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Bivalve mollusks of Ussuriysky Bay (Sea of Japan). Part 2

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The second part of the paper deals with ecological and biogeographical analyses of the bivalve molluscan fauna of Ussuriysky Bay comprising 124 species from 36 families; three species were found to be regionally extinct in the Holocene. 11 species were collected intertidally (*Mytilus trossulus, Vilasina pillula, Modiolus kurilensis, Septifer keenae, Arca boucardi, Crassostrea gigas, Chlamys farreri, Turtonia minuta, Mactra chinensis, Potamocorbula amurensis, Hiatella arctica*). Most frequently found in bottom samples collected by bottom samplers and trawls were eleven species (*Nucula ovatotruncata, Musculus niger, Axinopsida subquadrata, Adontorhina filatovae, Clinocardium likharevi, Serripes groenlandicus, Liocyma fluctuosum, Callithaca adamsi, Macoma calcarea, M. scarlatoi, Mya japonica*). They represent a boreal and boreal-arctic assemblage characteristic of the open part of the bay. Complexes of dominant and common species of the upper subtidal zone of the bay in its environmentally different parts are briefly described. Zonal-geographical analysis shows that boreal species are predominant (45%) with a significant proportion of subtropical and subtropical-boreal mollusks (36%). Bathymetric distribution of species, families and biogeographical complexes of bivalve mollusks is discussed.

Двустворчатые моллюски Уссурийского залива (Японское море). Часть 2

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Во второй части статьи проведен эколого-биогеографический анализ фауны Bivalvia Уссурийского залива, в составе которой зарегистрировано 124 вида из 36 семейств; из них три вида являются регионально вымершими в голоцене. На литорали залива собрано 11 видов (*Mytilus trossulus, Vilasina pillula, Modiolus kurilensis, Septifer keenae, Arca boucardi, Crassostrea gigas, Chlamys farreri, Turtonia minuta, Mactra chinensis, Potamocorbula amurensis, Hiatella arctica*). Наиболее часто встречающимися в дночерпательных и траловых пробах были 11 видов (*Nucula ovatotruncata, Musculus niger, Axinopsida subquadrata, Adontorhina filatovae, Clinocardium likharevi, Serripes groenlandicus, Liocyma fluctuosum, Callithaca adamsi, Macoma calcarea, M. scarlatoi, Mya japonica*), которые представляют бореальный и бореально-арктический комплекс, характерный для открытой части залива. Кратко описаны с привлечением литературных данных комплексы доминирующих и обычных видов самой верхней сублиторали залива в биономически разных его частях. Зонально-географический анализ фауны показал, что в ее составе преобладают бореальные виды (45%) при значительной представленности субтропических и субтропическо-бореальных моллюсков (36%). Рассмотрено батиметрическое распределение видов, семейств и биогеографических групп двустворчатых моллюсков.

Environmental setting

Ussuriysky Bay is the largest secondary bay in the north-eastern part of Peter the Great Bay. The north-western coastline of Ussuriysky Bay extends along the Murav'yeva-Amurskogo Peninsula and its insular continuation – Russky, Popova, Reineke, Rikorda, and some other small islands (see Fig. 1 in the first part of this paper: Lutaenko, 2005). The total length of the bay coastline is about 125 km. Ussuriysky Bay is a typical ria bay formed during the post-glacial time by ingression of marine waters into the valley of a former river [Lymarev, 1966; Markov, 1983]. About 18000–20000 years BP (Late Pleistocene Würm epoch), the sea level was at about −110...−120 m below its present position, and the area of the bay was an alluvial plain with rivers and lakes; at the maximum of the Holocene transgression (5000–6000 years BP), the sea level was 1–2 m above the present, and waters of Ussuriysky Bay spread into the river valleys in its inner part beyond the present-day coastline. These paleo-bays have been replaced with low accumulative coastal plains.

Coasts of the bay are high, steep, with many cliffs and benches, except for the northern part, where there is a wide coastal plain (Fig. 1). Spurs of the southern part of the Sikhote-Alin Mountains approach the eastern coast of Ussuriysky Bay. A number of small streams and rivers flow into the bay, the largest – Artyomovka, Shkotovka, Petrovka and Sukhodol (Kangauz) – flow into the inner part of the bay. The north-western coast of Ussuriysky Bay (from Bosphor Vostochny Strait to Cape Obryvisty) stretches for about 40 km to the north-east; it is steep and little indented, low sandy terraces are found only in the inner parts of small bays (Gornostay, Lazurnaya Bays) (Fig. 2). Beaches are mostly gravelly, with many rocks in the intertidal zone (Figs. 3, 4), sometimes with a significant admixture of shelly material. The eastern coast of Ussuriysky Bay extends from Cape Obryvisty to Askold Strait for 50 km; it is steep and rocky, with many narrow sandy and gravelly beaches, and more indented as compared to the western coast. The largest bay here is Sukhodol Bay, and there are a number of smaller bays – Bolshogo Kamnya, Andreeva, Il'movaya, Dunay, etc. Ussuriysky Bay is rather shallow, with a maximum depth of 60–70 m at the entrance, about 35 m in the middle part, and 2–10 m in the inner part. Some of our samples were taken from the

Fig. 1. Coastal plain in the inner part of Ussuriysky Bay (near mouth of Shkotovka River). Photo by K.A. Lutaenko (July 1997).

Fig. 2. Sandy beach with gravel festons in Gornostay Bay (western coast of Ussuriysky Bay). Photo by K.A. Lutaenko (April 2002).

