Морской биологический журнал
Marine Biological Journal
2023, vol. 8, no. 1, pp. 76–92
https://marine-biology.ru

UDC 594.124(265.54.04)

FEATURES OF SPATIAL DISTRIBUTION OF *CRENOMYTILUS GRAYANUS* AND *MODIOLUS KURILENSIS* (BIVALVIA, MYTILIDAE) IN PETER THE GREAT BAY (THE SEA OF JAPAN)

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Received by the Editor 14.10.2021; after reviewing 24.03.2022;
accepted for publication 20.10.2022; published online 14.03.2023.

The bivalves of the family Mytilidae – *Crenomytilus grayanus* (Dunker, 1853) and *Modiolus kurilensis* Bernard, 1983 – are Pacific, Asian species and mass representatives of upper sublittoral epifauna in coastal waters of Peter the Great Bay (the Sea of Japan). *C. grayanus* is a traditional commercial species, and *M. kurilensis* is a promising one; resources of both molluscs are significant. The aim of the work is the comparative analysis of spatial distribution and biomass of *C. grayanus* and *M. kurilensis* on different types of bottom sediments and habitat depths in Peter the Great Bay. The investigation was carried out in 2007–2019 by scuba diving hydrobiological techniques at depths of down to 20 m. The data were analyzed for 5,911 stations; Mytilidae representatives were found at 1,635 stations. For mytilids, vital mass of each individual was determined, and mean biomass was estimated. The landscape diversity of Peter the Great Bay bottom determines an almost ubiquitous distribution of *C. grayanus* and *M. kurilensis*, and this reflects good adaptation of molluscs to conditions typical for this part of their area. Monospecific aggregations of *C. grayanus* prevailed both on hard and soft bottom sediments (78.6 and 38.2% of total stations with Mytilidae, respectively), while mixed aggregations of both species prevailed on soft bottom sediments (38.3%). On soft bottom sediments, monospecific aggregations of *M. kurilensis* were more common (23.5%) than on hard ones (8.1%). In Peter the Great Bay, mean biomass of *C. grayanus* on hard bottom sediments was (728 ± 47) g·m^{-2} varying from 524 g·m^{-2} (the Amur Bay) to 922 g·m^{-2} (eastern Peter the Great Bay). The value for mean biomass of *C. grayanus* on soft bottom sediments was (491 ± 51) g·m^{-2} varying from 228 g·m^{-2} (the Ussuri Bay) to 829 g·m^{-2} (the Amur Bay), except for southwestern Peter the Great Bay and Boisman Bay, where the value was below 50 g·m^{-2}. Mean biomass of *M. kurilensis* on hard bottom sediments was (370 ± 74) g·m^{-2} varying from 18 g·m^{-2} (Baklan Bay) to 656 g·m^{-2} (the Empress Eugénie Archipelago water areas). The value for mean biomass of *M. kurilensis* on soft bottom sediments was (335 ± 37) g·m^{-2} varying from 77 g·m^{-2} (southwestern Peter the Great Bay) to 456 g·m^{-2} (the Amur Bay), except for Boisman and Baklan bays where the species was rare. In Peter the Great Bay, maximum values of the mean biomass for both species were recorded at depths of 1–10 m (*C. grayanus*, 664–805 g·m^{-2}; *M. kurilensis*, 347–485 g·m^{-2}); with increasing habitat depth, the abundance of both species decreased. The mean biomass of *C. grayanus* inhabiting hard bottom sediments at 10–20 m was quite high as well – 431–507 g·m^{-2}. On soft bottom sediments, with a shift in depth from 10–15 to 15–20 m, its mean biomass decreased from (204 ± 33) to (27 ± 11) g·m^{-2}. The mean biomass of *M. kurilensis* inhabiting both types of bottom sediments at 10–15 m was 121–194 g·m^{-2}, and at 15–20 m, the value was 11–60 g·m^{-2}.

Keywords: mytilids, Mytilidae, Gray mussel, *Crenomytilus grayanus*, horsemussel, *Modiolus kurilensis*, biomass, distribution, bottom sediments, habitat depth, Peter the Great Bay, Sea of Japan

The bivalves of the family Mytilidae – the Gray mussel *Crenomytilus grayanus* (Dunker, 1853) and horsemussel *Modiolus kurilensis* Bernard, 1983 – are Pacific, Asiatic species and mass representatives of upper sublittoral epifauna in coastal waters of the Peter the Great Bay (hereinafter the PGB), the Sea of Japan. *C. grayanus* is a low-boreal species capable of entering subtropical waters, while *M. kurilensis* is a subtropical boreal species [Golikov, Skarlato, 1967; Skarlato, 1981]. Low-boreal species tend to inhabit bays and open shelf areas; warm-water (subtropical) species prefer the warmest areas of bays. *C. grayanus* and *M. kurilensis* coexistence in the PGB is due to the location of the bay at the junction of two climatic zones: there, waters of the cold Primorsky Current, which mostly affects this area, meet waters of the East Korea Warm Current [Zuenko, 2008]. During winter, the PGB waters have the characteristics of Arctic ones; during summer, of subtropical ones [Manuilov, 1990].

Off the coast of Primorsky Krai, the Gray mussel is a traditional commercial species [Razin, 1934; Sedova, 2020], while the horsemussel is a promising one. The resources of these species in the PGB are significant: *C. grayanus*, 54.8 thousand tons; *M. kurilensis*, 27.1 thousand tons [Sedova, Sokolenko, 2019, 2021a]. At present, these species are often not separated when harvesting the Gray mussel: visually, their shells and sizes are similar, as well as their taste qualities. However, there are several differences (Fig. 1).

