through Suez Canal) (Boltachev et al., 2009 ; Vinogradov et al., 2017); species composition and structure of fish communities, inhabiting the coastal zone, are changing. In this regard, it becomes necessary to revise the composition and to analyze the diversity of local fish communities in the coastal zone.

The aim of this work is to study species composition, species richness, and diversity of fish communities in the Laspi Bay.

MATERIAL AND METHODS

The work is based on ichthyological material, sampled in April – July 1990; May – October 1991; August – September 1994; March – August 2017; and August – September 2018. The water body was also fished in August 2006; January and November 2008; May 2009; August – October 2010; October 2012; and May and August 2016.

The material was sampled in the studied water area with net fishing gear, hook tackle, and traps (Fig. 1).

In 1990–1991, 158 nets were set, and 3,735 fish specimens were caught. Three-walled bottom fishing nets with the length of 20–75 m and a mesh size of 20–30 mm were used. They were set at various depths perpendicular to the shoreline at 18:00–20:00 and removed at 08:00–10:00 the next day. In 2017–2018, the material was gathered using fixed single-walled nets with a mesh size of 10–40 mm. The nets were set at different depths both perpendicular and parallel to the shoreline. They were set during the day (10:00 to 18:00) and at nighttime (18:00 to 06:00). Moreover, at nighttime (18:00 to 6:00), bottom traps with mesh size of 6–8 mm were set at depths of 1–2 m. In total, 1,123 fish specimens were caught.

In addition to fishing, visual observations (without quantitative accounting) were carried out. In 2017–2018, monitoring was carried out using photo and video equipment, which made it possible to record small, secretive species. The total duration of visual underwater observations was of 180 h in 1990–1991, 300 h in 1994, and 200 h in 2017–2018.

Data on the presence of rare species in the Laspi Bay in 2014–2017 [green wrasse *Labrus viridis* Linnaeus, 1758 and salema *Sarpa salpa* (Linnaeus, 1758)] were obtained during interviews with members of the Sevastopol Association of Underwater Hunters and analysis of their photographic material, confirming the fact of fish registration.

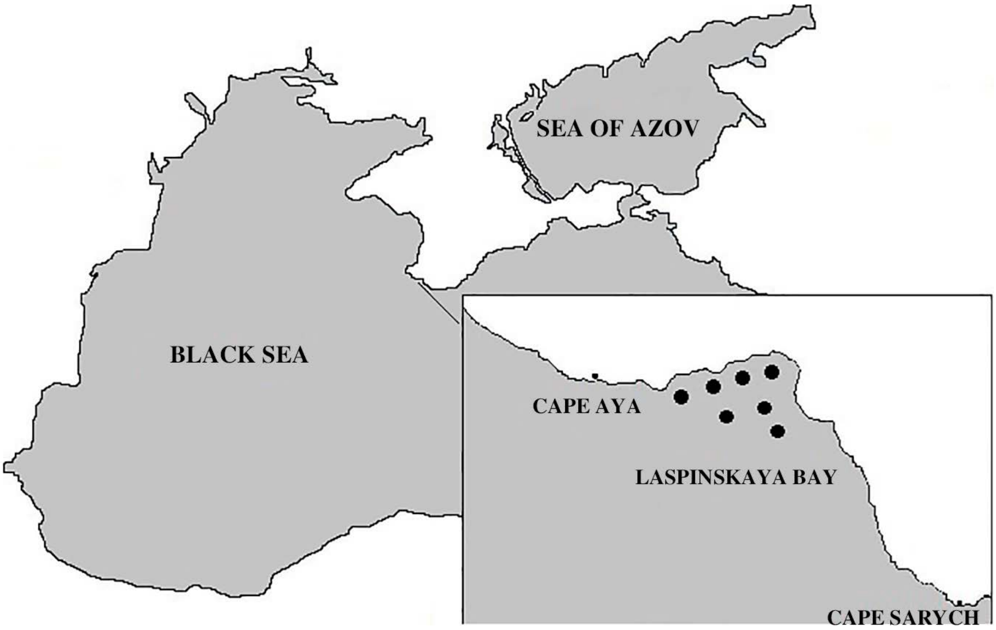

Fig. 1. Map of the Laspi Bay (points indicate sampling locations)

Fish species identification and taxonomic hierarchy are given in accordance with modern concepts (Vasil'eva, 2007 ; World Register of Marine Species, 2019).

To assess the degree of ichthyofauna similarity in different periods, the Sørensen – Czekanowski index was used (Bogolyubov, 1998):

$$K = \frac{2n(A \cap B)}{n(A) + n(B)}\,, \tag{1}$$

where n is the number of species;

A and B are analyzed fish communities.

For 2017–2018, the Margalef species richness index was calculated:

$$D = (S - 1)/\ln(N)\,, \tag{2}$$

where S is the total number of found species;

N is the total number of recorded specimens.

To calculate the uniformity of species distribution over the range, the Simpson diversity index was applied:

$$C = (\sum {p_i}^2)^{-1}\,, \tag{3}$$

where p_i is the ratio of species occurrence (abundance).

The Shannon diversity index was also calculated:

$$H = -\sum pi \times \log 2p_i\,, \tag{4}$$

where p_i is the ratio of specimens of the i-th species in the sample.

To determine the ratio of the dominant species in the catch, the Berger – Parker evenness index was used:

$$IBP = N_i/N_{max}\,, \tag{5}$$

where N_i is the total number of specimens in the sample;

N_{max} is the number of specimens of the dominant species (Pesenko, 1982 ; Rokitskii, 1973).

Indices of species richness and diversity were calculated on the basis of data, obtained in the spring-summer periods of 2017 and 2018. Species richness was estimated by the Margalef index, and species diversity – by the Simpson, Shannon, and Berger – Parker indices. In the calculations, the parameter of abundance was used, which made it possible to avoid the influence on the values of small species with a large biomass.

RESULTS AND DISCUSSION

The Laspi Bay is located between Sarych and Aya capes, the distance between which is about 8000 m. It is protected by mountains from the western, eastern, and northern winds (Atsikhovskaya & Chekmeneva, 2002 ; Klimova et al., 2011). The bay is located at the junction of the continental and subtropical climatic zones. Its depth gradually increases and reaches 60 m. The outer boundary of the bay coincides with the coastal boundary of the Main Black Sea Current, which determines intense water exchange with the open sea (Atsikhovskaya & Chekmeneva, 2002). In the bay water area, the concentration of pollutants is rather low, and the entire water column from the surface to the bottom is well aerated (Kuftarkova et al., 1990).

The coast is composed of volcanic rocks, gradually passing into the Upper Jurassic limestones, due to which the shores are characterized as highly durable (Agarkova-Lyakh, 2007) and are rather weakly subject to abrasion processes. The basis of bay bottom is rocky, boulder, and stony substrates, interspersed with small pebble areas. At the bay exit, there are small areas of sandy and silty bottom with boulders.

We have registered 70 fish species; in literature (Get'man, 2014 ; Salekhova et al., 1987), 84 species are indicated (Table 1). There were 56 common species, and the Sørensen – Czekanowski faunistic similarity index was 0.73. Totally, 14 species have not been previously recorded in the bay area, and 5 out of them [salema *S. salpa*, red-mouthed goby *G. cruentatus*, Bath's goby *Pomatoschistus bathi* Miller, 1982, mystery blenny *Parablennius incognitus* (Bath, 1968), and chestnut goby *Chromogobius quadrivittatus* (Steindachner, 1863)] are recent invaders, actively spreading in the Black Sea over the past 15–20 years only (Boltachev et al., 2009). Of particular interest is the first record of *Ch. quadrivittatus*. In recent years, an increase in abundance and occurrence of this species was noted along the entire Black Sea coast, and one of its reasons may be climate change (Boltachev & Karpova, 2017 ; Engin et al., 2016).

In literature (Salekhova et al., 1987), 28 species are indicated, which were not found during our studies. Previously (Salekhova et al., 1987), sampling was carried out in an area, including *inter alia* Sevastopol coast and bays. Probably, the list, given by the authors, includes species, that cannot be attributed to the Laspi Bay inhabitants: they are associated with the biotopes of other types, that are not represented in this water area, or do not inhabit the southern and southwestern coast of Crimea at all. These are straightnose pipefish *Nerophis ophidion* (Linnaeus, 1758), as well as syrman goby *Ponticola syrman* (Nordmann, 1840), ratan goby *Neogobius ratan* (Nordmann, 1840), Pinchuk's goby *Ponticola cephalargoides* (Pinchuk, 1976), flatsnout goby *Neogobius platyrostris* (Pallas, 1814), Bucchich's goby *Gobius bucchichi* Steindachner, 1870, grass goby *Zosterisessor ophiocephalus* (Pallas, 1814), and Caucasian dwarf goby *Knipowitschia caucasica* (Berg, 1916). The species, the findings of which in the Black Sea were sporadic, are as follows: grey triggerfish *Balistes capriscus* Gmelin, 1789, thicklip grey mullet *Chelon labrosus* (Risso, 1827), Adriatic blenny *Microlipophrys adriaticus* (Steindachner & Kolombatovič, 1883), and pikeperch *Sander lucioperca* Linnaeus, 1758 (Gudimovich, 1953 ; Oven & Salekhova, 1969 ; Puzanov, 1967). Finally, angler *Lophius piscatorius* Linnaeus, 1758 and John dory *Zeus faber* Linnaeus, 1758 have not been found off the coast of Crimea for more than 30 years. Probably, their local populations have disappeared, which is associated with the intensive trawling on the Crimean shelf (Boltachev & Karpova, 2017 ; Boltachev et al., 2009). The population of Risso's dragonet *Callionymus risso* Lesueur, 1814, inhabiting the biotopes of sandy and silty sediments, also almost disappeared in the 1990s (Boltachev & Karpova, 2017).

We cannot exclude the entry in the bay water area of some rare and numerically small species, which are registered off the coast of Crimea. These are: beluga *Huso huso* (Linnaeus, 1758), Russian sturgeon *Acipenser gueldenstaedtii* Brandt et Ratzeburg, 1833, round sardinella *Sardinella aurita* Valenciennes, 1847, Black Sea salmon *Salmo labrax* Pallas, 1814, European eel *Anguilla anguilla* (Linnaeus, 1758), leaping mullet *Chelon saliens* (Risso, 1810), bogue *Boops boops* (Linnaeus, 1758), shi drum *Umbrina cirrosa* (Linnaeus, 1758), European barracuda *Sphyraena sphyraena* (Linnaeus, 1758), Atlantic bonito *Sarda sarda* (Bloch, 1793), three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758, thickly snouted pipefish *Syngnathus variegatus* Pallas, 1814, and Schmidt's pipefish *Syngnathus schmidti* Popov, 1928.

Thus, according to our and published data, the Laspi Bay ichthyofauna accounts for at least 83 species (Table 1).

Table 1. Species composition of the Laspi Bay fish in 1981–2018

No.	Species	Published data	Our data	Origin	Environment
Squalidae – dogfish sharks					
1	*Squalus acanthias* Linnaeus, 1758 – picked dogfish	+	+	As	M, B
Rajidae – skates					
2	*Raja clavata* Linnaeus, 1758 – thornback ray	+	+	As	M
Dasyatidae – stingrays					
3	*Dasyatis pastinaca* (Linnaeus, 1758) – common stingray	+	+	Mm	M, B
Acipenseridae – sturgeons					
4	*Acipenser gueldenstaedtii* Brandt et Ratzeburg, 1833 – Russian sturgeon	+		IPCs	M, B, F
5	*Acipenser stellatus* Pallas, 1771 – starry sturgeon	+	+	IPCs	M, B, F
6	*Huso huso* (Linnaeus, 1758) – beluga	+		IPCs	M, B, F
Engraulidae – anchovies					
7	*Engraulis encrasicolus* (Linnaeus, 1758) – European anchovy	+	+	As	M, B
Clupeidae – herrings, sardines, pilchards, shads, menhadens, and allies					
8	*Alosa tanaica* (Grimm, 1901) – Black Sea shad		+	IPCs	M, B, F
9	*Alosa immaculata* Bennett, 1835 – Pontic shad	+	+	IPCs	M, B, F
10	*Sprattus sprattus* (Linnaeus, 1758) – European sprat	+	+	As	M, B
11	*Sardinella aurita* Valenciennes, 1847 – round sardinella	+		As	M, B
Salmonidae – salmonids					
12	*Salmo labrax* Pallas, 1814 – Black Sea salmon	+		IPCs	M, B, F
Anguillidae – freshwater eels					
13	*Anguilla anguilla* (Linnaeus, 1758) – European eel	+		As	M, B, F
Lotidae – rocklings					
14	*Gaidropsarus mediterraneus* (Linnaeus, 1758) – shore rockling	+	+	As	M
Gadidae – cods					
15	*Merlangius merlangus* (Linnaeus, 1758) – whiting	+	+	As	M
Lophiidae – goosefishes					
16	*Lophius piscatorius* Linnaeus, 1758 – angler	+		As	M
Ophidiidae – cusk-eels					
17	*Ophidion rochei* Muller, 1845 – Roche's snake blenny	+	+	As	M
Mugilidae – mullets					
18	*Chelon auratus* (Risso, 1810) – golden grey mullet	+	+	As	M, B, F
19	*Planiliza haematocheila* (Temminck & Schlegel, 1845) – so-iuy mullet		+	As	M, B, F
20	*Mugil cephalus* Linnaeus, 1758 – flathead grey mullet	+	+	As	M, B, F
21	*Chelon saliens* (Risso, 1810) – leaping mullet	+		As	M, B

Continue on the next page…

No.	Species	Published data	Our data	Origin	Environment
22	*Chelon labrosus* (Risso, 1827) – thicklip grey mullet	+		Rs	M, B, F
Atherinidae – Old World silversides					
23	*Atherina boyeri* Risso, 1810 – big-scale sand smelt		+	As	M, B, F
24	*Atherina hepsetus* Linnaeus, 1758 – Mediterranean sand smelt		+	As	M, B, F
Belonidae – needlefishes					
25	*Belone belone* (Linnaeus, 1760) – garfish	+	+	As	M, B
Zeidae – true dories					
26	*Zeus faber* Linnaeus, 1758 – John dory	+		Mi	M, B
Syngnathidae – seahorses, pipefishes, and seadragons					
27	*Syngnathus typhle* Linnaeus, 1758 – broadnosed pipefish	+	+	As	M, B
28	*Syngnathus abaster* Risso, 1827 – black-striped pipefish	+	+	As	M, B, F
29	*Syngnathus variegatus* Pallas, 1814 – thickly snouted pipefish	+		As	M
30	*Syngnathus schmidti* Popov, 1928 – Schmidt's pipefish	+		As	B, F
31	*Nerophis ophidion* (Linnaeus, 1758) – straightnose pipefish	+		As	M, B
32	*Hippocampus hippocampus* (Linnaeus, 1758) – short-snouted seahorse	+	+	As	M
Scorpaenidae – scorpionfishes					
33	*Scorpaena porcus* Linnaeus, 1758 – black scorpionfish	+	+	As	M
Triglidae – gurnards					
34	*Chelidonichthys lucerna* Linnaeus, 1758 – tub gurnard	+	+	As	M
Percidae – perches					
35	*Sander lucioperca* Linnaeus, 1758 – pikeperch	+		Rs	B, F
Serranidae – sea basses and groupers					
36	*Serranus scriba* (Linnaeus, 1758) – painted comber	+	+	As	M
Pomatomidae – bluefishes					
37	*Pomatomus saltatrix* (Linnaeus, 1766) – bluefish	+	+	As	M, B
Carangidae – jacks, pompanos, jack mackerels, runners, and scads					
38	*Trachurus mediterraneus* (Steindachner, 1868) – horse mackerel	+	+	As	M, B
Sparidae – porgies					
39	*Diplodus annularis* (Linnaeus, 1758) – annular sea bream	+	+	As	M, B
40	*Diplodus puntazzo* (Walbaum, 1792) – sharpsnout sea bream	+	+	As	M, B
41	*Sarpa salpa* (Linnaeus, 1758) – salema		+	Mi	M, B
42	*Boops boops* (Linnaeus, 1758) – bogue	+		As	M
Centracanthidae – picarels					
43	*Spicara flexuosa* Rafinesque, 1810 – blotched picarel	+	+	As	M

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No.	Species	Published data	Our data	Origin	Environment
44	*Spicara maena* (Linnaeus, 1758) – blotched picarel	+	+	As	M
	Sciaenidae – drums (croakers)				
45	*Sciaena umbra* Linnaeus, 1758 – brown meagre	+	+	As	M, B
46	*Umbrina cirrosa* (Linnaeus, 1758) – shi drum	+		As	M, B
	Mullidae – goatfishes				
47	*Mullus barbatus ponticus* Essipov, 1927 – red mullet	+	+	As	M
	Pomacentridae – damselfishes and clownfishes				
48	*Chromis chromis* (Linnaeus, 1758) – damselfish	+	+	As	M
	Labridae – wrasses				
49	*Symphodus cinereus* (Bonnaterre, 1788) – grey wrasse	+	+	As	M, B
50	*Symphodus ocellatus* Forsskål, 1775 – ocellated wrasse	+	+	As	M
51	*Symphodus roissali* (Risso, 1810) – five-spotted wrasse	+	+	As	M, B
52	*Symphodus tinca* (Linnaeus, 1758) – East Atlantic peacock wrasse	+	+	As	M, B
53	*Symphodus rostratus* (Bloch, 1791) – pointed-snout wrasse	+	+	As	M
54	*Ctenolabrus rupestris* (Linnaeus, 1758) – goldsinny wrasse	+	+	As	M
55	*Labrus viridis* Linnaeus, 1758 – green wrasse	+	+	As	M
	Ammodytidae – sand lances				
56	*Gymnammodytes cicerelus* (Rafinesque, 1810) – Mediterranean sand eel	+	+	As	M
	Trachinidae – weevers				
57	*Trachinus draco* Linnaeus, 1758 – greater weever	+	+	As	M
	Uranoscopidae – stargazers				
58	*Uranoscopus scaber* Linnaeus, 1758 – Atlantic stargazer	+	+	As	M
	Tripterygiidae – triplefin blennies				
59	*Tripterygion tripteronotum* (Risso, 1810) – red-black triplefin	+	+	As	M
	Blenniidae – combtooth blennies				
60	*Aidablennius sphynx* (Valenciennes, 1836) – sphinx blenny	+	+	As	M
61	*Salaria pavo* (Risso, 1810) – peacock blenny	+	+	As	M, B
62	*Parablennius incognitus* (Bath, 1968) – mystery blenny		+	Mi	M
63	*Parablennius sanguinolentus* (Pallas, 1814) – rusty blenny	+	+	As	M
64	*Parablennius tentacularis* (Brünnich, 1768) – tentacled blenny	+	+	As	M, B
65	*Parablennius zvonimiri* (Kolombatovič, 1892) – Zvonimir's blenny	+	+	As	M
66	*Coryphoblennius galerita* (Linnaeus, 1758) – Montagu's blenny	+	+	As	M

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No.	Species	Published data	Our data	Origin	Environment
67	*Microlipophrys adriaticus* (Steindachner & Kolombatovič, 1883) – Adriatic blenny	+		Rs	M
Gobiesocidae – clingfishes and singleslits					
68	*Diplecogaster bimaculata bimaculata* (Bonnaterre, 1788) – two-spotted clingfish		+	As	M
69	*Lepadogaster candolii* Risso, 1810 – connemarra clingfish	+	+	As	M
70	*Lepadogaster lepadogaster* (Bonnaterre, 1788) – shore clingfish		+	As	M
Callionymidae – dragonets					
71	*Callionymus pusillus* Delaroche, 1809 – sailfin dragonet	+	+	As	M
72	*Callionymus risso* Lesueur, 1814 – Risso's dragonet	+		As	M
Gobiidae – gobies					
73	*Aphia minuta* (Risso, 1810) – transparent goby	+	+	As	M, B
74	*Knipowitschia caucasica* (Berg, 1916) – Caucasian dwarf goby	+		As	M, B, F
75	*Zosterisessor ophiocephalus* (Pallas, 1814) – grass goby	+		As	M, B
76	*Chromogobius quadrivittatu*s (Steindachner, 1863) – chestnut goby		+	Mi	M
77	*Gobius bucchichi* Steindachner, 1870 – Bucchich's goby	+		As	M
78	*Gobius cobitis* Pallas, 1814 – giant goby	+	+	As	M, B
79	*Gobius cruentatus* Gmelin, 1789 – red-mouthed goby		+	Mi	M
80	*Gobius niger* Linnaeus, 1758 – black goby	+	+	As	M, B
81	*Gobius paganellus* Linnaeus, 1758 – rock goby	+	+	As	M, B, F
82	*Mesogobius batrachocephalus* (Pallas, 1814) – knout goby	+	+	IPCs	M, B
83	*Ponticola eurycephalus* (Kessler, 1874) – mushroom goby		+	IPCs	M, B
84	*Neogobius melanostomus* (Pallas, 1814) – round goby	+	+	IPCs	M, B, F
85	*Neogobius platyrostris* (Pallas, 1814) – flatsnout goby	+		IPCs	M, B
86	*Ponticola cephalargoides* (Pinchuk, 1976) – Pinchuk's goby	+		IPCs	M
87	*Neogobius ratan* (Nordmann, 1840) – ratan goby	+		IPCs	M, B
88	*Ponticola syrman* (Nordmann, 1840) – syrman goby	+		IPCs	M, B, F
89	*Pomatoschistus marmoratus* (Risso, 1810) – marbled goby		+	As	M, B
90	*Pomatoschistus bathi* Miller, 1982 – Bath's goby		+	Mi	M, B
Gasterosteidae – sticklebacks					
91	*Gasterosteus aculeatus* Linnaeus, 1758 – three-spined stickleback	+		IPCs	M, B, F
Scombridae – mackerels, tunas, and bonitos					
92	*Sarda sarda* (Bloch, 1793) – Atlantic bonito	+		Mi	M, B

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No.	Species	Published data	Our data	Origin	Environment
	Sphyraenidae – barracudas				
93	*Sphyraena sphyraena* (Linnaeus, 1758) – European barracuda	+		As	M
	Balistidae – triggerfishes				
94	*Balistes capriscus* Gmelin, 1789 – grey triggerfish	+		Rs	M
	Scophthalmidae – turbots				
95	*Scophthalmus maeoticus* (Pallas, 1814) – Black Sea turbot	+	+	As	M
	Bothidae – lefteye flounders				
96	*Arnoglossus kessleri* Schmidt, 1915 – scaldback		+	As	M
	Pleuronectidae – righteye flounders				
97	*Platichthys flesus* (Linnaeus, 1758) – European flounder	+	+	As	M, B, F
	Soleidae – true soles				
98	*Pegusa nasuta* (Pallas, 1814) – blackhand sole	+	+	As	M, B
	In total	**84**	**70**		

Note: As – allochthonous species; IPCs – indigenous Ponto-Caspian species; As – acclimatized species; Rs – random species; Mi – modern invaders; M – marine water; B – brackish water; F – freshwater [according to (World Register of Marine Species, 2019)].

Seventy fish species, recorded and reliably identified for the Laspi Bay coastal zone in 1990–1994 and 2017–2018, belong to 15 orders and 36 families. The family Gobiidae was characterized by the maximum number of species – eleven (Fig. 2). Seven species each were registered for the families Blenniidae and Labridae; three species each were noted for the families Mugilidae, Sparidae, Clupeidae, Gobiesocidae, and Syngnathidae; two species each were recorded for the families Atherinidae and Centracanthidae. Each other family was represented by one species. Thus, representatives of eight families make up 57 % of the Laspi Bay species composition.

In foreign sources (FishBase, 2020), *S. flexuosa* is considered as a junior synonym of *S. maena*. Nevertheless, the presence of significant morphometric and genetic differences between these species was established (Bektas et al., 2018 ; Minos et al., 2013).

The basis of the Laspi Bay ichthyofauna is formed by allochthonous species (58 species, 83 % of the total composition). Ponto-Caspian endemics, that inhabited the Pontian Sea-Lake, are represented by 6 species (9 %). The ratio of modern invaders (spreading since the XX century) is 7 % (5 species). Acclimatized species are represented by so-iuy mullet only, introduced from the Sea of Japan.

In relation to salinity, marine euryhaline fish (64 species, 92 %) prevailed in the bay, mainly migrants from the Mediterranean Sea. The brackish-water group was represented by three species, indigenous to the Black Sea: mushroom goby, round goby, and knout goby. Out of anadromous fish, starry sturgeon was recorded, as well as two species of the family Clupeidae: Black Sea shad and Pontic shad. Since the Black Sea salinity is lower (18–19 ‰) than the oceanic one (32–33 ‰), the marine fauna there is represented by euryhaline species, capable of living in such conditions. It should be noted that most of the species, which we classified as marine, can tolerate strong desalination and sometimes form populations in freshwater bodies (Leonardos, 2001), but high salinity values remain optimal for them.

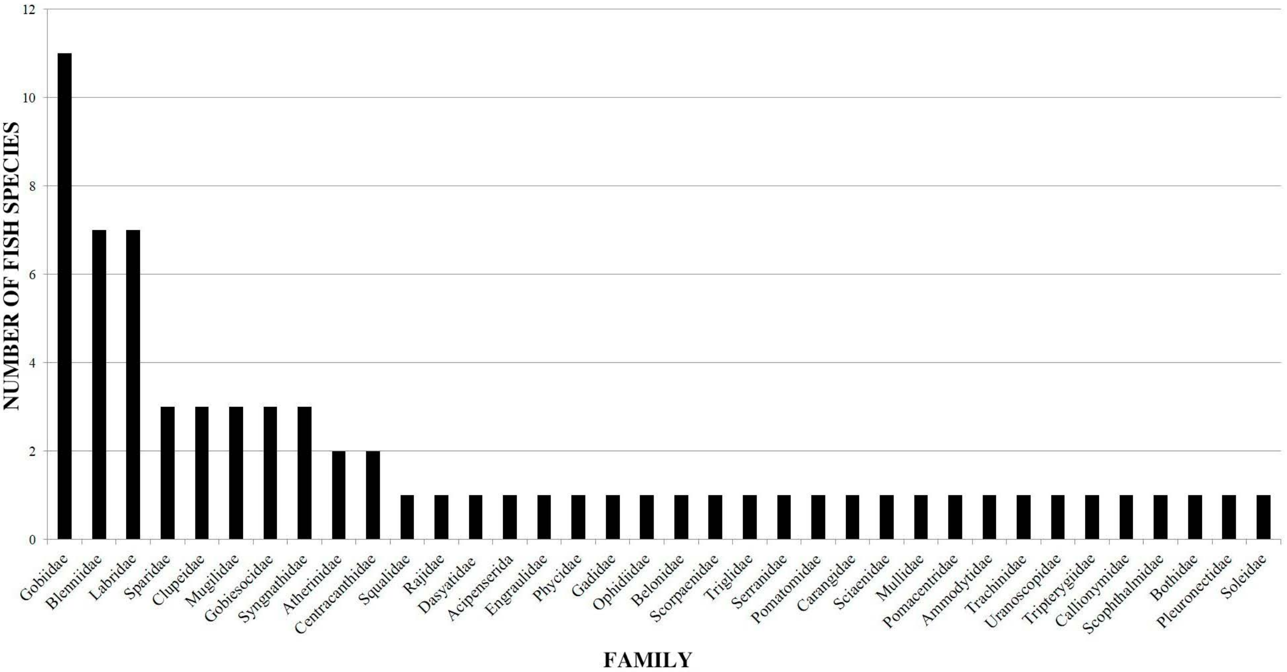

Fig. 2. Taxonomic structure of the Laspi Bay ichthyofauna

The ratio of sedentary fish species (not making significant migrations) accounted for 49 %, and moderately migratory (moving over short distances) – for 20 %. The ratio of highly migratory species (making significant migrations during feeding and spawning) was of 31 %.

Most of ichthyofauna representatives (31 species, 44 %) are rare ones: during the entire period of observations, only sporadic captures or photo and video recordings were registered. Another 26 species (37 %) can be categorized as common; these were sporadic specimens. In total, 13 species (19 %) are regularly found in the bay and are common. Out of them, horse mackerel and black scorpionfish predominate by abundance and biomass, sometimes constituting more than half of the catch. In control catches, 16 species (23 %) were represented by both juvenile and older age groups, and another 12 species (17 %) – by mature individuals only.

Depending on the season, the species diversity indices (Table 2) had values, characteristic of both a well-being community and a depressed one. First of all, criteria of diversity assess the predominance of one species; the lower the value, the higher the well-being of the community. Accordingly, such changes in the values of diversity indices are possibly associated with changes in the abundance of common fish species. The number of species in the spring period was approximately the same as in the summer season. Meanwhile, in spring, horse mackerel approached the shoreline en masse, and values of indices became low; in summer, the values were high.

Table 2. Indicators of species richness and diversity of fish communities in the Laspi Bay coastal zone in 2017–2018

Value	Margalef species richness index (D)	Simpson diversity index (C)	Shannon diversity index (H)	Berger – Parker evenness index (IBP)
Minimum	0.9	1.1	0.3	1.0
Maximum	2.9	9.2	5.5	6.6
Mean	1.7 ± 0.33	4.0 ± 1.37	2.6 ± 0.88	2.8 ± 0.98

Conclusions:

1. In the Laspi Bay during the research period (1991–1994 and 2017–2018), 70 fish species were registered. The family Gobiidae is represented by the maximum number of species (about 16 % of the species recorded). Ichthyofauna is mostly represented by marine euryhaline species (92 %); anadromous and brackish-water species account for 8 %. Of 70 species noted, 14 were recorded in this water area for the first time. Most of them are invaders, which indicates the ongoing acclimatization of representatives of the fauna of other water basins, registered in the first half of the XX century.
2. The total abundance of the Laspi Bay ichthyofauna representatives is subject to seasonal variability, and the main contributor is fluctuations in the abundance of horse mackerel. This variability directly affects the indicators of diversity, causing their significant decrease in the spring period.
3. Out of ichthyofauna representatives, found in the bay water area, 44 % belong to the category of rare: over the entire observation period, they were recorded only sporadically. Common species accounted for 19 %; out of them, horse mackerel was characterized by the highest abundance and biomass in spring, and black scorpionfish – in summer.

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ИХТИОФАУНА ПРИБРЕЖНОЙ ЗОНЫ ЧЁРНОГО МОРЯ В РАЙОНЕ БУХТЫ ЛАСПИНСКАЯ (КРЫМ)

Э. Р. Аблязов[1], А. Р. Болтачев[1], Е. П. Карпова[1],
А. Н. Пашков[2], О. Н. Данилюк[1]

[1]ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН»,
Севастополь, Российская Федерация
[2]Азово-Черноморский филиал ФГБНУ «Всероссийский научно-исследовательский институт
рыбного хозяйства и океанографии» («АзНИИРХ»), отдел «Краснодарский»,
Краснодар, Российская Федерация
E-mail: *e_ablyazov@mail.ru*

В настоящее время в Чёрном море протекают процессы осолонения и изменения среднегодовой температуры, которые уже обусловили естественное расселение различных представителей фауны Средиземноморского бассейна и Индийского океана и привели к изменению видового состава и структуры сообществ рыб, населяющих прибрежную зону Крымского полуострова. Вследствие этого возникла необходимость в изучении современного состава ихтиофауны и в оценке показателей её видового богатства и разнообразия. Бухта Ласпинская выбрана в качестве модельного полигона на основании следующих причин: относительно невысокий уровень антропогенной нагрузки; принадлежность части её акватории к особо охраняемым природным территориям и отсутствие рыбопромысловой деятельности прибрежными ставными орудиями лова; постоянный свободный заход пелагических видов рыб; наличие разнообразных биотопов; плавный переход глубин. Вышеперечисленные особенности бухты позволяют оценить наличие рыб разных экологических групп и обеспечивают условия для проведения мониторинга. Исследование выполняли в весенне-осенние периоды 1990–1994 и 2017–2018 гг. Материал собирали сетными орудиями лова, крючковыми снастями и ловушками. Постановку сетей проводили на разных глубинах перпендикулярно и параллельно берегу в дневное (10:00–18:00) и ночное (18:00–06:00) время. Также осуществляли визуальные наблюдения. Всего зарегистрировано 70 видов рыб. Из них 14 ранее не были отмечены в данном районе; пять из них [сальпа *Sarpa salpa* (Linnaeus, 1758), красноротый бычок *Gobius cruentatus* Gmelin, 1789, лысун Бата *Pomatoschistus bathi* Miller, 1982, зелёная морская собачка *Parablennius incognitus* (Bath, 1968) и четырёхполосый хромогобиус *Chromogobius quadrivittatus* (Steindachner, 1863)] являются недавними вселенцами, активно распространяющимися в Чёрном море только на протяжении последних 15–20 лет. Бóльшая часть проанализированных видов (64) — морские эвригалинные рыбы. Солоноватоводная группа представлена тремя аборигенными для Чёрного моря видами — бычком-рыжиком *Ponticola eurycephalus* (Kessler, 1874), бычком-кругляком *Neogobius melanostomus* (Pallas, 1814) и бычком-мартовиком *Mesogobius batrachocephalus* (Pallas, 1814). Среди проходных рыб зарегистрированы севрюга *Acipenser stellatus* Pallas, 1771 и два вида семейства Сельдевые — черноморский пузанок *Alosa tanaica* (Grimm, 1901) и сельдь черноморско-азовская проходная *Alosa immaculata* Bennett, 1835. Установлено, что сезонная динамика видового разнообразия рыб изучаемой акватории связана с изменением численности локальных скоплений ставриды *Trachurus mediterraneus* (Steindachner, 1868). В апреле — мае, во время подхода данного вида на мелководье для нагула и размножения, индексы имеют наименьшие значения; в августе, когда численность ставрид уменьшается, отмечены максимальные значения.

Ключевые слова: Чёрное море, бухта Ласпинская, ихтиофауна, состав, численность, видовое богатство, разнообразие, вселенцы

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

© 2021 **I. P. Bondarev and N. A. Boltachova**

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
E-mail: *igor.p.bondarev@gmail.com*

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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.