Fig. 3. Rocky coast in Sobol' Bay (south-western coast of Ussuriysky Bay). Photo by K.A. Lutaenko (April 2001).

161–240 m depth (sta. 77, 78 of the R/V *Lugovoye*, see: Lutaenko, 2005) near outer Ussuriysky Bay.

The bottom deposits in Ussuriysky Bay are predominantly aleurite and pelitic mud occupying the middle and outer parts of the bay, as well as central areas in its inner part and in Sukhodol Bay; in the outer part, mud may have an admixture of sand [Likht et al., 1983]. Sandy bottom is characteristic for two large bays on the western coast – Gornostay and Lazurnaya, fine-grained sand is distributed along the eastern coast. At abrasion coasts, sandy bottom is patchy, usually with an admixture of shell debris and gravel. Underwater surveys show the presence of large rocks and extensive rocky platforms with crevices traced down to the 10 m depth [Tarasov et al., 2005].

The meteorological regime of Ussuriysky Bay is determined by monsoonal circulation of the atmosphere, geographical position of the area, summer typhoons, and sea currents. In October–March, cold air transferred from the continent to the sea (winter monsoon) brings about cold, frosty weather with limited snow and prevailing northern and north-western winds. Summer monsoon occurs from May–June to August–September and is accompanied

Fig. 4. Gravelly beach and cliff in Desantnaya Bay (western coast of Ussuriysky Bay). Photo by K.A. Lutaenko (July 2002).

Fig. 5. Salinity (‰) in the near-bottom layer of Ussuriysky Bay in August (after: Podorvanova et al., 1989, fig. 60b).

by humid and foggy weather. Autumn is warm, dry, and sunny. Annual average precipitation in the area of Vladivostok City reaches 830 mm, with 85% of total annual precipitation during the summer period. Annual average air temperature is 6° C, with a minimum of −16...−17°C (to −36°C in the inner bay) in January and a maximum of +29…+31°C in August.

The hydrological regime of Ussuriysky Bay largely depends on geographical position and geomorphology, climate, river discharge, and currents [Biryulin et al., 1970; Vinokurova, 1977; Podorvanova et al., 1989; Zuenko, 1994; Danchenkov et al., 2003; Gayko, 2005; et al.]. Tidal range is small, with a maximum of up to 0.4–0.5 m, the velocity of tidal currents do not exceed 10–15 cm/s. In winter, the temperature of coastal waters decreases to −1…−2°C; waters in the open part are warmer. Surface water temperatures in spring are from +4 to +14°C. In summer, surface water is well warmed-up, especially in the inner part of the bay, where surface water temperature can increase to +24…+26°C in August. At the same time, coastal upwelling of cold waters occurs in the central part of the bay in summer [Danchenkov et al., 2003]. The cold Primorskoe Current influences the southern, open part of Ussuriysky Bay [Ivaschenko, 1993]. In winter (December–March), inner part is covered by ice.

Salinity in the open areas of Ussuriysky Bay is close to normal marine, varying from 32 to 33‰ in surface layer and from 33 to 33.5‰ near bottom [Podorvanova et al., 1989]. However, due to river runoff, salinity in the inner part decreases to 27.5–31‰ at the water surface (Fig. 5) and to 10–20‰ in the near-bottom layer; in the mouth of Artyomovka River, it is only about 9‰ [l.c.]. During heavy rainfalls in summer, surface water salinity may decrease significantly. During winter, salinity tends to be homogenous in the entire area of the bay.

Ecological and distributional aspects

In total, 124 species of bivalve mollusks belonging to 76 genera and 36 families were recorded for Ussuriysky Bay (Table 1). Three species (*Anadara inaequivalvis, A. kagoshimensis*, and *Meretrix lusoria*) are only found on beaches; they are regionally extinct in the Holocene and their shells are washed out to the beach by river and wave action [Lutaenko, 1992]. The number of species found is higher, compared to Possjet Bay (southwestern Peter the Great Bay) – 97 species [Golikov, Scarlato, 1967; Scarlato, 1981] and Vostok Bay (eastern Peter the Great Bay) – 88 species [Evseev, 1981]; but it close to the figure obtained for Amursky Bay – 119 species [Lutaenko, 2003] (Table 2). However, some species have not been collected in Ussuriysky Bay, perhaps, due to the inadequate sampling technique or rarity. Among possible inhabitants of the bay, we mention *Megayoldia thraciaeformis* (Storer, 1838), *Macoma loveni* (Jensen, 1905), *Pandora pulchella* Yokoyama, 1926, *Periploma fragilis* (Totten, 1845), and some others living in deeper areas (mostly below 70–100 m) and found in neighboring Amursky Bay. O.A. Scarlato [1972] described several species of cuspidariids from Peter the Great Bay including those living at depths of 50–100 m (*Cuspidaria ascoldica* Scarlato, 1972, *Cardiomya lindbergi* Scarlato, 1972).