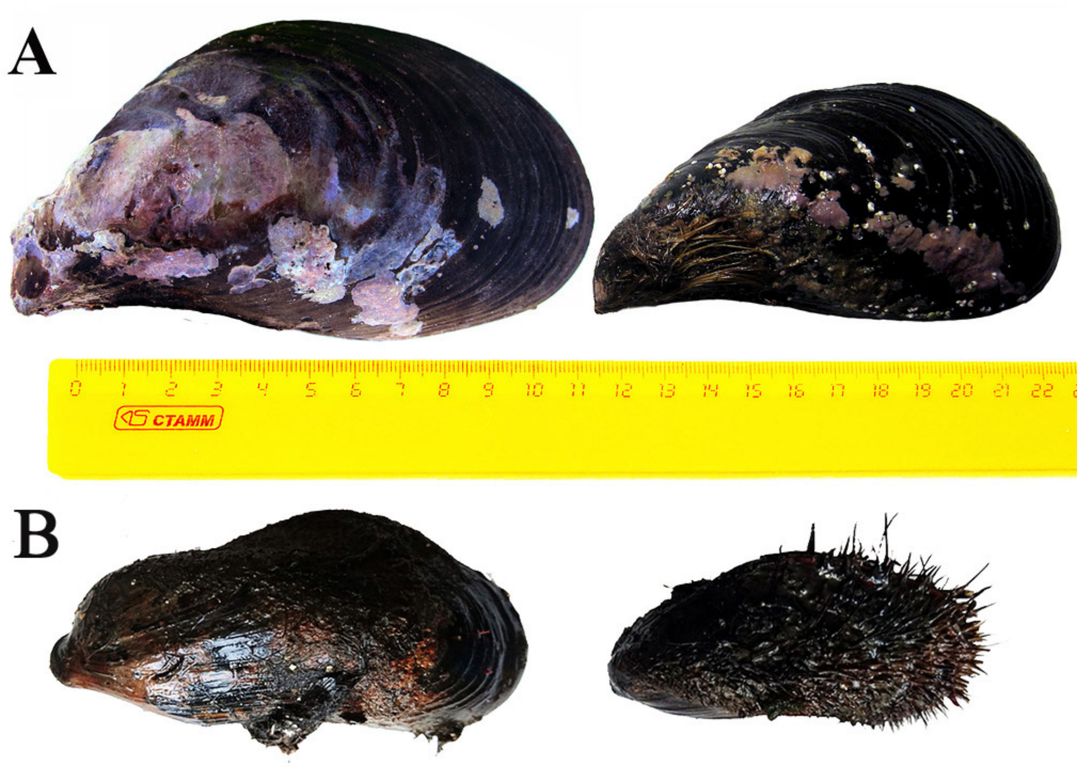


Fig. 1. *Crenomytilus grayanus* (A) and *Modiolus kurilensis* (B)

In *C. grayanus*, the upper edge of the shell is arcuate, and the lower is usually concave. The vertex is pulled down; the shell surface is smooth. In *M. kurilensis*, the front of the shell protrudes in front of the vertexes. The valves are covered with black and brown periostracum, with its brush-shaped setae being long and thick, which is more pronounced in younger molluscs [Volova, Skarlato, 1980]. With the same length, *C. grayanus* has a more massive shell.

Mytilidae are rarely found as single individuals; they usually form druses (Fig. 2) consisting of molluscs fastened with byssus filaments (the abundance of mussels can reach tens or even hundreds). Sometimes, druses form "brushes" of significant length or "banks."

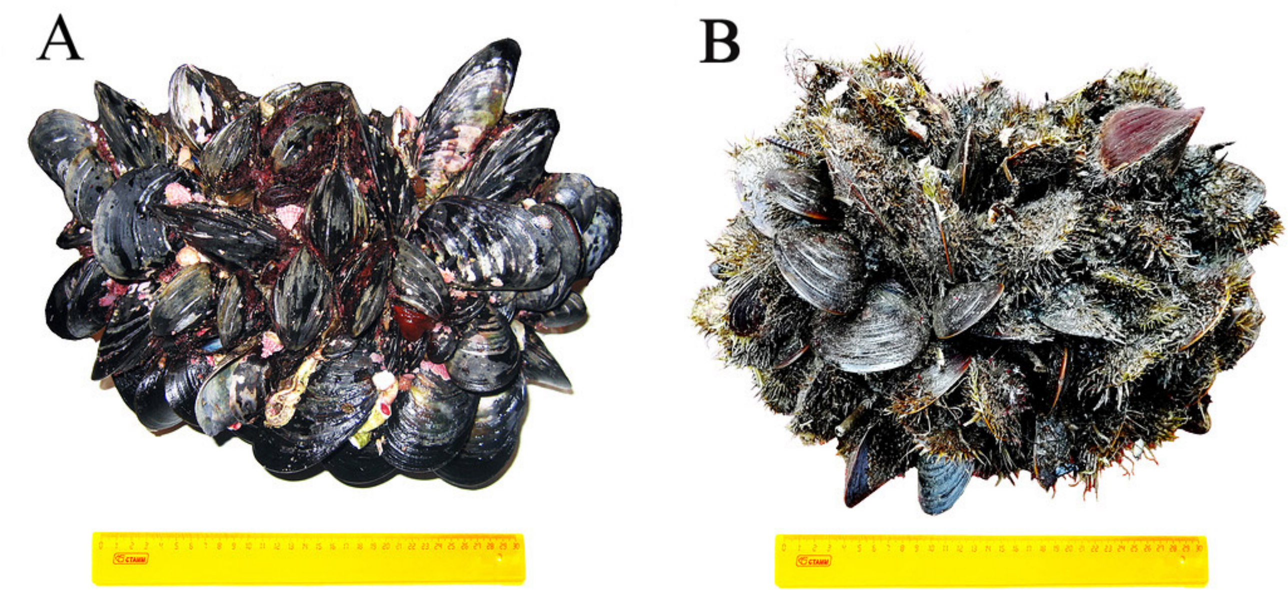


Fig. 2. Aggregations (druses) of *Crenomytilus grayanus* (A) and *Modiolus kurilensis* (B)

C. grayanus and *M. kurilensis* distribution in the PGB depends on both the variety of bottom sediments in the coastal area and hydrological conditions [Manuilov, 1990; Preobrazhensky et al., 2000; Razin, 1934; Skarlato, 1981]. An essential factor determining the composition of bottom sediments is the isolation of water areas which results from the indentation of the PGB coastline with secondary bays and adjacent islands. Due to different abilities of *C. grayanus* and *M. kurilensis* to inhabit hard and soft substrates, these species usually occur in different biotopes; however, they can form monospecific and mixed settlements on various types of bottom sediments [Kutishchev, Gogolev, 1983; Sedova, Sokolenko, 2018a, b, c, 2020a, b, 2021b; Selin, 2018a; Selin, Vekhova, 2002]. In the published works, Mytilidae settlement are considered only in certain PGB areas. To date, there is no complete picture of *C. grayanus* and *M. kurilensis* distribution throughout the PGB depending on the type of bottom sediments and the habitat depths. Interestingly, this is of great practical importance for organizing rational harvesting and planning measures to preserve Mytilidae resources.

The aim of this work is to conduct a comparative analysis of *C. grayanus* and *M. kurilensis* spatial distribution and abundance on different types of bottom sediments and habitat depth in the Peter the Great Bay.

MATERIAL AND METHODS

The work is based on the results of regular research carried out on the RV "Ubezhdenny" of the TINRO Base of Research Fleet in August–October 2007–2019 in different PGB sections by scuba diving. Mytilidae settlements that have an attached lifestyle maintain for a long time their spatial structure and abundance in the absence of unfavorable abiotic conditions, anthropogenic load, and intensive harvesting [Sedova, Sokolenko, 2019].