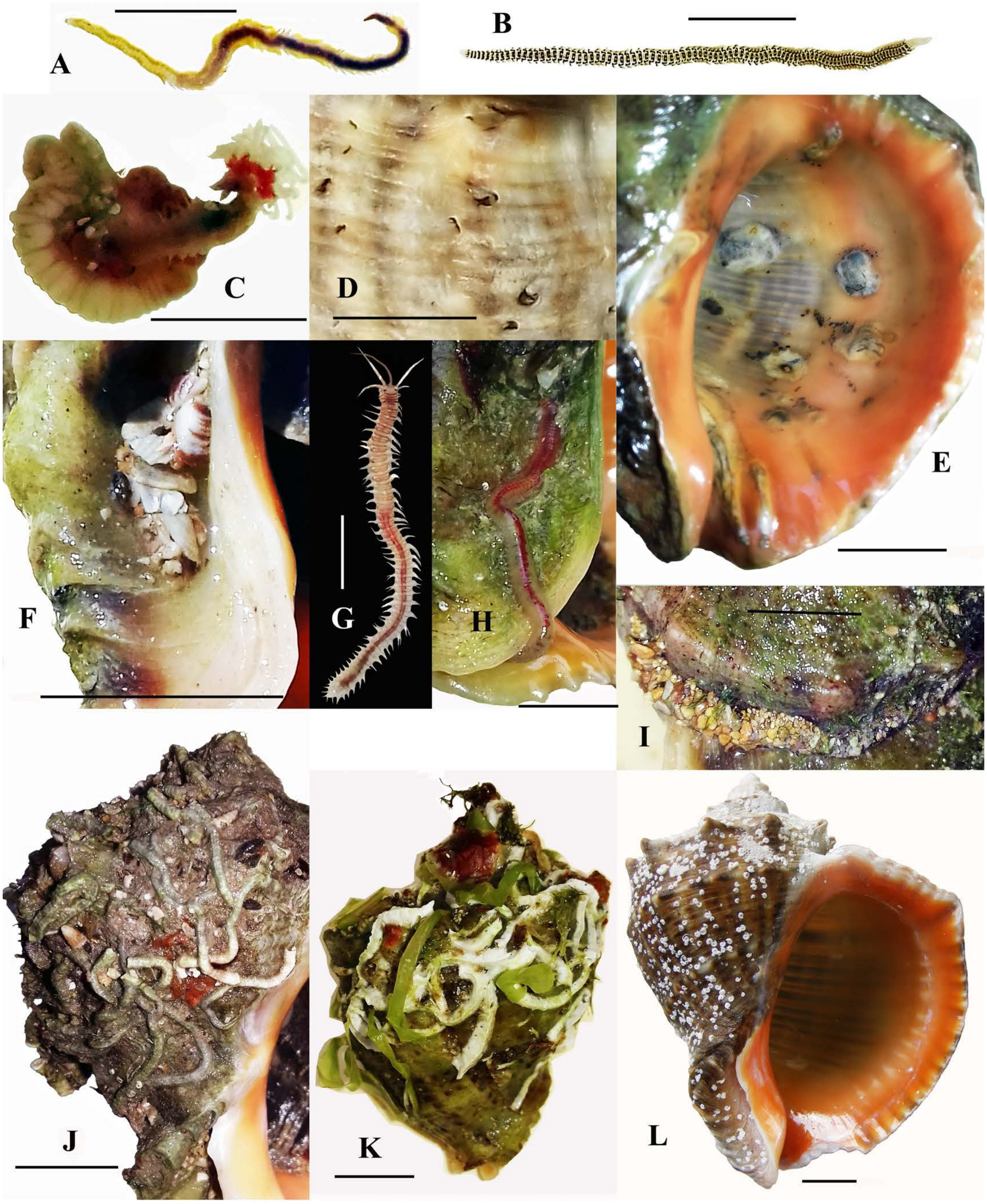

Fig. 2. Polychaetes of *R. venosa* consortium: A – *Genetyllis tuberculata*; B – *Mysta picta*; C – *Amphitritides gracilis*; D – *Polydora* sp. boring on a shell surface cleaned from fouling; E – blisters at the shell mouth blocking *Polydora* sp. passages; F – leathery tube encrusted with mollusc shell 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)

И. П. Бондарев, Н. А. Болтачева

ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН»,
Севастополь, Российская Федерация
E-mail: *igor.p.bondarev@gmail.com*

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

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INTRA- AND INTERPOPULATION VARIABILITY OF CYSTS AND ADULTS OF *ARTEMIA* (BRANCHIOPODA: ANOSTRACA) IN SIBERIAN POPULATIONS (MORPHOMETRY)

© 2021 **L. I. Litvinenko[1,2], K. V. Kutsanov[1], L. F. Razova[1], A. Sh. Gadiadullina[1], A. G. Gerasimov[1], and E. V. Brazhnikov[1]**

[1]Tyumen branch of the FSBSI "Russian Federal Research Institute of Fisheries and Oceanography" ("Gosrybtsentr"), Tyumen, Russian Federation
[2]Northern Trans-Ural State Agricultural University, Tyumen, Russian Federation
E-mail: *opb@gosrc.ru*

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The size of *Artemia* cysts is an important indicator of their value as a food resource; to some extent, it allows to identify populations. The data on cysts of *Artemia* parthenogenetic populations (diameter, chorion thickness, and presence of spots on a shell), sampled in hyperhaline lakes of Western Siberia in different years, were analyzed, as well as the data on the morphometry of *Artemia* adults, reared from cysts at the same salinity. Significant intra- and interpopulation variability in the indicators was established. The absolute values of the cyst diameter were in the range of 210–330 μm, the mean values for the samples – 243.5–282.9 μm, the mean values for populations – 257.8–279.6 μm; the absolute values of the decapsulated cyst diameter were in the range of 196–294 μm, the mean values for the samples – 236.5–262.6 μm, the mean values for populations – 239.9–253.2 μm; the absolute values of the cyst chorion thickness were in the range of 3.3–16.9 μm, and the mean values for populations – 6.6–12.4 μm. In the main commercial fishing lakes, which account for about 70 % of the total catch of *Artemia* cysts in Russia, the cysts had similar mean population sizes: 262–268 μm. The absence of intrapopulation anchoring of the cyst diameter and chorion thickness values is concluded; so, they cannot serve as reliable indicators, identifying Siberian populations. Statistically significant correlation ($r = -0.5$) was established between salinity of a mother water body and *Artemia* embryo diameter. Cyst spotting, not exceeding 5 % in almost all the samples, reached 24 % in cysts of Kuchukskoye Lake. Analysis of morphometric indicators of *Artemia* adults, reared from cysts, showed as follows: the mean body length (9.27–11.63 mm), abdomen width (0.53–0.69 mm), and distance between eyes (1.36–1.52 mm) were closely correlated with salinity of a water body (r values were of −0.76; −0.62; and −0.67, respectively). Cluster analysis of a set of morphometric indicators of *Artemia* adults showed the unification of populations based on salinity.

Keywords: *Artemia parthenogenetica*, cyst diameter, morphometry of *Artemia* adults, chorion thickness, salinity, population variability, Western Siberia

Out of seven *Artemia* species, living on the planet, three are found in Russia: in Crimean water bodies – *Artemia salina* (Linnaeus, 1758) and *Artemia urmiana* Günther, 1899; in Tuva (Svatikovo Lake) – *Artemia sinica* Cai, 1989 (Litvinenko et al., 2009, 2016 ; Shadrin et al., 2012 ; Shadrin & Anufriieva, 2012). In Russia, most populations belong to the group of those, unspecified to species level and reproducing parthenogenetically – *Artemia parthenogenetica* Bowen & Sterling, 1978. The need to identify commercial samples of *Artemia* cysts was highlighted as early as 2004 (Xiaomei et al., 2004). By that time, various *Artemia* species and geographical races began to enter the world market, both from the American continent and Asia (Western Siberia, Kazakhstan, Turkmenistan, and China). These cysts differed significantly in some characteristics from cysts of *Artemia franciscana* Kellog, 1906 from Great Salt Lake (USA), which are considered "standard" in aquaculture practice (Xiaomei et al., 2004). It concerned the peculiarities of diapause, chorion color, cyst and nauplius size, content of highly unsaturated fatty acids, buoyancy, hatching ratio and rate, *etc.* Later, due to illegal, unreported, and unregulated fishing, it became necessary to identify parthenogenetic populations in Russia. Numerous publications appeared (Egorkina et al., 2008 ; Litvinenko et al., 2018 ; Starovoitova & Burmistrova, 2017 ; etc.), which focused either on significant interpopulation differences in cyst diameter, allowing to identify populations, or on instability of this indicator in the same population in different years. A common drawback of these works was a small number of studied populations in different years.

In this regard, we were faced with the aim to study intra- and interpopulation variability of *Artemia* cysts, using an extended data series, and, on the basis of the results obtained, consider possible ways of identifying *Artemia* population by the cyst diameter, chorion thickness, chorion structure, and size of *Artemia* adults, reared from cysts up to mature stage.

MATERIAL AND METHODS

The cysts of *Artemia* parthenogenetic populations from 13 hyperhaline lakes of Western Siberia were studied. These lakes are as follows: Bolshoye Medvezhye (in the years of sampling, salinity was of 168–293 $g \cdot L^{-1}$), Maloye Medvezhye (164–321), Gashkovo (132–164), Nevidim (112–175), Sorochie (213–263), Aktoban (83–190), Siverga (74–86), Ulzhay (105–235), Ebeyty (135–344), Bolshoye Yarovoye (147–155), Maloye Yarovoye (201), Kuchukskoye (240), and Kulundinskoye (80 $g \cdot L^{-1}$) (Fig. 1). Cyst samples were collected in 2008–2019. The analysis was carried out by cyst diameter (43 samples), chorion thickness (31 samples), and morphometry of *Artemia* adults (7 samples).

Before measuring the diameter, cysts were placed in NaCl solution (10 $g \cdot L^{-1}$), with 1 % Lugol's iodine added, for 2 hours; then, they were filtered and placed in a Petri dish with 1 % Lugol's iodine and left in the dark for 12 hours. The next day, using an Altami SM0870 stereoscope, the diameter of hydrated cysts was measured (300 cysts from each sample).

To determine the chorion thickness, first, the diameter of hydrated cysts was measured; then, sodium hypochlorite (5 % of active chlorine) was added to remove cyst shell; 10–15 minutes later, embryo diameter was measured. The sample was of 100 cysts in each population. The chorion thickness (T_{ch}) was determined by the formula:

$$T_{ch} = (d_c - d_e)/2 \,, \tag{1}$$

where d_c is cyst diameter;

d_e is embryo diameter.

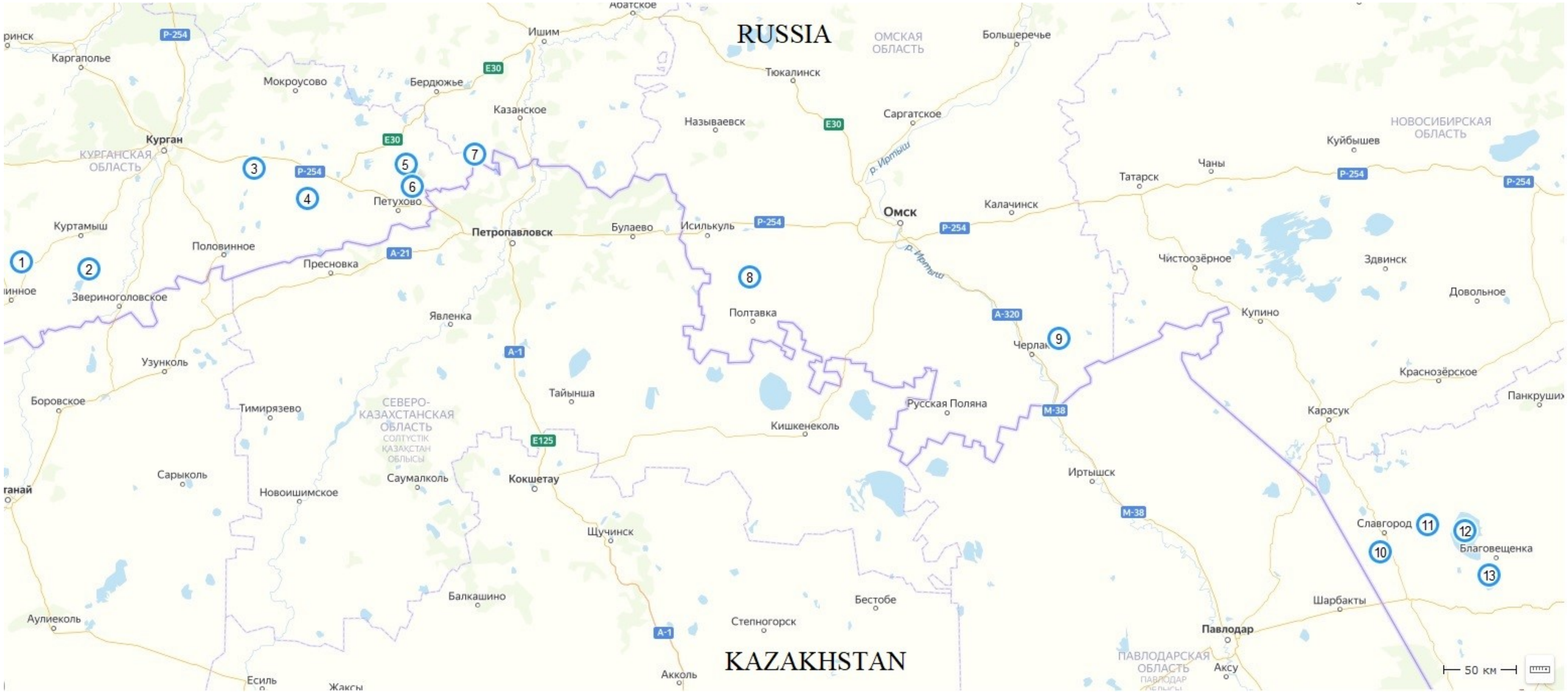


Fig. 1. Location of hyperhaline lakes (sources of *Artemia* cysts studied): 1 – Sorochie; 2 – Gashkovo; 3 – Aktoban; 4 – Nevidim; 5 – Maloye Medvezhye; 6 – Bolshoye Medvezhye; 7 – Siverga; 8 – Ebeyty; 9 – Ulzhay; 10 – Bolshoye Yarovoye; 11 – Maloye Yarovoye; 12 – Kulundinskoye; and 13 – Kuchukskoye

To breed *Artemia* nauplii, cysts were incubated in conical vessels under artificial light (1000 lux), at the temperature of +23…+25 °C, aeration, and in a saline solution (sea salt – 20 $g \cdot L^{-1}$, $NaHCO_3$ – 2 $g \cdot L^{-1}$) for 24 hours. Cultivation of *Artemia* adults was carried out in glass 2-L flasks at +23…+25 °C, aeration, and salinity of 100 $g \cdot L^{-1}$ (in salt solution: sea salt – 55 $g \cdot L^{-1}$, NaCl – 15 $g \cdot L^{-1}$, $MgSO_4$ – 11.9 $g \cdot L^{-1}$, $NaHCO_3$ – 10 $g \cdot L^{-1}$, $CaCl_2$ – 4.5 $g \cdot L^{-1}$, and KCl – 3.6 $g \cdot L^{-1}$). *Artemia* adults were fed with rice flour and *Scenedesmus* sp. suspension. Nauplii stocking density was of 100 $ind. \cdot L^{-1}$; as *Artemia* grew, the density was reduced to 10–20 $ind. \cdot L^{-1}$.

Artemia adults, that reached maturity, were fixed with Lugol's iodine and measured under an MBS-10 stereoscopic microscope with ocular micrometer. Out of each population, 10–30 *Artemia* adults were measured. In total, nine indicators were analyzed: eight plastic (body length, tl; abdomen length, al; abdomen width, aw; distance between eyes, de; eye diameter, ed; furka length, fl; length of the first antenna, la; and head width, hw) and one meristic (number of setae on furka, sf).

Statistical data processing was carried out by generally accepted methods (Lakin, 1990). Intrapopulation variability (cyst samples from one lake in different years and different dates of the same year) and interpopulation variability (cyst samples from different lakes) were analyzed by the main statistical indicators of quantitative variability: arithmetic mean (*M*), minimum (*min*) and maximum (*max*) values, arithmetic mean error (*m*), coefficient of variation (*CV*, %), standard deviation (*SD*), and sample size (*n*). Correlation coefficient (*r*) was calculated between salinity of a mother water body (source of cysts) and morphometric indicators of *Artemia* cysts and adults. The significance of the differences between the samples was assessed by the Student's *t*-test (t_{st}) at a significance level of $p \leq 0.05$ and $p \leq 0.001$. Cluster analysis was performed by Statistica 13.3 software.

RESULTS

1. Morphometry of cysts.

Diameter. In the samples studied, the absolute values of the cyst diameter were in the range of 210–330 µm, the mean values for the samples – 243.5–282.9 µm, and the mean values for populations – 257.8–279.6 µm (Table 1, Fig. 2). The largest cyst diameter was registered in the populations of Maloye Yarovoye [(279.6 ± 0.8) µm], Kuchukskoye [(278.9 ± 0.8) µm], and Aktoban [(275.9 ± 7.0) µm] lakes. The cysts in the populations of Nevidim and Ulzhay lakes were somewhat smaller: (273.3 ± 1.4) and (272.9 ± 2.1) µm, respectively. The smallest cysts were recorded in the populations of Gashkovo [(257.8 ± 4.5) µm] and Maloye Medvezhye [(258.4 ± 2.0) µm] lakes. Cysts from Bolshoye Yarovoye, Ebeyty, Bolshoye Medvezhye, and Kulundinskoye lakes had similar values: (261.6 ± 9.0), (265.2 ± 2.1), (265.8 ± 1.8), and (267.8 ± 0.8) µm, respectively. Consequently, cysts of the main commercial fishing lakes with an annual mean catch of 783 tons in total (Bolshoye Medvezhye – 102 tons, Ebeyty – 133, Bolshoye Yarovoye – 308, and Kulundinskoye – 240), accounting for about 70 % of the total catch in Russia, had similar sizes: 262–268 µm.

Analysis of the cyst diameter variability (Table 1) in an individual sample (*n* = 300) showed that the standard deviation of the indicator was in the range of 8.8–17.0 (mean $SD_1 = 12.6$), and the coefficient of variation was 3–6 % (mean $CV_1 = 4.7$ %).

Analysis of the cyst diameter variability (see Table 1) in an individual population (*n* = 3…7) showed that the standard deviation of the indicator was in the range of 3.5–15.7 (mean $SD_2 = 7.3$), and the coefficient of variation was 1.3–6.0 % (mean $CV_2 = 2.7$ %).

Table 1. Estimates of the cyst diameter variability in individual samples and lake populations (μm, unless otherwise stated)

Lake population	Year of sampling	Variability in samples						Intrapopulation variability					
		M_1	*min*	*max*	SD_1	CV_1, %	m_1	M_2	*min*	*max*	SD_2	CV_2, %	m_2
Gashkovo	2015	253.45	221	281	10.1	4	0.58	257,76	247	266	9.0	3.5	5.18
	2017	264.45	234	303	11.7	4	0.68						
	2018	265.95	242	287	8.8	3	0.51						
	2019	247.19	210	314	12.0	5	0.69						
Nevidim	2009	274.6	243	301	12.0	4	0.69	273.27	266	276	3.5	1.3	1.55
	2011	273.3	241	318	14.0	5	0.81						
	2012	275.23	247	303	10.8	4	0.63						
	2014	266.39	234	298	10.6	4	0.61						
	2015 (1)*	275.55	250	309	12.7	5	0.73						
	2015 (2)*	274.53	250	312	12.4	5	0.71						
Aktoban	2017	282.87	235	326	17.0	6	0.98	275.92	234	235	9.8	3.6	9.83
	2019	268.97	234	330	14.0	5	0.81						
Ebeyty	2008	270.87	226	313	13.8	5	0.8	265.16	257	271	5.6	2.1	2.28
	2011	261.84	228	298	11.6	4	0.67						
	2009	269.66	219	297	14.8	5	0.85						
	2013	256.64	223	289	13.1	5	0.76						
	2015	262.69	212	309	15.2	6	0.87						
	2017 (1)*	271.43	240	306	12.6	5	0.73						
	2017 (2)*	262.99	219	300	13.1	5	0.76						
Bolshoye Medvezhye	2008	268.83	226	298	12.7	5	0.73	265.84	260	272	4.8	1.8	1.95
	2009	264.47	228	298	13.8	5	0.79						
	2010	261.48	219	300	12.9	5	0.75						
	2011	263.63	226	294	12.5	5	0.72						
	2012	259.60	216	326	13.9	5	0.8						
	2014	272.01	237	302	12.4	5	0.71						
	2017	270.88	219	295	12.0	4	0.69						
Maloye Medvezhye	2009	257.10	221	291	12.9	5	0.75	258.43	253	265	4.9	1.9	2.19
	2011	252.57	216	292	13.2	5	0.76						
	2013	253.55	212	296	12.3	5	0.71						
	2014	261.49	227	286	11.4	4	0.66						
	2015	260.87	217	289	12.0	5	0.69						
	2017	265.11	215	288	11.4	4	0.66						
Ulzhay	2009	274.96	226	306	12.8	5	0.74	272.88	267	280	4.8	1.7	2.39
	2012	270.98	227	314	12.0	4	0.69						
	2013	267.39	236	295	9.6	4	0.55						
	2015	271.12	233	304	12.1	4	0.70						
	2018	279.95	239	315	13.6	5	0.78						

Continue on the next page…

Lake population	Year of sampling	Variability in samples						Intrapopulation variability					
		M_1	*min*	*max*	SD_1	CV_1, %	m_1	M_2	*min*	*max*	SD_2	CV_2, %	m_2
Bolshoye Yarovoye	2014	269.48	215	302	13.7	5	0.79	261.55	244	272	15.7	6.0	11.0
	2017	243.52	212	289	10.7	4	0.62						
	2018	271.66	231	309	13.7	5	0.79						
Maloye Yarovoye	2017	279.55	240	309	13.0	5	0.75	279.55					
Kuchukskoye	2017	278.89	236	314	13.5	5	0.78	278.89					
Kulundinskoye	2018	267.76	219	297	13.7	5	0.79	267.76					
In total:													
mean		266.02	227.44	301.95	12.58	4.7	0.73	268.82	253.5	267.1	7.3	2.7	4.54
minimum		243.52	210	281	8.8	3.0	0.51	257.76	234	235	3.5	1.3	1.55
maximum		282.87	250	330	17.0	6.0	0.98	279.55	267	280	15.7	6.0	11.0

Note: * – samples were taken in the same year with an interval of one month.

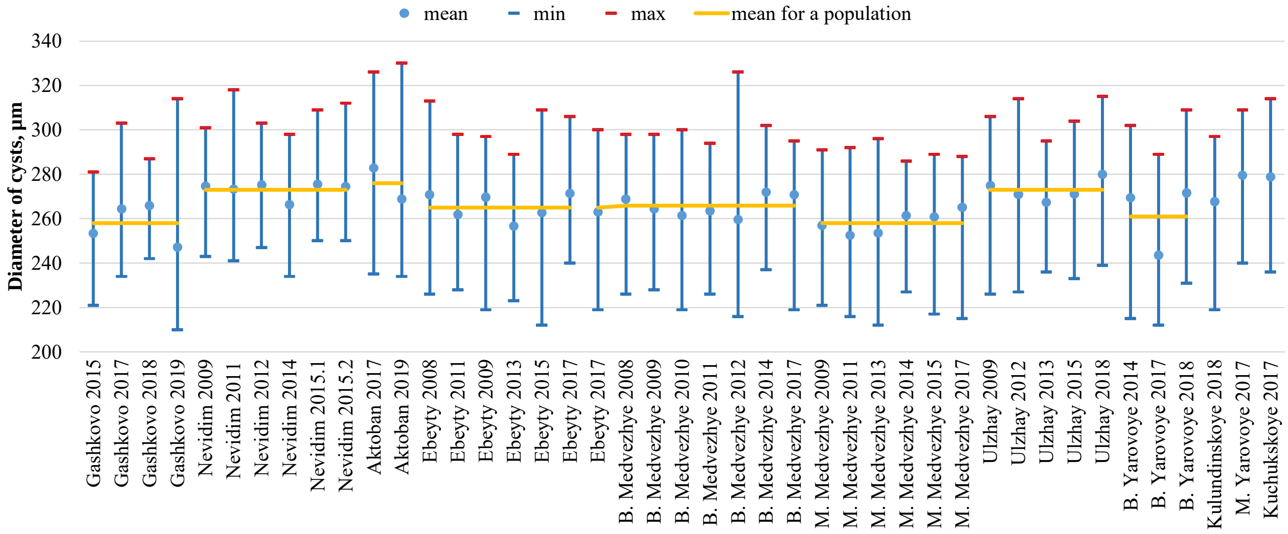


Fig. 2. Diameter of *Artemia* cysts from 11 lakes of Western Siberia

Comparative analysis of the data on interpopulation variability of the Siberian populations studied ($n = 11$) (M_3 within 258–280 µm; $M_3 \pm m_3 = 268.82 \pm 2.47$; $SD_3 = 7.8$; $CV_3 = 2.9$ %) with the data of intrapopulation variability, *inter alia* variability of individual samples, showed that the variability in the indicators is ranked as follows: $SD_1 > SD_3 > SD_2$ and $CV_1 > CV_3 > CV_2$.

The results of our study show that the variability in the mean values of the cyst diameter between populations is somewhat higher than in an individual population in different years and much lower than in an individual sample.

The analysis of the significance of the differences between all the samples (43 cyst samples) showed as follows: 78 % of the compared pairs have differences at a significance level $p \leq 0.001$, and 86 % of the compared pairs – at a significance level $p \leq 0.05$.

The analysis of the significance of intrapopulation differences showed that cysts from Nevidim Lake differ the least of all (only the sample of 2014 stood out). In other populations, the ratio of significantly different samples of different years was, at a high significance level, within 62–100 % (on average 75 %), which is close to the comparison estimates for the entire dataset.

Cluster analysis of the data similarity by the cyst diameter (Fig. 3) showed that the same populations in different years could be included in different clusters. There were no differences on the territorial basis either. The populations of Altai lakes, the most distant from other ones, were present in all the clusters, except for D. Cysts from Nevidim (2015) and Ebeyty (2017) lakes, sampled with an interval of one month (see Table 1), got into different clusters on the dendrogram.

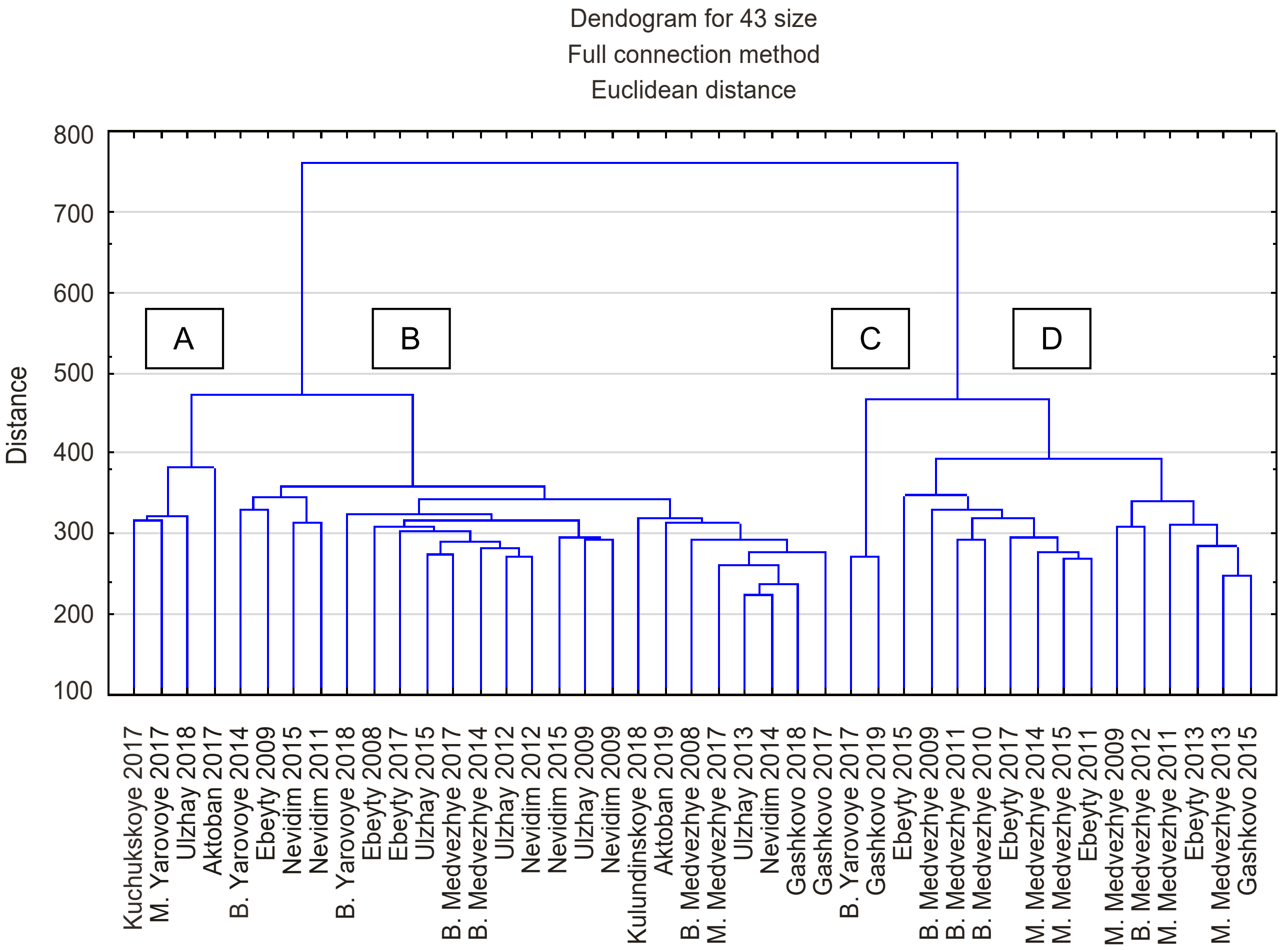
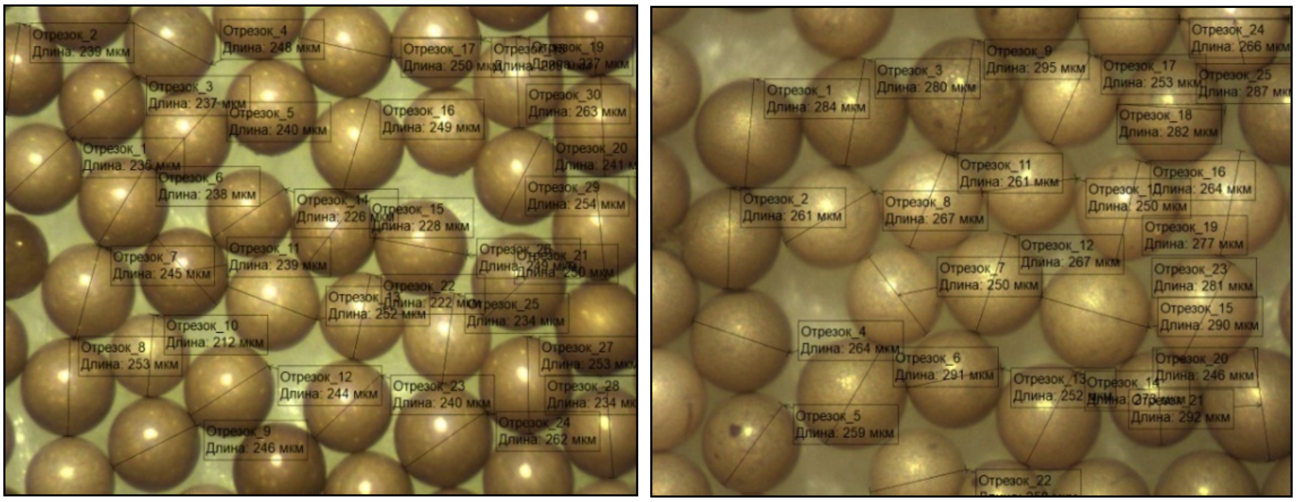


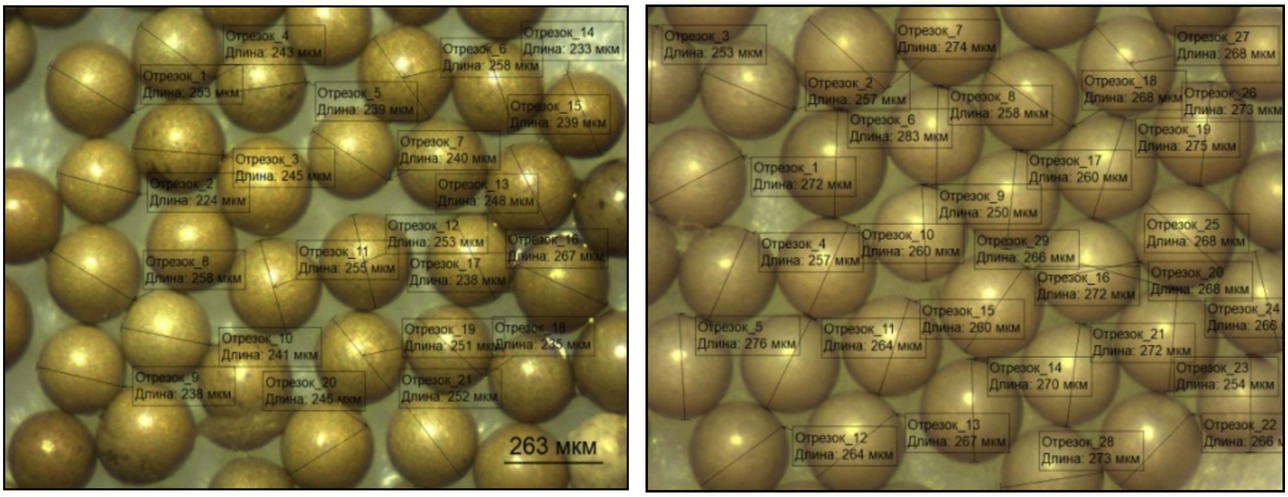
Fig. 3. Dendrogram of cluster analysis by the diameter of *Artemia* cysts of the populations studied

From the photographs (Fig. 4), a conclusion can be drawn about a morphological non-uniformity of cysts in size, both in different *Artemia* populations and in the same population in different years.



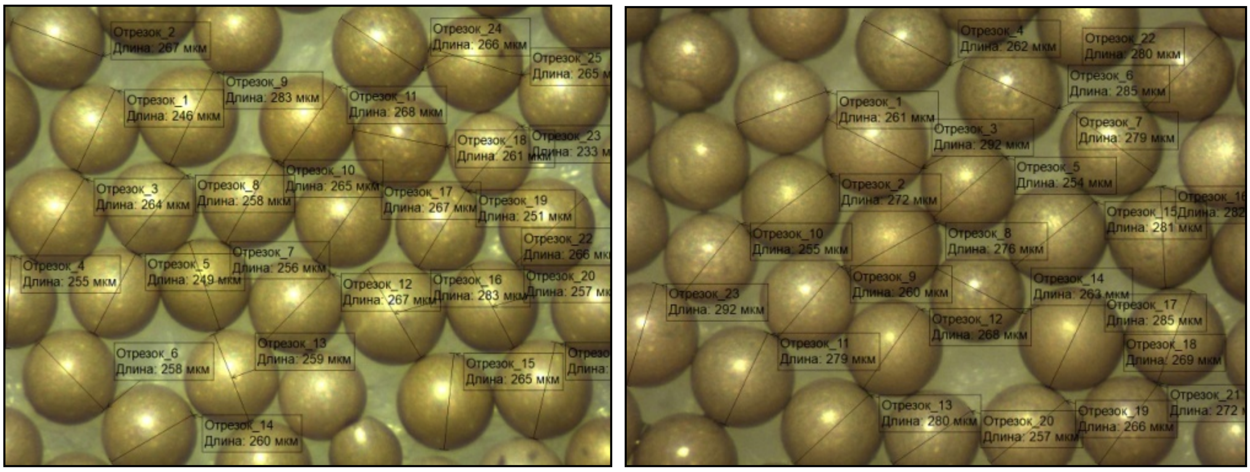
Bolshoye Yarovoye, 2017, (243.52 ± 0.62) μm

Bolshoye Yarovoye, 2018, (271.66 ± 0.79) μm



Gashkovo, 2019, (247.19 ± 0.69) μm

Gashkovo, 2017, (264.45 ± 0.68) μm

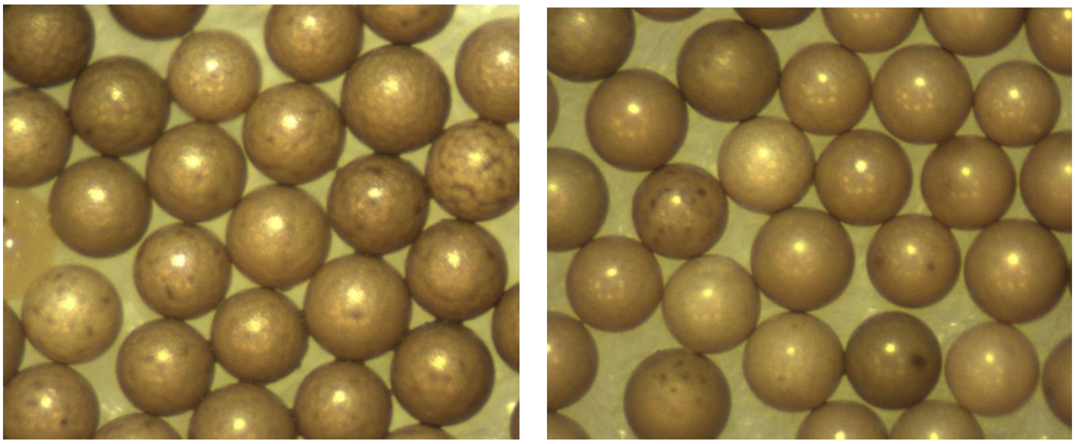


Bolshoye Medvezhye, 2012, (259.60 ± 0.80) μm

Bolshoye Medvezhye, 2014, (272.01 ± 0.71) μm

Fig. 4. Photos of cysts of the populations, studied in different years, with the greatest size variability (отрезок is segment; длина is length, μm)

Cyst spotting. Cysts with dark spots (Fig. 5) were rare in most populations; their ratio generally did not exceed 5 % and reached 24 % in Kuchukskoye Lake only (Fig. 6). This indicator can probably be used as one of the identifying for *Artemia* population of Kuchukskoye Lake.



Kuchukskoye, 2017, (278.89 ± 0.78) μm, 24 % of cysts with spots

Maloye Yarovoye, 2017, (279.55 ± 0.75) μm, 4 % of cysts with spots

Fig. 5. Cysts with spots on a shell

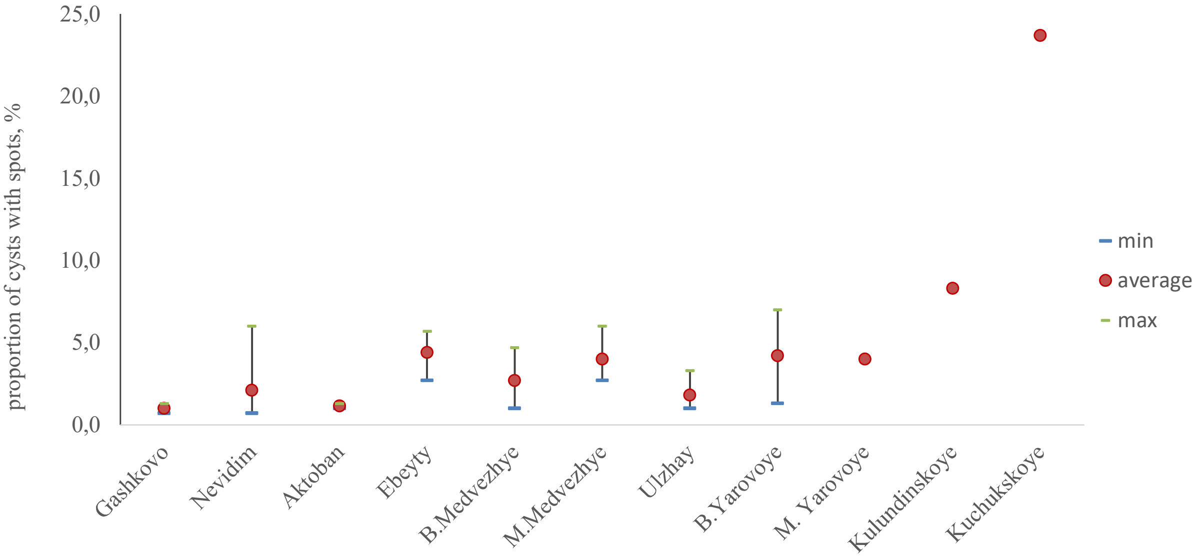


Fig. 6. Ratio of cysts with spots in *Artemia* populations, studied in different years

Embryo (decapsulated cyst) diameter. The absolute values of the embryo diameter were in the range of 196–294 μm (Table 2). The largest embryos were registered in the populations of Ulzhay (253 μm) and Nevidim (249 μm) lakes; medium-sized ones were recorded in Ebeyty, Bolshoye Medvezhye, and Maloye Medvezhye (244–245 μm) lakes; and the smallest ones were found in Lake Gashkovo (240 μm).