Bivalves found intertidally are mostly inhabitants of rocky shores in bays located in the southwestern part of Ussuriysky Bay – Sobol' and Tikhaya Bays. They are byssally attached species (*Mytilus trossulus, Vilasina pillula, Modiolus kurilensis, Septifer keenae, Arca boucardi, Chlamys farreri, Turtonia minuta, Hiatella arctica*) and one cemented bivalve – an oyster *Crassostrea gigas*. The majority of intertidal mollusks were collected in small quantitites and only juvenile and young individuals were found. Thus, *A. boucardi* had a shell length between 3 and 7 mm, *C. gigas* – 20–40 mm. *S. keenae, A. boucardi, C. gigas* and *H. arctica* occur only under rocks and boulders, attached to their lower surfaces. However, some species form dense settlements in the intertidal zone: *M. trossulus* in Tikhaya and Sobol' Bays can form mussel beds, and *T. minuta*

Table 1

List of species, bathymetric distributions and zonal-biogeographical characteristics of bivalve mollusks from Ussuriysky Bay, Sea of Japan

Species	Depth range, m	Zonal-biogeographical characteristics
Acila insignis	5–27	Subtropical-lowboreal
Nucula ovatotruncata	19–60	Lowboreal
N. tenuis	70–74	Widely distributed boreal-artcic
Nuculana sadoensis	70–74	Subtropical-lowboreal
Yoldia hyperborea	60	Widely distributed boreal-arctic
Y. notabilis	40–52	Subtropical-lowboreal
Y. keppeliana	28–45	Lowboreal
Y. johanni	26–30	Lowboreal
Y. seminuda	40–60	Widely distributed boreal
Y. toporoki	70	Lowboreal
Portlandia toyamaensis	50–70	Subtropical
Yoldiella derjugini	46–70	Widely distributed boreal
Arca boucardi	0	Subtropical-lowboreal
Anadara kagoshimensis	–	[Locally extinct]
A. inaequivalvis	–	[Locally extinct]
A. broughtonii	–	Subtropical
Glycymeris yessoensis	30	Lowboreal
Mytilus galloprovinciallis	–	Amphiboreal (circumboreal)
M. trossulus	0–52	Amphiboreal (circumboreal)
M. coruscus	–	Subtropical
Crenomytilus grayanus	–	Lowboreal
Musculista senhousia	–	Subtropical-lowboreal
Musculus niger	50–70	Widely distributed boreal
M. laevigatus	70	Widely distributed boreal
M. discors	70	Widely distributed boreal-arctic
M. glacialis	50–60	Widely distributed boreal-arctic
M. koreanus	70–74	Lowboreal
Vilasina pillula	0	Lowboreal
Modiolus kurilensis	0	Subtropical-boreal
Septifer keenae	0	Subtropical
Adula falcatoides	2.5–3	Lowboreal
Crassostrea gigas	0–30	Subtropical-lowboreal
Chlamys chosenica	–	Lowboreal
Ch. farerri	0	Subtropical
Ch. swiftii	–	Lowboreal

Table 1 (continued)

Species	Depth range, m	Zonal-biogeographical characteristics
Mizuhopecten yessoensis	–	Lowboreal
Pododesmus macrochisma	–	Widely distributed boreal
Pillucina pisidium	–	Subtropical
Conchocele scarlatoi	–	Lowboreal
Axinopsida subquadrata	5–70	Widely distributed boreal-arctic
Adontorhina filatovae	60–88	Lowboreal
Mendicula ferruginosa	88	Widely distributed boreal+circumboreal
Thyasira flexuosa	53	Boreal-arctic
Felaniella usta	–	Subtropical-lowboreal
Diplodonta semiasperoides	–	Lowboreal
Nipponomysella obesa	0	Subtropical
Mysella planata	50–70	Widely distributed boreal-arctic
Alvenius ojianus	0–74	Subtropical
Astarte elliptica	40	Widely distributed boreal-arctic
A. montagui	40	Widely distributed boreal-arctic
Cyclocardia rjabininae	122	Widely distributed boreal
C. crassidens	40	Widely distributed boreal
Clinocardium californiense	–	Widely distributed boreal
C. ciliatum	70	Widely distributed boreal-arctic
C. likharevi	40–74	Lowboreal
Serripes groenlandicus	21–70	Widely distributed boreal-arctic
S. notabilis	68–71	Widely distributed boreal
Trapezium liratum	–	Tropical-subtropical
Corbicula japonica	–	[Brackish-water]
Callista brevisiphonata	–	Lowboreal
Saxidomus purpuratus	–	Subtropical
Dosinia japonica	–	Subtropical
D. penicillata	5	Tropical-subtropical
Venerupis philippinarum	3–6	Subtropical-lowboreal
Liocyma fluctuosum	21–240	Widely distributed boreal-arctic
Mercenaria stimpsoni	5–8	Lowboreal
Protothaca euglypta	–	Subtropical
P. jedoensis	–	Subtropical
Callithaca adamsi	5–45	Lowboreal
Meretrix lusoria	–	–
Turtonia minuta	0	Circumboreal
Cadella lubrica	–	Subtropical-lowboreal

Table 1 (continued)