The bay was conditionally divided into following sections: 1, the southwestern PGB (from the Tumen River mouth to Cape Suslov); 2, Posyet Bay (from Cape Suslov to Cape Gamov); 3, Boisman Bay; 4, Baklan Bay; 5, the Amur Bay (the southern border is a line connecting the Cape Bruce and the Zheltukhin Island); 6, the Empress Eugénie Archipelago water areas (Russky, Shkot, Popov, Reyneke, and Rikord islands, as well as adjacent smaller islands); 7, the Ussuri Bay (the southern border is a line connecting southern tips of the Zheltukhin and Askold islands); 8, the eastern PGB (from the Cape Sysoev to the Cape Povorotny, including water areas of Putyatin and Askold islands) [Lotsiya severo-zapadnogo berega Yaponskogo morya, 1984] (Fig. 3).

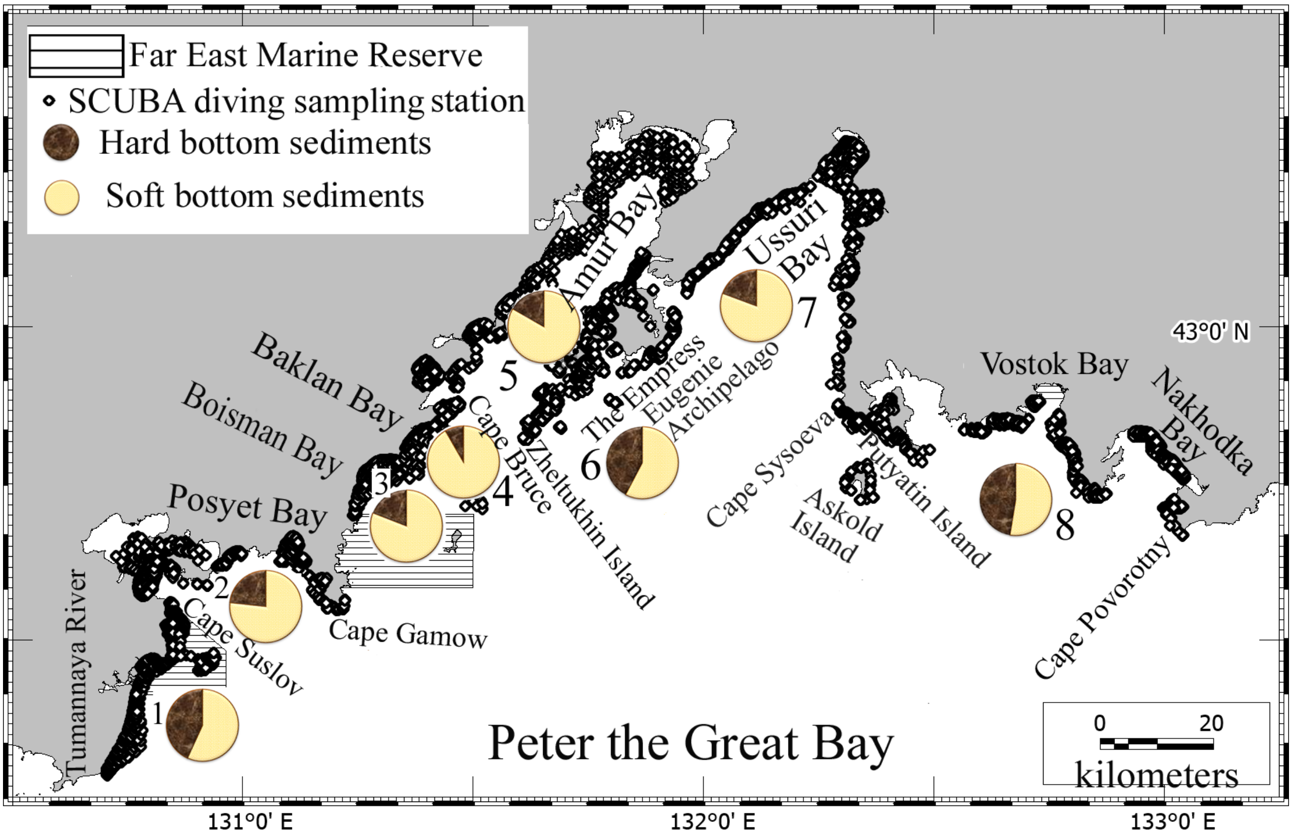


Fig. 3. Map of the research and sampling area; ratio of hard and soft bottom sediments in Peter the Great Bay (the Sea of Japan)

Standard scuba diving hydrobiological techniques were applied to obtain data on spatial distribution and abundance of molluscs. Depending on the orography and nature of bottom landscapes, the distance between the stations on the cuts perpendicular to the coastline was of 100–500 m [Sedova, Sokolenko, 2019]. In the vast areas of the relative flat bottom of bays, a regular grid of stations was used. Considering this and taking into account the areas of the studied spots at depths of 1–20 m, a different number of stations was carried out (Table 1). In total, the data from 5,911 stations located along the entire coast of the PGB were analyzed, except for areas prohibited for navigation (Fig. 3).

In areas with dense mollusc settlements, the diver used for sampling a measuring frame from one m^2 (in three replicates). In sparse settlements, the transect method was applied: the calculation and periodic sampling of animals were carried out in the field of view on a certain bottom area. The type of bottom sediments was determined visually. Sandy, silty-sand, and silty substrates were attributed to soft bottom sediments. Rocks, blocks, boulders, stones, and pebbles were attributed to hard bottom sediments. In total, 1,708 stations were carried out on hard bottom sediments, and 4,203 were carried out on soft ones (Table 1).

All sampled hydrobionts were analyzed onboard the RV. Druses were disassembled, the species composition of molluscs was determined, and lifetime mass of each mytilid was established. The mean Mytilidae biomass was determined considering the stations where the mussels were found (Table 1). Then, live molluscs were released back to the spots of sampling. *C. grayanus* and *M. kurilensis* were recorded at 1,635 stations (Table 1).

To prepare cartographic material, GIS MapInfo Pro software (https://mapinfo.ru/product/mapinfo-professional) was used. The obtained data were statistically processed in Microsoft Excel and Statistica (http://statsoft.ru/). The mean values of indicators, standard deviation, and standard error of the mean (*SEM*) with a significance level of 0.05 were determined. The ratio of Mytilidae biomass was evaluated by the two-sample independent *t*-test. To compare biomass of *C. grayanus* and *M. kurilensis* living under different conditions, Mann–Whitney *U* test was used – a non-parametric analogue of the *t*-test [Borovikov, 2003]. The null hypothesis was rejected at a significance level of 0.05 ($p \leq 0.05$).

RESULTS

***C. grayanus* and *M. kurilensis* spatial distribution depending on the type of bottom sediments.** The PGB stretches from the Tumen River mouth in the west to the Cape Povorotny in the east in the northwestern Sea of Japan [Lotsiya severo-zapadnogo berega Yaponskogo morya, 1984] (Fig. 3). Bottom sediments in the bay are very diverse. Rocks, blocks, and boulders are common off the steep shores and capes at depths of down to 10–14 m. With an increase in depth, those are replaced by pebbles or sandy, silty-sand, or silty substrates. In the tops of the bays, soft bottom sediments prevail – sand, silty-sand, and silt. The bottom sediment composition for each PGB section is described in detail in our previous publications [Sedova, Sokolenko, 2018a, b, c, 2020a, b, 2021b]. Throughout the PGB at depths of down to 20 m, the prevalence of soft bottom sediments was noted: on them, 71.1% of stations were carried out (on hard bottom sediments, 28.9%, respectively) (Table 1). For individual PGB sections, this ratio varied. Hard bottom sediments were most represented (42.3–47.4%) in the southwestern and eastern PGB and in the Empress Eugénie Archipelago water areas (Table 1, Fig. 3).