The analysis of the embryo diameter variability in an individual sample (n = 100) showed that the standard deviation of the indicator was in the range of 9.3–19.1 (mean SD_1 = 13.3), and the coefficient of variation was 3.9–7.9 % (mean CV_1 = 5.4 %).

Table 2. Limit and mean values of the decapsulated cyst (embryo) diameters in the populations studied and their variability

Lake	Years of sampling	Variability in the decapsulated cyst diameter (μm)		
		in the sample, absolute values	intrapopulation, mean values by years	interpopulation, mean values for populations
Ulzhay	2009, 2012, 2013, 2015, 2017	196–294	245.1–262.6	253.2
Ebeyty	2008, 2009, 2011, 2013, 2015	210–280	238.7–251.0	243.9
Bolshoye Medvezhye	2008, 2009, 2010, 2011, 2012, 2014	210–294	240.8–246.1	243.7
Maloye Medvezhye	2009, 2011, 2013, 2014, 2015 (1)*, 2015 (2)*, 2017	210–280	237.0–250.0	245.2
Nevidim	2009, 2011, 2012, 2014, 2015	210–280	244.4–255.6	249.0
Gashkovo	2015, 2017, 2018	196–266	236.5–242.3	239.9

Note: * – see explanation to Table 1.

The analysis of intrapopulation variability in the embryo diameter in an individual population (n = 3…7) showed that the standard deviation of the indicator was in the range of 2.3–6.3 (mean $SD_2 = 4.4$), and the coefficient of variation was 0.9–2.5 % (mean $CV_2 = 1.8$ %).

The analysis of interpopulation variability in the embryo diameter of the populations studied ($n = 6$) showed that $SD_3 = 4.7$ and $CV_3 = 1.9$ %.

Comparative analysis of the above data showed that the variability in the indicators is ranked as follows: $SD_1 > SD_3 > SD_2$ and $CV_1 > CV_3 > CV_2$.

According to the results of the study, the variability in the embryo sizes in individual samples is maximum, and the interpopulation variability in the mean values exceeds the intrapopulation one.

Statistically significant differences were recorded for 87 % of the compared pairs of the mean values for populations; differences were insignificant for the pairs Ebeyty – Bolshoye Medvezhye and Ebeyty – Maloye Medvezhye only (at $p \leq 0.05$).

Thus, to identify the populations, it is possible to use the embryo diameters, the interpopulation variability in which, as in the case with the cyst diameter, exceeds the intrapopulation one. It should be borne in mind that the main commercial fishing lakes (Ebeyty, Bolshoye Medvezhye, and Maloye Medvezhye) are characterized by the presence of embryos of similar sizes.

Cyst chorion thickness. In *Artemia* populations studied, the absolute values of the cyst chorion thickness ranged from 3.3 μm (Ulzhay Lake, 2017) to 16.9 μm (Ebeyty Lake, 2009). When comparing the mean chorion thickness for all the populations studied, the thinnest chorion was found in the populations from Gashkovo and Ulzhay lakes [(6.56 ± 0.29) and (7.01 ± 1.22) μm, respectively], and the thickest chorion – in the cysts of Lake Ebeyty [(12.43 ± 1.13) μm]. Cysts from Bolshoye Medvezhye, Maloye Medvezhye, and Nevidim lakes had medium thickness values [(8.08 ± 0.74), (8.54 ± 0.75), and (9.56 ± 1.38) μm, respectively] (Fig. 7).

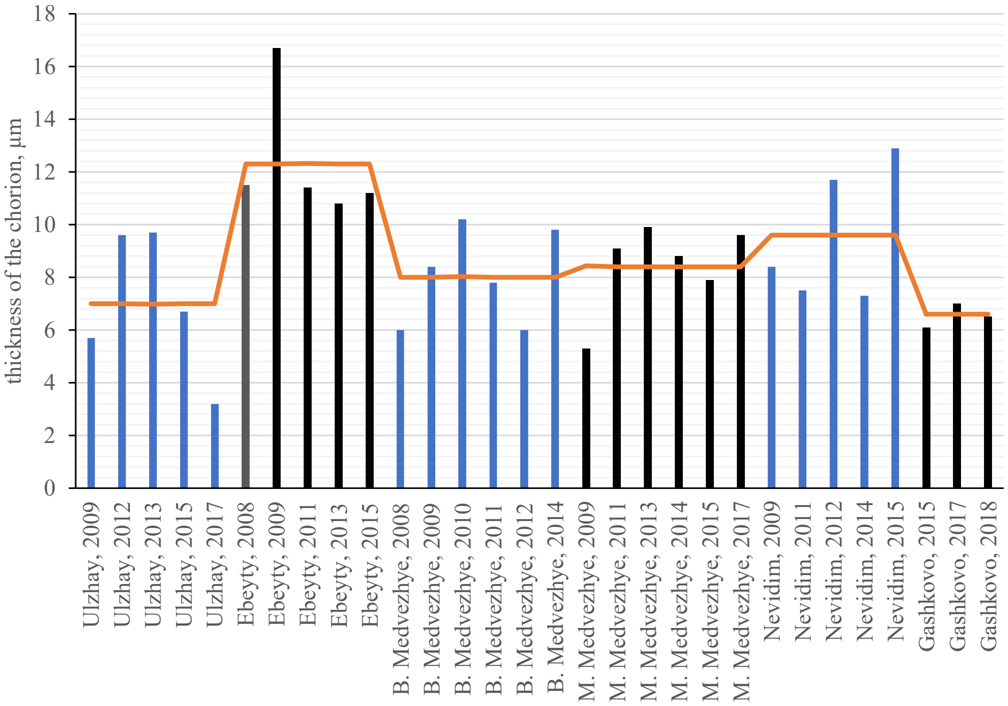


Fig. 7. Chorion thickness of *Artemia* populations studied

The intrapopulation range of the chorion thickness variability, expressed through the ratio of the maximum and minimum values in the lakes in different years, was insignificant in the population of Gashkovo Lake (1.2), average in the populations of Nevidim, Maloye Medvezhye, and Bolshoye Medvezhye lakes (1.8–2.0), and significant in the populations of Ulzhay and Ebeyty lakes (2.9–3.0).

Significant differences in the chorion thickness were established for 33 % of pairs: for Gashkovo – Maloye Medvezhye lakes and for Ebeyty with all the lakes, except for Nevidim.

Thus, of the cysts studied, the most detached in terms of several indicators are the cysts of Gashkovo Lake, as the smallest ones, with a thin chorion and small spotting, as well as the cysts of Kuchukskoye Lake, with a pronounced spotting.

Effect of salinity. It is known that salinity strongly affects *Artemia* rearing and breeding in the natural environment, and it was important to establish the degree of salinity effect of the mother water body brine on morphometry of cyst. On Fig. 8, the graphs are given of the dependence of morphometric indicators of cysts on salinity. Correlation analysis showed a weak negative correlation ($r = -0.21$) between salinity and cyst diameter and a weak positive correlation ($r = 0.25$) between salinity and chorion thickness. A statistically significant negative correlation ($r = -0.5$) was established between salinity and embryo diameter at a significance level of $p \leq 0.05$.

2. Morphometry of *Artemia* adults.

Salinity of the environment is known to be the main morpho-forming factor for *Artemia* adults. To eliminate its effect, we compared the indicators of *Artemia* adults, reared at the same salinity. In Table 3 and Fig. 9, the data are given on the morphometry of *Artemia* adults of Siberian parthenogenetic populations, reared at a salinity of 100 $g \cdot L^{-1}$. Correlation analysis of the morphometric indicators and salinity of the mother water bodies showed as follows: body length of *Artemia* adults was in a significant strong negative correlation with salinity; for abdomen width and distance between eyes, a mean negative correlation with salinity was recorded.

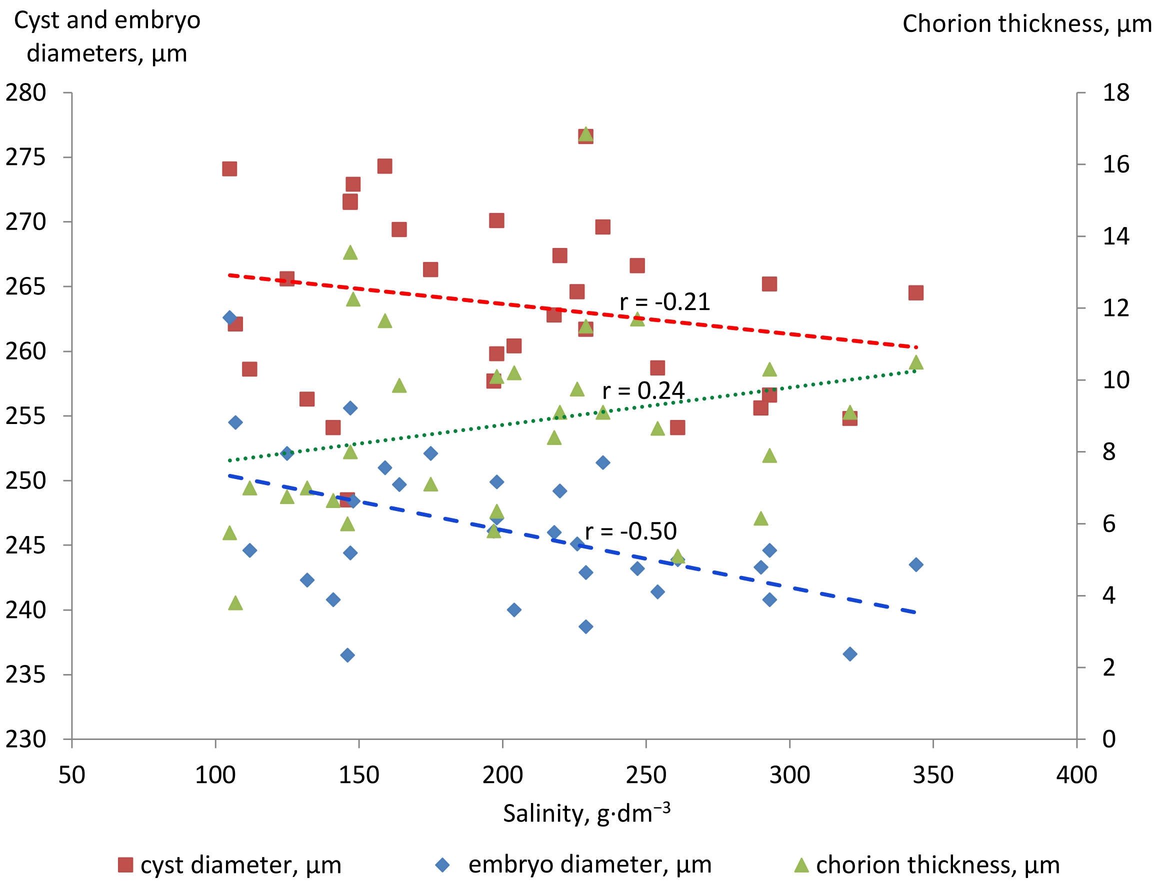


Fig. 8. Diagram of the dependence of morphometric indicators of cysts on brine salinity in a lake (source of cysts)

Table 3. Morphometric indicators of *Artemia* adults of the populations studied (mm, unless otherwise stated)

Lake, year	tl	al	aw	de	ed	sf, pcs	fl	la	hw	Σu, g·L^{-1}
Sorochie, 2009	9.46 ± 0.09	5.38 ± 0.07	0.53 ± 0.01	1.37 ± 0.02	0.24 ± 0.01	7.31 ± 0.28	0.30 ± 0.02	0.91 ± 0.02	0.64 ± 0.01	213
Sorochie, 2015	9.28 ± 0.12	5.24 ± 0.07	0.54 ± 0.01	1.36 ± 0.02	0.24 ± 0.01	7.19 ± 0.51	0.27 ± 0.01	0.96 ± 0.02	0.59 ± 0.01	263
Bolshoye Medvezhye, 2017	9.27 ± 0.64	4.43 ± 0.35	0.63 ± 0.03	1.48 ± 0.04	0.23 ± 0.02	9.0 ± 0.00	0.20 ± 0.01	0.92 ± 0.07	0.62 ± 0.02	168
Ebeyty, 2017	9.50 ± 0.31	4.96 ± 0.41	0.58 ± 0.04	1.48 ± 0.01	0.23 ± 0.01	10.6 ± 0.4	0.26 ± 0.01	0.86 ± 0.03	0.63 ± 0.03	135
Ulzhay, 2015	9.55 ± 0.26	5.02 ± 0.14	0.56 ± 0.03	1.45 ± 0.03	0.24 ± 0.01	10.7 ± 0.45	0.30 ± 0.01	0.91 ± 0.02	0.64 ± 0.03	125
Siverga, 2012	11.63 ± 0.17	5.73 ± 0.13	0.69 ± 0.02	1.52 ± 0.02	0.26 ± 0.01	7.08 ± 0.4	0.24 ± 0.03	0.87 ± 0.03	0.69 ± 0.01	86
Siverga, 2013	10.4 ± 0.14	5.46 ± 0.10	0.59 ± 0.02	1.41 ± 0.02	0.25 ± 0.01	5.33 ± 0.58	0.25 ± 0.01	0.95 ± 0.03	0.57 ± 0.01	74
Correlation with salinity, *r*	−0.76*	−0.25	−0.62	−0.67	−0.48	0.04	0.25	0.40	−0.22	

Note: * – statistically significant correlation. Abbreviations are explained in "Material and Methods" section.

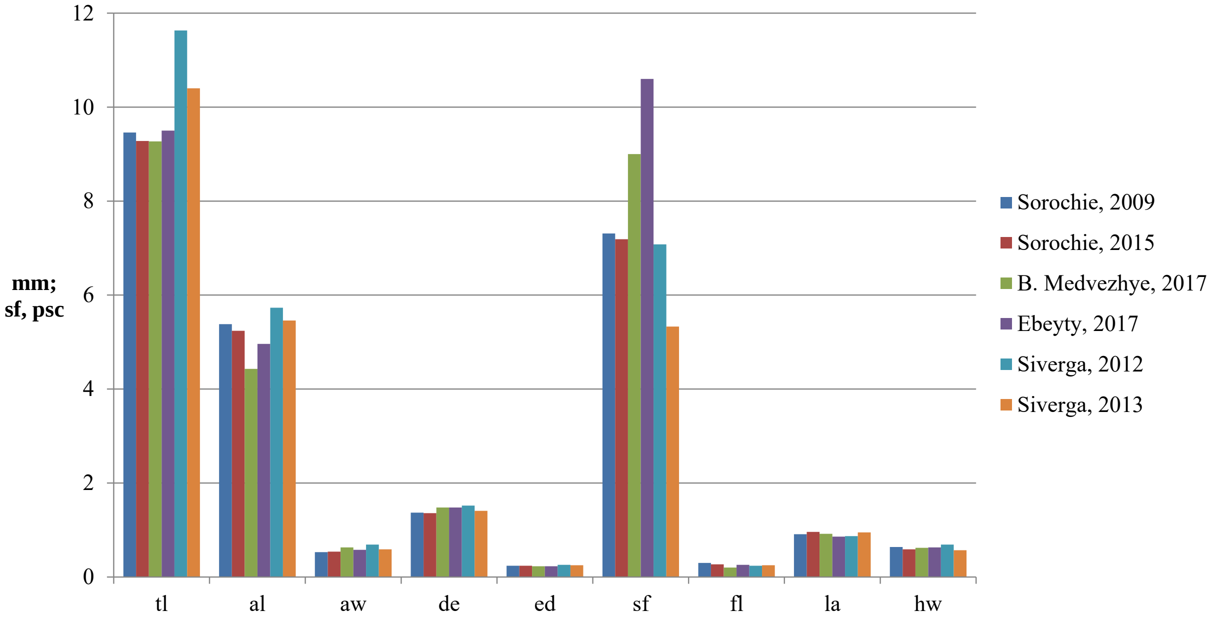


Fig. 9. Morphometric indicators of *Artemia* adults, reared from cysts of different populations

To assess the set of morphometric indicators, cluster analysis was carried out (Fig. 10). It showed the presence of a separate cluster A, formed by the population of Siverga Lake (2012 and 2013, with the lowest salinity of the natural water body: 74–86 $g \cdot L^{-1}$), and cluster B, which in turn was divided into subclusters B_1 (Ulzhay Lake, 2015 and 2017, 125–135 $g \cdot L^{-1}$), B_2 (Sorochie Lake, 2009 and 2015, 213–263 $g \cdot L^{-1}$), and B_3 (Bolshoye Medvezhye, 2017, 168 $g \cdot L^{-1}$).

Thus, *Artemia* adults, reared from cysts at the same salinity, carry information about the habitat conditions, under which they were formed.

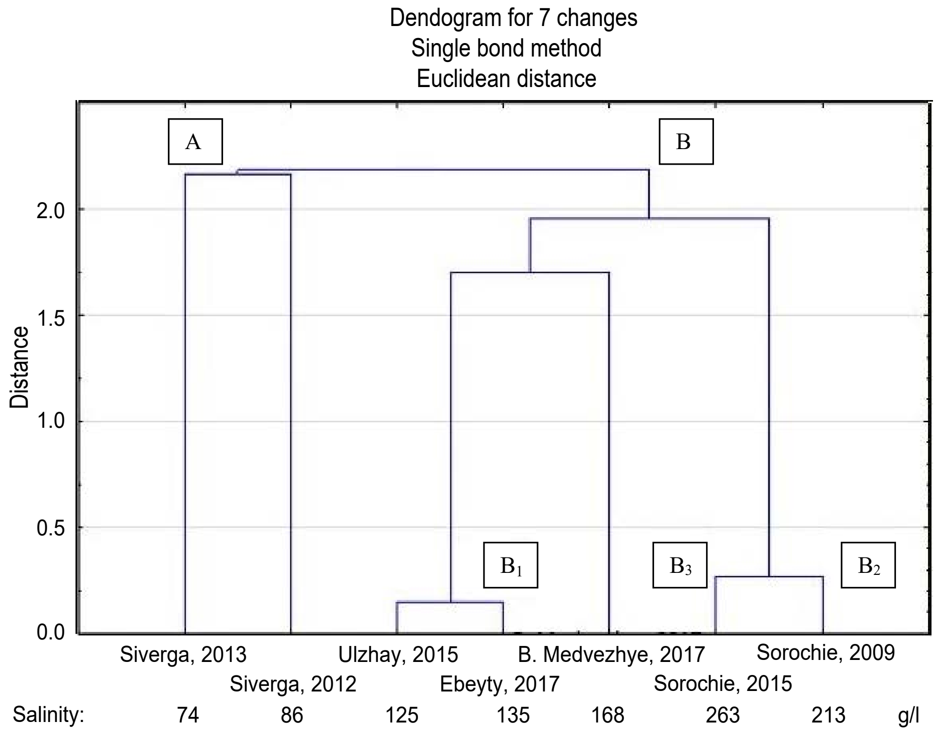


Fig. 10. Cluster analysis of morphometric data on *Artemia* adults, reared from cysts of different West Siberian populations

DISCUSSION

According to several researchers (Vanhaecke & Sorgeloos, 1980), the size of cysts and embryos, as well as chorion thickness, are the indicators, which determine the species and are basically unchanged under new environmental conditions. Practice has shown that there are difficulties both in *Artemia* species identification and in cyst population differentiation. As known (Amat, 1980 ; Asem et al., 2007 ; Camargo et al., 2005 ; Eskandari & Saygi, 2019 ; Litvinenko et al., 2016 ; Pilla & Beardmore, 1994 ; etc.), *Artemia tibetiana* Abatzopoulos, Zhang & Sorgeloos, 1998 is morphologically isolated, with the largest cyst size (up to 330 μm). The smallest cysts (on average 220–250 μm) are found in three species: *Artemia salina*, *Artemia persimilis* Piccinelli & Prosdocimi, 1968, and *Artemia franciscana* Kellog, 1906. The cysts of other species (*A. urmiana* and *A. sinica*) and parthenogenetic populations are mostly in the range of 250–280 μm. In the water bodies, studied by us, the cyst diameter varied in the range of 210–330 μm, with the mean value of 244–283 μm.

Considering *Artemia* bisexual species and parthenogenetic populations, living in Russia, there are difficulties in cyst differentiation by size due to the lack of clear divisions. According to literature sources (Anufriieva, 2014 ; Klepikov, 2012 ; Litvinenko et al., 2018, 2009 ; Solovov & Studenikina, 1990 ; Starovoitova & Burmistrova, 2017 ; Litvinenko et al., 2016), the size range of the cyst diameter absolute values fits into the gradation 220 to 290 μm, and mean for a population – 240 to 280 μm. Larger sizes for *A. parthenogenetica* populations were recorded in Bolshoye Yashaltinskoye and Dzhama water bodies (Kalmykiya): 225 to 370 μm, on average (300 ± 30) μm (Ivanova et al., 2012). For bottom sediments of Crimean water bodies (Anufriieva, 2014), two size groups of the cysts, belonging to *A. parthenogenetica*, are given: 243 μm for diploid races and 279 μm for polyploid ones. All this indicates a genetic non-uniformity of parthenogenetic races. Analysis of the cyst diameter of 25 *Artemia* parthenogenetic populations of Siberia (Litvinenko et al., 2018) showed as follows: more than 50 % of the populations have close (on average 253–261 μm) cyst sizes to that of the main commercial fishing lakes and cannot be identified by this indicator (the differences are insignificant); 33 % of populations have smaller cysts (240–245 μm); and 14 % have larger cysts (265–278 μm). As shown in our study, in the main commercial fishing lakes (Bolshoye Medvezhye, Ebeyty, Bolshoye Yarovoye, and Kulundinskoye), which account for about 70 % of the total catch of *Artemia* cysts in Russia, cysts have similar mean population sizes: 262–268 μm.

Our study has revealed significant intrapopulation variability of cysts in different years. When compared to previously published data, the difference turned out to be even greater than in our study. Thus, according to (Starovoitova & Burmistrova, 2017), in Kulundinskoye Lake over the period 1998–2005, the mean annual cyst diameter was in the range of 233–245 μm, in Bolshoye Yarovoye Lake in 1997–2012 – 235–249 μm, and in Maloye Yarovoye Lake in 1998–2016 – 226–256 μm, that is on average 1.1 times (in some years, even 1.2 times) lower than recorded by us. Such a difference might be related not only to the variability in the cyst size in the same population in different years, but also to the choice of measurement technique. In our research, a more accurate microscopic technique was used, and a large sample (300 pcs) was studied. All this illustrates the difficulty of using the cyst diameter as an identifying indicator.

Identity of cysts of Nevidim Lake, sampled with an interval of one month in 2015, and a significant difference in the sizes of cyst of Ebeyty Lake, sampled in 2017, also raise doubts about the possibility of identifying populations, even when having a cyst bank for each water body during all the periods of commercial fishing.

Cyst spotting, not exceeding 5 % in almost all the samples, reached 24 % in cysts of Kuchukskoye Lake. This fact may be of great importance in identifying a population. This is also evidenced by the data on structural differences in the surface of cysts of Kuchukskoye Lake, revealed by scanning electron microscopy (Egorkina et al., 2008).

As known (Vanhaecke & Sorgeloos, 1980), the chorion thickness does not always depend on the cyst diameter: there are populations with a small diameter and a thick chorion. Basically, the chorion thickness is in the range of 4.7–11.2 μm (Vanhaecke & Sorgeloos, 1980), but there are populations with a smaller and greater mean thickness: 1.31–9.37 μm – in Urmia Lake (Asem et al., 2007); 3.1–13.2 μm – in lakes of Columbia (Camargo et al., 2005); 0.6–8.6 μm – in water bodies of Turkey (Eskandari & Saygi, 2019). The absolute (3.3–16.9 μm) and mean (6.56–12.43 μm) values, obtained by us, expand the range of known values of the chorion thickness upward, which is likely to be due to more severe living conditions of Siberian populations. Comparison of our data with those published earlier (Litvinenko et al., 2000) has shown that the thickness of the cyst shell in several lakes can vary significantly. Thus, the intrapopulation variability in the chorion thickness in Ebeyty Lake had a range of fluctuations from 3.9 μm in 2007 (Litvinenko et al., 2009) to 12.4 μm in 2009; in Ulzhay Lake – from 11.4 μm in 1999 (Litvinenko et al., 2000) to 3.3 μm in 2017. In other populations, fluctuations were not so significant: in Bolshoye Medvezhye and Maloye Medvezhye lakes in 1999 – 9.3 μm, in 2007 – 7.6 μm, and in 2008–2015 – in the range of 5.1–10.3 μm (on average 8.3 μm); in Nevidim Lake in 1999 – 11.6 μm, in 2007 – 8.6 μm, and in 2009–2015 – 7.0–13.5 μm (on average 9.6 μm). The data obtained show a weak fixation of this morphometric indicator for the population, probably resulting from the effect of a set of natural factors, *inter alia* salinity, on a shell thickness. Thus, for *Artemia* populations of lakes of North Kazakhstan Region, where the mean chorion thickness ranged 4.0 to 8.4 μm, with a cyst diameter of 279–307 μm, it was established as follows: with an increase in salinity, the chorion thickness decreases (Volf, 2010). In our study, a weak positive correlation between these indicators was revealed.

Morphometric polymorphism of *Artemia* adults under the effect of environmental factors, primarily salinity, was noted at the turn of the XIX–XX centuries (Gajewskaya, 1916 ; Schmankewitsch, 1875). As shown in numerous studies (Boiko et al., 2016 ; Voronov, 1979 ; Ronzhina, 2009 ; Solovov & Studenikina, 1990 ; Boyko et al., 2012 ; Litvinenko & Boiko, 2008 ; Litvinenko et al., 2016 ; etc.), the sizes of mature *Artemia* adults differ within the same species and, to a large extent, depend on salinity of natural water bodies. An analysis of the morphometry of *Artemia* adults from different water bodies of Asia, Europe, Africa, and America, reared under laboratory conditions at the same salinity (Litvinenko & Boiko, 2008), has shown as follows: the formation of the phenotype of bisexual and parthenogenetic populations depends on the genotype as well, as evidenced by the established differentiation between American and all other populations of the Old World. In our experiments with *Artemia* adults, reared at the same salinity, a clear division into clusters by populations could be explained by the influence both of the genotype and salinity of a mother water body, in which the cysts were formed.

The dendrogram of similarity (Fig. 11), based on literature data on the morphometry of *Artemia* adults of the first generation (Razova, 2019), showed as follows: the American population allocated into a separate cluster, and the B_3 subcluster (Bolshoye Medvezhye Lake, 2017) (see Fig. 10) was joined by the populations of Bolshoye Yarovoye (2016) and Bolshoye Medvezhye (2016) lakes with a similar salinity of natural brine of 150–160 $g{\cdot}L^{-1}$. Since the sizes of *Artemia* adults of subsequent generations tended to decrease (Razova, 2019), it can be assumed that *Artemia* phenotype, which carries information about the environment, in which cysts were formed, is manifested in the first generation and partially in the second.

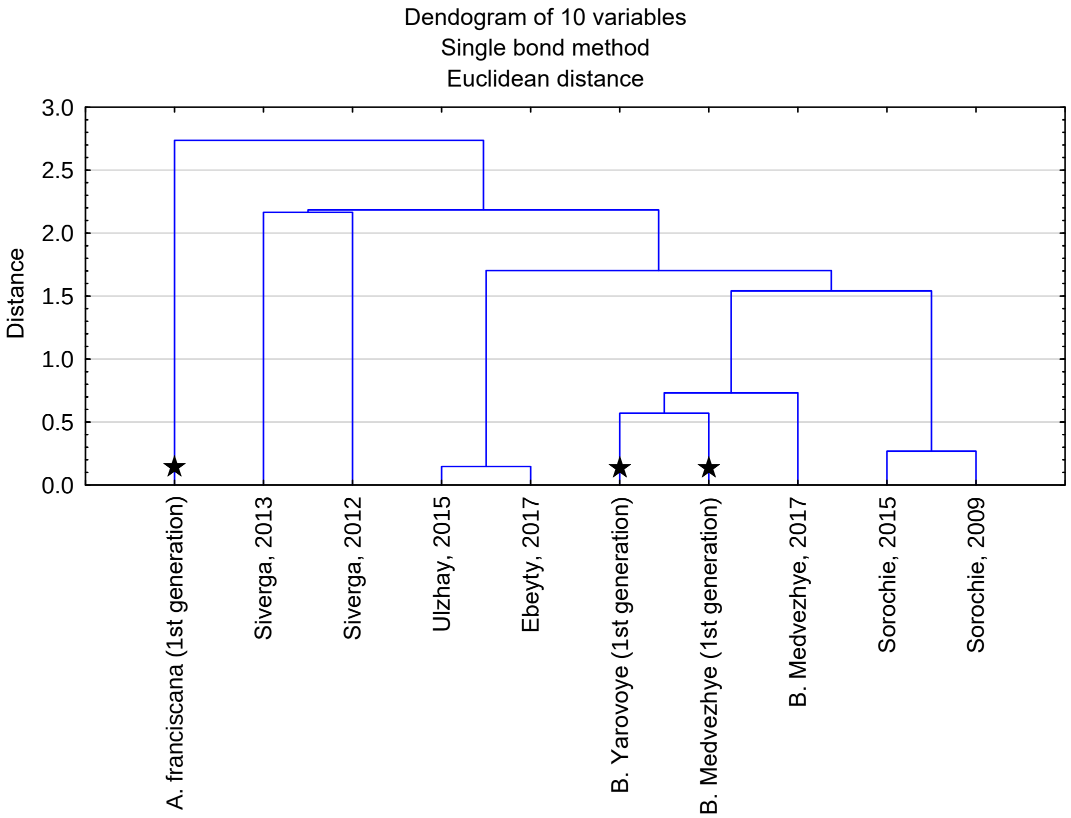


Fig. 11. Dendrogram of morphometric indicators of reared *Artemia* adults (★ – referenced literature data)

Conclusions:

1. *Artemia* cysts of Siberian populations are characterized by significant intra- and interpopulation variability in the diameter of the cysts and embryos and the chorion thickness.
2. Morphometric indicators of cysts, sampled from a water body at different dates of the same year, demonstrate seasonal variability.
3. In the main commercial fishing lakes, which account for about 70 % of the total catch of *Artemia* cysts in Russia, cysts have similar mean population sizes (262–268 μm).
4. Negative significant medium-strength correlation is established between salinity of a mother water body and the embryo diameter.
5. Significant interannual variability in the indicators of *Artemia* cysts in the same population shows that morphological characteristics of cysts cannot serve as reliable indicators, identifying a population.
6. Cyst spotting, possibly resulting from sample preparation, may further be used in differentiation of several *Artemia* populations.
7. Morphometric parameters of *Artemia* adults of the first generation, reared from cysts at the same salinity, carry information about salinity of a mother water body, which should be taken into account when identifying a population.

The work has been carried out within the framework of the state assignment of the Tyumen branch of Russian Federal Research Institute of Fisheries and Oceanography ("Gosrybtsentr") on the applied topic "Improving the fishing regulation system and increasing the efficiency of using the resources of commercial invertebrates of hyperhaline water bodies of the Russian Federation" (No. 076-00005-20-ПР).

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ВНУТРИ- И МЕЖПОПУЛЯЦИОННАЯ ИЗМЕНЧИВОСТЬ ЦИСТ И ВЗРОСЛЫХ СТАДИЙ АРТЕМИИ (BRANCHIOPODA: ANOSTRACA) В СИБИРСКИХ ПОПУЛЯЦИЯХ (МОРФОМЕТРИЯ)

Л. И. Литвиненко[1,2], К. В. Куцанов[1],
Л. Ф. Разова[1], А. Ш. Гадиадуллина[1],
А. Г. Герасимов[1], Е. В. Бражников[1]

[1]Тюменский филиал ФГБНУ «Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии» («Госрыбцентр»), Тюмень, Российская Федерация
[2]Государственный аграрный университет Северного Зауралья, Тюмень, Российская Федерация
E-mail: *opb@gosrc.ru*

Размеры цист артемии являются важным показателем ценности их как кормового ресурса и в некоторой степени позволяют идентифицировать популяции. В статье проанализированы показатели цист артемии партеногенетических популяций (диаметр, толщина хориона, наличие пятен на оболочке), отобранных в гипергалинных озёрах Западной Сибири в разные годы, и морфометрические показатели рачков, выращенных из цист при одинаковой солёности. Установлена значительная внутри- и межпопуляционная изменчивость рассмотренных показателей. Абсолютные значения диаметра цист находились в пределах 210–330 мкм, средние значения по пробам — 243,5–282,9 мкм, средние по популяциям — 257,8–279,6 мкм; абсолютные значения диаметра декапсулированных цист — в пределах 196–294 мкм, средние значения по пробам — 236,5–262,6 мкм, средние по популяциям — 239,9–253,2 мкм; абсолютные значения толщины хориона цист — 3,3–16,9 мкм, средние значения по популяциям — 6,6–12,4 мкм. В основных промысловых озёрах, на которые приходится около 70 % от всего вылова цист артемии в России, цисты имели близкие среднепопуляционные размеры (262–268 мкм). Дано заключение об отсутствии внутрипопуляционной закреплённости таких признаков, как диаметр цист и толщина хориона, то есть они не могут служить надёжными показателями, идентифицирующими сибирские популяции. Установлена статистически значимая связь ($r = -0{,}5$) между солёностью материнского водоёма и диаметром эмбрионов артемии. Пятнистость цист, не превышающая 5 % почти во всех их пробах, у цист озера Кучукское составила 24 %. Анализ морфометрических показателей рачков, выращенных из цист, показал, что средняя длина рачков (9,27–11,63 мм), ширина абдомена (0,53–0,69 мм) и расстояние между глазами (1,36–1,52 мм) тесно коррелировали с солёностью материнского водоёма (значения r составили –0,76; –0,62; –0,67 соответственно). Кластерный анализ совокупности морфометрических признаков рачков указывает на объединение популяций по признаку солёности.

Ключевые слова: *Artemia parthenogenetica*, диаметр цист, морфометрия рачков, толщина хориона, солёность, популяционная изменчивость, Западная Сибирь

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CETACEANS OF THE BARENTS SEA: FAUNA AND POPULATION STATUS AT THE BEGINNING OF THE XXI CENTURY

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Polar branch of the FSBSI "Russian Federal Research Institute of Fisheries and Oceanography"
(PINRO named after N. M. Knipovich), Murmansk, Russian Federation
E-mail: *mishin.tv@gmail.com*

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The Polar branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) carries out annually comprehensive surveys in the Barents Sea. This allows obtaining relevant data on distribution and occurrence of marine mammals, in particular cetaceans – the key link in the World Ocean ecosystem. In recent years, marine mammals monitoring has become increasingly important due to climate change and temperature rise in seas and oceans, that can result in habitat displacement and even possible extinction of certain species. This article summarizes the results of the vessel surveys of cetaceans carried out by the Polar branch of VNIRO in the Barents Sea in 2010–2019, as well as provides retrospective data on baleen whales (Mysticeti) and toothed whales (Odontoceti). Based on vessel survey material and taking into account data from literature sources, the current composition of the Barents Sea cetacean fauna is presented; at the beginning of the XXI century, it may include up to 16 species of 7 families. The analysis of vessel survey data made it possible to determine the status of marine mammals of this water area and to identify the frequency of their occurrence. The article presents population abundance for most species of baleen and toothed whales and shows the most likely spots of cetacean occurrence. According to the data obtained, white-beaked dolphin *Lagenorhynchus albirostris* is the most abundant, frequently sighted, and a year-round species: it accounts for more than 80 % of the total number of surveyed animals and about 50 % of all sighted cetaceans. Beluga whale *Delphinapterus leucas* and harbor porpoise *Phocoena phocoena* are also classified as permanent residents of the water area, and their localization is mainly confined to the Kola Peninsula coastal zone. May to October, the Barents Sea is regularly visited by species arriving from other Atlantic Ocean areas for feeding: minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus*, and humpback whale *Megaptera novaeangliae*. Narwhal *Monodon monoceros* and northern bottlenose whale *Hyperoodon ampullatus* are rarely sighted in the Russian Arctic western area.