Species	Depth range, m	Zonal-biogeographical characteristics
Megangulus luteus	40	Widely distributed boreal
M. venulosus	–	Lowboreal
M. zyonoensis	–	Lowboreal
Macoma calcarea	30–81	Widely distributed boreal-arctic
M. balthica	–	Amphiboreal (circumboreal)
M. incongrua	3–30	Subtropical-lowboreal
M. loveni	40	Widely distributed boreal-arctic
M. lama	–	Widely distributed boreal
M. golikovi	–	Widely distributed boreal
M. nipponica	–	Subtropical
M. scarlatoi	19–50	Widely distributed boreal
M. tokyoensis	5	Subtropical
M. contabulata	–	Subtropical
M. coani	–	Subtropical-lowboreal
M. hokkaidoensis	1.5–2	Lowboreal
M. irus	–	Subtropical
Macoma sp.	–	–
Gari californica	–	Widely distributed boreal
Nuttallia obscurata	–	Subtropical
N. ezonis	–	Lowboreal
N. commoda	40–45	Widely distributed boreal
Theora lubrica	27	Subtropical-lowboreal
Solen strictus	–	Subtropical
S. krusensterni	–	Subtropical-lowboreal
Siliqua alta	–	Widely distributed boreal
Mactra chinensis	–	Subtropical-lowboreal
M. quadrangularis	–	Subtropical
Spisula sachalinensis	–	Lowboreal
Mactromeris polynyma	–	Widely distributed boreal
Raeta pulchella	27–39	Tropical-subtropical
Mya truncata	40	Widely distributed boreal-arctic
M. uzenensis	8–45	Widely distributed boreal
M. japonica	28–70	Widely distributed boreal
Cryptomya busoensis	21	Subtropical
Anisocorbula venusta	30	Subtropical-lowboreal
Potamocorbula amurensis	0–27	Subtropical-lowboreal
Hiatella arctica	0–74	Widely distributed boreal-arctic

Table 1 (continued)

Species	Depth range, m	Zonal-biogeographical characteristics
Panomya norvegica	–	Widely distributed boreal-arctic
P. nipponica	45	Lowboreal
Panopea abrupta	–	Subtropical-boreal
Barnea manilensis	–	Tropical-subtropical
B. japonica	–	Subtropical
Zirfaea cf. *subconstricta*	–	Subtropical
Teredo navalis	–	Circumsubtropical-lowboreal
Bankia setacea	–	Boreal (amphipacific)
Zachsia zenkewitschi	0.5–0.6	Subtropical
Pandora pulchella	–	Subtropical-lowboreal
Lyonsia arenosa	70	Widely distributed boreal-arctic
Entodesma navicula	0	Widely distributed boreal
Thracia itoi	–	Lowboreal
Th. kakumana	–	Lowboreal
Laternula marilina	–	Subtropical

Note. «–» – data are not available.

Table 2

Species richness of bivalve mollusks in different parts of Peter the Great Bay, Sea of Japan

Area	Number of species	Source	Notes
Peter the Great Bay	135	Scarlato [1981]	Including upper bathyal findings
Possjet Bay and adjacent areas	97	Golikov and Scarlato [1967]; Scarlato [1981]	Samples were taken at depth down to 120 m [Golikov and Scarlato, 1967]
Central and western part of Peter the Great Bay	91	Klimova [1984]	Samples were taken at depths down to 460 m
Vostok Bay	88	Evseev [1981]	Samples were taken at depth down to 90 m
Amursky Bay and adjacent areas	119	Lutaenko [2002, 2003]	Samples were taken at depth down to 162 m
Ussuriysky Bay and adjacent areas	124	Present study	Samples were taken at depth down to 240 m

is very abundant among seaweeds. The winter coastal ice (from December to March), usually completely destroys mussel beds, being thus an additional factor, along with wave action and surf, which have been shown to be responsible for cyclic changes in the distribution pattern, size composition, and abundance of intertidal mussels in Peter the Great Bay [Selin, 1990].

Among soft-bottom dwellers, *Mactra chinensis* was found in a sandy intertidal area of Gornostay Bay. In the inner part of Ussuriysky Bay, *Potamocorbula amurensis* was recorded intertidally. Another infaunal bivalve might occur intertidally, *Venerupis philippinarum*; it is sometimes collected in this bathymetric zone in southern Primorye [Ponurovsky, 1993].

Thus, 11 species of bivalves are known from the intertidal zone of Ussuriysky Bay. This is 38% of the total number of species (29) occurring in this zone in Peter the Great Bay [Kussakin et al., 1997]. *A. boucardi* and *Ch. farreri* are absent from the list of above-mentioned authors and, therefore, are first intertidal records for the area.

The most common and abundant species (found, at least, at 5 stations) in the subtidal zone of Ussuriysky Bay were *Nucula ovatotruncata* (7 sta., up to 52 specimens/station; hereafter – spec./sta.), *Musculus niger* (5 sta., up to 3 spec./sta.), *Axinopsida subquadrata* (18 sta., up to 24–26 spec./sta.), *Adontorhina filatovae* (7 sta., up to 24 spec./sta.), *Clinocardium likharevi* (6 sta., up to 5 spec./sta.), *Serripes groenlandicus* (9 sta., up to 15 spec./sta.), *Liocyma fluctuosum* (24 sta., up to 18 spec./sta.), *Callithaca adamsi* (8 sta., up to 9 spec./sta.), *Macoma calcarea* (6 sta., up to 4 spec./sta.), *Macoma scarlatoi* (7 sta., up to 4 spec./sta.), and *Mya japonica* (5 sta., up to 6 spec./sta.). These mollusks were collected at depths of 5–240 m, but mostly below the 20–30 m depth. Thus, the above complex of species is characteristic of relatively cold-water zone, and these species can be regarded as dominant in the bottom communities in the open part of the bay. They are boreal and boreal-arctic in their distribution and do not penetrate in the southern subtropical area of the Sea of Japan, except for *M. japonica*.