In other PGB sections, the number of stations carried out on hard bottom sediments varied from 8.3% (Baklan Bay) to 23.3% (Posyet Bay). Mytilidae were found at 27.7% of all the surveyed stations (Table 1). There were both monospecific and mixed druses of molluscs.

In different PGB sections on hard bottom sediments (rocks, boulders, stones, and pebbles), monospecific druses of the Gray mussel accounted for 47.4–90.7%; for monospecific druses of the horsemussel, the value ranged within 2.7–13.7% (except for Baklan Bay); mixed druses accounted for 1.7–18.6%; and in Baklan Bay, the value was 52.6% (Table 2). The occurrence of monospecific druses of the Gray mussel on soft bottom sediments was 25.0–73.1%; monospecific druses of the horsemussel, 9.7–50.0%; and mixed druses, 7.7–48.7%. On both types of bottom sediments, monospecific druses of the Gray mussel prevailed in the southwestern PGB and the Amur and Ussuri bays; monospecific druses of the horsemussel prevailed on soft substrates in Boisman Bay and the eastern PGB (Table 2). Mixed druses prevailed on soft bottom sediments in Posyet Bay and the Empress Eugénie Archipelago water areas, as well as on hard substrates in Baklan Bay.

Table 1. Number of stations surveyed and Mytilidae biomass in Peter the Great Bay (2007–2019)

Section	Area, km^2	Number of stations, in parentheses, percentage of stations surveyed				Mean Mytilidae biomass ± *SEM*, in parentheses, standard deviation, below the line, range of values, g·m^{-2}	
		surveyed	hard bottom sediments	soft bottom sediments	on which Mytilidae were found	*C. grayanus*	*M. kurilensis*
Peter the Great Bay	1,005.8	5,911	1,708 (28.9%)	4,203 (71.1%)	1,635 (27.7%)	645 ± 36 (1,333) 0.1–14,120	347 ± 35 (869) 0.1–8,512
1. Southwestern PGB	70.2	475	205 (43.2%)	270 (56.8%)	133 (28.0%)	628 ± 141 (1,519) 3.5–14,120	84 ± 20 (71) 1.2–242
2. Posyet Bay	129.2	1,164	271 (23.3%)	893 (76.7%)	352 (30.2%)	563 ± 59 (1,017) 0.3–6,000	252 ± 57 (729) 0.5–6,000
3. Boisman Bay	41.1	440	84 (19.1%)	356 (80.9%)	67 (15.2%)	593 ± 129 (954) 0.6–4,555	46 ± 39 (153) 0.4–600
4. Baklan Bay	40.9	240	20 (8.3%)	220 (91.7%)	27 (11.2%)	660 ± 156 (767) 1–2,600	14 ± 11 (41) 0.5–150
5. Amur Bay	348.7	934	156 (16.7%)	778 (83.3%)	194 (20.8%)	671 ± 122 (1,508) 0.1–9,610	350 ± 118 (1,062) 0.1–8,000
6. Empress Eugénie Archipelago water areas	109.9	1,043	441 (42.3%)	602 (57.7%)	504 (48.3%)	597 ± 61 (1,272) 0.2–11,180	493 ± 67 (1,023) 0.3–8,512
7. Ussuri Bay	168.1	837	162 (19.4%)	675 (80.6%)	156 (18.6%)	739 ± 111 (1,356) 0.1–9,500	344 ± 100 (560) 0.2–2,360
8. Eastern PGB	97.7	778	369 (47.4%)	409 (52.6%)	202 (26.0%)	832 ± 135 (1,754) 0.1–11,448	228 ± 71 (533) 0.1–3,018

In total for the PGB (Fig. 4), the prevalence of monospecific druses of the Gray mussel was revealed at 783 stations (79% of the total stations with Mytilidae) on hard bottom sediments which this species prefers; the prevalence of mixed druses was recorded on soft substrates. These differences are statistically significant ($p = 0.001$ and $p = 0.002$, respectively). There were no noticeable differences in *M. kurilensis* distribution on hard and soft bottom sediments ($p = 0.341$).

Table 2. Ratio of stations with monospecific and mixed aggregations of Mytilidae and biomass values for *Crenomytilus grayanus* and *Modiolus kurilensis* on hard and soft bottom sediments in Peter the Great Bay

Section	Number of stations, in parentheses, percentage of stations with Mytilidae			Mean Mytilidae biomass ± *SEM*, in parentheses, standard deviation, below the line, range of values, g·m^{-2}	
	C. grayanus	*M. kurilensis*	*C. grayanus* + *M. kurilensis*	*C. grayanus*	*M. kurilensis*
Hard bottom sediments					
1. Southwestern PGB	97 (90.7%)	7 (6.5%)	3 (2.8%)	743 ± 166 (1,637) 4–14,120	88 ± 21 (56) 1–121
2. Posyet Bay	133 (76.0%)	18 (10.3%)	24 (13.7%)	731 ± 87 (1,085) 0.1–6,000	393 ± 185 (1,197) 1–6,000
3. Boisman Bay	50 (84.7%)	8 (13.6%)	1 (1.7%)	639 ± 137 (976) 1–4,555	77 ± 65 (196) 0.1–600
4. Baklan Bay	9 (47.4%)	0	10 (52.6%)	743 ± 196 (832) 1–2,600	18 ± 15 (46) 1–150
5. Amur Bay	70 (73.7%)	13 (13.7%)	12 (12.6%)	524 ± 147 (1,309) 0.1–9,610	115 ± 30 (148) 0.1–580
6. Empress Eugénie Archipelago water areas	202 (73.7%)	21 (7.7%)	51 (18.6%)	614 ± 84 (1,336) 0.1–11,180	656 ± 177 (1,498) 0.1–8,512
7. Ussuri Bay	97 (84.3%)	3 (2.7%)	15 (13.0%)	907 ± 140 (1,477) 1–9,500	362 ± 119 (506) 0.1–1,940
8. Eastern PGB	125 (85.2%)	11 (7.2%)	16 (10.6%)	922 ± 158 (1,874) 0.1–11,448	113 ± 77 (402) 0.1–2,068
Soft bottom sediments					
1. Southwestern PGB	19 (73.1%)	5 (19.2%)	2 (7.7%)	41 ± 20 (86) 4–353	77 ± 43 (95) 12–242
2. Posyet Bay	57 (32.2%)	38 (21.5%)	82 (46.3%)	374 ± 76 (901) 0.1–5,040	203 ± 42 (464) 1–3,110
3. Boisman Bay	2 (25.0%)	4 (50.0%)	2 (25.0%)	3.3 ± 1.1 (2.1) 1–5	1.3 ± 0.2 (0.4) 1–2
4. Baklan Bay	5 (62.5%)	2 (25.0%)	1 (12.5%)	411 ± 204 (500) 2–1,199	1.8 ± 0.6 (1.1) 1–3
5. Amur Bay	43 (43.4%)	26 (26.3%)	30 (30.3%)	829 ± 198 (1,692) 0.1–8,000	456 ± 169 (1,263) 1–8,000
6. Empress Eugénie Archipelago water areas	69 (30.0%)	49 (21.3%)	112 (48.7%)	575 ± 88 (1,180) 0.1–7,252	420 ± 56 (710) 0.1–3,762
7. Ussuri Bay	28 (68.3%)	4 (9.7%)	9 (22.0%)	228 ± 114 (692) 0.1–3,870	320 ± 180 (649) 1–2,360
8. Eastern PGB	21 (42.0%)	22 (44.0%)	7 (14.0%)	379 ± 155 (823) 2–3,843	334 ± 115 (620) 1–3,018