Keywords: marine mammals, cetaceans, Cetacea, vessel surveys, distribution, occurrence, abundance, Barents Sea

The Barents Sea is one of the most productive areas of the World Ocean. High estimates of zooplankton biomass are recorded here, and a large number of commercial fish species is registered: Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, capelin *Mallotus villosus*, Arctic cod *Boreogadus saida*, Atlantic herring *Clupea harengus*, *etc*. This makes the Barents Sea a preferred habitat for marine mammals staying. Cetaceans traditionally feed in the high-latitude areas of the North-East Atlantic, arriving there in spring from other Atlantic Ocean areas.

Analyzing literature data on cetacean species composition in the Barents Sea since the XX century, it is necessary to mention A. G. Tomilin's publication (1975) and the Atlas of Marine Mammals of the USSR, edited by V. A. Zemsky (1980), which describe 14 and 18 species, respectively. At the beginning of the XXI century, according to the works of V. N. Svetochev et al. (2003) and V. L. Mishin (2004), the Barents Sea cetacean fauna was represented by 18 and 17 species, respectively. According to K. M. Kovach et al. (2009), the cetacean fauna may include up to 15 species. The most up-to-date data on the species diversity of baleen and toothed whales in the area analyzed are presented in the Atlas of Marine Mammals of the Russian Arctic and the Far East (2017): 16 cetacean species can be sighted in the Barents Sea (Table 1).

Table 1. Cetacean fauna composition of the Barents Sea according to various literature sources

Species	Tomilin, 1975[1]	Atlas, 1980[2]	Mishin, 2004[3]	Kovacs et al., 2009[4]	Morskie mlekopitayushchie, 2017[4]
Atlantic white-sided dolphin *Lagenorhynchus acutus*	+	+	+	+	+
White-beaked dolphin *Lagenorhynchus albirostris*	+	+	+	+	+
Short-beaked common dolphin *Delphinus delphis*	–	+	+	+	+
Harbor porpoise *Phocoena phocoena*	+	+	+	+	+
Bottlenose dolphin *Tursiops truncatus*	–	+	+	–	–
Killer whale *Orcinus orca*	+	+	+	+	+
Long-finned pilot whale *Globicephala melas*	–	+	+	+	+
Beluga whale *Delphinapterus leucas*	+	+	+	+	+
Narwhal *Monodon monoceros*	+	+	+	+	+
Sperm whale *Physeter catodon*	+	+	+	+	+
Northern bottlenose whale *Hyperoodon ampullatus*	+	+	+	+	+
Blue whale *Balaenoptera musculus*	+	+	+	+	+
Fin whale *Balaenoptera physalus*	+	+	+	+	+
Sei whale *Balaenoptera borealis*	+	+	+	–	+
Minke whale *Balaenoptera acutorostrata*	+	+	+	+	+

Continue on the next page…

Species	Tomilin, 1975[1]	Atlas, 1980[2]	Mishin, 2004[3]	Kovacs et al., 2009[4]	Morskie mlekopitayushchie, 2017[4]
Humpback whale *Megaptera novaeangliae*	+	+	+	+	+
North Atlantic right whale *Eubalaena glacialis*	–	+	–	–	–
Bowhead whale *Balaena mysticetus*	+	+	+	+	+
In total	**14**	**18**	**17**	**15**	**16**

Note: the given species composition corresponds to the following time period: [1] – the beginning of the XX century; [2] – mid XX century; [3] – the end of the XX century – the beginning of the XXI century; [4] – the beginning of the XXI century.

The aim of this work was to assess the current state of cetacean populations in the Barents Sea. To do this, the following tasks had to be solved:

- to determine the current species composition of baleen and toothed whales;
- to study their distribution and occurrence;
- to estimate the abundance of cetaceans;
- to reveal the pattern of their occurrence in the sea area.

MATERIAL AND METHODS

The article is based on the data of the vessel surveys of 2010–2019 of the Polar branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO), obtained mainly beyond the territorial waters, with the author participating, as well as on literature material.

To date, vessel surveys of cetaceans are carried out as part of annual comprehensive research in the Barents Sea in winter (February to March)[1], spring-summer (May to July)[2], and autumn (August to October)[3].

The survey period, as well as the routes of the research vessels, may change year to year due to weather, ice cover conditions, *etc.* As an example, Fig. 1 shows the survey routs of the RV "Vilnius" and "Fridtjof Nansen" during the comprehensive research in 2016; it is clearly seen that the survey has covered most of the Barents Sea area.

Vessel research of marine mammals was carried out by the method developed in the Polar branch of VNIRO (Zyryanov, 2004).

For each cetacean species, summarized data on the mass fraction and occurrence is presented (Table 2). The species mass fraction (%) is taken as a ratio of the number of surveyed marine mammals of one species to the total number of cetaceans of other species. Occurrence (%) is the ratio of the number of sightings (observations) of one cetacean species to the sum of all sightings of other species. To calculate the occurrence and mass fraction of most cetacean species, we used the data of the vessel surveys of the Polar branch of VNIRO. For those species that were not sighted during the research or were registered only once, literature material was used.

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[1] Regularly since 2012, within N69°–N76°, E30°–E52°.

[2] Regularly since 2008, within N69°–N74°, E20°–E45°.

[3] Regularly since 2004, within N69°–N82°, E35°–E75°.

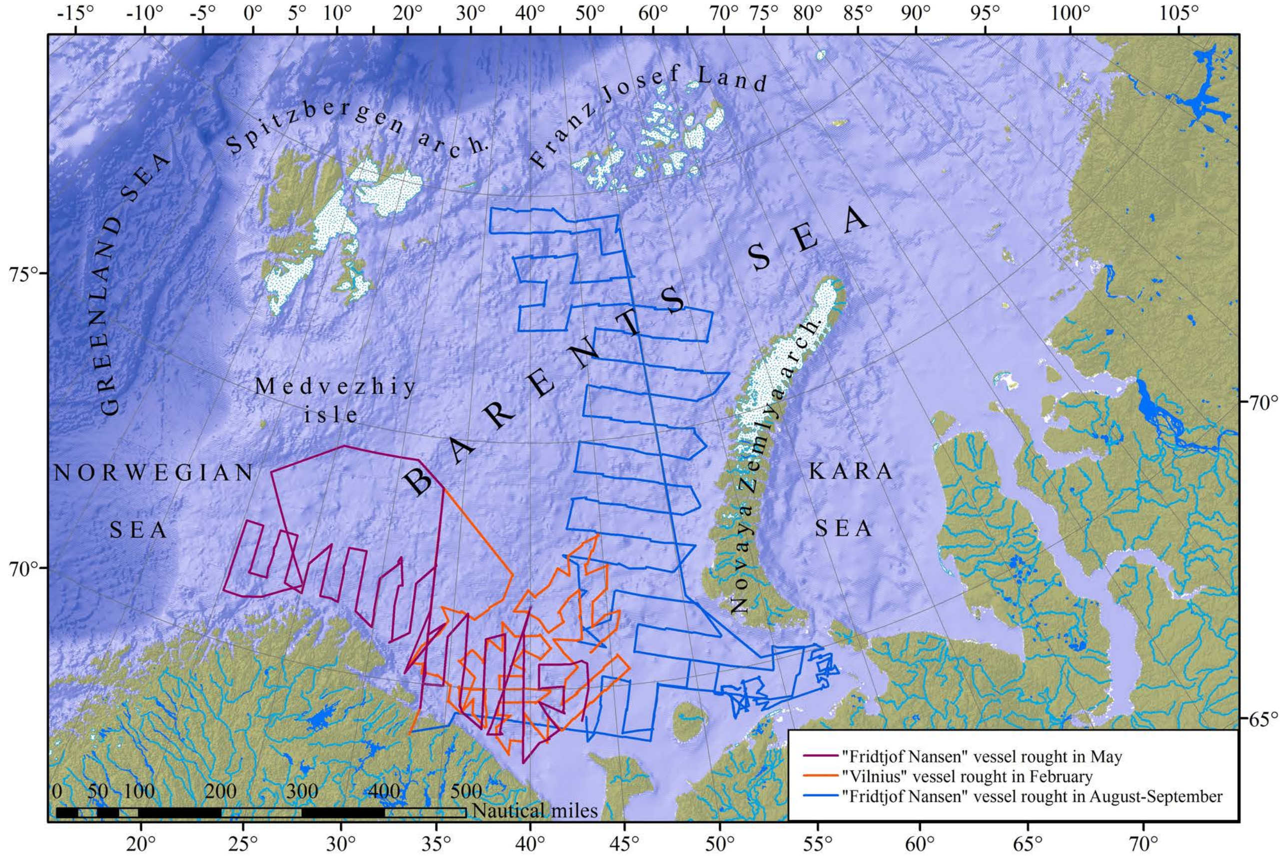

Fig. 1. Routes of the research vessels during the annual comprehensive surveys carried out by the Polar branch of VNIRO on the example of ecosystem surveys (2016)

RESULTS AND DISCUSSION

The Barents Sea cetacean fauna can be conditionally divided into three groups: permanent residents, seasonal migrants, and occasional visitors.

Permanent residents inhabit the sea area all year round. This group includes white-beaked dolphin, beluga whale, and harbor porpoise.

White-beaked dolphin is an inhabitant of the northern Atlantic Ocean; it occurs throughout all the Barents Sea (Fig. 2) and all year round. As a rule, it is distributed over the sea area in groups of 4–10 individuals. Sometimes, large pods are registered, up to several hundred individuals. Such sightings are related to dense aggregations of their main forage fish – capelin and Atlantic herring. The last time, a large pod (up to 500 individuals) was recorded in February 2018 at the Nordkinskaya Bank, in the southwestern sea area.

Considering the results of the vessel surveys over the past decade, we can say that white-beaked dolphin is the most abundant (82 %) and frequent (49 %) cetacean species (Table 2). According to our data, the total abundance of *L. albirostris* in the Barents Sea is about 50–60 thousand individuals (Klepikovsky et al., 2017), which corresponds to the Norwegian expert evaluation of previous years (Øien, 1993).

Beluga whale is a widespread species in the Arctic waters; it can be found in the Barents Sea all year round (Lukin & Ognetov, 2009). In total, not less than 20 isolated populations of this toothed whale are identified, with a total abundance up to 200 thousand individuals (Lowry et al., 2020).

Table 2. Species mass fraction and occurrence based on the vessel surveys of the Polar branch of VNIRO and literature material (2010–2019)

Species	Mass fraction, %	Occurrence, %
White-beaked dolphin *Lagenorhynchus albirostris*	82.18	49.14
Minke whale *Balaenoptera acutorostrata*	4.67	21.78
Fin whale *Balaenoptera physalus*	2.79	10.26
Humpback whale *Megaptera novaeangliae*	4.70	10.07
Harbor porpoise *Phocoena phocoena*	3.25	5.13
Killer whale *Orcinus orca*	0.79	1.18
Beluga whale *Delphinapterus leucas*	0.72	0.86
Sperm whale *Physeter catodon*	0.16	0.72
Bowhead whale *Balaena mysticetus*[1]	0.46	0.66
Northern bottlenose whale *Hyperoodon ampullatus*	0.13	0.13
Narwhal *Monodon monoceros*[2]	0.16	0.07

Note: [1] – based on the data of the Polar branch of VNIRO and literature material (Goryaev, 2017, 2019 ; Gavrilo & Ershov, 2010); [2] – based on literature material alone (Gavrilo & Ershov, 2010).

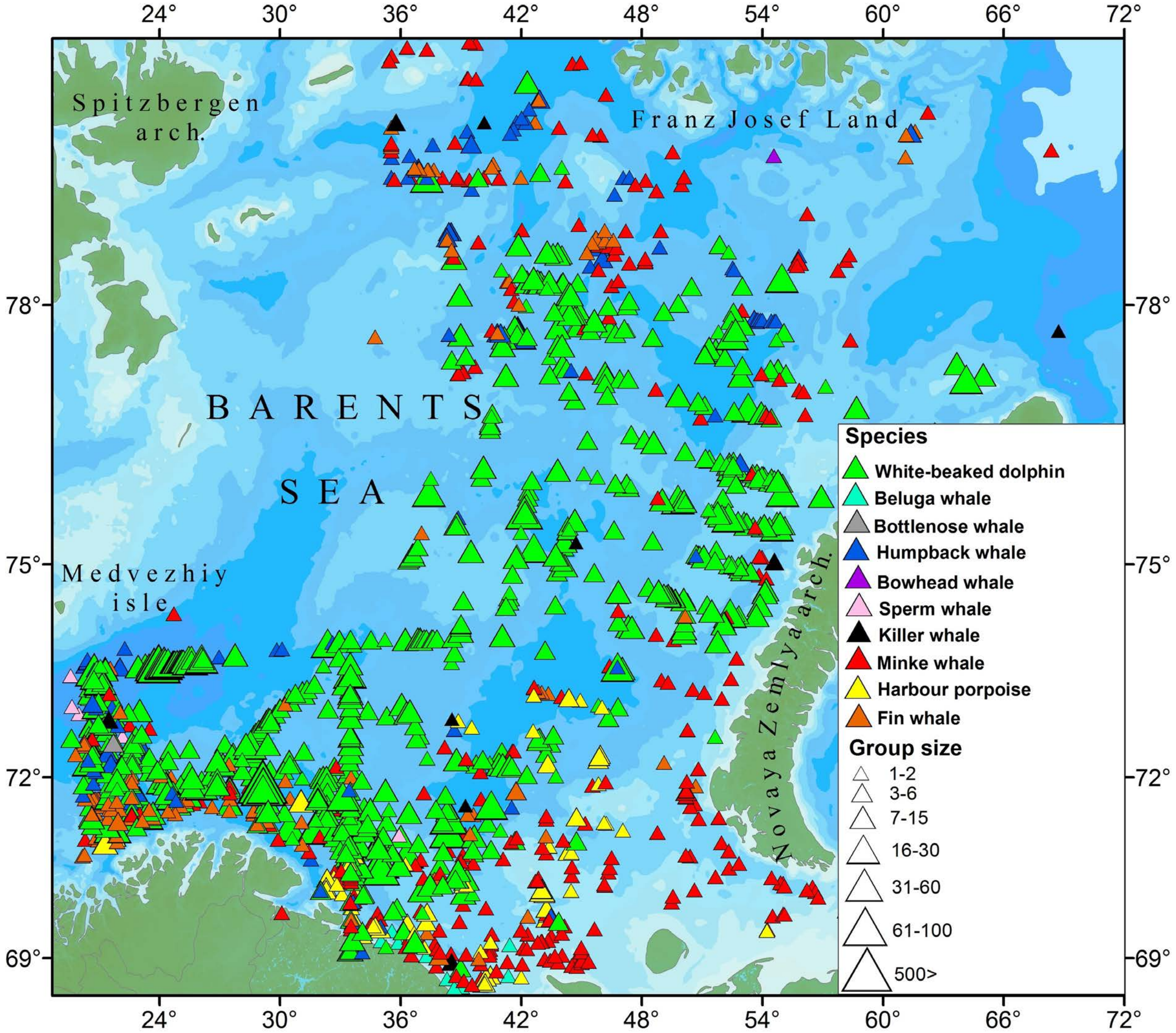

Fig. 2. Cetacean fauna of the Barents Sea based on the vessel surveys of the Polar branch of VNIRO (2010–2019)

The population structure of beluga whale inhabiting the western sector of the Russian Arctic is poorly studied, and the exact species abundance is not known (NAMMCO, 2018). According to some data, in summer in the Barents Sea there may be up to 10 thousand individuals (Kovacs et al., 2009), while in winter not more than 3–4 thousand remain (Matishov & Ognetov, 2006). During the surveys, beluga whales were mainly sighted in southeastern coastal areas (Fig. 1). *D. leucas* occurrence in relation to other cetaceans was less than 1 % (Table 2); however, despite a small number of surveyed animals over a long time period, the species cannot be classified as a rare one. The vessel surveys considered in this article were carried out mainly beyond the 12-mile zone, in open water; therefore, whales, that usually adhere to the coastline and ice edge (beluga whale, narwhal, and bowhead whale), were rare or nonexistent. Analyzing the data of coastal surveys carried out annually by the Polar branch of VNIRO, we can say that in the summer period beluga whale is quite common in southern and southeastern coastal areas of the Barents Sea. Its highest occurrence is observed during the migration period, April to July: beluga whale can be found in the areas adjacent to Franz Josef Land and Novaya Zemlya archipelagos, as well as in other areas (Kleinenberg et al., 1964).

Harbor porpoise is a typical species for coastal and southern Barents Sea areas. It has a small body size and a low dorsal fin; so, it can be sighted only under good weather conditions. The species prefers coastal waters and does not enter north of N76°; however, there is a recorded case of its occurrence beyond N80° (Gavrilo, 2008). According to the vessel surveys, harbor porpoise stays in the sea area February to October, which confirms the literature data on its year-round presence in the Barents Sea (Mlekopitayushchie Sovetskogo Soyuza, 1976 ; Kovacs et al., 2009). *P. phocoena* was mainly sighted in the southern sea areas, up to N74° (Fig. 2), where up to 15 individuals usually fed on Atlantic herring, capelin, and cods. According to 10-year survey data, the species mass fraction and occurrence were of 3 and 5 %, respectively (Table 2). According to annual surveys carried out by the Polar branch of VNIRO in the territorial waters, the highest occurrence of *P. phocoena* is observed in coastal sea areas, where in summer the animal is recorded along the entire Murmansk coast. The species abundance for the Barents Sea can be estimated at 11–12 thousand individuals (Klepikovsky et al., 2017 ; Kovacs et al., 2009).

Seasonal migrants arrive in the Barents Sea in the spring-summer period from the Atlantic for feeding (in autumn, they migrate in the opposite direction). This group includes most of the Barents Sea cetaceans. At this time, with varying degrees of probability, the following baleen and toothed whales can be sighted in the sea area: humpback whale, fin whale, bowhead whale, minke whale, sperm whale, northern bottlenose whale, killer whale, and narwhal.

Humpback whale is the most abundant baleen whale species, accounting for about 5 % of the total number of surveyed animals (Table 2). According to the vessel surveys, humpback whales are annually recorded in the Barents Sea May to October; however, according to satellite tagging data for the Svalbard archipelago area in 2018, some individuals may stay in the western sea areas at least until the end of December (Øien & Biuw, 2018). The highest number of the species sightings is registered in the southwestern and northern sea areas (Fig. 2): whales were recorded singly and in pairs, less often in groups of 3–14 individuals, in aggregations of capelin and macroplankton. The total abundance of *M. novaeangliae* in the North-East Atlantic waters during the feeding period is more than 10 thousand individuals (Leonard & Øien, 2019), and up to 1.5 thousand humpback whales may visit the Barents Sea (Klepikovsky et al., 2017).

Fin whale is a typical species for the Barents Sea. As shown by satellite tagging for the Svalbard archipelago area in autumn, most fin whales begin winter migration to warmer Atlantic waters in September-October; some whales may stay at high-latitude areas of the North-East Atlantic for winter (Lydersen et al., 2020). During vessel surveys, whales were recorded May to October singly and in pairs, way less often in groups of 3–5 individuals. The species was most frequently registered in the southwestern and northern sea areas (Fig. 2), which are related to aggregations of Atlantic herring, capelin, and macroplankton – fin whale usual diet (Aguilar & García-Vernet, 2018). During the feeding period, more than 11 thousand herring whales are feeding in the North-East Atlantic (Leonard & Øien, 2019). According to our expert evaluation, not more than 1 thousand individuals visit the Barents Sea annually (Klepikovsky et al., 2017).

Bowhead whale is an endemic species in the Arctic and Subarctic seas; it is the only baleen whale that can be sighted in the Arctic all year round. Vessel surveys showed a low species occurrence; thus, in August 2010 in the northeastern Barents Sea, polar whales were sighted only once – 2 individuals (Fig. 2). Franz Josef Land archipelago area is the spot of the most regular sightings of bowhead whale of the Svalbard species population (Belikov, 1985 ; De Korte & Belikov, 1994), the abundance of which, according to various estimates, can range from 100 (Boertmann et al., 2015) to more than 340 individuals (Vacquié-Garcia et al., 2017). In 2010, a total of 20 individuals were recorded in western Franz Josef Land archipelago area during aerial surveys (Gavrilo & Ershov, 2010). Analyzing recent literature data, we can highlight the results of vessel surveys carried out by the Murmansk Marine Biological Institute in the spring-summer periods of 2016 and 2018, during which 11 and 2 polar whales, respectively, were registered at ice edge in the northeastern Barents Sea (Goryaev, 2017, 2019). Yu. I. Goryaev considers the sighting of this species to be due to more favorable ice conditions in these areas with an overall low level of ice cover in their habitats; moreover, the researcher hypothesizes about possible wintering of bowhead whales in the ice adjacent to the Novaya Zemlya archipelago (Goryaev, 2017). Satellite tagging in May – June 2017 west of the Svalbard archipelago area (the Fram Strait) showed that some polar whales in the summer months migrate for wintering to Franz Josef Land archipelago. They spend the winter months in close proximity to the archipelago; with spring onset, they migrate southward, up to N78° (Kovacs et al., 2020).

Minke whale is a widespread species; it can be sighted in all oceans and at almost all latitudes – from S70° to N80° (Cooke, 2018). According to survey results, it is the most frequently sighted baleen whale in the Barents Sea: species occurrence is about 22 % (Table 2). During the surveys, whales were recorded May to October, mostly singly, and over the entire sea area. In northern areas, most *B. acutorostrata* occurrences were registered in aggregations of capelin and juvenile Arctic cod; in southern areas – in aggregations of Atlantic herring, juvenile cods (*Melanogrammus aeglefinus* and *Gadus morhua*), *etc.*; and in southeastern areas – in aggregations of Arctic cod, Atlantic herring, and sand lance *Ammodytes tobianus*. According to various estimates, the total abundance of minke whale arriving for feeding in the Barents, Norwegian, and North seas can range from 81 thousand individuals (Bøthun et al., 2009) to 90 thousand (Solvang et al., 2015); based on our data, not more than 10–13 thousand minke whales may visit the Barents Sea (Klepikovsky et al., 2017).

Sperm whale can be classified as an uncommon species (Table 2) with a local distribution. The animal was mainly sighted in the southwestern sea areas (northeastern Kopytov water area and the southern slope of the Medvezhinskaya Bank) (Fig. 2), where it was feeding on cephalopods and some demersal fish species. It is worth noting that sperm whales are more and more often recorded by Norwegian colleagues in the western Barents Sea in autumn during joint Russian-Norwegian ecosystem surveys (Survey Report, 2020). However, the main feeding spots are in the deep water in the southeastern Norwegian Sea, in particular in the Bleik Canyon area, near the Lofoten Islands, where dozens of individuals feed in summer and autumn (Rødland & Bjørge, 2015). According to research data of 2014–2018 (Leonard & Øien, 2019), up to 6 thousand sperm whales may visit the Norwegian Sea and adjacent water areas annually.

Northern bottlenose whale has recently been sighted rarely. In 2010–2019, only two sightings, with a total of 10 individuals, were recorded in the southwestern Barents Sea (Fig. 2), while in 1990–1993, 10 sightings of northern bottlenose whale were registered (Boiko, 2000). There is a known case of a dead whale found on the Rybachy Peninsula coastline in 2012; the animal was subsequently classified by specialists of the Polar branch of VNIRO. The main occurrence areas of this toothed whale are west of E16°, in the deep water (the western slope of the Medvezhinskaya Bank and western Kopytov water area), where northern bottlenose whales sometimes feed together with sperm whales on aggregations of halibut and squid (according to data from Russian fishing vessels). The total abundance of this toothed whale visiting the North-East Atlantic may account for about 8 thousand individuals (Leonard & Øien, 2019); the exact abundance of northern bottlenose whales in the Barents Sea is unknown.

Killer whale is a common, not numerous species; during the surveys, it was widely distributed over the Barents Sea area (Fig. 2). Whales were sighted both singly and in groups of 2–6 individuals; the occurrence of the species compared to other cetaceans was slightly higher than 1 % (Table 2). At the end of February 2019, a group of 8 killer whales was sighted by Murmansk fishermen off the Kola Peninsula coast; it is likely to be due to the availability of their favorite feed object – Atlantic herring *Clupea harengus* (following it, killer whales annually migrate from the East Atlantic). In the spring-summer period, the visits of killer whale to the Barents Sea may also be related to harp seal *Pagophilus groenlandicus* arriving from the White Sea Throat and beginning summer migration. Thus, in 2003, killer whales were recorded in spots of harp seal aggregations (Mishin, 2004). The total abundance of *O. orca* visiting the North-East Atlantic can be estimated at 15 thousand individuals (Leonard & Øien, 2019).

Narwhal inhabiting the western sector of the Russian Arctic is likely to belong to the Svalbard species population (Hobbs et al., 2019). Data on narwhal occurrence in the Barents Sea come mainly from annual monitoring cruises and tour cruises carried out by the Russian Arctic National Park. All sightings of this species in Russian waters are recorded in hard-to-reach areas of Franz Josef Land archipelago and are confined to ice edge. Narwhals sometimes visit the deep-water Cambridge Channel, *inter alia* the Dezhnev Bay off the southeastern Zemlya Aleksandry Island (Timoshenko, 2006). In September 2009, a dozen narwhals were sighted in the Topographs Bay in aggregations of Arctic cod (Gavrilo & Ershov, 2010). The lack of sightings of these whales during the vessel surveys, as well as scarce literature data on their occurrence, make it possible to classify narwhal as a rare species with a local distribution. The abundance of whales inhabiting the Svalbard archipelago areas may be more than 800 individuals (Vacquié-Garcia et al., 2017).

Occasional visitors are predominantly thermophilic species not typical for the Barents Sea; their rare visits could result from a deeper penetration of warm Atlantic waters and a wide distribution of food resources.

Blue whale is periodically sighted in small numbers by Norwegian colleagues in the deep water in the northern and western edges of the Svalbard archipelago in aggregations of krill (Survey Report, 2019). The proximity of whale occurrence areas to the Barents Sea, the conditional boundaries of which in northwestern area lie at the Leigh-Smith Cape on the Nordaustlandet Island (Svalbard archipelago) (Dobrovolskii & Zalogin, 1982), allows suggesting possible single visits of blue whales to the northwestern sea areas.

Atlantic white-sided dolphin, unlike white-beaked dolphin, prefers warmer waters of the Atlantic Ocean; so, it is an occasional visitor in the Barents Sea. Nevertheless, as literature data show, rare visits of Atlantic white-sided dolphin to the western sea areas are possible (Survey Report, 2017 ; Goryaev, 2017).

Short-beaked common dolphin is a fairly abundant species in the North-East Atlantic, and its distribution to the northeast is limited by the waters of Norway western coast and by N70° (Murphy et al., 2013). However, the study of video footage, made by the search and rescue team of the Ministry of Emergency Situations of Russia in the Kola Bay in the summer 2018, allows suggesting possible rare visits of short-beaked common dolphin to the southern Barents Sea.

Sei whale is the most thermophilic baleen whale species; as a rule, it inhabits warmer Atlantic waters. In the first half of the XX century, it was widely distributed over the Barents Sea, reaching Murmansk coast (Boiko, 2000). Currently, due to low abundance, it is practically not observed. The only sighting of this whale over the past decade was recorded in August 2015 by Norwegian colleagues during a joint Russian-Norwegian ecosystem survey (Complete Report, 2016).

Long-finned pilot whale is one of the most common cetacean species in the North-East Atlantic, with the main occurrence areas being confined to Greenland and Iceland waters (Pike et al., 2019). Sometimes, it visits the eastern Norwegian Sea (Nøttestad et al., 2015) – an area, which seems to be the border of the species range. Over the past decade, there is only one record of long-finned pilot whale sighting in the Barents Sea (Complete Report, 2016), which was most likely occasional.

Thus, taking into account the results of vessel surveys, as well as some literature data, we may conclude the possible presence in the Barents Sea of up to 16 cetacean species of 7 families: Balaenidae, Balaenopteridae, Delphinidae, Monodontidae, Phocoenidae, Physeteridae, and Hyperoodontidae.

The current cetacean composition and some peculiarities of the residence of baleen and toothed whales in the Barents Sea are presented in Table 3.

Since the beginning of the XX century, the Barents Sea cetacean fauna has undergone changes both in species composition (varying 14 to 18 species) and population abundance. The lowest biodiversity of cetaceans was recorded at the beginning of the last century (Tomilin, 1975). However, at that time, there was no information on the sightings of short-beaked common dolphin and long-finned pilot whale, whose visits to the southwestern sea areas were, nevertheless, possible, as was pointed out by K. M. Kovach et al. (2009) as well. At the same time, the fauna proposed by Norwegian colleagues does not include sei whale. It should be noted that for the entire survey period (2010–2019), we have registered neither long-finned pilot whale nor sei whale; however, in view of some literature data, possibility of rare visits of these species to the western sea areas can be assumed. The highest species diversity of cetaceans was recorded in the middle of the XX century (Atlas, 1980): at that time, North Atlantic right whale, blue whale, and bottlenose dolphin inhabited the Barents Sea; currently, they do not occur in this area. Moreover, several species of marine mammals, in particular bowhead whale, sei whale, long-finned pilot whale, and narwhal, were characterized by a wide distribution over the sea area, but the most abundant and frequently sighted species at present, white-beaked dolphin, was of a limited distribution. Later, sightings of several thermophilic species (bottlenose dolphin, long-finned pilot whale, and sei whale) in the Barents Sea were confirmed in the works of V. N. Svetochev et al. (2003) and V. L. Mishin (2004), with blue whale sightings being also mentioned. The most up-to-date information on the Barents Sea cetaceans is given in the Atlas of Marine Mammals of the Russian Arctic and the Far East (2017), which describes 16 species for the Barents Sea; our data correlate well with the results published in the Atlas.

Table 3. Cetacean fauna composition and some peculiarities of their residence in the Barents Sea (based on the vessel surveys of the Polar branch of VNIRO and literature sources of 2010–2019)

Species	Status of species / frequency of occurrence / type of distribution	The most likely sighting areas
Toothed whales (Odontoceti)		
White-beaked dolphin	PR / abundant / widespread	Everywhere
Atlantic white-sided dolphin	OV	Western areas
Harbor porpoise	PR / abundant / local	Coastal areas of the Kola Peninsula, southern areas
Short-beaked common dolphin	OV	Southwestern areas
Killer whale	SM / common / widespread	Everywhere, up to ice edge
Beluga whale	PO / common / local	Coastal areas of the Kola Peninsula (southern and southeasten areas)
Narwhal	SM / rare / local	Franz Josef Land archipelago (ice edge)
Sperm whale	SM / uncommon / local	Southwestern area (deep water), Bear Island
Northern bottlenose whale	SM / rare / local	Southwestern area (deep water), Bear Island
Long-finned pilot whale	OV	Western areas
Baleen whales (Mysticeti)		
Fin whale	SM / abundant / widespread	Everywhere
Humpback whale	SM / abundant / widespread	Everywhere
Blue whale	OV	Northwestern area, Nordaustlandet Island
Minke whale	SM / abundant / widespread	Everywhere
Bowhead whale	SM / uncommon / local	Northeastern area: Franz Josef Land archipelago and Novaya Zemlya archipelago (ice edge)
Sei whale	OV	Western areas

Note. Species by the type of residence: PR – permanent resident; SM – seasonal migrant; OV – occasional visitor, cetacean species, which does not inhabit the Barents Sea permanently in any season (is not typical for this water area). Species by the frequency of occurrence: abundant – is regularly observed during vessel surveys; common – is registered periodically, with the frequency of occurrence of 1–5 %; uncommon – is recorded sometimes in the Barents Sea, with the frequency of occurrence of 0.2–0.9 %; rare – single observations, with the frequency of occurrence less than 0.2 %.

We assume that up to 16 species of baleen and toothed whales can be currently sighted in the Barents Sea. However, it should be noted that only 11 species can be classified as typical ones for the area – except for Atlantic white-sided dolphin, short-beaked common dolphin, long-finned pilot whale, and sei whale (more thermophilic species, whose range is currently bounded by the eastern Norwegian Sea), as well as blue whale (at high latitudes, it occurs in the Arctic Ocean). Long-term surveys have shown that the highest occurrence of marine mammals is usually recorded in the spring-summer period, when conditions in the Barents Sea are the most favorable and a wide distribution of their food resources is observed.

Thus, comparison of retrospective materials with the data of current studies shows certain changes in the ranges of several cetacean species. These changes are likely to result from a decrease in the population abundance of baleen and toothed whales due to whaling in 1910–1972; this is indicated by the literature material (Mikhalev, 2009). According to official data alone, more than 220 thousand whales and dolphins were hunted in the northern Atlantic Ocean during that period, *inter alia* sei whales, blue whales, and long-finned pilot whales (Ivashin et al., 1972). The second reason for the ongoing changes in the ranges of marine mammals seems to be associated with climatic factors, which largely determine both seasonal and long-term distribution of cetaceans, as well as their migrations. Studies conducted by Australian scientists using the Model of Intermediate Complexity for Ecosystem assessments (MICE) have shown a significant decrease by the end of the XXI century in the abundance of blue whales, fin whales, and southern right whales of the Pacific population, as well as fin whales and humpback whales inhabiting Southern Atlantic and the Indian Ocean (Tulloch et al., 2019). The authors of the article associate the predicted decrease in the abundance of baleen whales with a reduction of krill *Euphausia superba* biomass due to global warming. The subsequent progressive interspecific competition of baleen whales for food resources may lead to changes in the migration routes of cetaceans and in their food spectrum.

As known, fluctuations in the Arctic water temperature, observed with some periodicity (Sherstyukov, 2016), as well as changes in the Barents Sea hydrological regime, directly affect both distribution of cetacean food recourses and its quantitative and qualitative composition (Boitsov et al., 2005 ; Bochkov, 2005 ; Prokopchuk & Trofimov, 2019). The occurrence of thermophilic marine mammals in the Barents Sea, which are not typical for the area, can be explained by the formation in a certain time period of more favorable oceanographic conditions for their habitation and a wide distribution of food resources.

As we can see, the Barents Sea cetacean fauna composition can vary over time. Annual vessel surveys of marine mammals, carried out by the Polar branch of VNIRO and covering most of the Barents Sea area, allow not only monitoring the state of cetacean populations, the key link in the ecosystem of seas and oceans, but also predicting their development trends. This is of great importance in the context of ongoing climatic changes and active hydrocarbon exploration in the World Ocean.

Conclusions:

1. Over the last century, the Barents Sea cetacean fauna has undergone certain changes, varying 14 to 18 species. Vessel surveys carried out in 2010–2019 and analysis of literature material made it possible to identify 16 species of baleen and toothed whales of 7 families, of which only 11 can be classified as typical species for the sea area. The changes in the abundance and species composition of baleen and toothed whales are likely to be related to both active whaling in 1910–1972 and periodically changing oceanographic conditions in the Barents Sea, which directly affect the distribution of food resources of cetaceans.

2. The distribution of cetaceans was studied, and the most probable areas of baleen and toothed whale sighting were determined. By the frequency of occurrence, all cetaceans were divided into four groups: abundant, common, uncommon, and rare species.
3. The abundance of most cetacean species was estimated, and the status of baleen and toothed whales in the Barents Sea was determined. As established, white-beaked dolphin, beluga whale, and harbor porpoise can be sighted in the Barents Sea all year round.
4. White-beaked dolphin was determined as the most abundant and widespread species: it accounts for 82 % of the total number of surveyed animals and 49 % of all cetacean sightings.

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КИТООБРАЗНЫЕ БАРЕНЦЕВА МОРЯ: ФАУНА И СОСТОЯНИЕ ПОПУЛЯЦИЙ В НАЧАЛЕ XXI ВЕКА

Т. В. Мишин

Полярный филиал ФГБНУ «Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии» (ПИНРО имени Н. М. Книповича), Мурманск, Российская Федерация
E-mail: *mishin.tv@gmail.com*

Комплексные научно-исследовательские работы, ежегодно проводимые Полярным филиалом ВНИРО (ПИНРО имени Н. М. Книповича) в Баренцевом море, позволяют получать актуальную информацию о распределении и встречаемости морских млекопитающих, в частности китообразных, которые являются важнейшим звеном в экосистеме Мирового океана. В последние годы необходимость проведения мониторинга морских млекопитающих приобретает всё бóльшую актуальность в связи с изменением климата и повышением температуры морей и океанов, что может привести к смещению ареалов и даже к возможному исчезновению тех или иных видов. В настоящей работе обобщены результаты судовых учётов китообразных, выполненных Полярным филиалом ВНИРО в Баренцевом море в 2010–2019 гг., а также приведены ретроспективные данные по фауне усатых (Mysticeti) и зубатых (Odontoceti) китов. На основе материалов судовых исследований и с учётом сведений из литературных источников определён современный состав китообразных Баренцева моря, который в начале XXI века может быть представлен 16 видами китообразных из 7 семейств. Анализ материалов судовых учётов позволил определить статус пребывания морских млекопитающих в акватории моря и выявить частоту их встречаемости. Приведена численность популяций большинства видов усатых и зубатых китов, указаны наиболее вероятные места их встреч. По данным исследований, самым массовым, часто и круглогодично встречающимся видом определён беломордый дельфин *Lagenorhynchus albirostris*: на его долю приходится более 80 % от общего количества учтённых морских млекопитающих и около 50 %

от всех встреченных китообразных. К постоянно присутствующим в акватории моря видам также отнесены белуха *Delphinapterus leucas* и обыкновенная морская свинья *Phocoena phocoena*, мести́ локализации которых приурочены преимущественно к прибрежной зоне Кольского полуострова. С мая по октябрь в акватории Баренцева моря регулярно встречаются виды, прибывающие сюда для нагула из других районов Атлантики, — малый полосатик *Balaenoptera acutorostrata*, финвал *Balaenoptera physalus* и горбач *Megaptera novaeangliae*. Крайне редко в западном секторе Российской Арктики можно увидеть нарвала *Monodon monoceros* и высоколобого бутылконоса *Hyperoodon ampullatus*.