As we mentioned, data on the ecology and distribution of bivalve mollusks in Ussuriysky Bay are limited. In the inner bay, in estuarine areas and in some inlets (Andreeva, Bolshogo Kamnya, Sukhodol), oyster beds are very common; they occupy depths between 0.75 and 4 m, though dead shells can be found at depths down to 36 m (between Shamora (Lazurnaya) and Andreeva Bays) due to ice dispersal [Razin, 1934]. We also observed abundant oyster settlements in Desantnaya Bay. Mean population density of oysters reached up to 12–21 spec./m^2 in the 1930s (Table 3). According to V.A. Rakov and D.L. Brodyansky [1985], present-day distribution of oyster beds in Ussuriysky Bay is similar to their distribution in the 1930s. *C. gigas* is not an object of commercial fishing in southern Primorye, although attempts to cultivate this species were made in the 1970s.

Among abundant infaunal species in the inner part of the bay, one should mention a large arcid *Anadara broughtonii*; its population density in the 1930s reached 13 spec./m^2 but in the 1990s decreased to 4.7 spec./m^2 due to overfishing (Table 3). The infaunal community here also includes common and characteristic *Spisula sacha-*

Table 3

Biological characteristics (density of settlements and biomasses) of bivalve mollusks in Ussuriysky Bay, Sea of Japan

Species	Area	Density (specimens/m²) and biomasses (g/m²)	Reference
Anadara broughtonii	Inner part of the bay	Up to 4.7 sp./m², mean – 1.02 sp./m²; 96.8–1972.9 g/m²	Gabaev, Olifirenko, 2001
A. broughtonii	Maytun (=Murav'yny) Bay (inner part of Ussuriysky Bay)	Mean – 1.34 sp./m², maximum up to 13 sp./m²	Razin, 1934 (as *Arca inflata* Reeve, 1844)
Vilasina pillula	Stark Strait	523.9 sp./m²; 5.7 g/m²	Ivanova et al., 1994
Crenomytilus grayanus	Shamora (=Lazurnaya) Bay	1959 – 27.4 sp./m² 1970 – 3.4 sp./m²	Biryulina, 1972
	Sukhodol Bay	1970 – 1.5–4.7 sp./m²	
	Andreeva Bay	1959 – 5.3 sp./m² 1970 – 3.7 sp./m²	
	Cape Kom-Piho-Saho (=Golyi)	1959 – 3.0 sp./m² 1970 – 6.5 sp./m²	
	Bezymyannaya Bay	1959 – 2.5 sp./m² 1970 – 1.8 sp./m²	
	Cape Veselkina	1970 – 0.7 sp./m²	
	Askold Island	1970 – mean 2.4–3 sp./m²	
Crassostrea gigas	Ussuriysky Bay	2.5–21 sp./m²	Razin, 1934 (as *Ostrea gigas* and *O. laperousi* Razin, 1934)
Mizuhopecten yessoensis	Andreeva Bay (eastern coast of Ussuriysky Bay)	Mean – 0.07–2.00 sp./m²	Bregman, 1979
M. yessoensis	Sukhodol Bay	0.2 sp./m²	Biryulina, Rodionov, 1972
	Andreeva Bay	0.7 sp./m²	
	Cape Kom-Piho-Saho (=Golyi)	0.3 sp./m²	
	Bezymyannaya Bay	1.0 sp./m²	
Alvenius ojianus	Stark Strait	34.0 sp./m²; 7.5 g/m²	Ivanova et al., 1994
Dosinia japonica	Maytun (=Murav'yny) Bay (inner part of Ussuriysky Bay)	Up to 6 sp./m²	Razin, 1934
Mercenaria stimpsoni	Lazurnaya Bay	1.0 sp./m²	Biryulina, 1975
	Shitau-Uay Bay	Mean – 3.3 sp./m²	
Liocyma fluctuosum	Around Askold Island, depth 85 m	82 sp./m²; 7.5 g/m²	Klimova, 1975

Table 3 (continued)

Species	Area	Density (specimens/m²) and biomasses (g/m²)	Reference
Megangulus spp.	Lazurnaya Bay Shitau-Uay Bay	0.2 sp./m² 0.3 sp./m²	Biryulina, 1975 (as *Peronidia*; may include 2 species – *M. venulosus* and *M. zyonoensis*)
Spisula sachalinensis	Ussuriysky Bay	Mean – 3.6 sp./m²	Razin, 1934
S. sachalinensis	Lazurnaya Bay	0.5–6.3 sp./m²; mean – 2.3 sp./m²	Biryulina, 1975
Mactra chinensis	Lazurnaya Bay Shitau-Uay Bay	0.4 sp./m² Mean – 0.2 sp./m²	Biryulina, 1975
Hiatella arctica	Stark Strait	30.6 sp./m²; 0.2 g/m²	Ivanova et al., 1994

linensis, M. chinensis, Mactra quadrangularis, Raeta pulchella, Dosinia penicillata, V. philippinarum, Siliqua alta, Solen krusensterni, P. amurensis, Macoma incongrua and *M. japonica*. Corbulid *P. amurensis* is especially abundant in the near-mouth areas of rivers. Our taphonomic studies on beaches in 1991–1995 show that its density can reach up to 707 valves+complete shells/m² near the mouth of the Shkotovka River.