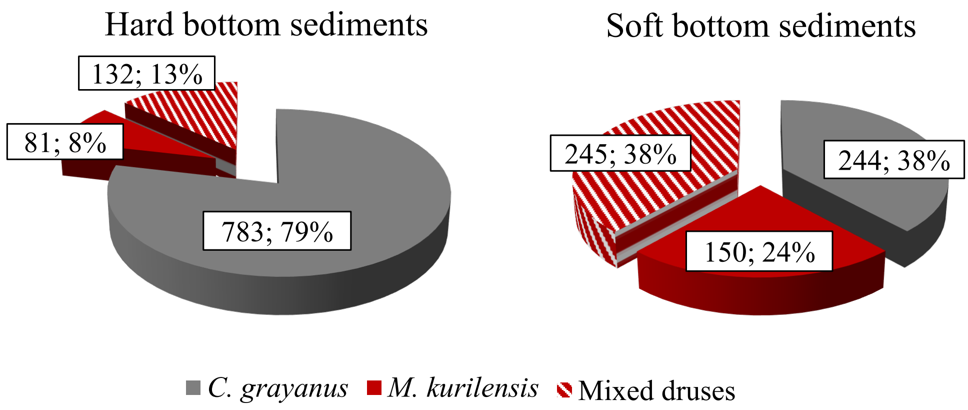


Fig. 4. Ratio of monospecific and mixed aggregations of *Crenomytilus grayanus* and *Modiolus kurilensis* on hard and soft bottom sediments in Peter the Great Bay (number of stations; percentage of total stations with Mytilidae)

The values of *C. grayanus* and *M. kurilensis* biomass in individual PGB sections, as well as ratios of hard and soft bottom sediments there, differed (Fig. 3, Tables 1, 2). On hard bottom sediments, the mean value of *C. grayanus* biomass varied from 524 g·m^{-2} in the Amur Bay to 922 g·m^{-2} in the eastern PGB (Table 2). On soft substrates, the highest value of the mean biomass of *C. grayanus* was recorded in the Amur Bay (829 g·m^{-2}), while the lowest ones (< 50 g·m^{-2}) were registered in Boisman Bay and the southwestern PGB. On hard bottom sediments, the mean biomass of *M. kurilensis* varied from 18 g·m^{-2} (Baklan Bay) to 656 g·m^{-2} (the Empress Eugénie Archipelago water areas); on soft bottom sediments, the value varied from 77 g·m^{-2} (the southwestern PGB) to 456 g·m^{-2} (the Amur Bay), except for open Boisman and Baklan bays, where the species was rare (Table 2). In the Amur, Posyet, and Ussuri bays, the Empress Eugénie Archipelago water areas, and the eastern PGB, the mean biomass of each of two species was > 100 g·m^{-2} both on hard and soft bottom sediments.

In the PGB, the mean values of the biomass of *C. grayanus* and *M. kurilensis* were statistically significantly different ($p = 0.0004$), amounting to 645 and 347 g·m^{-2}, respectively (Table 1). Comparison of species biomass values separately on hard and soft bottom sediments showed noticeable differences as well ($p = 0.001$ and $p = 0.019$, respectively). The values of the mean biomass of *C. grayanus* inhabiting hard and soft substrates differed significantly ($p = 0.001$), amounting to 728 and 491 g·m^{-2}, respectively. Interestingly, there were no noticeable differences in the values for *M. kurilensis* – 370 and 335 g·m^{-2} ($p = 0.643$) (Table 3).

Table 3. Mean Mytilidae biomass on hard and soft bottom sediments in Peter the Great Bay, g·m^{-2}

Bottom sediments	*C. grayanus*			*M. kurilensis*		
	Mean biomass ± *SEM*	Standard deviation	Range of values	Mean biomass ± *SEM*	Standard deviation	Range of values
Hard	728 ± 47	1,422	0.1–14,120	370 ± 74	1,070	0.1–8,512
Soft	491 ± 51	1,134	0.1–8,000	335 ± 37	741	0.1–8,000

Vertical distribution. On hard bottom sediments in the southwestern PGB, Posyet Bay, and Boisman Bay, higher values of the mean biomass for *C. grayanus* were recorded at depths of 1–14.9 m; in Baklan Bay, at 1–20 m; in the Empress Eugénie Archipelago water areas and the eastern PGB, at 1–9.9

and 15–20 m; and in the Ussuri Bay, at 1–9.9 m (Table 4). On soft bottom sediments, *C. grayanus* was not registered at all in the southwestern PGB and Boisman and Baklan bays at depths of down to 5 m. In Ussuri Bay and the eastern PGB, the biomass of the Gray mussel was low. Higher values were noted at depths of 1–9.9 m in the Amur and Posyet bays and in the Empress Eugénie Archipelago water areas, as well as at depths of 5–9.9 m in Baklan Bay and the eastern PGB (Table 4). On hard bottom sediments, *M. kurilensis* settlements with the biomass of > 300 g·m^{-2} were found at depths of down to 10 m in Posyet Bay and the Empress Eugénie Archipelago water areas, as well as at depths of 10–14.9 m in Boisman Bay. On soft bottom sediments, those were registered at depths of 5–9.9 m in the Amur Bay and the eastern PGB, as well as at 1–10 m in the Empress Eugénie Archipelago water areas (Table 5).