Ключевые слова: морские млекопитающие, китообразные, Cetacea, судовые учёты, распределение, встречаемость, численность, Баренцево море

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CHANGE IN PLUTONIUM SEDIMENTATION FLUXES INTO THE BOTTOM SEDIMENTS OF THE SEVASTOPOL BAY BEFORE AND AFTER THE CHERNOBYL NPP ACCIDENT

© 2021 **A. A. Paraskiv, N. N. Tereshchenko,**
V. Yu. Proskurnin, and O. D. Chuzhikova-Proskurnina

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
E-mail: *paraskiv@ibss-ras.ru*

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The Sevastopol Bay located in the northern Black Sea was exposed to radioactive contamination by anthropogenic radionuclides, *inter alia* $^{238,239+240}$Pu, and to other types of anthropogenic load. One of them was the construction of breakwaters at the bay mouth in 1975–1986, which resulted in a change in the hydrological regime. The aim of this work was to assess the change in ^{238}Pu and $^{239+240}$Pu sedimentation fluxes into the bottom sediments of the Sevastopol Bay mouth in the period before and after the Chernobyl NPP accident (1962–1986 and 1986–2013, respectively). Plutonium in sediments was determined by the radiochemical method, followed by measurement of the activity of radioisotopes with an alpha spectrometer. The sedimentation rate was defined by geochronological dating of sediment layers, accessing the change in ^{238}Pu/$^{239+240}$Pu activity ratio in the bottom sediment core. Then, the mass accumulation rate in the bottom sediments was calculated. As established, in the period after 1986, the mean annual sedimentation rate and mass accumulation rate in the bay mouth increased by 63 and 70 %, respectively. Assessment of $^{238,239+240}$Pu sedimentation fluxes during two research periods showed as follows: after 1986, ^{238}Pu and $^{239+240}$Pu fluxes into the bottom sediments increased by 150 and 49 %, respectively. The increased ^{238}Pu percentage in plutonium sedimentation flux after 1986 indicates Chernobyl origin of plutonium in the bottom sediment layers above 11 cm. In the post-Chernobyl period, the cumulative effect of an increase in $^{238,239+240}$Pu sedimentation flux into the bay mouth results both from an increase in the radioactive fallout intensity after the Chernobyl NPP accident and an effect of breakwaters on the regime of sedimentation processes in the water area (an increase in the mass accumulation rate).

Keywords: plutonium, Black Sea, Sevastopol Bay, sedimentation fluxes, bottom sediments, Chernobyl NPP accident

In recent decades, a regional focus has prevailed in radioecological studies of the World Ocean: the investigations are focused on the study of specific areas that have fallen into the zone of input of anthropogenic radionuclides. One of them is the Black Sea area (Eremeev et al., 2004 ; Radioekologicheskii otklik, 2008 ; Trapeznikov et al., 2018 ; Lukšienė et al., 2014 ; Tereshchenko et al., 2018 ; Zheng et al., 2008).

The Black Sea is a closed water body with narrow straits and limited water exchange with the World Ocean (Ivanov & Belokopytov, 2011). In the drainage sea basin, there are 54 nuclear facilities, which are potential sources of artificial radionuclides (Gulin et al., 2019). The coastal areas of the Black Sea – closed and semi-closed bays – are natural depots for radionuclides limiting their further transport (Tereshchenko et al., 2012).

Within the city of Sevastopol, the largest and most widely used bay is the Sevastopol Bay. This water area is of increased environmental risk caused by several factors: discharges of a significant amount of wastewater, anthropogenic load, the Chernaya River flow, and limitation of water exchange between the bay and the open sea resulting from the construction of breakwaters (Egorov et al., 2018a ; Ovsyanyi et al., 2001).

Anthropogenic radioactive isotopes that have entered the Black Sea include alpha-emitting isotopes of plutonium ^{238,239,240}Pu. By the behavior in the aquatic ecosystem, these are conservative substances: their concentration in water decreases only due to the processes of redistribution between ecosystem components (Radioekologicheskii otklik, 2008). One of the main ways of aquatic environment self-purification from conservative sorption-active substances is their elimination with the sedimentation flux into bottom sediments (Egorov et al., 2018a, b).

The key characteristic indicators of sedimentation processes in aquatic ecosystems are the sedimentation rate (SR) and mass accumulation rate (MAR). They can be estimated in different ways, being studying the layered deposits of unicellular algae valves in bottom sediments (Hay et al., 1991), as well as using chronological markers: aerosol particles formed as a result of massive combustion of hydrocarbon fuels (Rose, 1998) or stable isotopes of lead (Ritson et al., 1999), *etc.*

However, the inclusion of anthropogenic radionuclides in the circulation of matter allows to carry out fundamental studies of the processes occurring in ecosystems under natural conditions, using these radionuclides as radiotracers: not as a research object, but as a research tool.

The radiotracer method is applied in studying sedimentation processes using radioisotopes of both natural and anthropogenic origin (Proskurnin et al., 2018 ; Radioekologicheskii otklik, 2008 ; Appleby, 1998 ; Gulin et al., 2003). As a rule, it is based on an investigation of vertical distribution of one or more radioisotopes in bottom sediments, as well as on a study of the distribution character of separate isotopes ratio.

The use of plutonium radioisotopes for studying sedimentation processes in the Black Sea ecosystems became possible due to the time disunity of the maximums of radioactive fallout from two main sources of its input, as well as different values of ^{238}Pu/$^{239+240}$Pu activity ratio in them. Thus, in 1962–1963, a maximum of global radioactive fallout was registered resulting from nuclear weapon tests in open environments. At the same time, for the latitudinal zone in which the Black Sea is located, ^{238}Pu/$^{239+240}$Pu activity ratio was of 0.036 in 1971 (Hardy et al., 1973). In turn, in the release after the Chernobyl NPP accident in 1986, ^{238}Pu/$^{239+240}$Pu activity ratio was of 0.47, *i. e.* an order of magnitude greater than in global radioactive fallout (Aarkrog, 1988). This makes it possible to determine current mean annual rates of sedimentation processes in the sea on the scale of recent decades. Therefore, to study the processes of seawater sedimentation purification in Sevastopol coastal water area, anthropogenic long-lived plutonium radionuclides were used.

The aim of this work was to assess the change in ^{238}Pu and $^{239+240}$Pu sedimentation fluxes into the bottom sediments of the Sevastopol Bay mouth in the period before (1962–1986) and after the Chernobyl NPP accident (1986–2013).

MATERIAL AND METHODS

In the Sevastopol Bay, four areas are distinguished, of different hydrological and hydrochemical regimes and pollution degrees (Ivanov et al., 2006). According to this division, the distribution of $^{239+240}$Pu in the surface (0–5 cm) layer of bottom sediments was studied earlier (Fig. 1) (Tereshchenko et al., 2013). The maximum $^{239+240}$Pu activity concentration was registered at station 2a in the bay mouth, and that determined the choice of this particular water area for investigating the vertical distribution of plutonium in the bay bottom sediments. For this study, a 20-cm core of bottom sediments was sampled in the Sevastopol Bay mouth in 2013 (st. 2a) at a depth of 15 m (Fig. 1).

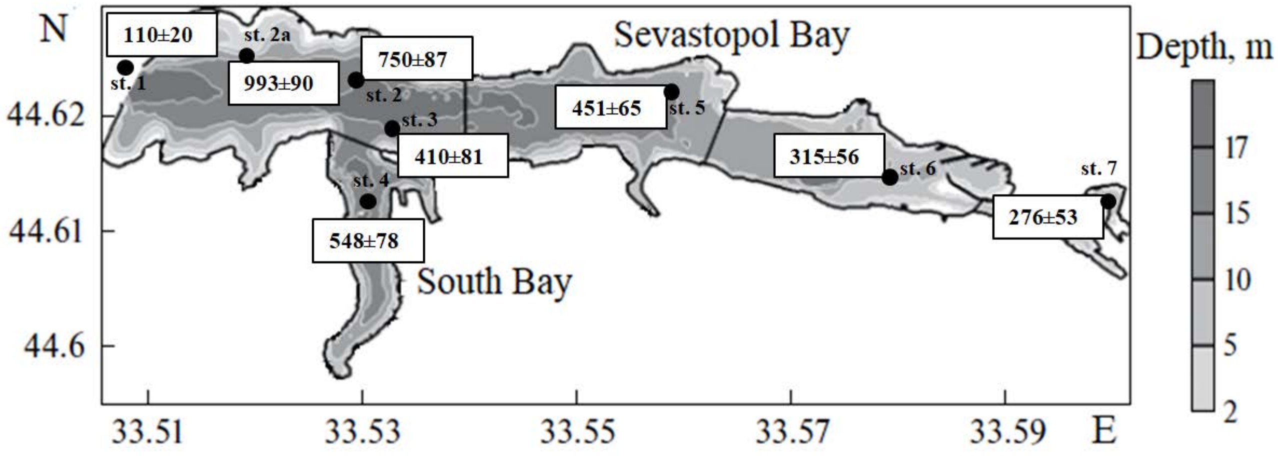


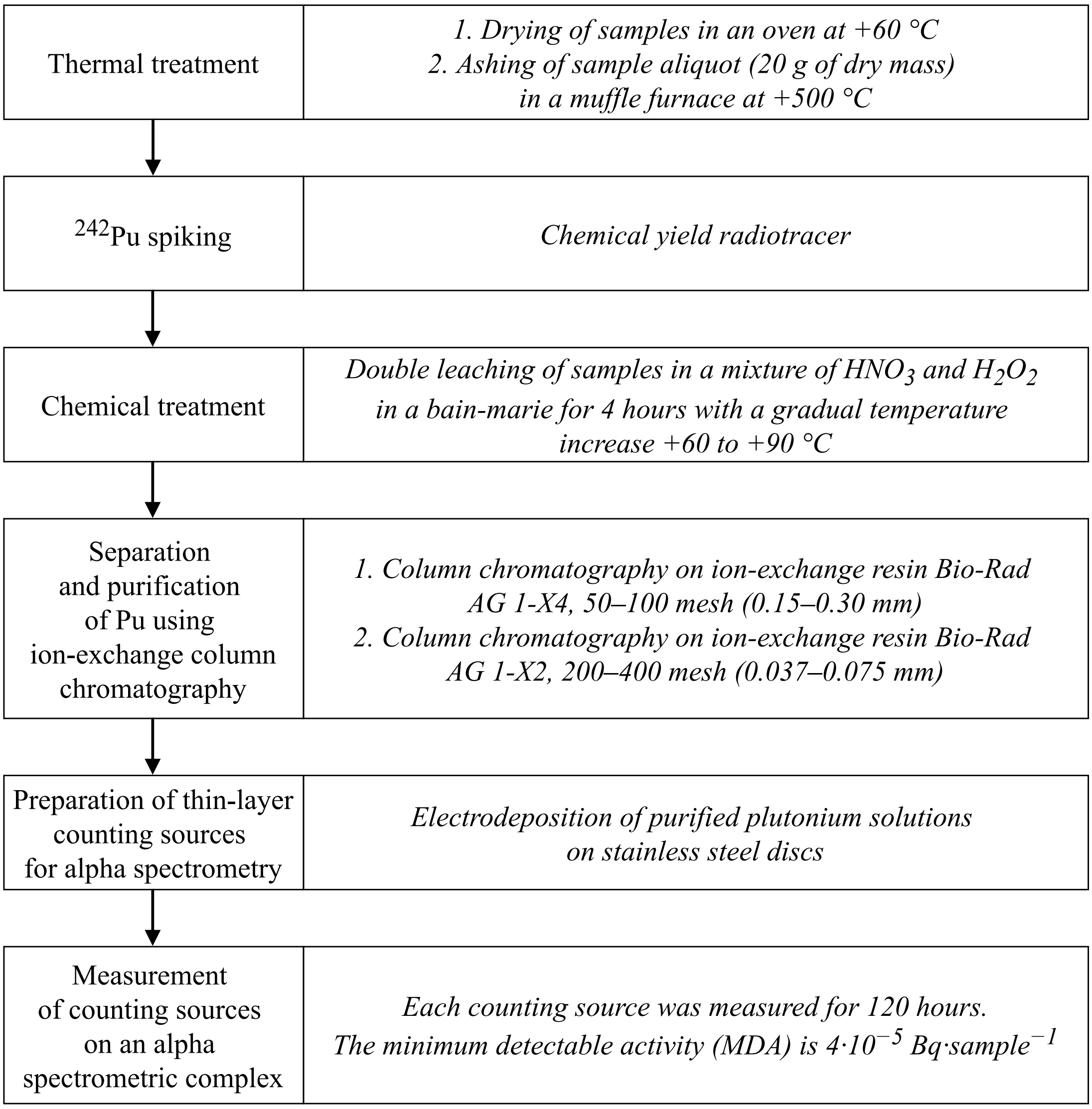
Fig. 1. Distribution of $^{239+240}$Pu activity concentration (mBq·kg^{-1}) in a 0–5-cm layer of the bottom sediments of the Sevastopol Bay (Tereshchenko et al., 2013)

Sampling was carried out with an acrylic tube, 57 mm in diameter, with a vacuum seal. Subsequently, the core was cut into 1-cm layers, and each sample was subjected to complex radiochemical treatment (Fig. 2) (Radioekologicheskii otklik, 2008 ; Tereshchenko et al., 2018).

The measurements were carried out on an ORTEC alpha spectrometer (USA). Based on the data obtained, activity concentration of alpha-emitting radioisotopes of plutonium in each layer was determined: ^{242}Pu (tracer of the chemical yield of plutonium), ^{238}Pu, and $^{239+240}$Pu. Activity concentration of ^{239}Pu and ^{240}Pu isotopes was measured in total, since these nuclides emit alpha particles with very close values of energy, within 5.11–5.17 MeV (Mefod'eva & Krot, 1987), and their energy spectra overlap. Activity concentration of plutonium radioisotopes in bottom sediments was expressed in Bq·kg^{-1} of sediment dry weight. The chemical yield of plutonium was 69–83 %, except for the 2–3-cm layer, where the value was 20 %. Such a low chemical yield in a single sample can be explained by the forced long break during the radiochemical treatment. The error in determining $^{239+240}$Pu activity concentration did not exceed 10 %; for ^{238}Pu, it was within 12–45 % due to low levels of their concentration.

Along with natural isotopes, isotope ratios and peaks of their activity resulting from the input of artificial radionuclides into the environment are widely used within the radiotracer method both for studying the migration of radioisotopes and investigating various natural processes in ecosystems (Hong et al., 2011 ; Isotopes in Hydrology, 2013). Moreover, they are used to study the dating of radioisotope contamination of bottom sediments, as well as sedimentation processes (Proskurnin et al., 2018 ;

Radioekologicheskii otklik, 2008 ; Baskaran et al., 1995 ; Isotopes in Hydrology, 2013 ; Zhang et al., 2018). The choice of the required radioisotopes ratio depends on the source of their input in the area studied and the method of their determination (Isotopes in Hydrology, 2013 ; Lindahl et al., 2010). For plutonium radioisotopes, ^{239}Pu/^{240}Pu ratio is used in mass spectrometry; ^{238}Pu/$^{239+240}$Pu ratio is used in case of determining radioisotopes by alpha spectrometry when studying their input resulting from nuclear disasters, in particular NPP accidents, and from nuclear weapon tests, since the relative amount of ^{238}Pu in the mixture of isotopes in reactor-grade plutonium is higher than that in weapons-grade plutonium. Geochronological dating of bottom sediments in the Sevastopol Bay mouth using ^{238}Pu/$^{239+240}$Pu ratio became possible due to our application of alpha spectrometry, as well as due to the unique radioecological situation in the Black Sea. It consists in the presence of two main sources of plutonium input (global radioactive fallout and radioactive input after the Chernobyl NPP accident), with the time disunity of their maximums (1962 and 1986, respectively) and different isotopic composition of plutonium radionuclides: ^{238}Pu/$^{239+240}$Pu activity ratios differ by an order of magnitude.



Thermal treatment	*1. Drying of samples in an oven at +60 °C* *2. Ashing of sample aliquot (20 g of dry mass) in a muffle furnace at +500 °C*
^{242}Pu spiking	*Chemical yield radiotracer*
Chemical treatment	*Double leaching of samples in a mixture of HNO_3 and H_2O_2 in a bain-marie for 4 hours with a gradual temperature increase +60 to +90 °C*
Separation and purification of Pu using ion-exchange column chromatography	*1. Column chromatography on ion-exchange resin Bio-Rad AG 1-X4, 50–100 mesh (0.15–0.30 mm)* *2. Column chromatography on ion-exchange resin Bio-Rad AG 1-X2, 200–400 mesh (0.037–0.075 mm)*
Preparation of thin-layer counting sources for alpha spectrometry	*Electrodeposition of purified plutonium solutions on stainless steel discs*
Measurement of counting sources on an alpha spectrometric complex	*Each counting source was measured for 120 hours.* *The minimum detectable activity (MDA) is $4 \cdot 10^{-5}$ Bq·sample^{-1}*

Fig. 2. Scheme of the main steps for determining plutonium alpha radioisotopes in bottom sediments (Radioekologicheskii otklik, 2008 ; Tereshchenko et al., 2018)

Thus, based on the data obtained on ^{238}Pu and $^{239+240}$Pu vertical distribution, as well as ^{238}Pu/$^{239+240}$Pu ratio, geochronological dating of bottom sediments in the Sevastopol Bay mouth was carried out according to the approach described earlier (Proskurnin et al., 2018 ; Radioekologicheskii otklik, 2008). Subsequently, biogeochemical indicators of sedimentation processes were determined: the sedimentation rate (SR) and mass accumulation rate (MAR). The sedimentation rate was calculated by the formula (Radioekologicheskii otklik, 2008):

$$SR = \frac{h_2 - h_1}{T_2 - T_1} , \tag{1}$$

where SR is sedimentation rate, mm·year^{-1};

h$_1$ is upper boundary of the layer studied, mm;

h$_2$ is lower boundary of the layer studied, mm;

T$_1$ is beginning of the study period, year;

T$_2$ is end of the study period, year.

The mass accumulation rate in the area studied was calculated by the formula (Radioekologicheskii otklik, 2008):

$$MAR = \frac{m_{w/s} \times SR}{S_d \times h} , \tag{2}$$

where MAR is mass accumulation rate, g·m^{-2}·year^{-1};

m$_{w/s}$ is salt-free mass of h-height sediment (mm) in a core, g;

SR is sedimentation rate, mm·year^{-1};

S$_d$ is cross-sectional area of a sampling tube, m^2.

These data made it possible to assess plutonium sedimentation fluxes into the bottom sediments of the bay mouth for two periods: before and after the Chernobyl NPP accident.

The flux of plutonium radioisotopes into bottom sediments (F, Bq·m^{-2}·year^{-1}) was calculated as the product of ^{238}Pu and $^{239+240}$Pu activity concentration in the layer of bottom sediments (A$_i$) and the mass accumulation rate (MAR):

$$F_i = A_i \times \mathrm{MAR} . \tag{3}$$

Plutonium inventory in the bay bottom sediments was calculated by the formula:

$$Z = \frac{\sum_{i=1}^{n} A_i \times m_{iw/s}}{S_d} , \tag{4}$$

where A$_i$ is ^{238}Pu or $^{239+240}$Pu activity concentration in the *i*-th layer of bottom sediments, Bq·kg^{-1};

m$_{iw/s}$ is salt-free mass of the *i*-th layer of bottom sediments, kg;

S$_d$ is cross-sectional area of a sampling tube, m^2.

RESULTS AND DISCUSSION

As a result of a layer-by-layer study of the bottom sediments in the Sevastopol Bay mouth, the data were obtained on the vertical distribution in them of alpha-emitting radioisotopes of plutonium ^{238}Pu and $^{239+240}$Pu (Fig. 3A).

Compared to activity concentration of $^{239+240}$Pu, activity concentration of ^{238}Pu in the vertical core was low. Its values were less than 0.1 $Bq \cdot kg^{-1}$, differing in the layers by more than two times (Fig. 3A). The distribution of the sum of $^{239+240}$Pu isotopes was characterized by the presence of two clearly expressed maximums: in the sediment layers of 10–11 and 17–18 cm. In the last two layers of the core, a trend is recorded for a decrease in $^{239+240}$Pu activity concentration, which corresponds to radioactive fallout from less powerful explosions during nuclear weapon tests in open environments in the 1950s (Transuranovye elementy, 1985).

The distribution of ^{238}Pu/$^{239+240}$Pu activity ratio in the bottom sediment core was analyzed as well (Fig. 3B). It can be seen from the graph that from the lower layers and up to the 10–11-cm layer, ^{238}Pu/$^{239+240}$Pu activity ratio was about 0.02. This is consistent with the data as follows: in 1971, the ratio for N40°–N50° was 0.036 (Hardy et al., 1973). By 1986, this ratio decreased to 0.02 due to ^{238}Pu radioactive decay (half-life is 87.7 years).

Above the 10–11-cm layer, an increase in ^{238}Pu/$^{239+240}$Pu activity ratio is observed; apparently, this was caused by the beginning of the influx of plutonium of Chernobyl origin, in which ^{238}Pu ratio was higher than in plutonium of global origin (Aarkrog, 1988). Since plutonium from these two sources mixed, ^{238}Pu/$^{239+240}$Pu activity ratio in bottom sediments of different Black Sea areas increased after the Chernobyl NPP accident. However, this ratio varied within 0.05–0.36, depending on sampling spot and date, due to the patchiness of the Chernobyl fallout (Radioekologicheskii otklik, 2008 ; Proskurnin et al., 2018).

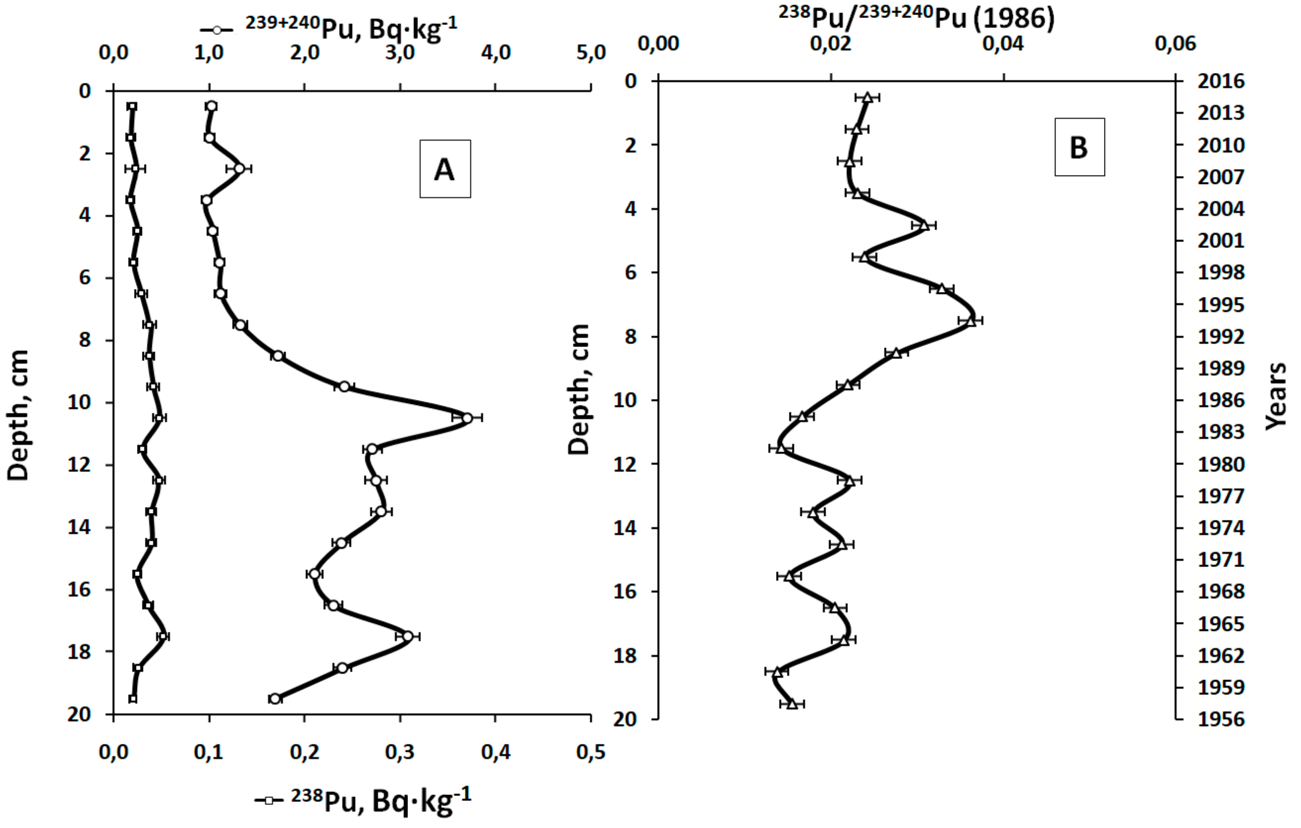


Fig. 3. Vertical distribution of ^{238}Pu and $^{239+240}$Pu activity concentration (A) and ^{238}Pu/$^{239+240}$Pu activity ratio (B) in the bottom sediments of the Sevastopol Bay mouth

Thus, based on the data on the beginning of an increase in ^{238}Pu/$^{239+240}$Pu activity ratio in the 10–11-cm layer, $^{239+240}$Pu peak observed at these depths was attributed to the period of the beginning of the Chernobyl fallout (1986). The second $^{239+240}$Pu maximum – in the 17–18-cm sediment layer – was attributed to the global fallout maximum (1962), since ^{238}Pu/$^{239+240}$Pu activity ratio in this layer corresponded to the isotopic composition of plutonium from global fallout.

On the basis of these two dates, as well as the date of core sampling, geochronological dating of the bottom sediments of the Sevastopol Bay mouth was carried out (Fig. 3); the key biogeochemical indicators of sedimentation processes in this water area were calculated (Table 1).

Table 1. Comparison of sedimentation rate and mass accumulation rate at the Sevastopol Bay mouth before and after the Chernobyl NPP accident

Period	Sediment layer	Sedimentation rate		Mass accumulation rate	
		SR, mm·year^{-1}	%	MAR, g·m^{-2}·year^{-1}	%
1986–2013	0–11	4.07	163	3,012	170
1962–1986	11–18	2.50	100	1,767	100

The data obtained indicate as follows: in the period after the Chernobyl NPP accident, the sedimentation rate and mass accumulation rate in the Sevastopol Bay area studied increased by 63 and 70 %, respectively.

Those results are consistent with the changes in the hydrological regime resulting from the construction of the breakwaters at the Sevastopol Bay mouth in 1975–1986. The bay exit was narrowed 1235 to 415 m, which led to a decrease in water exchange between the bay and the open sea by 40–70 % (Ivanov et al., 2006). Apparently, this resulted in an increase in the mass accumulation rate: in this bay area, a kind of sedimentation trap was formed.

Taking into account the quantitative indicators of the vertical distribution of plutonium radioisotopes in the column of bottom sediments, as well as the indicators of the key biogeochemical sedimentation processes, we have carried out a geochronological reconstruction of plutonium sedimentation fluxes into the bottom sediments of the Sevastopol Bay mouth (Fig. 4).

A slight increase in $^{239+240}$Pu sedimentation flux was noted back in the late 1970s – early 1980s, when the breakwaters were being constructed at the Sevastopol Bay mouth, which could cause roiling and re-sedimentation of bottom sediments. In subsequent years, such a strong increase in $^{239+240}$Pu sedimentation flux was likely caused by the cumulative effect of the new input of plutonium (after the Chernobyl NPP accident) and an increase in the mass accumulation rate resulting from the construction of the breakwaters (Fig. 4). The mass accumulation rate plays a leading role in plutonium redistribution into bottom sediments, since plutonium has an increased sorption capacity for suspended particles and is characterized by a pedotropic type of behavior. It was previously shown that more than 98 % of plutonium that has entered the water masses is deposited in the Black Sea bottom sediments (Tereshchenko et al., 2012).

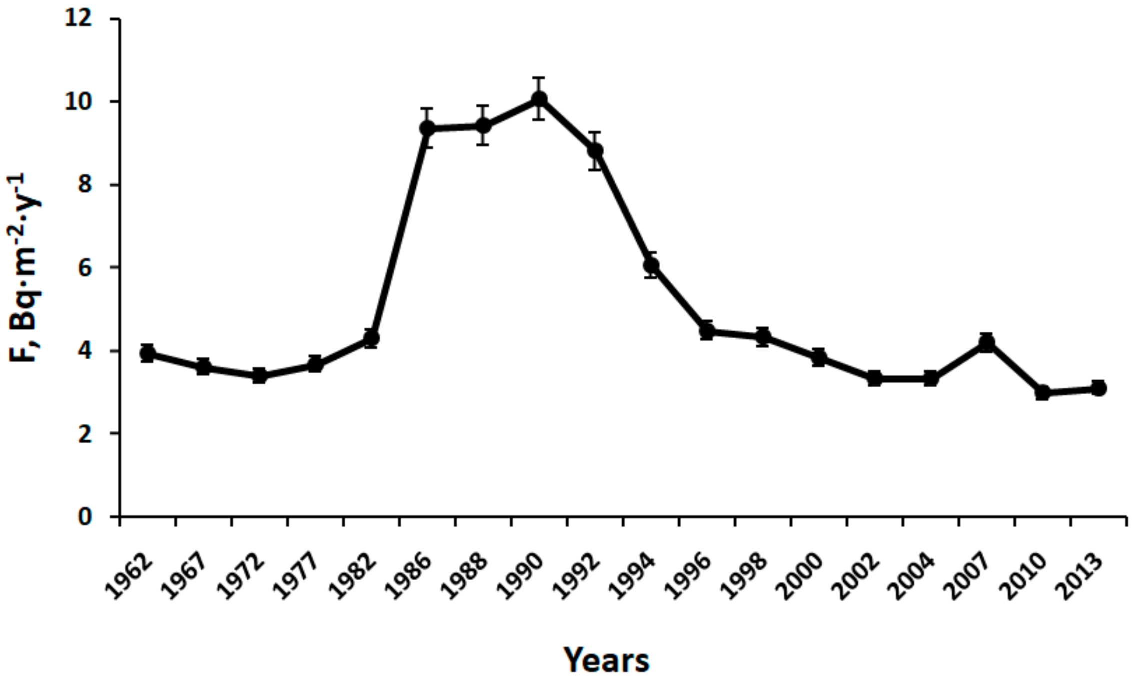


Fig. 4. Geochronological reconstruction of $^{239+240}$Pu sedimentation flux into the bottom sediments of the Sevastopol Bay mouth

We analyzed the mean values of sedimentation flux and plutonium inventory for two time intervals: before the Chernobyl NPP accident (1962–1986) and after it (1986–2013) (Table 2).

Table 2. Comparison of the mean values of plutonium sedimentation flux and inventory at the Sevastopol Bay mouth before and after the Chernobyl NPP accident

Period	Plutonium sedimentation flux				Plutonium inventory			
	^{238}Pu		$^{239+240}$Pu		^{238}Pu		$^{239+240}$Pu	
	Bq·m^{-2}·year^{-1}	%	Bq·m^{-2}·year^{-1}	%	Bq·m^{-2}	%	Bq·m^{-2}	%
1986–2013	0.15	250	5.65	149	2.82	204	152.45	167
1962–1986	0.06	100	3.80	100	1.38	100	91.08	100

It was established as follows: in the period after 1986, ^{238}Pu sedimentation flux into the bottom sediments of the Sevastopol Bay mouth increased by 150 %, and $^{239+240}$Pu sedimentation flux – by 49 %. Moreover, an increase in the inventory of ^{238}Pu (104 %) was higher than that of $^{239+240}$Pu (67 %). An increase in the ratio of ^{238}Pu in the radioisotopic composition of plutonium is characteristic of plutonium of Chernobyl origin, which confirms its presence in the flux of plutonium radioisotopes into bottom sediments after 1986. We should note that the mean Chernobyl radioactive fallout in the Black Sea was about 10 % of the global fallout. Therefore, the increase observed in sedimentation fluxes could not result from the input of plutonium of Chernobyl origin alone, but was associated with an increase in the sedimentation flux of suspended matter in this water area.

An analysis of two periods separately showed that each of them is characterized by its own dependence of the changes in plutonium flux in time (Fig. 5).

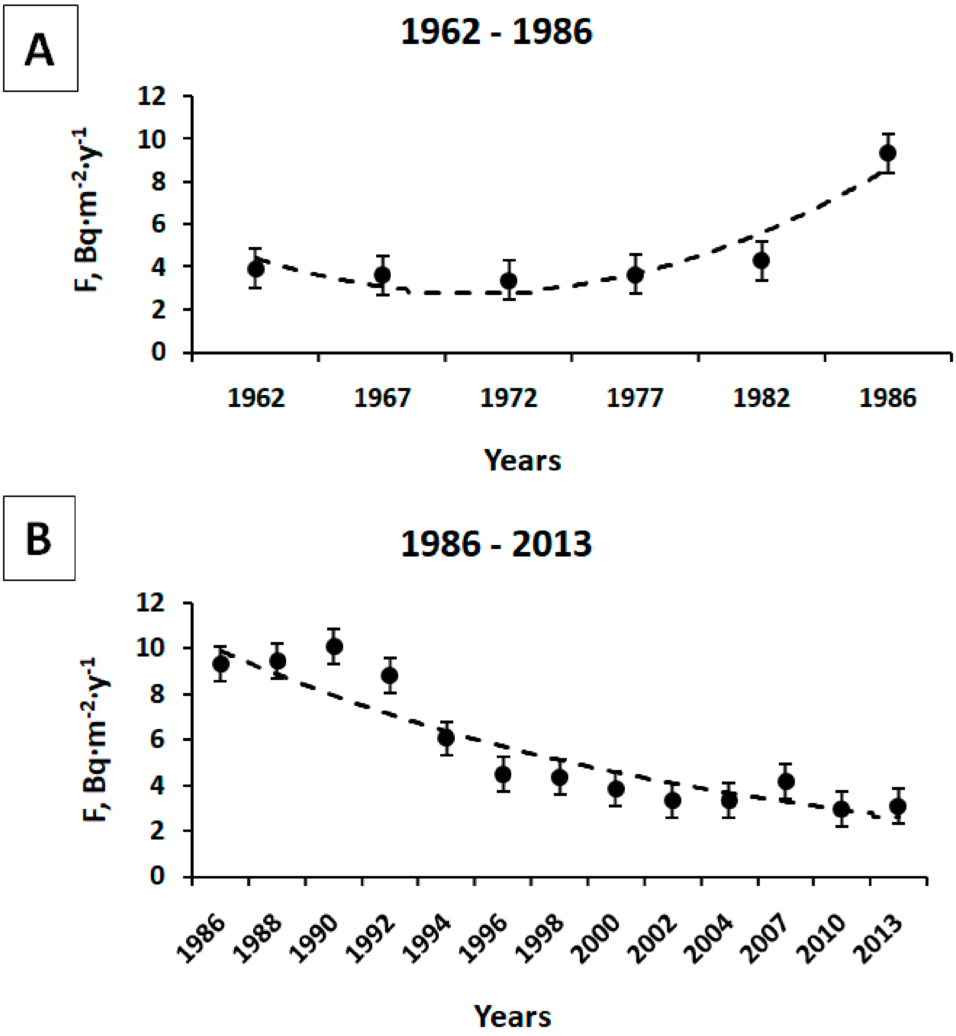


Fig. 5. Trends in $^{239+240}$Pu sedimentation flux into the bottom sediments of the Sevastopol Bay mouth during two periods: 1962–1986 (A) and 1986–2013 (B)

The trend in changes in $^{239+240}$Pu flux in the periods before and after the Chernobyl NPP accident is approximated with high reliability by curves described by polynomial ($R^2 = 0.84$) and exponential ($R^2 = 0.82$) functions (5) and (6), respectively:

$$F^{239+240}Pu = 0.0233 \times (t - 1962)^2 - 0.4419 \times (t - 1962) + 4.8727\,, \tag{5}$$

$$F^{239+240}Pu = 9.9192 \times e^{-0.05 \times (t-1986)}\,, \tag{6}$$

where F$^{239+240}$Pu is $^{239+240}$Pu sedimentation flux into bottom sediments;

t is a year for which the sedimentation flux is determined.