A brackish-water bivalve *Corbicula japonica* s.l. forms dense settlements in the mouths of rivers flowing into inner bay – Artyomovka, Shkotovka, and Petrovka [Yavnov, Rakov, 2002]. Density of populations in the lower reaches of Artyomovka River in 1990s was between 3–5 and 68 spec./m² (0.9–2 m depth), in Shkotovka River – 7–16 spec./m² (1.5–2.3 m depth), in Petrovka River (Sukhodol Bay) – 6–8 to 28 spec./m² [l.c.]. There is no fishing of this mollusk in Ussuriysky Bay though in early 1990s fishing of *C. japonica* was begun in neighboring Amursky Bay (Razdolnaya River estuary) for export to Japan.

Sandy bottom of open bays is occupied by the community of infaunal bivalves dominated by *S. sachalinensis, M. chinensis*; less common are *Nuttallia ezonis, Dosinia japonica, Felaniella usta, Panopea abrupta, Glycymeris yessoensis, Megangulus venulosus, Mercenaria stimpsoni.* Such an assemblage is typical for sandy beaches of Gornostay and Lazurnaya Bays. In Lazurnaya Bay, in 1970, settlements of *S. sachalinensis* with an area of about 140 hectares and average density of 2.3 spec./m² (0.5 to 6.3 spec./m²) occurred along the coastline at a depth of 1.5 to 6.2 m [Biryulina, 1975]. Commercial fishing of *S. sachalinensis* took place only in 1931–1934; at present, only non-regulated recreational summer harvesting exists. Data on the density of populations of some other bivalves in Ussuriysky Bay are summarized in Table 3.

Another assemblage of infaunal bivalves occurs on mixed substrata (sandy with admixture of shell debris, pebbles, gravels) and in sea-grass *Zostera* beds, widely distributed along rocky shores. Here, *Protothaca euglypta, Protothaca jedoensis, Saxidomus purpuratus, M. japonica, V. philippinarum,* and *Mya uzenensis* are abundant; *Diplodonta semiasperoides, Macoma irus, Gari californica, Anisocorbula venusta, Clinocardium californiense, Callista brevisiphonata* are less common. Epifaunal bivalves on rocky coast are represented by *Crenomytilus grayanus, Modiolus kurilensis, Septifer keenae, Mytilus coruscus*, and *Agriodesma navicula*. The giant mussel *C. grayanus* can reach a density of 27 spec./m^2, forming dense aggregations (Table 3). The Japanese scallop *Mizuhopecten yessoensis* is also a common member of the community of mixed substrata but its stock seems to have declined significantly in the second half of the 20th century due to poaching.

Comparison of the composition of common and abundant bivalves inhabiting different bays of the Sea of Japan (Table 4) may suggest that Japanese bays (Wakasa, Toyama, Tsukumo and Nanao) bear little similarity to Russian bays (Nakhodka, Ussuriysky, Amursky and Possjet) in this respect; only three species in common were found (*R. pulchella, Theora lubrica, Macoma tokyoensis*). This can be explained by the prevailence of warm-water, subtropical and tropical-subtropical, species in Japanese fauna owing to warming effect of the Tsushima Current, a branch of the Kuroshio. However, Korean Yeongil Bay is more similar to Russian bays by the composition of common/abundant species.

Table 4

Dominant and common species of bivalve mollusks in bays of the Sea of Japan

Locality	Dominant and common species	Reference
Wakasa Bay, Honshu	*Modiolus margaritaceus, Carditella hanzawai, Bathyarca kyurokusimana, Laevicirce soyoae, Crenulilimopsis oblonga, Variocorbula rotalis*	Ito, 1990
Toyama Bay, Honshu	<u>Euneritic zone (0–30 m)</u>: *Barbatia stearnsii, Limopsis japonica, Neopycnodonte musashiana, Pitar chordata, Fabulina nitidula* [=*Nitidotellina hokkaidoensis*], *Myadora fluctuosa*	Fujii, 1987
Tsukumo Bay, Noto Peninsula, Honshu	<u>Inner bay area</u>: *Anodontia stearnsiana, Pecten albicans, Laevicardium undatopictum, Fulvia hungerfordiana, Raetellops pulchella* [=*Raeta pulchella*], *Theora lubrica*, *Moerella iridescens, Nitidotellina minuta, Macoma tokyoensis;* <u>outer bay area</u>: *Oblimopa japonica, P. albicans, Pillucina yamakawai, Leptaxinus oyamai, L. undatopictum, Costellipitar chordatum, Nitidotellina nitidula* [=*N. hokkaidoensis*], *N. minuta*	Habe, 1973