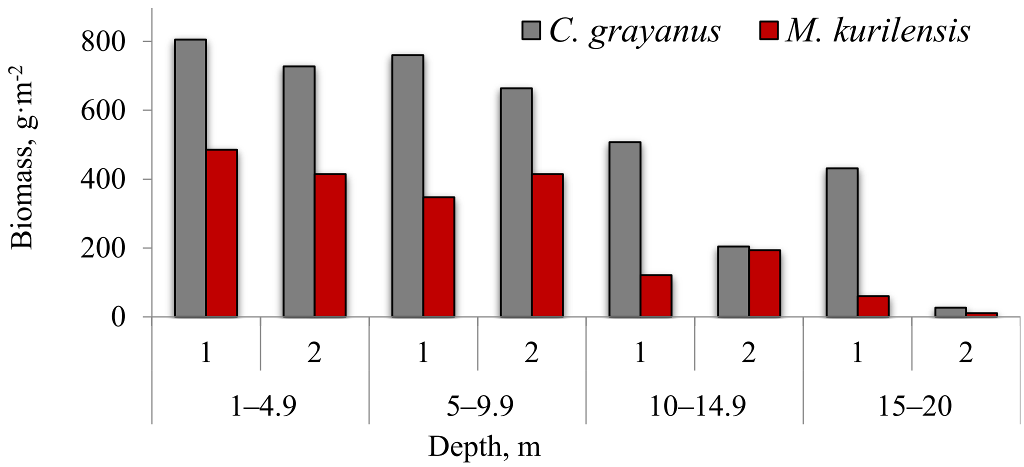
Table 4. Distribution of mean biomass of *Crenomytilus grayanus* on hard and soft bottom sediments depending on the habitat depth in Peter the Great Bay, g·m^{-2}

Section \ Depth	1–4.9 m	5–9.9 m	10–14.9 m	15–20 m
	Mean biomass ± *SEM*; in parentheses, standard deviation; below the line, range of values			
Hard bottom sediments				
1.Southwestern PGB	767 ± 161 (992) / 4–3,530	791 ± 394 (2,367) / 4–14,120	800 ± 302 (1,209) / 4–3,883	239 ± 155 (409) / 4–1,059
2. Posyet Bay	610 ± 104 (849) / 0.3–3,900	856 ± 168 (1,232) / 0.3–6,000	930 ± 278 (1,390) / 1–5,100	395 ± 220 (731) / 1–2,500
3. Boisman Bay	480 ± 191 (787) / 1–2,615	862 ± 259 (1,217) / 1–4,555	545 ± 216 (683) / 1–2,070	3 ± 2 (3) / 1–5
4. Baklan Bay	592 ± 405 (993) / 1–2,592	613 ± 124 (351) / 190–1,098	977 ± 813 (1,408) / 80–2,600	1,000
5. Amur Bay	639 ± 234 (1,533) / 0.2–9,610	418 ± 177 (1,019) / 0.7–5,760	58 ± 46 (80) / 3.4–150	0
6. Empress Eugénie Archipelago water areas	858 ± 158 (1,661) / 1–11,180	483 ± 119 (1,109) / 1–7,854	278 ± 103 (654) / 0.4–2,882	479 ± 241 (965) / 2–2,892
7. Ussuri Bay	506 ± 210 (1,092) / 0.6–5,325	994 ± 326 (1,459) / 1–5,000	325 ± 169 (478) / 1–1,320	282 ± 278 (393) / 3–560
8. Eastern PGB	964 ± 225 (1,770) / 0.1–9,562	1,162 ± 310 (2,280) / 1–11,448	200 ± 138 (572) / 0.1–2,336	502 ± 333 (941) / 1.2–2,450
Soft bottom sediments				
1. Southwestern PGB	0	107 ± 82 (165) / 4–353	4	34 ± 17 (55) / 4–177
2. Posyet Bay	555 ± 208 (1,247) / 0.3–5,040	392 ± 119 (916) / 0.3–5,000	248 ± 71 (421) / 0.7–1,582	29 ± 20 (61) / 0.6–189
3. Boisman Bay	0	0.6	2.5	5
4. Baklan Bay	0	493 ± 296 (591) / 2–1,199	247 ± 245 (347) / 2–492	0
5. Amur Bay	693 ± 305 (1,139) / 0.9–4,000	1,045 ± 302 (2,026) / 0.9–8,000	290 ± 115 (414) / 0.1–1,200	80
6. Empress Eugénie Archipelago water areas	1,012 ± 280 (1,731) / 1–7,252	736 ± 147 (1,246) / 0.2–7,200	218 ± 57 (408) / 0.2–2,060	32 ± 25 (104) / 0.5–436
7. Ussuri Bay	77 ± 63 (166) / 0.2–450	221 ± 146 (506) / 0.1–1,800	8 ± 3 (8) / 1.5–22	0.8 ± 0.3 (0.4) / 0.5–1.1
8. Eastern PGB	13 ± 10 (14) / 3–22	1,030 ± 475 (1,344) / 2–3,842	194 ± 74 (257) / 3–744	3 ± 0.4 (0.9) / 1.6–3.7

Analyzing the entire PGB, it has to be noted that *C. grayanus* forms settlements with the highest biomass at depths of 1–20 m on hard substrates (mean value is 431–805 g·m^{-2}) and at depths of down to 10 m on soft ones (Fig. 5). At the same time, mean biomass values at depths of 1–4.9 and 5–9.9 m did not differ significantly for *C. grayanus* inhabiting both types of bottom sediments (p = 0.495 and p = 0.425, respectively). There were no noticeable differences in these indicators (Fig. 5) in molluscs inhabiting hard substrates at depths of 10–14.9 and 15–20 m as well (p = 0.920). Interestingly, mean biomass values for *C. grayanus* inhabiting soft bottom sediments at same depths were significantly different (p = 0.0002).

Table 5. Distribution of mean biomass of *Modiolus kurilensis* on hard and soft bottom sediments depending on the habitat depth in Peter the Great Bay, g·m^{-2}