An analysis of the trends in changes in plutonium flux over time indicates that the cumulative effect of an increase in the fallout intensity and the construction of the breakwaters resulted in an increase in plutonium sedimentation flux from the water column of the bay photic layer. In this case, self-purification of the bay water occurs; however, plutonium is not removed from the ecosystem, but is deposited in bottom sediments (Egorov et al., 2018a, 2013). In the absence of additional sources of plutonium input, this leads to a decrease in its activity concentration in water and a decrease in the sedimentation flux of water self-purification from plutonium; plutonium sedimentation flux slows down. As shown earlier, provided that the accumulation factors are constant (with an element concentration below n×10^{-5} mol, which is typical for the levels of plutonium concentration in the Black Sea water), the sedimentation flux of plutonium removal from water masses into bottom sediments varies depending on the level of its concentration in water according to the Le Chatelier – Braun's principle (Egorov et al., 2013). At the same time, with a decrease in plutonium activity concentration in water, its residence time in water masses increases due to a decrease in the value of plutonium sedimentation flux into sediments (Tereshchenko et al., 2018).

Thus, in the current period, the use of plutonium isotopes as radiotracers of natural processes of conservative substance sedimentation into bottom sediments makes it possible to study both the quantitative characteristics of these processes (the sedimentation rate and mass accumulation rate) and the mechanisms of migration and redistribution of plutonium in marine ecosystems (plutonium sedimentation flux from the water column into bottom sediments).

Conclusions:

1. The vertical distribution of ^{238}Pu and $^{239+240}$Pu – alpha-emitting radioisotopes of plutonium – in the bottom sediments of the Sevastopol Bay mouth has been studied. The maximum activity concentration of $^{239+240}$Pu was determined in the layers of 10–11 and 17–18 cm. As an important characteristic indicator of plutonium input source, the profile of ^{238}Pu/$^{239+240}$Pu activity ratio was analyzed.
2. Geochronological dating of bottom sediments in the Sevastopol Bay mouth using the radiotracer method was carried out.
3. For the periods before and after the Chernobyl NPP accident, the quantitative characteristics of the key biogeochemical indicators of sedimentation processes in the bay water area studied – the sedimentation rate and mass accumulation rate – were determined.
4. It was established as follows: in the period after 1986, the mean annual sedimentation rate and mass accumulation rate in the bay area studied increased by 63 and 70 %, respectively.
5. Geochronological reconstruction of plutonium sedimentary fluxes into bottom sediments of the Sevastopol Bay mouth was carried out. It was found as follows: after the Chernobyl NPP accident, ^{238}Pu sedimentation flux into the bottom sediments of the Sevastopol Bay mouth increased by 150 %, and $^{239+240}$Pu sedimentation flux – by 49 %. The increased ^{238}Pu percentage in plutonium sedimentation flux, as well as increased values of ^{238}Pu/$^{239+240}$Pu activity ratio in the post-Chernobyl period, confirms the increase in plutonium concentration in the sediment layers above 11 cm due to plutonium of Chernobyl origin.
6. An analysis of the trends in changes in $^{239+240}$Pu flux in the period before and after the Chernobyl NPP accident indicates that the cumulative effect of an increase in the fallout intensity and the construction of the breakwaters resulted in an increase in plutonium sedimentation flux from the water column of the bay photic layer.

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ИЗМЕНЕНИЕ СЕДИМЕНТАЦИОННЫХ ПОТОКОВ ПЛУТОНИЯ В ДОННЫЕ ОТЛОЖЕНИЯ БУХТЫ СЕВАСТОПОЛЬСКАЯ В ПЕРИОД ДО И ПОСЛЕ АВАРИИ НА ЧАЭС

© 2021 г. **А. А. Параскив, Н. Н. Терещенко,**
В. Ю. Проскурнин, О. Д. Чужикова-Проскурнина

ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН»,
Севастополь, Российская Федерация
E-mail: *paraskiv@ibss-ras.ru*

Бухта Севастопольская, расположенная в северной акватории Чёрного моря, подвергалась радиоактивному загрязнению техногенными радионуклидами, включая $^{238,239+240}$Pu, и испытывала другие виды техногенной нагрузки. Одним из них явилось строительство заградительных молов на входе в бухту в 1975–1986 гг., которое привело к изменению её гидрологического режима. Целью данной работы было оценить изменение седиментационных потоков ^{238}Pu и $^{239+240}$Pu в донные отложения устьевой части бухты Севастопольская в период до и после аварии на Чернобыльской АЭС (1962–1986 и 1986–2013 соответственно). Плутоний в осадках определяли радиохимическим методом, с последующим измерением активности радиоизотопов на альфа-спектрометре. Скорость осадконакопления определяли с помощью геохронологической датировки слоёв осадка по изменению отношения активностей ^{238}Pu/$^{239+240}$Pu в керне донных отложений. Затем рассчитывали скорость седиментации осадочного вещества в донные осадки. Установлено, что в период после 1986 г. среднегодовая скорость осадконакопления и скорость седиментации осадочного вещества в устье бухты увеличились на 63 и 70 % соответственно. Оценка седиментационных потоков $^{238,239+240}$Pu за два исследуемых периода показала, что поток ^{238}Pu в донные отложения увеличился после 1986 г. на 150 %, а поток $^{239+240}$Pu — на 49 %. Повышенная процентная доля ^{238}Pu в седиментационном потоке плутония после 1986 г. указывает на чернобыльское происхождение плутония в слоях донных отложений выше 11 см. Суммарный эффект увеличения седиментационных потоков $^{238,239+240}$Pu в устье бухты в постчернобыльский период обусловлен ростом интенсивности радиоактивных выпадений после аварии на ЧАЭС и влиянием гидротехнических сооружений на режим седиментационных процессов в акватории (увеличением скорости седиментации осадочного вещества).

Ключевые слова: плутоний, Чёрное море, бухта Севастопольская, седиментационные потоки, донные отложения, авария на ЧАЭС

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RESOURCES AND STRUCTURE OF HORSEMUSSEL *MODIOLUS KURILENSIS* SETTLEMENTS IN PETER THE GREAT BAY (THE SEA OF JAPAN)

© 2021 **L. G. Sedova and D. A. Sokolenko**

Pacific branch of the FSBSI "Russian Federal Research Institute of Fisheries and Oceanography", Vladivostok, Russian Federation
E-mail: *ludmila.sedova@tinro-center.ru*

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Modiolus kurilensis F. R. Bernard, 1983 (Mollusca, Bivalvia) can be found in Peter the Great Bay (the Sea of Japan) both on soft and hard substrates, often together with the mussel *Crenomytilus grayanus* (Dunker, 1853); it is a promising commercial species. This mollusc is a by-catch when catching *C. grayanus*. The aim of the work was to assess *M. kurilensis* resources and settlement structure in Peter the Great Bay. The research was carried out in 2007–2018 by scuba-diving methods of hydrobiological research at the depths of down to 20 m. In total, the data were analyzed for 2,409 stations; *M. kurilensis* was found at 308 stations. Sampled molluscs were measured and weighed. The material was processed statistically and cartographically; the mean biomass and distribution density of *M. kurilensis* settlements were calculated. In total, 870 horsemussels were analyzed for studying the settlement structure. The following indicators were estimated: index of settling (ratio of the abundance of juvenile molluscs with a shell length of 1–30 mm (spat, yearlings) to the abundance of adults with a shell length of > 50 mm); index of maturation (ratio of the abundance of pre-reproductive molluscs with a shell length of 35–50 mm to the abundance of adults with a shell length of > 50 mm); index of replenishment of the commercial stock (ratio of the abundance of molluscs with a shell length of 95–100 mm (recruits) to the abundance of molluscs of commercial length of > 100 mm). The state of *M. kurilensis* population in Peter the Great Bay is stable: the ratio of molluscs of non-commercial length varies 52 to 86 % in most settlements, which indicates active natural reproduction and regular replenishment of the benthic part over many years. Replenishment of settlements with settling of both spat and yearlings depends on the presence of pelagic larvae in the plankton, while replenishment of the mature molluscs depends on favorable conditions for juvenile survival. In 2007–2018, the mean values of the indices of settling and maturation in *M. kurilensis* settlements in Peter the Great Bay were of (0.18 ± 0.07) and (0.05 ± 0.01), respectively. *M. kurilensis* resources are estimated at 27.1 thousand tons, and the commercial stock – at 16.4 thousand tons. The annual replenishment of the commercial stock of *M. kurilensis* in Peter the Great Bay is possible in a volume of more than 3 thousand tons. The mean value of the index of replenishment of the commercial stock is of (0.21 ± 0.03).

Keywords: horsemussel, *Modiolus kurilensis*, resources, commercial stock, settlement structure, replenishment, Peter the Great Bay, Sea of Japan

The bivalve mollusc *Modiolus kurilensis* F. R. Bernard, 1983 (Mytilidae) is a common representative of the upper sublittoral epifauna. It is distributed from the Yellow Sea to Peter the Great Bay, off the southwestern Sakhalin, from the northern Japanese archipelago to the Commander Islands, and off the Kamchatka coast. This eurytopic species is found on both soft and hard substrates, often together with the mussel *Crenomytilus grayanus* (Dunker, 1853) (Sedova & Sokolenko, 2018a, b, c ; Selin, 2018a ; Selin et al., 1991). The molluscs have an attached lifestyle, and they form aggregations (druses and "brushes"); singletons are found as well.

M. kurilensis is a promising commercial species; currently, it is a by-catch when catching *C. grayanus* off the Primorye coast (Gavrilova & Zhembrovskiy, 2000 ; Razin, 1934 ; Sedova, 2020 ; Sedova & Sokolenko, 2019a). Catches are not differentiated, since these two species are similar in shell morphology and comparable in size and taste (Vekhova, 2013). Compared to *C. grayanus*, horsemussels are characterized by a lighter shell and a relatively higher soft tissue content.

To date, there is no literature material on *M. kurilensis* resources in Peter the Great Bay; there are only some data on the composition of aggregations and biology of the species in its certain areas: in Posyet, Amur, Vostok, and Nakhodka bays, as well as in the Putyatin Island water area (Vekhova, 2013 ; Galysheva & Yakovleva, 2007 ; Sedova & Sokolenko, 2018a ; Selin, 2018a, b ; Selin & Ponurovsky, 1981 ; Selin et al., 1991).

The aim of the research is to assess *M. kurilensis* settlement structure and resources in Peter the Great Bay (the Sea of Japan).

MATERIAL AND METHODS

The research was carried out in Peter the Great Bay on the RV "Ubezhdenny" of the Base of Research Fleet of the Pacific branch of Russian Federal Research Institute of Fisheries and Oceanography in the summer-autumn periods of 2007–2018. Data on mollusc spatial distribution and abundance were obtained by standard scuba-diving methods of hydrobiological research at the depths of down to 20 m (Sedova & Sokolenko, 2019a). GIS MapInfo Pro software was used to prepare cartographic material. The research was planned based on the analysis of the data on the distribution of commercial invertebrates obtained by us earlier, during monitoring in Peter the Great Bay.

Most diving stations were surveyed in transects perpendicular to the shoreline, at a distance of 200–500 m (depending on the shoreline orography and the nature of bottom sediments). In each transect, 2 to 10 stations were surveyed, considering both depth changes and underwater landscape boundaries. On large areas of relatively flat seabed of the bay basins, a regular grid of stations was used.

In total, 2,409 stations along the entire shoreline were surveyed in Peter the Great Bay (spots on the map with no marked diving stations are specially protected areas, mariculture plantations, and port water areas; there, research was not carried out) (Fig. 1, Table 1). *M. kurilensis* was recorded at 308 stations (about 13 % of their total number).

In dense settlements, mollusc samples were collected at the station from three frames with an area of 1 m^2 each, located randomly in close proximity to each other. In sparse settlements, the transect method was used to estimate mollusc abundance: a diver examined a certain seabed area, counting and periodically sampling molluscs in visual range. The druses were cut off with a dive knife, trying to preserve their integrity. On the research vessel, the druses were sorted out, and the horsemussels were counted, including spat, if available.

Shell length of 1,186 specimens was measured with a caliper with an accuracy of 1 mm; total live weight of every individual was determined by weighing with an accuracy of 0.1 g.

After material statistical and cartographic processing, averaged data on the density and biomass of settlements were obtained. The calculation of horsemussel total biomass and abundance was carried out by Voronoi tessellation (Thiessen polygons), taking into account bathymetric ranges and boundaries of underwater landscapes (Sedova & Sokolenko, 2019a).

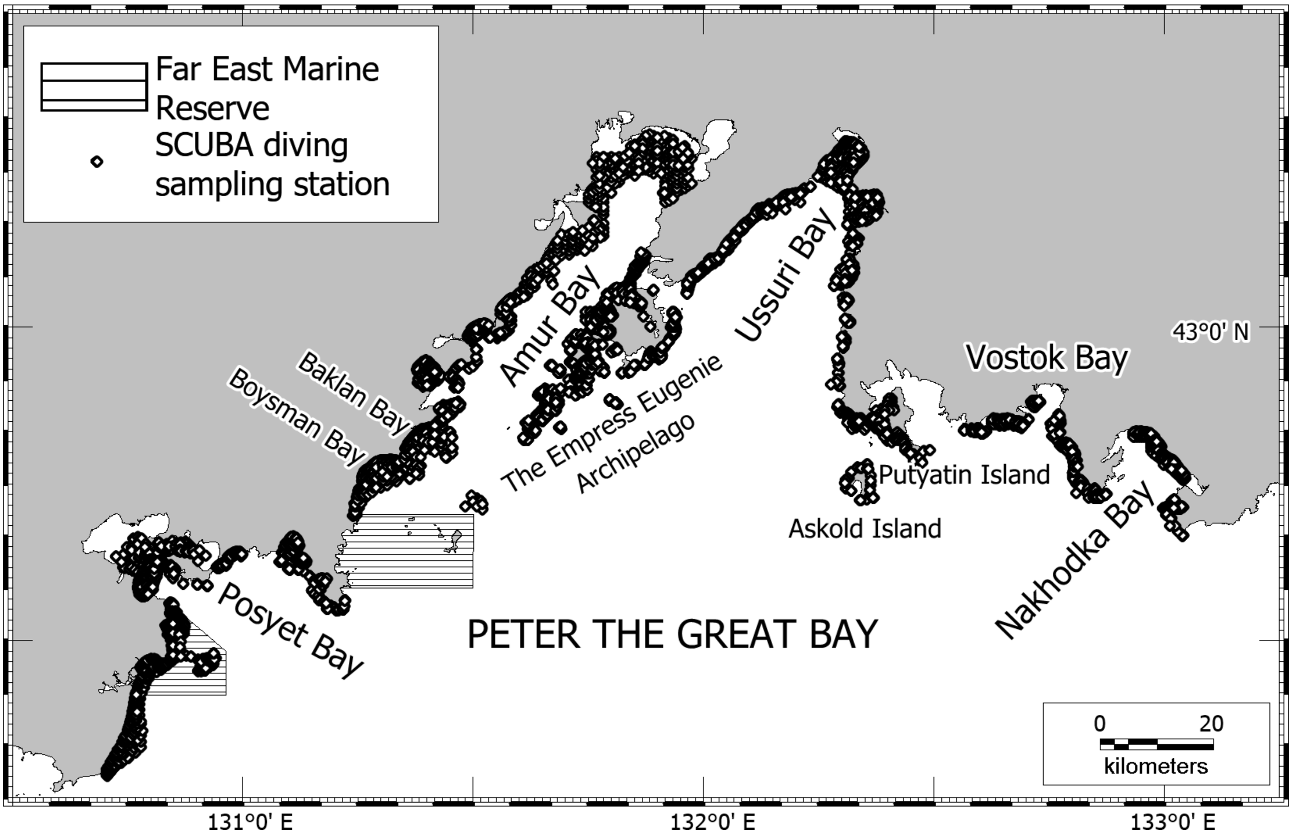

Fig. 1. Map of the area of research and sampling in Peter the Great Bay (the Sea of Japan)

Table 1. Number of stations surveyed in Peter the Great Bay

Area of research	Year	Number of diving stations investigated	Number of stations, where horsemussel was found	Total sample, specimens
Southwestern Peter the Great Bay	2007	290	14	40*
Posyet Bay	2015	172	53	236*
	2016	166	27	85
Boisman Bay	2014	294	13	17
Baklan Bay	2016	127	11	61
Amur Bay	2009	426	52	72
	2016	83	24	110*
Empress Eugénie Archipelago water area	2016	27	6	67
	2017	171	62	369*
Ussuri Bay	2018	230	21	62*
Putyatin Island water area	2007	63	8	14
Askold Island water area	2017	48	0	0
Eastern Peter the Great Bay	2012	312	17	53*
In total		**2,409**	**308**	**1,186**

Note: * – sample was used to analyze *M. kurilensis* settlement structure.

To study the settlement structure, 870 *M. kurilensis* specimens were analyzed. The structure of horsemussel settlements in the Boisman Bay and Putyatin Island water area was not considered due to the non-representativeness of the samples (Table 1). In the samples from the Baklan Bay, juveniles of 4–36 mm prevailed (95 %), while in the Askold Island water area, horsemussels were not recorded. The settlement structure in the Amur Bay and Empress Eugénie Archipelago water area was analyzed using research data of recent years; in the Posyet Bay, the analysis was based on the results of surveys of 2015 (Table 1).

M. kurilensis indices of settling and maturation were determined by the methods previously used for *C. grayanus* (Vigman, 1983 ; Vigman & Kutishchev, 1979 ; Gavrilova, 2002 ; Sedova & Sokolenko, 2019b). Considering minor differences in *M. kurilensis* and *C. grayanus* growth in the first years of life (Vekhova, 2013), the rate of replenishment of horsemussel settlements by settling juveniles (index of settling, IS) was determined as the ratio of the abundance of molluscs with a shell length of 1–30 mm (spat, yearlings) to the abundance of adults with a shell length of > 50 mm. The rate of replenishment of the mature part of the aggregations (index of maturation, IM) was calculated as the ratio of the abundance of pre-reproductive molluscs with a shell length of 35–50 mm to the abundance of adults with a shell length of > 50 mm.

According to various sources, a horsemussel reaches its commercial length (100 mm) in the age of 9 to 18 years, and the growth of mussels since 15 years is of 1–2 mm·year^{-1} (Vekhova, 2013 ; Selin & Ponurovsky, 1981 ; Selin et al., 1991). Therefore, the replenishment of the commercial stock was determined by the ratio of the abundance of molluscs ranging in length 95 to 100 mm (recruits), most of which will replenish the commercial stock in a year, to the abundance of individuals of the commercial length.

Statistical processing of the material obtained was carried out using the Statistica and Microsoft Excel software (mean values of the indices were established, as well as the error of the mean at a significance level of 5 %).

RESULTS AND DISCUSSION

Distribution and resources. For *M. kurilensis*, protected areas of the seabed, with a predominance of soft sediments, are favorable; in spots with active hydrodynamics, horsemussel is rare (Vekhova, 2013 ; Selin, 2018a ; Selin et al., 1991 ; Rees et al., 2008). In Peter the Great Bay, at the depths of down to 20 m, *M. kurilensis* is widespread, but its abundance varies significantly in different areas (Fig. 2). Horsemussel druses, both together with *C. grayanus* and monospecific, occupy significant areas (8.1–10.6 km^2) in Posyet and Ussuri bays, as well as in the Empress Eugénie Archipelago water area, with the widest distribution (36.0 km^2) in the Amur Bay (Table 2).

The highest values of the mean density of settlements (6.6–8.8 ind.·m^{-2}) and biomass (384–510 g·m^{-2}) were recorded in the Posyet, Amur, and Ussuri bays; the maximum values were registered in the Amur Bay settlements (100 ind.·m^{-2} and 8000 g·m^{-2}). In other areas, the abundance estimates were significantly lower (Table 2). In the Askold Island coastal area (spot with high hydrodynamics), *M. kurilensis* was not noted, which is likely to be due to environmental conditions, that are unsuitable for the species. In 2001–2005, the density of horsemussel settlements in eastern Peter the Great Bay (the Vostok and Nakhodka bays) varied 0.5 to 50 ind.·m^{-2} (Galysheva & Yakovleva, 2007).

M. kurilensis resources in Peter the Great Bay are estimated at 27.1 thousand tons, with most of them (66.8 %) recorded in the Amur Bay (Fig. 2, Table 2).

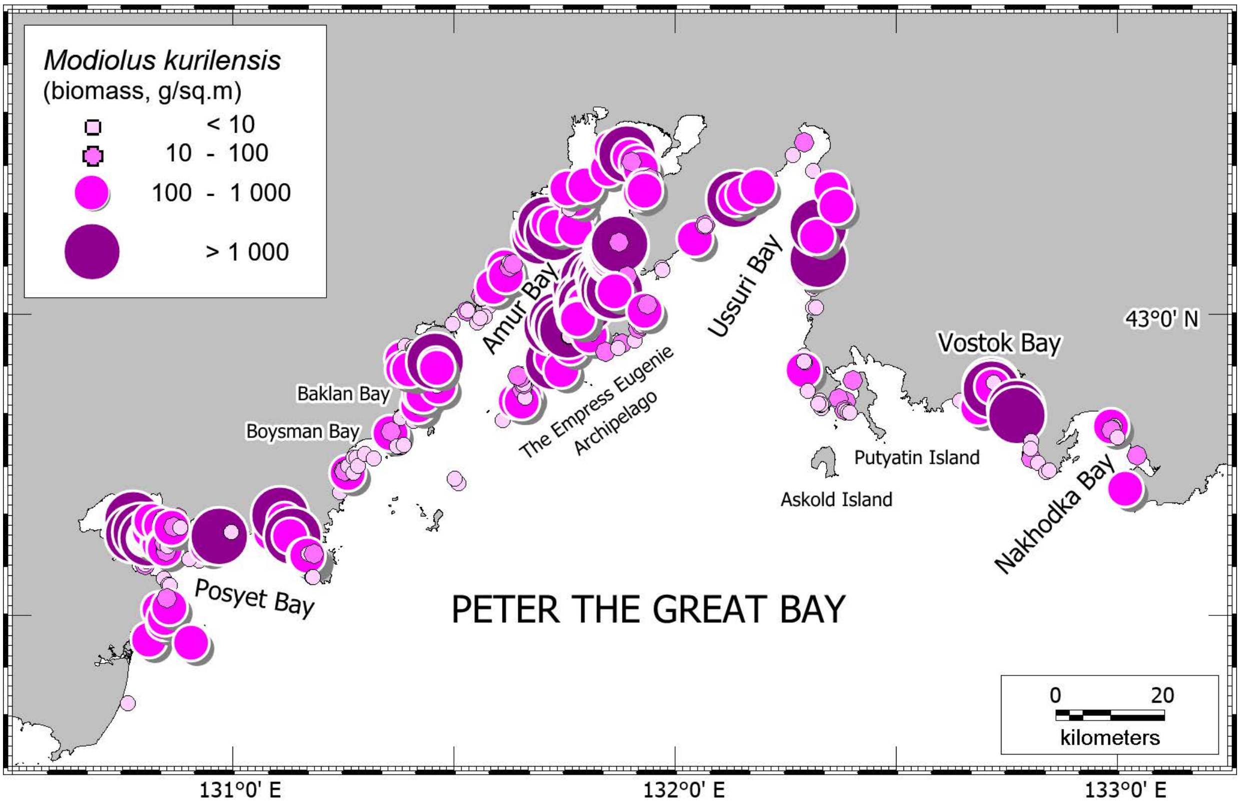

Fig. 2. *M. kurilensis* biomass distribution in Peter the Great Bay

Table 2. *M. kurilensis* biostatistical characteristics and resources in Peter the Great Bay

Locality and year	Area, km^2	Depth, m	Mean density, ind.·m^{-2}	Maximum density, ind.·m^{-2}	Mean biomass, g·m^{-2}	Maximum biomass, g·m^{-2}	Resources	
							thousand ind.	tons
1	0.9	1–15	0.5 ± 0.1	2	62 ± 16	230	249	34.7
2	8.1	1–20	6.7 ± 2.0	84	384 ± 131	5048	29322	2065.0
3	2.6	2–20	1.1 ± 0.5	15	32 ± 22	600	1554	108.6
4	36.0	1–18	8.8 ± 2.7	100	468 ± 179	8000	412134	18 116.0
5	10.6	1.4–19	2.8 ± 0.8	44	258 ± 62	3120	60396	4489.9
6	9.0	1.8–20	6.6 ± 2.3	40	510 ± 152	2360	20208	1678.7
7	0.8	9–19	0.03 ± 0.02	0.1	4 ± 2	13	36	5.5
8	1.7	2–19	3.6 ± 1.1	39	249 ± 78	3018	7566	614.2
In total	69.7	1–20					**531465**	**27112.6**

Note: 1 – southwestern Peter the Great Bay (2007); 2 – the Posyet Bay (2015–2016); 3 – the Boisman Bay (2014) and Baklan Bay (2016); 4 – the Amur Bay (2009, 2016); 5 – the Empress Eugénie Archipelago water area (2016–2017); 6 – the Ussuri Bay (2018); 7 – the Putyatin Island water area (2007); 8 – eastern Peter the Great Bay (2012).

Settlement structure. In our samples, *M. kurilensis* shell length varied 5 to 163 mm, and the individual weight varied 0.03 to 330 g (Table 3). In southwestern Peter the Great Bay, the maximum mean lengths of mollusc were recorded, and the ratio of non-commercial stock (individuals with a shell length of < 100 mm) was of 47.5 % (Table 4). In other horsemussel settlements, the ratio of non-commercial stock exceeded 72.7 %, which affected the mean shell length: it varied 69.0 to 82.5 mm (Table 3).

The mean individual size of commercial mussels varied as follows: shell length – from 110.3 mm (the Amur Bay) to 125.1 mm (Ussuri Bay), individual weight – from 160 g (the Posyet Bay and the Empress Eugénie Archipelago water area) to 241 g (the Ussuri Bay) (Table 3).

In different areas of Peter the Great Bay, *M. kurilensis* settlement structure differs. Over the research period, the ratio of juveniles of < 30 mm varied from 2.5 % (southwestern Peter the Great Bay) to 28.0 % (the Posyet Bay) (Table 4). In the Ussuri Bay, juveniles of < 50 mm were not registered. It might have been due to the timing of the research: it was carried out October to November 2018, while in other areas – from the second half of July to the early September. In different areas of Peter the Great Bay, the index of settling (IS) varied 0.03 to 0.42 (Table 3). The ratio of pre-reproductive juveniles in all areas, except for the Ussuri Bay, varied 2.5 to 7.5 %, and the index of maturation (IM) varied 0.03 to 0.11 (Tables 3, 4). The ratio of adult molluscs (with a shell length of > 50 mm) in all settlements was significant: from 67.4 % in the Posyet Bay to 100 % in the Ussuri Bay.

Table 3. *M. kurilensis* indicators, as well as indices of settling (IS), maturation (IM), and replenishment of the commercial stock (IRC) of horsemussel settlements (in brackets, ranges of values are given)

Locality and year	All molluscs		Molluscs of commercial length		IS	IM	IRC
	Mean shell length, mm	Mean individual weight, g	Mean shell length, mm	Mean individual weight, g			
1	101.1 ± 4.1 (27–163)	145 ± 12 (3–330)	119.5 ± 3.5 (100–163)	199 ± 14 (120–330)	0.03	0.03	0.19
2	69.0 ± 2.5 (5–133)	70 ± 4 (0.03–304)	111.5 ± 1.1 (100–133)	160 ± 6 (94–304)	0.42	0.05	0.30
3	72.2 ± 3.3 (11–131)	76 ± 6 (0.3–302)	110.3 ± 1.5 (100–131)	162 ± 8 (100–302)	0.29	0.06	0.13
4	80.3 ± 1.5 (10–137)	82 ± 3 (0.1–321)	111.5 ± 0.9 (100–137)	160 ± 5 (70–321)	0.09	0.06	0.30
5	82.5 ± 2.5 (59–143)	89 ± 9 (31–311)	125.1 ± 2.5 (120–143)	241 ± 16 (173–311)	0	0	0.11
6	73.6 ± 4.6 (20–123)	76 ± 10 (1–270)	115.9 ± 1.7 (105–123)	198 ± 13 (118–270)	0.27	0.11	0.25

Note: 1 – southwestern Peter the Great Bay (2007); 2 – the Posyet Bay (2015); 3 – the Amur Bay (2016); 4 – the Empress Eugénie Archipelago water area (2017); 5 – the Ussuri Bay (2018); 6 – eastern Peter the Great Bay (2012).

Table 4. Ratio of size groups in *M. kurilensis* settlements (frequency of occurrence, %)

Locality (year of research)	Shell length, mm					
	1–30	35–50	> 50	95–100	> 100	< 100
Southwestern Peter the Great Bay (2007)	2.5	2.5	95.0	10.0	52.5	47.5
Posyet Bay (2015)	28.0	3.4	67.4	6.8	22.9	77.1
Amur Bay (2016)	20.9	4.5	72.7	3.6	27.3	72.7
Empress Eugénie Archipelago area (2017)	7.9	5.7	83.2	7.3	24.4	75.6
Ussuri Bay (2018)	0	0	100.0	1.6	14.5	85.5
Eastern Peter the Great Bay (2012)	18.9	7.5	69.8	5.6	22.7	77.3

Note. Shell length: 1–30 mm – spat and yearlings; 35–50 mm – pre-reproductive molluscs; > 50 mm – adults; 95–100 mm – recruits; > 100 mm – molluscs of commercial length; < 100 mm – molluscs of non-commercial length.

The ratio of individuals of the commercial length varied 14.5 % in the Ussuri Bay to 52.5 % in southwestern Peter the Great Bay [(27.4 ± 5.3) % on average in the bay] (Table 4). Taking into account these values and horsemussel total abundance in Peter the Great Bay (Table 2), it can be concluded that the abundance of molluscs of the commercial length is of 145.6 million ind. Considering the minimum mean weight of horsemussel of the commercial length [(112.5 ± 14.2) g], calculated based on the total abundance of analyzed individuals in the surveyed aggregations, the commercial stock was of (16.4 ± 2.0) thousand tons.

The ratio of recruits in *M. kurilensis* settlements varied 1.6 % in the Ussuri Bay to 10.0 % in southwestern Peter the Great Bay (Table 4). The index of replenishment of the commercial stock (ICR) varied 0.11 to 0.30 (Table 3). Its highest value was recorded in 2015 in the Posyet Bay and in 2017 in the Empress Eugénie Archipelago water area, and the lowest one was registered in the Ussuri Bay in 2018. The mean ICR value in the Peter the Great Bay for different years was of (0.21 ± 0.03). Thus, the annual replenishment of the commercial stock of *M. kurilensis* in Peter the Great Bay can reach 3.4 thousand tons (21 % of the commercial stock of 16.4 thousand tons).

The study of *M. kurilensis* settlement structure in certain areas of Peter the Great Bay in different years showed as follows: despite several differences, the ratio of the non-commercial stock exceeds 70 % of the total abundance of horsemussel in almost all settlements (Table 4). The replenishment of the benthic part of a mollusc population occurs regularly over many years resulting from pelagic larvae settling in bottom settlements of adults (mainly *M. kurilensis* and *C. grayanus*) on their byssus filaments (Selin, 2018a, b ; Lindenbaum et al., 2008 ; Tsuchiya, 2002).

According to the literature data, the individual fecundity of *M. kurilensis* is about 1–2 million eggs (Mikulich & Rodin, 1963), which is significantly lower than that of *C. grayanus* [15–20 million eggs (Markovskaya, 1952)]. Reproductive maturation and spawning period of the mollusc in Peter the Great Bay vary depending on environmental conditions. In plankton, larvae are found June to October, at a seawater temperature of +17…+22 °C. When reaching a size of 300 μm, larvae settle on the shells of adult mytilids, fixing with byssus filaments; there, their further growth takes place (Evseev & Kolotukhina, 2008 ; Selin, 2018a).

In southwestern Peter the Great Bay, *M. kurilensis* pelagic larvae were recorded in August (Kolotukhina et al., 2015), and in the Posyet Bay – June to September, with a density of 70–250 ind.·m^{-3} in different years (Radovets & Khristoforova, 2008). In the Amur Bay, they were found June to September, with a maximum density in July (in the upper bay area – 865 ind.·m^{-3}; in the open bay area – 825 ind.·m^{-3}) (Kulikova et al., 2014). In the upper Ussuri Bay area, *M. kurilensis* pelagic larvae were registered July to October, with a maximum density in October (210 ind.·m^{-3}); in the open bay area, they were noted August to October, with a low density (Kulikova et al., 2013). In the Vostok Bay, pelagic larvae were recorded August to September, with the maximum concentration in early August (703 ind.·m^{-3}) (Radovets & Khristoforova, 2008).

The presence of juveniles (shell length up to 30 mm) in horsemussel settlements can indicate the intensity of larvae settling in the previous year. Over the research period, the lowest settling intensity was recorded in 2017 in the Ussuri Bay and in 2006 in southwestern Peter the Great Bay, while the highest settling intensity was registered in 2014 in the Posyet Bay (Table 4). Thereunder, in different years and areas, the index of settling (IS) of *M. kurilensis* juveniles varied considerably (Table 3), averaging (0.18 ± 0.07). In *C. grayanus* populations under similar conditions, the mean IS value (Sedova & Sokolenko, 2019b) was more than 3 times higher, which is likely to result from a higher density of *C. grayanus* populations.

When horsemussel larvae settle in *C. grayanus* druses or mixed druses, horsemussel juveniles often die since they cannot compete with molluscs of the upper druse layer and with *C. grayanus* juveniles (Kutishchev & Gogolev, 1983). The survival rate of settled juveniles is affected not only by their positions in the druse, which ensures a proper filtering activity of molluscs, but by the level of the substrate siltation and hydrodynamic and hydrological conditions (Avdeeva-Markovskaya, 1979 ; Vigman, 1983 ; Selin, 2018a). Moreover, mollusc juveniles can be devoured by various predators: starfish, crustaceans, and fish. Individuals with a shell length of 62–130 mm predominate in the lower druse layer, whereas settled juveniles are concentrated in the central layer, which protects them from predators and promotes survival (Selin, 2018a, b ; Dinesen & Morton, 2014 ; Lindenbaum et al., 2008).

Over the research period, the highest value of the index of maturation (IM) was registered for *M. kurilensis* settlement in eastern Peter the Great Bay (Table 3). This indicates as follows: within 3–4 years *prior* to IM calculation, the most favorable conditions for the successful growth of juveniles were formed in this area. The mean value for *M. kurilensis* in Peter the Great Bay was of (0.05 ± 0.01). In the same years, the mean value of IM in *C. grayanus* settlements was of (0.25 ± 0.05) (Sedova & Sokolenko, 2019b), which is 5 times higher than in *M. kurilensis* settlements and results from the lower survival rate of *M. kurilensis* juveniles.

For Peter the Great Bay, the ratio of the commercial stock of *M. kurilensis* settlements was of (27.4 ± 5.3) % (Table 4); for *C. grayanus* settlements, it was of (34.0 ± 4.8) % in the same period (Sedova & Sokolenko, 2019b). The mean value of the replenishment of the commercial stock of *M. kurilensis*, equal to (0.21 ± 0.03), was almost at the same level as the value for *C. grayanus* settlements – (0.17 ± 0.04) (Sedova & Sokolenko, 2019b). As noted above, the annual replenishment of the commercial stock of *M. kurilensis* in Peter the Great Bay is possible in a volume of more than 3 thousand tons. However, neither commercial nor natural mortality of molluscs is taken into account (which can result from unfavorable abiotic conditions and anthropogenic load), though they may make their own adjustments. For comparison, the data on the possible annual replenishment of the commercial stock of *C. grayanus* in Peter the Great Bay is presented. With the current state of the commercial stock (32.6 thousand tons), it is estimated at 5 thousand tons (Sedova & Sokolenko, 2019b).

Conclusion. The state of *M. kurilensis* population in Peter the Great Bay in 2007–2018 was stable. In most settlements, the ratio of individuals of non-commercial length varied 52.5 to 85.5 %, which indicates the ongoing processes of active natural reproduction and regular replenishment of the benthic part over many years.

Replenishment of *M. kurilensis* settlements with settling juveniles depends on the presence of pelagic larvae in the plankton, while replenishment of the mature part depends on favorable conditions for juvenile survival. In 2007–2018, the mean values of the indices of settling and maturation in *M. kurilensis* settlements in Peter the Great Bay were of (0.18 ± 0.07) and (0.05 ± 0.01), respectively.

M. kurilensis resources are estimated at 27.1 thousand tons, and the commercial stock – at 16.4 thousand tons. The annual replenishment of the commercial stock of *M. kurilensis* settlements in Peter the Great Bay is possible in a volume of more than 3 thousand tons. The mean value of the index of the commercial stock replenishment is of (0.21 ± 0.03).