Locality	Dominant and common species	Reference
Nanao Bay, Noto Peninsula, Honshu	*Nucula paulula, Theora lubrica*, *Paphia undulata, Microcirce gordonis*	Habe, 1956
Possjet Bay, northwestern Sea of Japan, Russia	Semi-enclosed bays: *Pillucina pisidium, Arca boucardi, Crenomytilus grayanus, Chlamys farreri nipponensis, Venerupis japonica* [=*V. philippinarum*], *Musculista senhousia, Macoma incongrua, Macoma sicca* [=*M. contabulata*], *Anadara broughtonii, Theora lubrica, Alvenius ojianus, Axinopsida subquadrata, Anisocorbula venusta, Raeta pulchella, Laternula limicola* [=*L. marilina*]; open part of the bay: *C. grayanus, Modiolus difficilis* [=*M. kurilensis*], *Acila insignis, Ennucula cyrenoides* [=*Nucula ovatotruncata*], *P. pisidium, Macoma orientalis* [=*M. scarlatoi*], *Mercenaria stimpsoni, Felaniella usta, Siliqua alta, Turtonia minuta, Peronidia venulosa* [=*Megangulus venulosus*], *Patinopecten yessoensis* [=*Mizuhopecten yessoensis*], *Spisula sachalinensis, Mactra sulcataria* [=*M. chinensis*], *Macoma calcarea, Callista brevisiphonata, Serripes groenlandicus, Callithaca adamsi, Panope japonica* [=*Panopea abrupra*]	Scarlato et al., 1967; Golikov and Scarlato, 1967; Klimova, 1980; Komendantov and Orlova, 1990
Nakhodka Bay, northwestern Sea of Japan, Russia	*Macoma scarlatoi, Axinopsida subquadrata, Clinocardium californiense, Raeta pulchella, Callithaca adamsi, Liocyma fluctuosum, Theora fragilis* [=*Th. lubrica*]	Lutaenko, 1999
Amursky Bay, northwestern Sea of Japan, Russia	*Nucula ovatotruncata, Nucula tenuis, Yoldia notabilis, Yoldia seminuda, Musculus laevigatus, Serripes groenlandicus, Axinopsida subquadrata, Dosinia penicillata, Liocyma fluctuosum, Callithaca adamsi, Alvenius ojianus, Macoma calcarea, Macoma incongrua, Macoma scarlatoi, Macoma tokyoensis, Theora lubrica, Raeta pulchella, Potamocorbula amurensis, Mya uzenensis, Mya japonica*	Lutaenko, 2002, 2003
Yeongil Bay, southwestern Sea of Japan, Korea	*Acila insignis*, *Nucula tenuis*, *Yoldia notabilis*, *Mytilus galloprovincialis*, *Arca boucardi*, *Axinopsida subquadrata*, *Felaniella usta*, *Mactra chinensis*, *Raeta pulchella*, *Nitidotellina hokkaidoensis*, *Theora fragilis* [=*Th. lubrica*], *Alvenius ojianus*, *Callithaca adamsi*, *Ruditapes philippinarum*, *Laternula anatina*	Lutaenko et al., 2003

Biogeography and vertical distribution

Ussuriysky Bay is situated in the boreal region [Kussakin, 1990] or the cold-temperate zone, according to bioclimatic zonation [Kafanov et al., 2000]. Based on the zonal-geographical (latitudinal-zonal) approach, the bay fauna belongs to the North-Japanese Lowboreal Subregion and the North-Japanese Province [Scarlato, 1981] or the Manchurian (=Ainian) Subregion of the Pacific Boreal Region [Kussakin, 1990]. A.I. Kafanov [1991] regarded the bivalve molluscan fauna of Peter the Great Bay as belonging to the Primorian Subprovince of the Korean-Primorian Province in Japanese-Manchurian Subregion. However, afterwards he recognized South Primorian Province based on ichthyofaunistic zoning [Kafanov et al., 2000]. We use herein the zonal-geographical terminology for the purposes of classification of distributional ranges of bivalve mollusks, which were categorized into five main types following O.A. Scarlato [1981]: (1) tropical-subtropical; (2) subtropical and subtropical-boreal; (3) lowboreal; (4) widely distributed boreal and circumboreal; and (5) boreal-arctic species. The clarification of these terms is given elsewhere [Lutaenko, 1993]. Despite this terminology is generally accepted only in the Russian biogeographical literature and ignored by western biogeographers, it is very useful in understanding complicated zoogeographical structure of the shelf fauna in temperate latitudes. To avoid confusion, we would like to emphasize that findings of tropical-subtropical and subtropical species in temperate waters merely mean that the **main** part of their distributional ranges lies in the respective climatic zones, but they can survive in winter and can reproduce in certain, warmed-up in summer, areas of the boreal Pacific. In Russian literature, these areas are termed inter-zonal regions [Scarlato, 1981].

When analyzing the zonal-geographical composition of bivalve molluscan fauna of Ussuriysky Bay, we used a list consisting of 119 species; the remaining species were excluded because three of them are regionally extinct, one species (*C. japonica*) is a brackish-water inhabitant, and *Macoma sp*. cannot be assigned to any group. Boreal mollusks are predominant – 54 species (45%), being represented by nearly equal number of lowboreal (28 species, or 23%) and widely distributed boreal and circumboreal (26 species, or 22%) (Fig. 6). Warm-water mollusks play a significant role in the fauna and their proportion reaches 40%; these include a

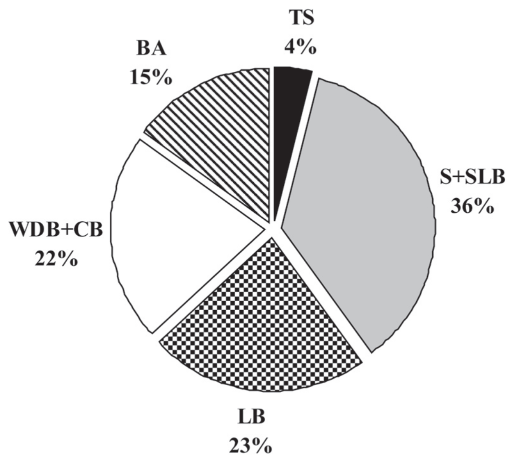

Fig. 6. Zonal-geographical composition of the bivalve molluscan fauna of Ussuriysky Bay (**TS** – tropical-subtropical species; **S+SLB** – subtropical and subtropical-lowboreal species [including subtropical-boreal and circumsubtropical-lowboreal]; **LB** – lowboreal species; **WDB+CB** – widely distributed boreal and circumboreal species [including boreal-amphipacific]; **BA** – boreal-arctic species.

numerous group of subtropical and subtropical-boreal species (43, or 36%) and four tropical-subtropical bivalves (*Trapezium liratum, D. penicillata, R. pulchella, Barnea manilensis*) (4%). The share of cold-water, boreal-arctic species is quite high – 15% (18 species), but most of them inhabit deeper areas of the bay.