Section \ Depth	1–4.9 m	5–9.9 m	10–14.9 m	15–20 m
	Mean biomass ± *SEM*; in parentheses, standard deviation; below the line, range of values			
Hard bottom sediments				
1. Southwestern PGB	81 ± 40 (69) 1–121	121	121	12
2. Posyet Bay	341 ± 216 (1,146) 1–6,000	860 ± 507 (1,717) 1–5,048	22 ± 14 (24) 6–50	2.4 ± 0.4 (0.8) 2–3.3
3. Boisman Bay	14 ± 1 (2) 12–15	15 ± 1 (1) 14–17	301 ± 299 (423) 2–600	0.4
4. Baklan Bay	5 ± 4 (8) 1–15	24 ± 21 (56) 1–150	0	0
5. Amur Bay	132 ± 54 (179) 0.1–580	128 ± 38 (127) 0.2–350	1.3 ± 0.4 (0.6) 0.8–2	0
6. Empress Eugénie Archipelago water areas	1,002 ± 369 (2,055) 0.4–8,512	490 ± 174 (936) 1–4,204	155 ± 59 (166) 1–417	182 ± 180 (360) 0.5–722
7. Ussuri Bay	40	29 ± 14 (24) 2–50	190 ± 187 (266) 2–378	0
8. Eastern PGB	205 ± 186 (618) 0.7–2,068	57 ± 53 (151) 0.1–432	85 ± 82 (143) 2–250	18 ± 17 (39) 0.7–88
Soft bottom sediments				
1. Southwestern PGB	242	61	0	28 ± 16 (28) 12–61
2. Posyet Bay	267 ± 83 (557) 0.5–3,110	205 ± 68 (467) 0.6–2,496	116 ± 50 (229) 0.5–900	7 ± 2 (6) 1–16
3. Boisman Bay	0	0.7	1.4	1.5
4. Baklan Bay	0	1.1	1.2	3.0
5. Amur Bay	271 ± 127 (458) 0.5–1,640	615 ± 280 (1,609) 0.9–8,000	235 ± 71 (188) 2–500	18 ± 15 (27) 2–50
6. Empress Eugénie Archipelago water areas	668 ± 185 (1,095) 1.6–3,762	464 ± 68 (584) 0.3–2,738	254 ± 82 (506) 0.3–1,933	13 ± 10 (36) 0.6–126
7. Ussuri Bay	0	157 ± 87 (150) 1–300	8	1.4 ± 0.3 (0.5) 1.1–1.8
8. Eastern PGB	219 ± 68 (205) 1–532	609 ± 276 (917) 1–3,018	168 ± 136 (332) 1–834	1.2 ± 0.03 (0.05) 1.2–1.3



Species	Mean biomass ± *SEM*; in parentheses, standard deviation; below the line, range of values, g·m^{-2}			
1, hard bottom sediments				
C. grayanus	805 ± 72 (1,460) 0.1–11,180	760 ± 88 (1,579) 0.1–14,120	507 ± 85 (952) 0.1–5,100	431 ± 118 (806) 1–2,892
M. kurilensis	485 ± 136 (1,357) 0.1–8,512	347 ± 98 (842) 0.1–5,048	121 ± 37 (175) 1–600	60 ± 51 (192) 0.1–722
2, soft bottom sediments				
C. grayanus	727 ± 141 (1,418) 0.1–7,252	664 ± 94 (1,348) 0.1–8,000	204 ± 33 (374) 0.1–2,060	27 ± 11 (72) 1–436
M. kurilensis	415 ± 76 (787) 1–3,762	415 ± 66 (874) 0.1–8,000	194 ± 44 (392) 0.1–1,933	11 ± 4 (25) 1–126

Fig. 5. Distribution of mean biomass of *Crenomytilus grayanus* and *Modiolus kurilensis* depending on the habitat depth in Peter the Great Bay

M. kurilensis prevailed at depths of 1–10 m on both types of bottom sediments (Fig. 5). There were no significant differences in mean biomass values for *M. kurilensis* inhabiting both hard and soft substrates at depths of 1–4.9 and 5–9.9 m ($p = 0.508$ and $p = 0.985$, respectively), while at 10–14.9 and 15–20 m, mean biomass values for this species were noticeably different ($p = 0.019$ and $p = 0.001$, respectively).

DISCUSSION

The results of the study and analysis of literary sources confirmed the existence of both monospecific and mixed settlements of *C. grayanus* and *M. kurilensis*. According to the data obtained, in the PGB, monospecific druses of *C. grayanus* prevailed both on hard and soft bottom sediments, while mixed druses prevailed on soft substrates (Fig. 4). Similar studies on spatial distribution of Mytilidae on different types of bottom sediments throughout the PGB have not been carried out earlier.

The stable position of mytilids on bottom sediments is ensured by their byssus filaments which reduce unfavorable hydrodynamic load of the environment [Vekhova, 2007]. *C. grayanus* is known to attach more successfully to hard bottom sediments, while *M. kurilensis*, to soft ones [Rees et al., 2008; Selin, 2018b; Selin, Vekhova, 2002, 2004; Vekhova, 2013, 2019]. It is related to the morphology and size of byssus filaments. The Gray mussel – with its streamlined mytiloid-shaped shell and strong attachment to substrates with the help of a powerful byssus apparatus – prefers to settle on hard rocky and boulder sediments in coastal areas with moderate wave action [Skarlato, 1981]. On soft bottom sediments, the Gray mussel can form settlements only when it finds a hard base: rare boulders, stone-strewn area, or mollusc shells [Selin, Vekhova, 2004]. The horsemussel – with its wide and light shell with periostracum setae and numerous long and thin byssus filaments (those are capable of penetrating deep into bottom sediment, thereby facilitating the mollusc staying on its surface) – usually inhabits deeper areas of bay bottom sheltered from waves [Selin, 2018a; Vekhova, 2007]. When a single horsemussel tries to attach to hard substrates, the thickness of its byssus filaments does not allow either to stay on their surface or to form druses.

The formation of mixed druses is due to the fact that *C. grayanus* and *M. kurilensis* larvae can settle on druses of both species; this allows molluscs to inhabit unusual biotopes [Kutishchev, Gogolev, 1983; Lindenbaum et al., 2008; Selin, 1977, 2018a; Tsuchiya, 2002]. According to the literature data, in mixed druses formed on hard substrates, the structure of *C. grayanus* druses is usually preserved; on soft bottom sediments, the structure of *M. kurilensis* druses is preserved. More stable aggregations are formed mainly on hard substrates (rocks, blocks, boulders, and stones) and consist of medium and large druses with a dense spatial structure, which increases the efficiency of Mytilidae larvae settling [Kutishchev, Gogolev, 1983; Vigman, 1983]. In mixed druses on hard substrates, the horsemussel can live due to the compensation of its attachment by a more powerful byssus apparatus of the Gray mussel.

C. grayanus and *M. kurilensis* larvae settle on bottom settlements of adult mussels. After the metamorphosis is complete, those attach with their byssus filaments to a shell surface, to byssus filaments of larger Mytilidae, or among the periostracum setae of the horsemussel [Selin, 2018a]. However, on soft bottom sediments, the conditions for juvenile settling are hampered by the fact that adults are contaminated with silty sand (therefore, the larvae settle less than on hard substrates). Settling of *C. grayanus* larvae on *M. kurilensis* druses occurs annually; when the horsemussel specimens are displaced from mixed druses, the Gray mussel can form monospecific druses on soft bottom sediments [Selin, 1991]. Under favorable conditions of hydrodynamic load, *C. grayanus* can form extensive settlements on soft substrates as well [Selin, 2018a; Selin, Vekhova, 2003; Skarlato et al., 1967]. The successful coexistence of Mytilidae on different types of bottom sediments was shown by N. Selin [2018a] for a local area of Vostok Bay (the PGB).