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РЕСУРСЫ И СОСТАВ ПОСЕЛЕНИЙ МОДИОЛУСА КУРИЛЬСКОГО *MODIOLUS KURILENSIS* В ЗАЛИВЕ ПЕТРА ВЕЛИКОГО (ЯПОНСКОЕ МОРЕ)

Л. Г. Седова, Д. А. Соколенко

Тихоокеанский филиал ФГБНУ «Всероссийский научно-исследовательский институт рыбного хозяйства и океанографии», Владивосток, Российская Федерация
E-mail: *ludmila.sedova@tinro-center.ru*

Модиолус курильский *Modiolus kurilensis* F. R. Bernard, 1983 (Mollusca, Bivalvia) — двустворчатый моллюск семейства Mytilidae; он встречается в заливе Петра Великого (Японское море) на мягких и твёрдых субстратах, зачастую совместно с мидией Грея *Crenomytilus grayanus* (Dunker, 1853), и является перспективным промысловым видом. Его добывают в качестве прилова при добыче *C. grayanus*. Цель работы — оценить ресурсы и состав поселений *M. kurilensis* в заливе Петра Великого. Исследования проводили в 2007–2018 гг. с применением стандартных водолазных гидробиологических методов, изучая глуби́ны до 20 м. Выполнено 2409 станций, модиолус обнаружен на 308 из них. Собранных моллюсков измеряли и взвешивали. В результате статистической и картографической обработки материала получены усреднённые данные о плотности и биомассе поселений *M. kurilensis*. Для изучения состава поселений модиолуса проанализировано 870 экз. Определяли следующие параметры: показатель оседания молоди (отношение численности молоди размером 1–30 мм (сеголетки, годовики) к числу взрослых особей с длиной раковины более 50 мм); показатель созревания (отношение численности молодых моллюсков препрепродуктивного возраста (35–50 мм) к числу взрослых особей с длиной раковины более 50 мм); пополнение промысловой части поселений (отношение рекрутов (95–100 мм) к числу особей промыслового размера с длиной раковины > 100 мм). Состояние популяции *M. kurilensis* в заливе Петра Великого стабильно: доля особей непромыслового размера в разных поселениях варьирует от 52 до 86 %, что свидетельствует об активном естественном воспроизводстве и регулярном пополнении бентосной части популяции на протяжении многих лет. Пополнение поселений оседающей молодью зависит от наличия пелагических личинок в планктоне, а их половозрелой части — от благоприятных условий для выживания молоди. Средние значения показателей оседания и созревания в поселениях *M. kurilensis* в заливе Петра Великого в 2007–2018 гг. составляли (0,18 ± 0,07) и (0,05 ± 0,01) соответственно. Ресурсы *M. kurilensis* оценены в 27,1 тыс. т, а промысловый запас — в 16,4 тыс. т. Ежегодное пополнение промысловой части поселений *M. kurilensis* в заливе Петра Великого возможно в объёме более 3 тыс. т. Среднее значение показателя пополнения промысловой части — (0,21 ± 0,03).

Ключевые слова: модиолус курильский, *Modiolus kurilensis*, ресурсы, промысловый запас, состав поселений, пополнение, залив Петра Великого, Японское море

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COMPARATIVE CHARACTERISTICS OF THE ULTRASTRUCTURE OF NEPHRON CELLS IN SOME SPECIES OF PELAGIC, EPIBENTHIC, AND DEMERSAL FISH (THE KARANTINNAYA BAY, THE BLACK SEA)

© 2021 **E. A. Flerova**[1] **and G. M. Chuyko**[2]

[1]Yaroslavl Scientific Research Institute of Livestock Breeding and Forage Production – Federal Williams Research Center of Forage Production and Agroecology, Mikhailovsky, Russian Federation
[2]Papanin Institute for Biology of Inland Waters Russian Academy of Sciences, Borok, Russian Federation
E-mail: *katarinum@mail.ru*

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The ultrastructure of the main sections of the mesonephros nephron in Black Sea teleost fish is studied. The species investigated are as follows: pelagic *Trachurus mediterraneus* (Steindachner, 1868) and *Chelon auratus* (Risso, 1810); epibenthic *Diplodus annularis* (Linnaeus, 1758) and *Spicara flexuosa* Rafinesque, 1810; and demersal *Scorpaena porcus* Linnaeus, 1758, *Gobius niger* Linnaeus, 1758, and *Mullus barbatus ponticus* Essipov, 1927. It is shown that in Black Sea fish, which inhabit different depths and are under different conditions of environmental osmotic pressure, nephrons at the tissue level of organization have a single structure and form glomerular kidneys. Fish adaptability to the habitat at certain depths is primarily manifested in an increase in the number and size of mitochondria of all types of nephron epithelial cells. A decrease in the renal corpuscles area, the length of podocytes, and height of tubular epithelial cells, as well as the brush border length of type I proximal tubules is also recorded. Nephron cytological peculiarities of pelagic, epibenthic, and demersal fish characterize a high adaptive capacity of the mesonephros cellular structures.

Keywords: teleost fish, pelagic fish, epibenthic fish, demersal fish, kidney, nephron, ultrastructure, Black Sea

Determining the mechanisms of fish adaptation to diverse biotic and abiotic factors does not seem possible without a comprehensive study of the structure of various organs, tissues, and especially cells. Fish kidneys serve as a leading effector component of the physiological system of water-salt metabolism, due to which fish have acquired a certain habitat independence and inhabited both seawater and freshwater (Natochin, 1976, 2002 ; Wood et al., 2020). As known, the structure and function of the kidneys of freshwater and marine fish are determined by the peculiarities of their phylogenetic development and ecology. Freshwater teleost fish have a well-developed glomerular kidney, that excretes excess water and reabsorbs filtered ions. On the contrary, marine teleost fish have to save water and excrete excess salts; therefore, glomeruli are reduced in the kidneys of several species, up to their complete disappearance (Natochin, 1976, 2002 ; Erisson & Olsen, 1968 ; Ericsson & Olsen, 1970 ; Marshall, 1930).

Currently, special attention is given to the study of fish adaptations to a complex of environmental factors at the cellular level, since fish evolution is closely related to a high degree of specialization and adaptive plasticity of this level of organization of living matter. To develop a general pattern of kidneys functioning of teleost fish inhabiting water of various salinity, information is required on peculiarities of fine structures forming the nephron. Unfortunately, works focused on the study of ultrastructure of marine fish kidneys are still fragmentary. There is no data on the correlation between the nephron fine structure and the lifestyle of marine fish inhabiting different depths within the same water area characterized by different hydrochemical indicators, *inter alia* salinity (Kuftarkova et al., 2008). The present work is aimed at revealing common and specific features of the submicroscopic structure of the nephron in pelagic, epibenthic, and demersal teleost fish of the Black Sea.

MATERIAL AND METHODS

The ultrastructure of the mesonephros nephrons was studied in 7 species of Black Sea teleost fish. Pelagic species investigated are Mediterranean horse mackerel *Trachurus mediterraneus* (Steindachner, 1868) (7 ind., (10.1 ± 0.20) cm, (1.6 ± 0.80) g) and golden grey mullet *Chelon auratus* (Risso, 1810) (5 ind., (15.4 ± 7.7) cm, (49.0 ± 7.26) g). Epibenthic species are annular sea bream *Diplodus annularis* (Linnaeus, 1758) (10 ind., (5.60 ± 0.20) cm, (5.90 ± 0.50) g) and picarel *Spicara flexuosa* Rafinesque, 1810 (17 ind., (9.95 ± 0.19) cm, (18.3 ± 1.17) g). Demersal species are black scorpionfish *Scorpaena porcus* Linnaeus, 1758 (10 ind., (11.9 ± 0.46) cm, (67.4 ± 7.56) g), black goby *Gobius niger* Linnaeus, 1758 (3 ind., (8.70 ± 0.31) cm, (18.2 ± 0.92) g), and red mullet *Mullus barbatus ponticus* Essipov, 1927 (12 ind., (12.2 ± 0.44) cm, (62.6 ± 7.17) g).

Samples were taken in the summer-autumn period in the Karantinnaya Bay (the Black Sea, Sevastopol), which is characterized by the difference in temperature and salinity between surface and bottom. The temperature difference reaches 13.39 °C in summer. During this period, an inflow to the bottom layer of cooled and more saline (18.24 ‰) deep water with a reduced dissolved oxygen content (89 %) and pH value of 8.15 is clearly observed, while in the surface layer, salinity value averages 17.12 ‰, dissolved oxygen content – 96 %, and pH value – 8.24 (Kuftarkova et al., 2008).

Fish were caught with traps and transported to the laboratory to determine their size and weight characteristics. Then, kidneys were removed, and kidney pieces were dissected with a scalpel from the middle area of the mesonephros for electron microscopy. Samples were fixed in 2.5 % glutaraldehyde in 0.1 M phosphate buffer and treated by an electron microscopy standard technique (Timakova et al., 2014). Ultrathin sections were prepared using a Leica EM UC7 microtome, contrasted with uranyl acetate and lead citrate, and examined under a JEM-1011 electron microscope. Measurements were carried out by digital photographs; data obtained were statistically processed using Microsoft Excel and Statistica 10 software.

During statistical processing, mean values and their standard errors ($M \pm m$) were calculated. The data analysis on outliers was performed *prior* to statistical analysis. Compliance with the normal distribution was assessed by the Shapiro – Wilk test (W). To determine the statistical significance of the difference in sample mean values, the Student's t-test was used. To assess the difference in sample mean values, multiple pairwise post hoc comparisons were performed, by the least significant difference test (LSD-test). If the distribution deviated from the normal, the Kruskal – Wallis test was used. In this case, the difference in sample mean values was assessed by multiple pairwise post hoc comparisons by the Dunnett's test. As a critical significance level, $p \leq 0.05$ was taken.

RESULTS

The renal corpuscle is the beginning of the nephron in all the species studied and is built according to a single principle. The wall of the renal corpuscle consists of two layers, parietal and visceral, very tightly contiguous to each other. Between the layers, there is a cavity, 2.03–2.45 μm thick (Fig. 1a, Table 1). The outer layer of the capsule is formed by a single-layer squamous epithelium located on the 0.66–0.77-μm thick basement membrane (Table 1). The inner layer of the capsule is formed by podocytes very tightly contiguous to each other (Fig. 1a). The podocyte body is oval; it is elongated along the nuclear membrane (Fig. 1b). The largest cells were identified on sections of renal corpuscles in pelagic species, *T. mediterraneus* and *Ch. auratus*. The length of T. *mediterraneus* podocytes significantly exceeds this indicator in epibenthic and demersal fish, while the length of *Ch. auratus* podocytes significantly exceeds this indicator in epibenthic *D. annularis*. The podocyte nucleus is rounded and occupies most of the cells; the length of the nuclei varies 2.82 to 4.34 μm, and the width varies 1.41 to 2.15 μm (Table 1). Heterochromatin is clumpy; it is concentrated mainly on the nucleus periphery. Dense cytoplasm of most cells contains two large mitochondria (Fig. 1b). On sections of renal corpuscles, a small number of capillary loops is observed (Fig. 1a).

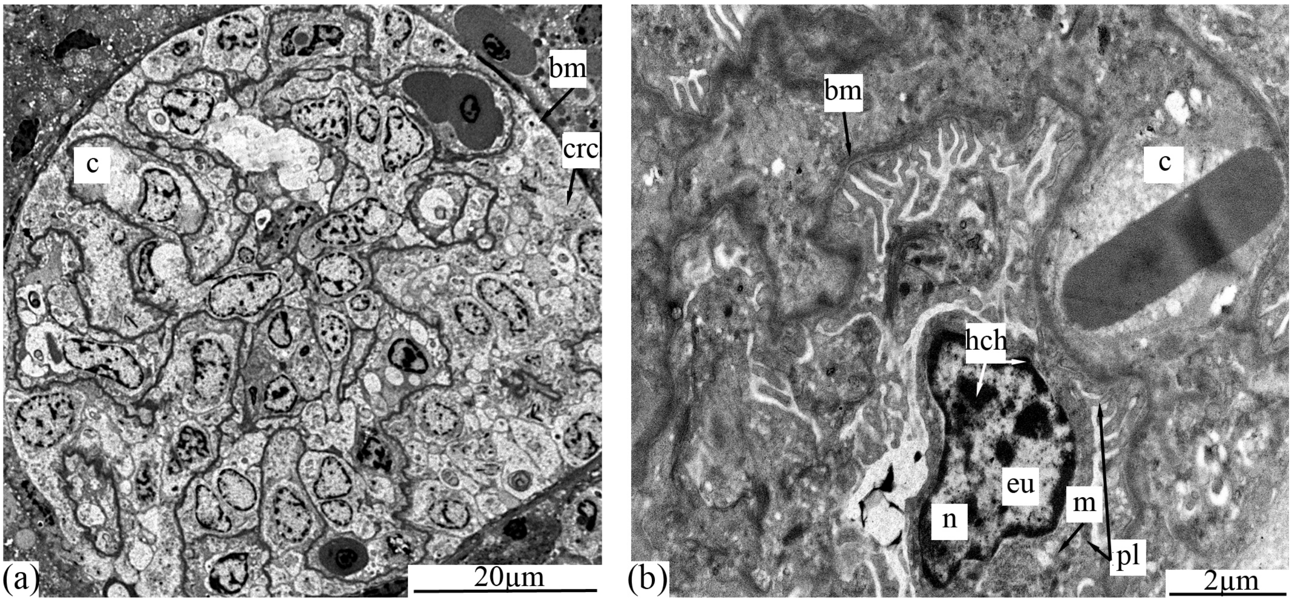

Fig. 1. Ultrastructure of the nephron: a – renal corpuscle in *Scorpaena porcus*; b – podocyte of the renal corpuscle in *Spicara flexuosa*. Bm – basement membrane of the parietal layer; hch – heterochromatin; c – capillary; m – mitochondrion; pf – podocyte feet; crc – cavity of renal corpuscle; eu – euchromatin; n – nucleus

The proximal tubule epithelial cells are built according to the plan typical for the cells of this nephron area (Figs 2a, 3a). They differ from the distal tubule cells by the presence of a brush border, which is the tallest in the initial area and gradually decreases as approaching the distal tubule epithelial cells.

Analysis of the ultrastructure of the cells lining this area of the tubule showed as follows: epithelial cells can be divided into 2 types (Figs 2a, 3a).

Table 1. Morphometric indicators of the renal corpuscle structures, μm

Species	Renal corpuscle diameter, *n* = 10	Renal corpuscle cavity, *n* = 10	Basement membrane thickness, *n* = 20	Podocyte	
				Cell, *n* = 10	Nucleus, *n* = 20
Trachurus mediterraneus	49.2 ± 3.60	2.08 ± 0.10	0.77 ± 0.05	$5.09 \pm 0.24^{1,2,3,4} \times 2.97 \pm 0.40$	4.34 ± 0.32 × 2.15 ± 0.30
Chelon auratus	$49.0 \pm 0.41^{1,2,3,4,5}$	2.16 ± 0.07	0.73 ± 0.07	$4.76 \pm 0.34^{5} \times 2.86 \pm 0.19$	3.60 ± 0.16 × 2.07 ± 0.21
Diplodus annularis	47.4 ± 0.48^{1}	2.03 ± 0.09	0.71 ± 0.05	$4.65 \pm 0.09^{5} \times 2.34 \pm 0.27$	2.77 ± 0.26 × 1.41 ± 0.21
Spicara flexuosa	47.1 ± 0.66^{2}	2.08 ± 0.11	0.66 ± 0.06	$3.59 \pm 0.14^{1} \times 2.72 \pm 0.25$	2.82 ± 0.33 × 1.92 ± 0.12
Gobius niger	47.0 ± 0.35^{3}	2.45 ± 0.22	0.67 ± 0.02	$4.19 \pm 0.34^{2} \times 2.49 \pm 0.29$	3.11 ± 0.44 × 1.56 ± 0.24
Mullus barbatus ponticus	46.3 ± 0.17^{4}	2.42 ± 0.16	0.69 ± 0.01	$4.42 \pm 0.37^{3} \times 2.40 \pm 0.25$	3.30 ± 0.41 × 1.57 ± 0.20
Scorpaena porcus	46.9 ± 0.82^{5}	2.33 ± 0.23	0.66 ± 0.03	$4.12 \pm 0.42^{4} \times 2.58 \pm 0.37$	3.11 ± 0.36 × 1.81 ± 0.28

Note: hereinafter in the tables, the same numerical indices in different columns denote statistically significant differences between indicators, $p \leq 0.05$.

Type I epithelial cells form the beginning of the proximal tubule. These are elongated, pyramidal cells tightly contiguous to each other (Fig. 2a). The tallest epithelial cells were identified in pelagic species (*Ch. auratus*), and the shortest ones were recorded in demersal species (*S. porcus*). As revealed, the cells in *T. mediterraneus* and *Ch. auratus* are significantly longer than cells in other species studied (Table 2). The nuclei of epithelial cells are rounded; nuclei sizes differ insignificantly between the species (Table 2). The nuclei are located in the basal part of cells; there is little heterochromatin, and it is located mainly along the nuclear membrane, between nuclear pores (Fig. 1a). The cytoplasm contains a large number of large mitochondria located along the longitudinal axis of the cells (Fig. 2b). As established, the number and size of mitochondria on sections of epithelial cells increase in the series pelagic – epibenthic – demersal fish. Differences in the number and size of mitochondria between pelagic and demersal fish are significant (Table 2). Mitochondria in *D. annularis*, having an epibenthic lifestyle, are statistically significantly larger than those in demersal species, *G. niger* and *M. barbatus ponticus* (Table 2). Forming complex weaves, numerous folds of the smooth endoplasmic reticulum stretch from the basal part along the cells (Fig. 2b). In the basal part of cells, electron-transparent vesicles were revealed (Fig. 2b). In the apical part of cells, large electron-dense secretory granules were found, typical for this nephron area (Fig. 2a). The number of secretory granules varied insignificantly (Table 2). No correlation was revealed between the size of secretory granules and the lifestyle of the species studied. The largest granules were found on cell sections of *G. niger*, while the smallest secretory granules were recorded on cell sections of *M. barbatus ponticus* (Table 2). A well-developed endocytosis zone is located in the apical part of cells, at the edge of the brush border; it reaches the greatest length in *S. flexuosa*, while the lowest one – in *M. barbatus ponticus* (Table 2). This zone is characterized by the presence of a well-developed tubulovesicular system, which is formed by a large number of vesicles and single segments of tubular reticulum localized along the longitudinal axis of the cell (Fig. 2c).

Table 2. Morphometric indicators of type I epithelial cells of the proximal tubule, μm

Indicator	*Trachurus mediterraneus*	*Chelon auratus*	*Diplodus annularis*	*Spicara flexuosa*	*Gobius niger*	*Mullus barbatus ponticus*	*Scorpaena porcus*
Cell, $n = 10$	$13.4 \pm 0.51^{1,2,3,4,5} \times 10.5 \pm 0.70$	$13.8 \pm 0.62^{6,7,8,9,10} \times 9.15 \pm 0.44$	$12.5 \pm 0.38^{1,6} \times 9.57 \pm 0.42$	$12.0 \pm 0.20^{2,7} \times 9.57 \pm 0.30$	$11.7 \pm 0.29^{3,8} \times 9.32 \pm 0.28$	$11.3 \pm 0.18^{4,9} \times 8.40 \pm 0.88$	$11.0 \pm 0.39^{5,10} \times 9.04 \pm 0.62$
Nucleus, $n = 20$	5.92 ± 0.38 × 4.40 ± 0.39	4.27 ± 0.20 × 3.86 ± 0.24	5.71 ± 0.12 × 4.02 ± 0.26	4.78 ± 0.42 × 3.45 ± 0.31	5.45 ± 0.22 × 4.80 ± 0.28	4.13 ± 0.11 × 3.74 ± 0.18	4.99 ± 0.30 × 3.53 ± 0.41
Mitochondrion, $n = 20$	$1.15 \pm 0.16 \times 0.59 \pm 0.04^{1,2,3,4}$	$1.02 \pm 0.08 \times 0.65 \pm 0.06^{5,6,7,8}$	$1.36 \pm 0.15 \times 0.79 \pm 0.05^{9,10}$	$1.82 \pm 0.62 \times 1.12 \pm 0.19^{1,5}$	$2.00 \pm 0.18 \times 1.26 \pm 0.11^{2,6,9}$	$2.10 \pm 0.21 \times 1.26 \pm 0.14^{3,7,10}$	$1.93 \pm 0.23 \times 1.49 \pm 0.14^{4,8}$
Number of mitochondria on cell section, $n = 20$	$48.7 \pm 7.28^{1,2}$	$45.3 \pm 3.48^{3,4}$	57.5 ± 3.19	52.0 ± 8.04	63.7 ± 4.83	$74.6 \pm 2.66^{1,3}$	$73.2 \pm 3.75^{2,4}$
Secretory granule, $n = 20$	1.58 ± 0.13 × 1.35 ± 0.13	0.68 ± 0.06 × 0.59 ± 0.10	1.17 ± 0.07 × 0.93 ± 0.06	1.08 ± 0.20 × 0.99 ± 0.18	1.65 ± 0.07 × 1.47 ± 0.13	0.63 ± 0.03 × 0.52 ± 0.05	1.04 ± 0.05 × 0.95 ± 0.05
Number of secretory granules on cell section, $n = 20$	4.00 ± 0.45	4.00 ± 0.50	5.25 ± 1.31	5.29 ± 1.31	4.00 ± 0.49	3.20 ± 0.20	3.75 ± 0.68
Endocytosis zone, $n = 20$	3.81 ± 0.79	3.41 ± 0.21	3.25 ± 0.40	5.07 ± 0.25	4.65 ± 0.34	2.84 ± 0.32	4.64 ± 0.31
Brush border length, $n = 20$	$2.87 \pm 0.31^{1,2,3,4,5}$	2.69 ± 0.12	2.35 ± 0.14^{1}	1.99 ± 0.21^{2}	2.10 ± 0.18^{3}	1.95 ± 0.16^{4}	2.14 ± 0.12^{5}
Cilia, $n = 20$	0.23 ± 0.00	0.24 ± 0.00	0.22 ± 0.00	0.24 ± 0.00	0.23 ± 0.00	0.24 ± 0.00	0.24 ± 0.01
Microvilli, $n = 20$	0.32 ± 0.04	0.26 ± 0.01	0.40 ± 0.01	0.23 ± 0.03	0.31 ± 0.03	0.24 ± 0.02	0.23 ± 0.01

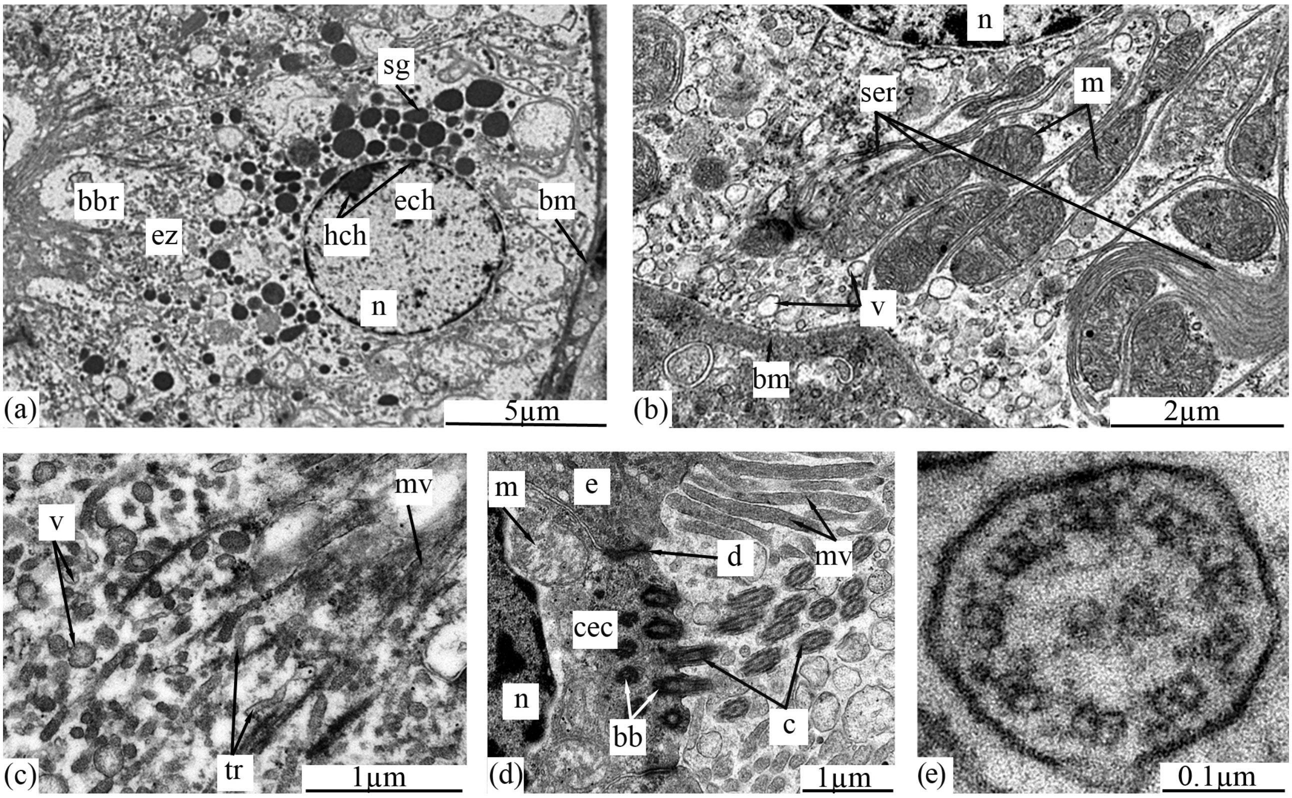

Fig. 2. Ultrastructure of type I proximal tubule epithelial cells: a – fragment of the proximal tubule with type I epithelial cells in *Chelon auratus*; b – basal part of type I epithelial cell in *Gobius niger*; c – endocytosis zone of *Mullus barbatus ponticus*; d – apical part of ciliated epithelial cell in *Diplodus annularis*; e – cross section of the cilium in *Diplodus annularis*. Bm – basement membrane; bb – basal body; v – vesicle; hch – heterochromatin; ser – smooth endoplasmic reticulum; d – desmosome; ez – endocytosis zone; m – mitochondrion; mv – microvilli; c – cilia; cec – ciliated epithelial cell; sg – secretory granules; bbr – brush border; tr – tubular reticulum; e – type I epithelial cell; ech – euchromatin; n – nucleus

The brush border is the tallest in the proximal tubules in pelagic fish: its length in *T. mediterraneus* is significantly larger than in epibenthic and demersal fish (Table 2). The brush border consists of a large number of cilia and microvilli facing the tubule lumen (Fig. 2d). As shown, the microvilli thickness differs in the species studied; thus, the indicator in *T. mediterraneus* significantly differs from that in *D. annularis*, *S. flexuosa*, and *S. porcus*. No correlation was revealed between the microvilli thickness and the lifestyle of the species (Table 2). Cilia are outgrowths of ciliated epithelial cells, which form the proximal tubule (Fig. 2d). The structure of ciliated epithelial cells is somewhat different from that of epithelial cells carrying microvilli on apical surface. The cytoplasm of ciliated cells is lighter, and there is no endocytosis zone; in the apical part of cells, large mitochondria are found located above cilia basal bodies (Fig. 2d). The structure of cilia is typical for these organelles, and they are formed by an axoneme; at the base of the cilium, there is a basal body (Fig. 2e).

Type II epithelial cells are structurally similar to type I cells, but are shorter (Fig. 3a, Table 3).

The shortest epithelial cells were recorded in the nephrons in *Ch. auratus*, and the tallest – in the nephrons in *S. porcus* (Table 3). Epithelial cells in *T. mediterraneus* were found to be significantly taller than those in *G. niger*, *M. barbatus ponticus*, and *S. porcus*. Epithelial cells in *Ch. auratus* were significantly taller than those in *T. mediterraneus* and in all epibenthic and demersal species studied (Table 3). The nuclei of epithelial cells are rounded, and they are located in the central area of the cells; nuclei sizes differ insignificantly between the species studied (Table 3, Fig. 3a). There is little heterochromatin,

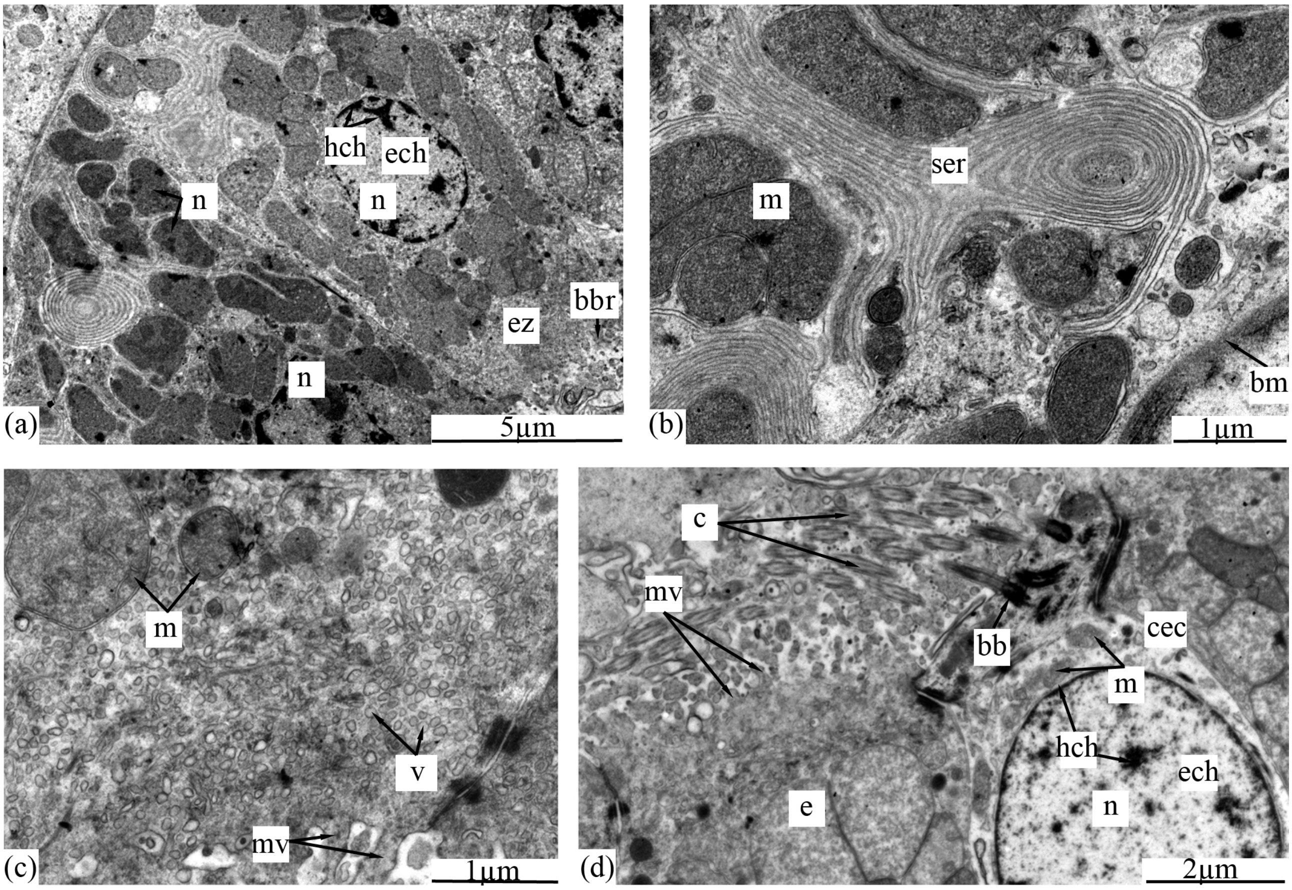

Fig. 3. Ultrastructure of type II proximal tubule epithelial cells: a – fragment of the proximal tubule with type II epithelial cells in *Mullus barbatus ponticus*; b – basal part of type II epithelial cell in *Gobius niger*; c – endocytosis zone of *Trachurus mediterraneus*; d – apical part of ciliated epithelial cell in *Trachurus mediterraneus*. Bm – basement membrane; bb – basal body; v – vesicle; hch – heterochromatin; ser – smooth endoplasmic reticulum; ez – endocytosis zone; m – mitochondrion; mv – microvilli; c – cilia; cec – ciliated epithelial cell; bbr – brush border; e – epithelial cell of the intermediate tubule; ch – euchromatin; n – nucleus

and it is located mainly along the nuclear membrane, between nuclear pores. The cytoplasm contains a large number of mitochondria; their mean number in type II epithelial cells exceeds that in type I cells. As revealed, the number of mitochondria on sections of epithelial cells in epibenthic and demersal fish significantly exceeds that on sections of epithelial cells in *T. mediterraneus* and *Ch. auratus* (Table 3). For type II epithelial cells, no pattern of changes in the size of mitochondria depending on lifestyle of the species studied was established. The largest mitochondria were registered on sections of *M. barbatus ponticus*, while the smallest ones – on sections of *T. mediterraneus*. The sizes of *S. flexuosa* and *M. barbatus ponticus* mitochondria were shown to significantly exceed those for *T. mediterraneus*. The sizes of *D. annularis* mitochondria significantly exceeded those for *S. flexuosa* and *M. barbatus ponticus* (Table 3). The folds of the smooth endoplasmic reticulum in the basal part of type II epithelial cells occupy a larger area compared to those of type I epithelial cells (Fig. 3b). A characteristic feature of type II epithelial cells is the absence of secretory granules in the cytoplasm (Fig. 3a). The endocytosis zone is less developed than in type I cells (Table 3), although a large number of vesicles are clearly visible (Fig. 3c). The endocytosis zone reaches the highest length values in *S. flexuosa*, and the lowest – in *T. mediterraneus* (Table 3). The brush border is shorter compared to that of type I cells (Table 3); it includes both cilia, which are the formation of ciliated epithelial cells, and microvilli (Fig. 3d). Microvilli of type II cells are wider compared to microvilli of type I cells (Table 3). No correlation was found between the endocytosis zone length, brush border length, and microcilia thickness and the lifestyle of the species studied.

The intermediate tubule epithelial cells were found in the nephron in *Ch. auratus* and *S. porcus* (Fig. 4a, Table 4). The structure of these epithelial cells is the most different from the structure of the cell types considered above. These are the lowest cells, with nuclei in the central part. The epithelial cells of the nephron in *Ch. auratus* are significantly taller than those of the nephron in *S. porcus*. The nuclei structure of these epithelial cells is similar to that of types I and II cells (Fig. 4a).

On cell sections, a less developed, than in type I and II epithelial cells, system of tubules of the smooth endoplasmic reticulum was registered, which surrounds electron-dense mitochondria (Fig. 3b). *S. porcus* mitochondria are larger than those in *Ch. auratus*. The number of mitochondria on cell sections of *S. porcus* is more than 1.5 times higher than that on cell sections of *Ch. auratus*; the differences are significant. There is no formed endocytosis zone. Single microvilli are located on cell apical surface (Fig. 4a). The microvilli length of the intermediate tubule cells is 2 times less than that of the microvilli of types I and II epithelial cells. *Ch. auratus* microvilli are significantly taller than those of *S. porcus* (Table 4). In the intermediate tubule structure, there are no ciliated epithelial cells.

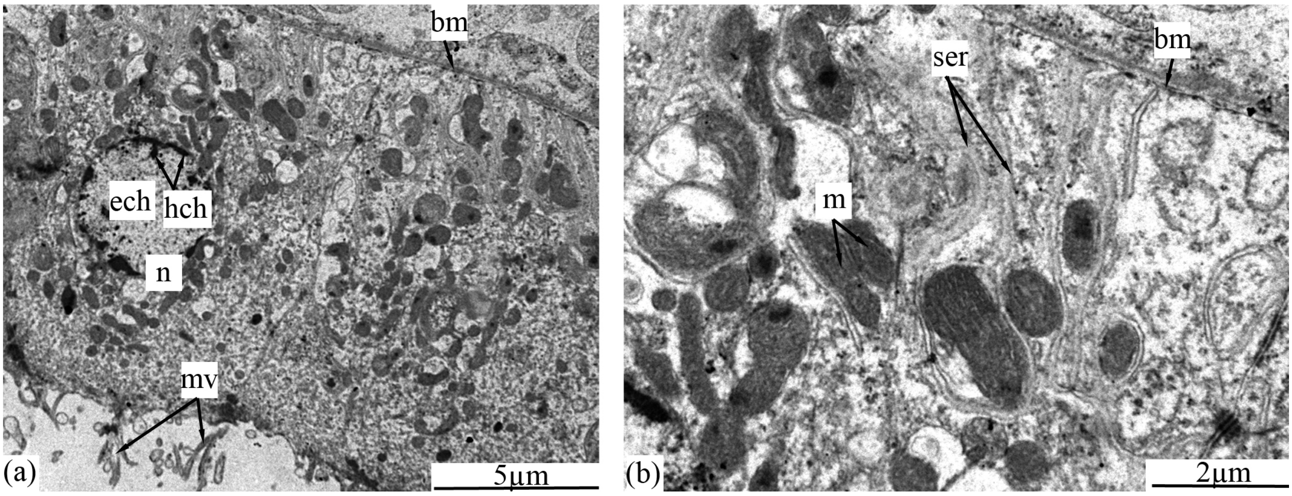

Fig. 4. Ultrastructure of the intermediate tubule epithelial cells: a – fragment of the intermediate tubule in *Chelon auratus*; b – basal part of the intermediate tubule epithelial cell in *Chelon auratus*. Bm – basement membrane; hch – heterochromatin; ser – smooth endoplasmic reticulum; m – mitochondrion; mv – microvilli; ech – euchromatin; n – nucleus

The distal tubule is formed by cells, that are tall and very wide at the base (Fig. 5a, Table 5).