The ratio of *C. grayanus* biomass (of the total biomass of two species) in different PGB sections ranged within 54.8–97.9%, averaging 76.9% throughout the bay. On hard substrates, the value was higher (79.0%); on soft ones, it was lower (61.0%). The lower mean values of *M. kurilensis* biomass, compared to that of *C. grayanus* (Table 3), can be explained by its subtropical origin as well, since the water area of most of the PGB is suitable for the habitat of low-boreal species, while subtropical boreal species inhabit mainly shallow coastal areas, which are well warmed up during summer, and sheltered bays [Golikov, Skarlato, 1967; Skarlato, 1981].

At depths of 1–10 m, the biomass of the studied species in the PGB, both on hard and soft substrates, mostly reached its highest values; at depths of 10–20 m, only *C. grayanus* biomass on hard bottom sediments reached its maximum (Fig. 5). This is consistent with the literature data. As known, with increasing depth, there is a decrease in the occurrence and biomass of almost all benthic species, except for boreal-Arctic ones [Golikov, Skarlato, 1967]. As a rule, subtropical species inhabit the depths of down to 5 m; deeper (down to 20 m), low-boreal species prevail [Skarlato et al., 1967].

In the southwestern PGB, as well as in Posyet, Boisman, and Baklan bays, the highest biomass of the Gray mussel on hard bottom sediments was recorded at depths of down to 15 m; in other sections, down to 10 m; on soft substrates in the Amur and Posyet bays, down to 10 m; and in Baklan Bay and the eastern PGB, at depths of 5–10 m (Table 4). The highest biomass of the horsemussel was registered at depths of down to 10 m in Posyet Bay on hard bottom sediments; in the Empress Eugénie Archipelago water areas on both types of bottom sediments; and at depths of 5–10 m in the Amur Bay and the eastern PGB on soft substrates (Table 5).

Conclusion. The landscape diversity of the bottom of the Peter the Great Bay (the Sea of Japan) is the reason for the almost ubiquitous distribution of *C. grayanus* and *M. kurilensis*, and this reflects good adaptation of molluscs to the conditions typical for this part of their area. *C. grayanus* and *M. kurilensis* abundance in different sections of the bay varies widely. However, the mean biomass of the Gray mussel on hard bottom sediments exceeds its value for soft substrates by 1.5 times, and the biomass of the horsemussel, both on hard and soft bottom sediments, by 2 times. There was no difference in mean biomass values of *M. kurilensis* on hard and soft substrates. Both on hard and soft bottom sediments, monospecific druses of the Gray mussel prevail; on soft substrates, mixed druses prevail.

When planning Mytilidae harvesting in the Peter the Great Bay, it should be taken into account as follows: both species form settlements with a maximum biomass at depths of down to 10 m (*C. grayanus*, on hard bottom sediments; *M. kurilensis*, on soft substrates). This makes it possible to collect molluscs by diving.

Acknowledgement. The authors are sincerely grateful to the anonymous reviewers for their constructive comments and recommendations, which were taken into account when preparing this article for publication.

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ОСОБЕННОСТИ ПРОСТРАНСТВЕННОГО РАСПРЕДЕЛЕНИЯ *CRENOMYTILUS GRAYANUS* И *MODIOLUS KURILENSIS* (BIVALVIA, MYTILIDAE) В ЗАЛИВЕ ПЕТРА ВЕЛИКОГО (ЯПОНСКОЕ МОРЕ)

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Двустворчатые моллюски семейства Mytilidae — мидия Грея *Crenomytilus grayanus* (Dunker, 1853) и модиолус курильский *Modiolus kurilensis* Bernard, 1983 — тихоокеанские, приазиатские виды, массовые представители эпифауны верхней сублиторали прибрежных вод залива Петра Великого Японского моря. Мидия Грея является традиционным, а модиолус — перспективным объектом промысла; оба вида имеют значительные ресурсы. Цель работы — выполнить сравнительный анализ пространственного распределения и обилия *C. grayanus* и *M. kurilensis* на разных типах грунта и глубинах обитания в заливе Петра Великого. Исследования проводили в 2007–2019 гг. с использованием стандартных водолазных гидробиологических методов на глубинах до 20 м. Выполнено 5911 станций; на 1635 из них обнаружены митилиды. У митилид определяли прижизненную массу каждой особи и среднюю биомассу. Ландшафтное разнообразие дна залива Петра Великого обуславливает почти повсеместное распространение *C. grayanus* и *M. kurilensis*, что отражает хорошую адаптацию моллюсков к условиям, характерным для этой части их ареала. Моновидовые друзы *C. grayanus* преобладали как на твёрдых, так и на мягких субстратах (78,6 и 38,2 % от общего количества станций с митилидами соответственно), а смешанные друзы обоих видов — на мягких грунтах (38,3 %). Моновидовые друзы *M. kurilensis* на мягких субстратах встречались чаще (23,5 %), чем на твёрдых (8,1 %). В заливе Петра Великого средняя биомасса *C. grayanus* на твёрдых грунтах составляла (728 ± 47) г·м$^{-2}$, варьируя от 524 г·м$^{-2}$ (Амурский залив) до 922 г·м$^{-2}$ (восточная часть залива Петра Великого); на мягких грунтах — (491 ± 51) г·м$^{-2}$, изменяясь от 228 г·м$^{-2}$ (Уссурийский залив) до 829 г·м$^{-2}$ (Амурский залив), за исключением юго-западной части залива Петра Великого и бухты Бойсмана, где значение было ниже 50 г·м$^{-2}$. Средняя биомасса *M. kurilensis* на твёрдых грунтах составляла (370 ± 74) г·м$^{-2}$, варьируя от 18 г·м$^{-2}$ (бухта Баклан) до 656 г·м$^{-2}$ (акватории архипелага Императрицы Евгении); на мягких грунтах — (335 ± 37) г·м$^{-2}$, изменяясь от 77 г·м$^{-2}$ (юго-западная часть залива Петра Великого) до 456 г·м$^{-2}$ (Амурский залив), за исключением бухт Бойсмана и Баклан, где вид встречался единично. В заливе Петра Великого максимальные значения средней биомассы обоих видов отмечены на глубинах 1–10 м (*C. grayanus* — 664–805 г·м$^{-2}$, *M. kurilensis* — 347–485 г·м$^{-2}$); с возрастанием глубины их обилие снижалось. Значения средней биомассы *C. grayanus*, обитающей на глубинах от 10 до 20 м на твёрдых субстратах, также достаточно высоки — 431–507 г·м$^{-2}$. На мягких грунтах с изменением глубины от 10–15 до 15–20 м её средняя биомасса уменьшалась от (204 ± 33) до (27 ± 11) г·м$^{-2}$. Средняя биомасса *M. kurilensis* на глубинах 10–15 м составляла 121–194 г·м$^{-2}$, а на глубинах 15–20 м — 11–60 г·м$^{-2}$ на обоих типах грунта.

Ключевые слова: митилиды, Mytilidae, мидия Грея, *Crenomytilus grayanus*, модиолус курильский, *Modiolus kurilensis*, биомасса, распределение, грунт, глубина обитания, залив Петра Великого, Японское море