The tallest epithelial cells of this part of the tubule were found in the nephron in *D. annularis*, and the shortest ones – in the nephron in *M. barbatus ponticus*. It was shown as follows: the height of epithelial cells decreases in the series pelagic – epibenthic – demersal fish. When comparing the sizes of epithelial cells in pelagic and demersal fish, it was revealed that the epithelial cells in *T. mediterraneus* were significantly taller than those in *G. niger* and *M. barbatus ponticus*. Epithelial cells in *D. annularis* were significantly taller than those in *G. niger*, *M. barbatus ponticus*, and *S. porcus*. Comparing the sizes of epithelial cells in epibenthic and demersal fish, it was recorded as follows: *Ch. auratus* cells were statistically significantly taller than those of demersal fish, and *S. flexuosa* epithelial cells were significantly taller than those of *M. barbatus ponticus* (Table 5).

Table 3. Morphometric indicators of type II epithelial cells of the proximal tubule, μm

Indicator	*Trachurus mediterraneus*	*Chelon auratus*	*Diplodus annularis*	*Spicara flexuosa*	*Gobius niger*	*Mullus barbatus ponticus*	*Scorpaena porcus*
Cell, *n* = 10	11.2 ± 0.24^{1,2,3,4} × 9.74 ± 1.50	12.8 ± 0.37^{1,5,6,7,8,9} × 9.74 ± 0.19	11.2 ± 0.78^{5} × 7.55 ± 0.61	10.2 ± 1.10^{6} × 7.85 ± 0.60	9.76 ± 0.56^{2,7} × 8.38 ± 0.75	9.55 ± 0.14^{3,8} × 8.46 ± 0.22	9.16 ± 0.18^{4,9} × 7.32 ± 0.42
Nucleus, *n* = 20	4.54 ± 0.24 × 3.29 ± 0.12	4.43 ± 0.05 × 3.70 ± 0.16	3.33 ± 0.12 × 3.01 ± 0.02	4.98 ± 0.43 × 3.94 ± 0.34	4.70 ± 0.16 × 3.56 ± 0.31	4.52 ± 0.13 × 3.45 ± 0.19	5.44 ± 0.21 × 4.99 ± 0.04
Mitochondrion, *n* = 20	1.19 ± 0.21 × 0.73 ± 0.10^{1,2}	1.39 ± 0.10 × 1.19 ± 0.11	1.26 ± 0.21 × 0.83 ± 0.09^{3,4}	1.57 ± 0.07 × 1.17 ± 0.05^{1,3}	1.61 ± 0.13 × 0.80 ± 0.03	1.72 ± 0.21 × 1.23 ± 0.19^{2,4}	2.74 ± 0.74 × 0.89 ± 0.05
Number of mitochondria on cell section, *n* = 20	50.0 ± 3.55^{1,2,3,4,5}	48.0 ± 4.24^{6,7,8,9,10}	75.0 ± 3.77^{1,6}	72.3 ± 0.76^{2,7}	78.7 ± 3.54^{3,8}	76.2 ± 2.29^{4,9}	76.6 ± 1.60^{5,10}
Endocytosis zone, *n* = 20	1.24 ± 0.31^{1,2}	2.01 ± 0.23	1.83 ± 0.18	4.19 ± 0.30^{1}	1.41 ± 0.20	2.01 ± 0.15	2.64 ± 0.12^{2}
Brush border length, *n* = 20	1.58 ± 0.19	1.81 ± 0.27	1.45 ± 0.15	1.96 ± 0.40	1.58 ± 0.22	1.39 ± 0.03	1.57 ± 0.11
Cilia, *n* = 20	0.23 ± 0.00	0.24 ± 0.00	0.22 ± 0.00	0.24 ± 0.00	0.23 ± 0.00	0.24 ± 0.01	0.24 ± 0.00
Microvilli, *n* = 20	0.33 ± 0.02	0.27 ± 0.02	0.45 ± 0.04	0.26 ± 0.03	0.37 ± 0.03	0.27 ± 0.02	0.48 ± 0.02

Table 4. Morphometric indicators of the intermediate tubule epithelial cells, μm

Indicator	*Chelon auratus*	*Scorpaena porcus*
Cell, *n* = 10	11.8 ± 0.26 × 9.32 ± 0.22	9.07 ± 0.22* × 7.50 ± 0.23
Nucleus, *n* = 20	4.97 ± 0.30 × 4.61 ± 0.16	4.96 ± 0.61 × 4.60 ± 0.33
Mitochondrion, *n* = 20	1.20 ± 0.10 × 1.03 ± 0.05	1.54 ± 0.09 × 1.24 ± 0.08*
Number of mitochondria on cell section, *n* = 20	36.6 ± 3.65	63.4 ± 2.77*
Microvilli length, *n* = 20	0.85 ± 0.17	0.50 ± 0.07*
Microvilli, *n* = 20	0.33 ± 0.04	0.29 ± 0.01

Note: * – the differences between the indicators for *Chelon auratus* and *Scorpaena porcus* are statistically significant, $p \leq 0.05$.

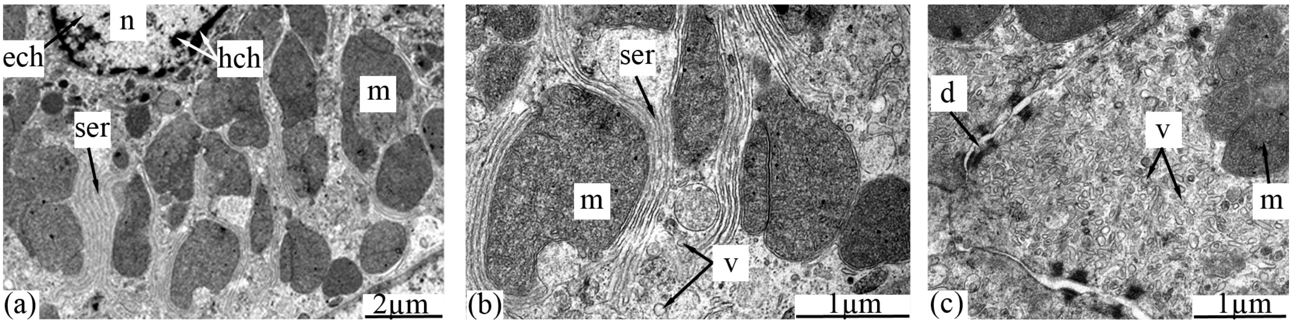

Fig. 5. Ultrastructure of the distal tubule epithelial cells: a – basal part of the distal tubule epithelial cells in *Mullus barbatus ponticus*; b – cytoplasm of the distal tubule epithelial cells in *Mullus barbatus ponticus*; c – lobe-like outgrowths of the distal tubule epithelial cells in *Mullus barbatus ponticus*. V – vesicles; hch – heterochromatin; ser – smooth endoplasmic reticulum; d – desmosome; m – mitochondrion; mv – microvilli; ech – euchromatin; n – nucleus

Table 5. Morphometric indicators of the distal tubule epithelial cells, µm

Indicator	Cell, *n* = 10	Nucleus, *n* = 20	Mitochondrion, *n* = 20	Number of mitochondria on cell section, *n* = 20
Trachurus mediterraneus	$14.9 \pm 0.19^{1,2} \times$ 9.80 ± 0.94	$6.33 \pm 0.22 \times$ 4.90 ± 0.16	$1.48 \pm 0.16 \times$ $0.62 \pm 0.12^{1,2}$	$49.6 \pm 4.59^{1,2,3,4,5,6}$
Chelon auratus	$15.3 \pm 0.64^{3,4,5} \times$ 15.2 ± 1.63	$6.16 \pm 0.35 \times$ 4.92 ± 0.66	$1.49 \pm 0.21 \times$ 0.74 ± 0.05	$47.2 \pm 5.20^{1,7,8}$
Diplodus annularis	$14.5 \pm 0.76^{6,7,8} \times$ 12.8 ± 1.38	$5.38 \pm 0.18 \times$ 4.88 ± 0.24	$1.83 \pm 0.07 \times$ $0.92 \pm 0.07^{3,4}$	$77.2 \pm 4.07^{2,7,9,10,11}$
Spicara flexuosa	$13.4 \pm 0.71^{9} \times$ 11.0 ± 1.71	$5.34 \pm 0.49 \times$ 4.93 ± 0.57	$1.55 \pm 0.16 \times$ $0.81 \pm 0.16^{5,6}$	$63.6 \pm 2.28^{3,8}$
Gobius niger	$13.2 \pm 0.15^{1,3,6} \times$ 9.63 ± 0.34	$5.82 \pm 0.33 \times$ 4.57 ± 0.26	$2.14 \pm 0.10 \times$ 1.28 ± 0.06	$84.4 \pm 1.33^{4,9}$
Mullus barbatus ponticus	$12.5 \pm 0.06^{2,4,7,9} \times$ 9.11 ± 0.87	$5.47 \pm 0.93 \times$ 3.50 ± 0.18	$1.99 \pm 0.12 \times$ $1.22 \pm 0.11^{1,3,5}$	$77.3 \pm 2.98^{5,10}$
Scorpaena porcus	$13.1 \pm 0.27^{5,8} \times$ 9.50 ± 0.19	$4.54 \pm 0.35 \times$ 3.60 ± 0.21	$2.01 \pm 0.18 \times$ $1.22 \pm 0.11^{2,4,6}$	$84.2 \pm 1.34^{6,11}$

The nuclei of most cells occupy a central position; sometimes, they are displaced towards the basal part. There is little heterochromatin, and it is concentrated mainly on the nucleus periphery, between nuclear pores. In cytoplasm, large electron-dense mitochondria were found, which were less ordered than mitochondria of type I and II epithelial cells. Mitochondria are surrounded by a tubular system of the smooth endoplasmic reticulum, which is developed similarly to the system of type I proximal tubule epithelial cells (Fig. 5a, b). The number and size of mitochondria increase in the series pelagic – epibenthic – demersal fish. As revealed, the number of mitochondria on cell sections of *T. mediterraneus* was statistically significantly smaller than in other species studied. The number of mitochondria on cell sections of *D. annularis* was statistically significantly smaller than that of *Ch. auratus* and *S. flexuosa*. The number of mitochondria on cell sections of *Ch. auratus* was significantly smaller than in the epibenthic species (Table 5). It was revealed that mitochondria on cell sections of *M. barbatus ponticus* and *S. porcus* were statistically significantly larger compared to those in *T. mediterraneus* and epibenthic fish (Table 5). There is no endocytosis zone. A characteristic feature of this type of cells is a large number of vesicles localized in the apical part of cells, which, in turn, forms lobe-like cytoplasmic outgrowths facing the tubule lumen. The largest number of vesicles, that fill the entire cytoplasm of lobe-like outgrowths, was recorded in demersal fish (Fig. 5c).

DISCUSSION

Cytological analysis of the mesonephros of pelagic, epibenthic, and demersal fish of the Black Sea, with the mean salinity of surface layers of 17.58–18.09 ‰ and of deeper layers of 22.33 ‰ (Ivanov & Belokopytov, 2011), has shown as follows: the nephrons of the trunk kidney of the species studied have a single structure. At the same time, the analysis of the results obtained unambiguously indicates several peculiarities of the nephron cell ultrastructure in the species, which depend on the confinement to a certain depth and salinity.

All kidneys are glomerular; the nephron includes both proximal and distal tubules. For all the species, a similar change in the length of epithelial cells, endocytosis zone, brush border, and microvilli diameter from proximal to distal nephron section is shown. Kidneys of marine teleost fish are known to be of two types, glomerular and aglomerular. Aglomerular kidneys were described for demersal ambush predators, angler *Lophius piscatorius* and oyster toadfish *Opsanus tau*, which inhabit ocean waters, with the mean annual salinity of about 35 ‰ at depth reaching 200 m, as well as for *Nerophis ophidian* inhabiting the Atlantic Ocean, depth of down to 30 m (Erisson & Olsen, 1968 ; Ericsson & Olsen, 1970 ; Marshall, 1930). Well-developed renal corpuscles were described for many species of freshwater and anadromous fish, as well as euryhaline species *Sparus auratus*, *Trachurus mediterraneus*, and *Diplodus annularis*, with a range mainly confined to the Black Sea (Flerova, 2012 ; Flerova et al., 2020 ; Zuasti & Agulleiro, 1983). Based on literature data and on our results, we can assume that renal corpuscles are characteristic of the nephrons in all teleost fish, inhabiting seawater with salinity up to 22 ‰, regardless of their lifestyle. Previously, a correlation between the salinity of the habitat and the level of glomeruli development was shown (Lozovik, 1963 ; Oğuz, 2015). Moreover, it was established that the diameter of the renal corpuscles and the body size of podocytes (the cells involved in the formation of the filtration barrier of the kidney) are larger in freshwater fish than in marine fish. This is primarily due to the fact that the kidneys of freshwater teleost fish filter larger volumes of fluid than the kidneys of marine fish (Flerova, 2012). Differences in the diameter of the renal corpuscle and the length of podocytes for pelagic, epibenthic, and demersal fish are likely to be related to the regulation of water-salt metabolism, when inhabiting various depths, with different salinity and water column pressure.

The proximal tubule turned out to be the most differentiated; it is formed by two types of epithelial cells, differing in their morphology. Such a structural organization of the proximal tubule is conservative for teleost fish. Thus, two types of epithelial cells were previously described for species of the orders Salmoniformes, Cypriniformes, and Perciformes inhabiting freshwater and seawater and performing anadromous migrations (Flerova, 2012 ; Flerova et al., 2020 ; Anderson & Loewen, 1975 ; Maksimovich et al., 2000 ; Ojeda et al., 2006). It is known that the brush border of the proximal tubules regulates the rate of active fluid transport (Natochin, 1976). In the proximal tubule, ciliated cells of all studied types were found, due to which both epithelial cells bearing microvilli on the apical surface and a brush border are formed; this demonstrates the similarity of its ultrastructure with the ultrastructure of freshwater fish (Flerova, 2012). No correlation was revealed between the frequency of occurrence of ciliated cells in the proximal tubules in the species studied and their lifestyle. Nevertheless, a shorter brush border of type I proximal tubules of the nephron in *T. mediterraneus* and *Ch. auratus* was recorded compared to brush borders in other species studied; both this fact and a lower height of epithelial cells indicate a decrease in the volume of the glomerular filtrate coming from renal corpuscles of epibenthic and demersal fish compared to the volume of the glomerular filtrate of pelagic fish.

As known, the degree of development of a smooth endoplasmic reticulum and of associated mitochondria number directly depends on the intensity of the mechanisms of reabsorption and secretion of the proximal tubule epithelial cell ions (Natochin, 1976). For all the species studied, the higher degree of development of a smooth endoplasmic reticulum is revealed compared to similar organoid in Salmoniformes, Cypriniformes, and Perciformes freshwater fish, as well as Salmonidae smolts performing anadromous migrations (Flerova, 2012 ; Flerova et al., 2020, 2019). No correlation was found between the development of a smooth endoplasmic reticulum and the lifestyle. Pattern of an increase in the number and size of mitochondria with an increase in the depth and salinity of the habitat was noted. These structural changes indicate intensification of the work of pumps, which provide active transport of ions, under increased osmotic load; these pumps are located mainly in the basal part of cells (Natochin, 1976).

The next section of the tubule, which was found in *Ch. auratus* and *S. porcus* only, is formed by epithelial cells that have similar structure with the intermediate tubule epithelial cells in Salmoniformes, Cypriniformes, and Perciformes freshwater fish (Vinnichenko, 1980 ; Maksimovich et al., 2000). It can be assumed that the intermediate tubule is present in all the species studied, but since the epithelial cells of this section form a small segment of the nephron, it is extremely difficult to identify and describe them. Both the proximal tubule cells and intermediate tubule epithelial cells in *S. porcus* are characterized by lower height and shorter microvilli length, as well as by a significantly larger number of larger mitochondria compared to those in *Ch. auratus*. Previously, it was shown that the structure of epithelial cells indicates their similarity with the thin segment cells of the loop of Henle of nephrons in warm-blooded animals, with the main function being to transport water (Vinnichenko, 1980). The specialization of these cells in *Ch. auratus* and *S. porcus* allows suggesting that demersal fish, as compared to pelagic ones, have a more perfect system of anti-gradient processes, which, along with a larger flattening of cells, makes it possible to shorten the water path (Erisson & Olsen, 1968 ; Ojeda et al., 2006).

The distal tubule epithelial cells of the species studied have a similar structure with the cells, that were previously described for Salmoniformes, Cypriniformes, and Perciformes species of different ecological groups (Flerova, 2012 ; Flerova et al., 2020 ; Anderson & Loewen, 1975 ; Flerova et al., 2019 ; Maksimovich et al., 2000 ; Ojeda et al., 2006). As shown earlier, a large number of vesicles distributed throughout the cytoplasm of cells, a larger number of mitochondria on sections of the distal tubule epithelial cells as compared to a number in proximal tubules, and a more developed system of membranes of the smooth endoplasmic reticulum on sections of the distal tubule epithelial cells in marine fish compared to freshwater fish indicate the peculiarities of functioning of distal tubule related to the regulation of the excreted urine volume (Natochin, 1976). For the species studied, a pattern of an increase in the number and size of mitochondria and the number of vesicles with an increase in the depth and salinity of the habitat was registered. These structural changes can be cytological markers of an increase in salinity and water column pressure as well.

It should be noted as follows: the differences in the basement membrane thickness, width of the renal corpuscle cavity, length of the endocytosis zone, size of the nuclei of all types of cells, number and size of secretory granules in the cytoplasm of type I proximal tubules, and microvilli thickness were statistically insignificant and most likely related not to the systematic or ecological peculiarities of the species, but to the functioning of structures at a certain point in time.

Conclusion. Comparison of the ultrastructural peculiarities of the mesonephros in the Black Sea fish, which inhabit different depths and are under different conditions of environmental osmotic pressure, allows suggesting as follows: at the tissue level of organization, nephrons have a single structure and form glomerular kidneys. The confinement to the habitat at certain depths is primarily manifested in an increase in the number and size of mitochondria of all types of nephron epithelial cells. Smaller area of renal corpuscles, length of the podocytes, and height of tubular epithelial cells, as well as length of the brush border of type I proximal tubules are registered. Nephron cytological peculiarities of pelagic, epibenthic, and demersal fish characterize a high adaptive capacity of the mesonephros cellular structures.

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СРАВНИТЕЛЬНАЯ ХАРАКТЕРИСТИКА УЛЬТРАСТРУКТУРЫ КЛЕТОК НЕФРОНА НЕКОТОРЫХ ВИДОВ ПЕЛАГИЧЕСКИХ, ПРИДОННЫХ И ДОННЫХ РЫБ (БУХТА КАРАНТИННАЯ, ЧЁРНОЕ МОРЕ)

Е. А. Флёрова[1], Г. М. Чуйко[2]

[1]Ярославский научно-исследовательский институт животноводства и кормопроизводства — филиал ФНЦ ВИК имени В. Р. Вильямса, пос. Михайловский, Российская Федерация
[2]Институт биологии внутренних вод имени И. Д. Папанина Российской академии наук, пос. Борок, Российская Федерация
E-mail: *katarinum@mail.ru*

Изучена ультраструктура основных отделов нефрона мезонефроса костистых рыб Чёрного моря (пелагических *Trachurus mediterraneus* (Steindachner, 1868) и *Chelon auratus* (Risso, 1810); придонных *Diplodus annularis* (Linnaeus, 1758) и *Spicara flexuosa* Rafinesque, 1810; донных *Scorpaena porcus* Linnaeus, 1758, *Gobius niger* Linnaeus, 1758 и *Mullus barbatus ponticus*

Essipov, 1927). Показано, что у рыб Чёрного моря, обитающих на разных глубинах и находящихся в различных условиях осмотической нагрузки среды, на тканевом уровне организации нефроны имеют единый план строения и формируют гломерулярные почки. Приспособленность рыб к обитанию на определённых глубинах в первую очередь проявляется в увеличении количества и размеров митохондрий всех типов эпителиальных клеток нефрона. Кроме того, отмечено уменьшение площади почечных телец, длины подоцитов и высоты эпителиоцитов канальцев, а также длины щёточной каёмки проксимальных канальцев I типа. Цитологические особенности нефрона пелагических, придонных и донных рыб характеризуют высокую адаптационную способность клеточных структур мезонефроса.

Ключевые слова: костистые рыбы, пелагические рыбы, придонные рыбы, донные рыбы, почка, нефрон, ультраструктура, Чёрное море

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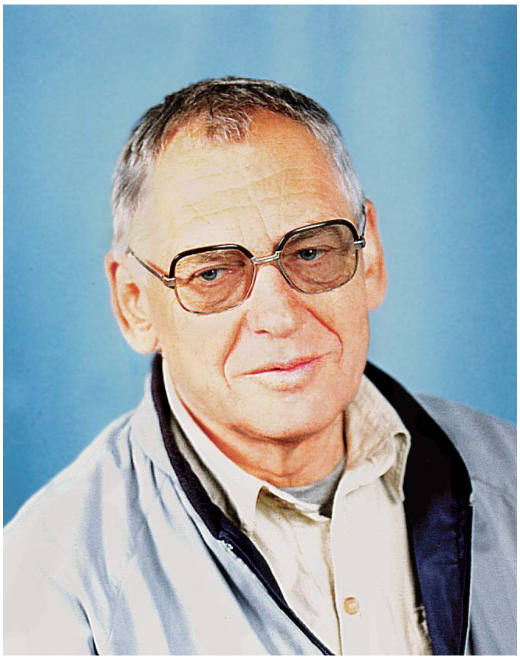
TO THE JUBILEE OF D. SC. GERMAN ZUYEV



On 27 June, 2021, German Zuyev, D. Sc., Professor, and one of the oldest researchers at the A. O. Kovalevsky Institute of Biology of the Southern Seas, is celebrating his 85th birthday.

German Zuyev was born on 27 June, 1936, in Chita into a military family. In 1954, he graduated from school in Chita and entered the faculty of ichthyology at the A. I. Mikoyan Moscow Technical Institute for the Fishery Industry. In 1959, G. Zuyev received a diploma of an ichthyologist and fish breeder and was sent to work at the Atlantic Scientific and Commercial Perspective Exploration (Kaliningrad) as an engineer-ichthyologist. Within two years (September 1959 to June 1961), he took part in four research cruises to the North Atlantic.

In 1961, he moved to Sevastopol and entered the PhD graduate school at the Sevastopol Biological Station of the Academy of Sciences of the Ukrainian SSR (hereinafter the AS of the USSR). During the graduate studies, he took part in two cruises on the RV "Akademik A. Kovalevsky" – to the Mediterranean and Red seas. In August 1964, German Zuyev presented to the Scientific Council the PhD thesis "Functional Foundations of the External Structure of Cephalopods", which served as the basis for his enrollment in the nekton department of the Institute of Biology of the Southern Seas of the AS of the USSR as a junior researcher. In February 1965, he successfully defended the PhD thesis at the Dissertation Council of the Zoological Institute of the Academy of Sciences of the Soviet Union, specializing in invertebrate zoology; in July 1965, he was awarded the degree of PhD in biology. In 1966, his first monograph – "Functional Foundations of the External Structure of Cephalopods" – was published.

In September 1967, G. Zuyev was transferred from the nekton department to the ichthyology department, where he continued studying morphology and ecology of cephalopods, as well as prospects of their commercial use.

In 1961–1968, he was taking an active part in research cruises to the northwestern Indian Ocean, *inter alia* the Red and Arabian seas, the Persian Gulf, and the Gulf of Aden, where he has amassed a large collection of cephalopods. The results obtained formed the basis for his monograph "Cephalopods of the Northwestern Indian Ocean" (1972).

In 1972, German Zuyev was promoted to senior researcher at the IBSS ichthyology department. He was involved in the study of the orange-back squid intraspecific structure based on morphophysiological, ecological, and genetic variability. He analyzed the main biological peculiarities of epipelagic squid populations (growth rate, age, and natural mortality) and developed methods of visual observation and quantitative accounting of epipelagic squids.

Since 1976, he was the scientific supervisor and main executor of several topics, being developed in the ichthyology department on the instructions of the State Committee for Science and Technology. Moreover, he was the executor of contractual topics with the research institutes of the Ministry of Fisheries, aimed at studying the productivity of pelagic oceanic communities, as well as identifying and rationally use of their resources.

In 1981, G. Zuyev was appointed the head of the laboratory of productivity of nekton animals. In 1982, he defended D. Sc. dissertation “Species Structure, Ecology, and Productivity of Nekton Oceanic Squids”, specializing in hydrobiology.

In 1983–1984, he was in an assignment in Conakry (the Republic of Guinea), where he headed the laboratory of hydrobiology of the Scientific Research Center of the Marine Hydrophysical Institute of the AS of the USSR and carried out ichthyological research. The results obtained formed the basis of the collective monograph, as well as many scientific articles and abstracts.

In 1996, German Zuyev became the head of the IBSS ichthyology department. Since that time, his scientific interests are related to studying the commercial fish of the Black Sea, identifying the patterns of the formation of commercial fish aggregations, and scientific substantiation of the optimization of the fishing. He developed and successfully tested an ecological and geographical method for determining the populations of Black Sea mass fish species of commercial importance. In recent years, he is involved in assessing and predicting the state of populations of mass and commercial fish species in the Sea of Azov – Black Sea basin under anthropogenic load and climatic changes. The results obtained by him made a significant contribution to modern ideas about the dynamics of the intraspecific structure of anchovy and sprat. Thus, the reproductive potential of mass pelagic fish species of the Black Sea was studied. An assessment of the effect of fishing and climatic changes on their biological peculiarities and population dynamics was given. Valuable recommendations for the organization of rational fishing and conservation of biological resources were developed.

In 2001, G. Zuyev was awarded the title of Professor. For 60 years of work at the IBSS, he has gone from graduate student to head of the department and wrote more than 240 scientific articles. German Zuyev is the author of two individual monographs and two popular science books, co-author of five collective monographs, and editor of two monographs. He took part in research cruises on the RV "Mikhail Lomonosov", "Akademik Vernadsky", and "Professor Vodyanitsky" to the Red and Mediterranean seas and Indian and Atlantic oceans; he worked in challenging expedition conditions. He has extensive experience in scientific and pedagogical activities: for some years, he gave lecture courses to students of Sevastopol universities and supervised the practice, coursework, and diploma work of students representing biological faculties of several universities in the country. Six PhD theses were defended under his supervision.

Dear German Vasilyevich, we sincerely admire your purposefulness, initiative, high professionalism, and dedication to science! On the day of your jubilee, we wish you good health, active longevity, success, family well-being, and fulfillment of desires!

Colleagues from IBSS ichthyology department

К ЮБИЛЕЮ ДОКТОРА БИОЛОГИЧЕСКИХ НАУК ГЕРМАНА ВАСИЛЬЕВИЧА ЗУЕВА

27 июня 2021 г. исполняется 85 лет Герману Васильевичу Зуеву, доктору биологических наук, профессору, одному из старейших сотрудников ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН».

1871
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TRIBUTE TO PROFESSOR VICTOR ZAIKA

> Don't leave a stone unturned.
> It's always something,
> to know you have done the most you could.
>
> *Charles Dickens*

Victor Evghenievich Zaika turned 85 this year. He's been gone for seven years. V. Zaika lived a long and very intensive life in science. His mind had no peace in studying the various manifestations of life that he loved and could feel it pulse. Victor Zaika enriched science with his ideas and works, striving for possible perfection in everything he did. Generously gifted by nature, creatively charming, and inspiring colleagues by his own example, he was constantly in a state of scientific inquiry. And those, who were fortunate enough to work with him, are infinitely grateful to fate for that.

The analytical mind of the researcher manifested itself from an early age. Victor Evghenievich accompanied his mother on veterinary expeditions, listened to the lectures she gave to the students, and assisted her in the work, which later determined his interest in studying various biological processes. He graduated from school in Ulan-Ude with the medal and entered the Leningrad State University (now – Saint Petersburg State University), becoming a bright representative of the classical generation of Professor V. A. Dogiel zoological school.

In 1962, he began research activities at the Institute of Biology of the Southern Seas, and for over 50 years his life was associated with the Black Sea. In this significant period of his life, the theory of *Productivity of Aquatic Invertebrates* was developed. Subsequently, Professor V. Zaika proposed a theory describing *the Basic Processes of Energy Balance*, further developing the study of *the Animals Growth* equations, initiated in science by Ludwig von Bertalanffy. For the first time in the country, he initiated research on marine microzooplankton and phototrophic picoplankton. Further, these studies were developed extensively.

V. E. Zaika and the permanent captain of the RV "Professor Vodyanitsky", Captain of Long-Distance Navigation V. G. Tyninika

He created his own scientific school. Among his students, there are 24 Doctors of Science. They are currently continuing their research on the structure and biodiversity of communities: E. A. Kolesnikova, N. A. Boltachova, N. N. Shalovenkov, S. A. Mazlumian, A. N. Petrov, E. L. Nevrova, I. P. Bondarev, as well as students of his students, M. V. Makarov and V. G. Kopiy. Grateful memory carefully preserves the invaluable experience gained during the years of our scientific formation. Victor Evghenievich was alien to mentorship, working in expeditions alongside colleagues, he brought up by his personal example of hard work and hesitation in scientific research.

Over the years of work at IBSS have been carried out: long-term field studies of zoobenthos; experimental work on the rate of different nature single-celled organisms division; on the growth of hydrobionts. The results obtained have significantly enriched our knowledge of the Black Sea ecosystem in the second half of the XX century.

For a long time Professor Zaika headed A. O. Kovalevsky Institute of Biology of the Southern Seas (IBSS) of the National Academy of Sciences of Ukraine and determined the research strategy in the study of marine and oceanic ecosystems. Much of his creative energy he devoted to organizational activities, reorganizing the academic departments of IBSS and the expansion international scientific cooperation.

As part of the research groups, Professor Zaika has headed complex International Projects on the Black Sea Ecosystem. His creative efforts have always found understanding and appreciation by the long-term international initiative: "Black Sea Commission". Research carried out on the RV "Mikhail Lomonosov", "Akademik A. Kovalevsky", "Vityaz", and "Professor Vodyanitsky" covered areas from the NW part of the Black Sea to the Bosporus outlet, including the Mediterranean Sea, the Atlantic and the Indian Ocean. The materials obtained during the complex of expeditions conducted under the leadership of Victor Evghenievich subsequently served as a basis for further research.

Benthos department (1986)

Shelf ecosystems department (2006)

His research interests overlapped with those of such renowned oceanographers as Academician Jean-Marie Perez (director of the Andum biological station), and Prof. G.S. Tregubov (director of Villefranche-sur-Mer Marine Station), Jacques-Yves Cousteau (explorer) and many others. He worked fruitfully in the Commission on "Scientific Research of the Black Sea and Mediterranean Sea". A special milestone was the joint work with the Turkish scientists of the Institute of Marine Sciences in Erdemli (1975) and his creative friendship with the prof. Umit Unluata (head of section at Intergovernmental Oceanographic Commission of UNESCO).

Victor Zaika and Jean-Marie Perez

Academic activity of Professor Zaika is reflected in more than 300 articles and 18 monographs. He was a member of the editorial boards of a number of international journals and chairman of the specialized Scientific Councils on Hydrobiology and Ichthyology. V. E. Zaika was known as an encyclopedic scholar and an outstanding naturalist, author of fascinating scientific essays. His rich life experience he realized in scientific works and essays, including popular books about inhabitants of the Black Sea, and the Sevastopol Biological Station and "our closest overseas neighbors" (*V. E. Z.*). Here he expressed all the strength of his love of life. Fellow zoologists noted the contribution of V. E. Zaika into taxonomy, and named after three new species.

If everyone who is "devoted to science" (*V. E. Z.*)* is compared with a star, V. Zaika was the most organic in this hypothetical constellation. Unfortunately, no consciousness can fully restore human life, with its details, which are always hidden from the outside eye. Life is a wave-like mystery; when it crashes on the shore of memory, it can reproduce only the captured splashes, and the whole boundless wave of life will remain a mystery forever.

ПАМЯТИ ПРОФЕССОРА ВИКТОРА ЕВГЕНЬЕВИЧА ЗАИКИ

В 2021 г. исполнилось 85 лет Виктору Евгеньевичу Заике, члену-корреспонденту НАН Украины и лауреату Государственной премии Украины в области науки и техники. Уже семь лет его нет с нами. Виктор Евгеньевич прожил долгую и очень интенсивную жизнь в науке. Его ум не знал покоя в изучении различных проявлений жизни, которую он любил и пульс которой чутко чувствовал. Во всём добиваясь возможного совершенства, В. Е. Заика обогатил науку своими идеями и трудами. Щедро одарённый от природы, обаятельный, собственным примером воодушевляющий коллег, он непрерывно находился в состоянии поиска. И те, кому посчастливилось с ним работать, бесконечно благодарны за это судьбе.

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*By definition of V. Zaika. Very rare and the only praise he allowed himself.

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IN MEMORIAM: ALEXANDRA SHMELEVA
(17.05.1926 – 04.01.2021)

On 4 January, 2021, Alexandra Shmeleva, one of the world's most famous copepodologists, PhD, the oldest researcher at the A. O. Kovalevsky Institute of Biology of the Southern Seas, passed away at the age of 94.

All the scientific activity of Alexandra Shmeleva for almost half a century (since 1957) was inseparably connected with the Institute of Biology of the Southern Seas. Her research was focused on the copepods of the World Ocean, in particular *Calocalanus* (Calanoida) and *Oncaea* (Cyclopoida). The study of copepods was the meaning and purpose of her life, and such dedication to science aroused great respect.

In 1960–1970, A. Shmeleva processed the materials of the cruises of the RV "Akademik A. Kovalevsky", "Mikhail Lomonosov", and "Akademik Vernadsky", as well as the International Indian Ocean Expedition (UNESCO) and many other research cruises. It was during this time that she became known as a world-class taxonomist. She has described 43 copepod species, new to science, from the Indian Ocean, Antarctic, Atlantic, and Mediterranean Sea; she has clarified the weight characteristics of the Adriatic Sea copepods. Thanks to these studies, the number of known Copepoda species in the Mediterranean alone increased from 200 in 1957 to 425 in 1980. She found more than 30 new Copepoda species off the coast of Turkey, and some of them are supposed to be mass migrants who had entered the Mediterranean Sea through the Suez Canal. More than 150 Mediterranean Copepoda species were discovered away from the Bosporus area, on shipping routes up to Crimea and the Tsemes Bay; probably, they ended up in the Black Sea with the ballast water of merchant ships.

She is the author and co-author of more than 80 scientific publications, *inter alia* four monographs. The identification guide of fauna of the Iberian Peninsula in two volumes "Crustacea, Copépodos marinos. Calanoida" by Professor Francisco Vives and Alexandra Shmeleva is a successful compendium of a lifetime, dedicated to science and copepods in particular. This fundamental publication is a useful tool for current and future copepodologists.

At the IBSS, she has raised several generations of highly qualified specialists. In her presentation, systematics turned from a routine science into an exciting experience. She was proud of the collection of copepods of the World Ocean, many of which she had no time to describe. She generously shared knowledge, experience, and unique scientific materials with Spanish, Greek, and Turkish colleagues, as well as specialists from many other countries. With warmth and love, she reminisced the French Professor Grégoire Trégouboff (1886–1969), a well-known specialist in the Mediterranean zooplankton. The identification guide of copepods of the Mediterranean Sea, which he co-authored with Maurice Rose, is still of great relevance. In one of the letters, G. Trégouboff wrote: "…I am very grateful to you for your intention to dedicate to me one of the new Copedoda species you have discovered, *Oncaea tregoubovi* Shmeleva, 1968." As a sign of special gratitude and deep respect to Vladimir Vodyanitsky, the outstanding scientist, Corresponding Member of the Academy of Sciences of the Ukrainian SSR, and director of the Sevastopol Biological Station and IBSS, she named one of cyclopoid copepods discovered by her *Oncaea vodjanitskii* Shmeleva & Delalo, 1965.

A. Shmeleva was a person of great vitality, optimism, and erudition. Her stories of travel, books, and history were as engaging and informative as her conversations about science and Copepoda studies. At one time, she lived in the Sevastopol district Gollandiya. From the windows of her house, she saw the blue expanses of the Sevastopol Bay – a mysterious and always alluring sea, without which she could not live…

We have to remember and honor our teachers, on whose ideas and research today's science is based. The bright memory of Alexandra Shmeleva will forever remain in our hearts.

Zh. P. Selifonova,
Admiral Ushakov Maritime State University, Novorossiysk;
A. O. Kovalevsky Institute of Biology of the Southern Seas, Sevastopol

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ПАМЯТИ АЛЕКСАНДРЫ АЛЕКСАНДРОВНЫ ШМЕЛЁВОЙ (17.05.1926 – 04.01.2021)

4 января 2021 г. на 95-м году ушла из жизни Александра Александровна Шмелёва — один из наиболее известных специалистов по систематике копепод в мире, к. б. н., старейший научный сотрудник Института биологии южных морей имени А. О. Ковалевского.

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