In general, biogeographical composition of the bivalve fauna of Ussuriysky Bay is similar to that of entire Peter the Great Bay [Scarlato, 1981]. Among 135 species occurring in the latter, 42 species (31%) are lowboreal. This figure is higher, compared to Ussuriysky Bay (27 species). The share of widely distributed boreal and boreal-arctic mollusks in Peter the Great Bay was 23.7% and 14.8%, respectively (52 species). The higher proportion of subtropical and subtropical-boreal mollusks in Ussuriysky Bay (37%), compared to that of Peter the Great Bay (28.3%), can be explained by inclusion in O.A. Scarlato's (1981) list species recorded at the entrance of the bay, at depths down to 1000–2000 m. Thus, bivalve molluscan fauna of Ussuriysky Bay in general can be characterized as boreal (temperate), with a significant addition of warm-water elements.

It should also be mentioned that there are certain faunal differences between open and inner parts of Ussuriysky Bay. This phenomenon was first shown for Possjet Bay molluscan fauna [Golikov, Scarlato, 1967]. Thus, 55% of the total number of warm-water, subtropical species inhabit only semi-enclosed bays, 35% are known throughout the bay, and only 10% are found in open parts. This is easily traced in beach molluscan thanatocoenoses of both Possjet and Ussuriysky Bays, and in Recent fauna of Amursky Bay [Lutaenko, 1994a, b; 2003]. The phenomenon is related to intense summer warming of semi-enclosed bays and inner parts of secondary bays which is necessary for successful reproduction of warm-water species (tropical-subtropical and subtropical); winter cooling in itself does not prevent subtropical fauna from living in temperate latitudes [Scarlato, 1981]. Remnants of the mid-Holocene warming still existing in Ussuriysky and Amursky Bays concentrate in their inner parts. However, they never penetrated into the eastern part of Peter the Great Bay – Vostok and Nakhodka Bays – due to strong influence of the cold Primorskoe Current [Lutaenko, 1999, 2003; see also detailed maps of local distributions in the latter work]. Thus, the difference between western and eastern parts of Peter the Great Bay is an important faunal feature of the region. Our new data on the molluscan faunas of Amursky and Ussuriysky Bays disprove the opinion about the unique, warm-water nature of the fauna of Possjet Bay [Scarlato, 1981; Kafanov, 1991].

The distribution of bivalve mollusks and their shells in different depth zones along the Russian coast of the Sea of Japan has been studied by a number of researchers [Golikov and Scarlato, 1967; Evseev, 1981; Scarlato, 1981; Kafanov, 1991; Lutaenko, 1999, 2003]. Some authors paid much attention to bathymetric distribution of biogeographical assemblages, others emphasized individual species distributions or compared empty shells and live mollusks distributions. Two vertical zones are generally accepted in vertical division of the shelf fauna: upper shelf fauna and lower shelf fauna; the boundary between these zones lies at a depth of 20 m or 30 m in Sagami and Tokyo Bays (Pacific coast of Japan), respectively [Horikoshi, 1957; 1962]. This corresponds to the boundary between euneritic and mesoneritic areas (20–30 m) in the vertical zonation scheme for marine mollusks proposed by K. Oyama [1952]. A.N. Golikov and O.A. Scarlato [1967] found that at a depth range of 25–30 m in Possjet Bay, there is a well-defined faunal boundary, which is characterized by the total dissapperance of subtropical species prevailing above this depth range and the appearance of boreal-arctic species. According to O.A. Scarlato [1981], the highest number of bivalve species (256) in the Russian Far Eastern seas is found in the depth range of 10–25 m. A.I. Kafanov [1991] noted an important synperate (zone of concentration of species ranges) at a depth of 25 m in the entire North Pacific. On a larger scale, the segregation of northern and southern elements is observed in the Sea of Japan on the continental slope over the 150–200 m depth and represents the boundary between so-called «taraba» and «okaba» communities [Nishimura, 1966]. The same conclusion was drawn by Y. Kogure and I. Hayashi [1998] for echinoderms and by O.G. Kussakin [1990] for isopods: the shallow water fauna mostly occurs to 200 m depths. This is in accord with the scheme of K. Oyama [1952] who drew the boundary between «Shallow Sea Province» and «Deep Sea Province» (i.e., bathyneritic, or hemibathyal zone and bathyal zone) at a depth of 200–250 m. Another boundary is known at a depth of 50–60 m [Oyama, 1952; mesoneritic – subneritic boundary] or 60 m [Scarlato, 1981]. This vertical zonation is used in other Japanese faunal studies on mollusks [e.g., Fujii, 1987]. Thus, we subdivided the area of Ussuriysky Bay into three bathymetric zones: 0–30 m, 31–60 m, and deeper than 61 m. According to hydrographic maps, maximum depth at the entrance of the bay itself reaches 75 m.

When considering the bathymetric distribution of mollusks in Ussuriysky Bay, we took into account data on 116 species. All mollusks found on beaches are regarded as living in the depth range of 0–30 m; information about *Chlamys chosenica* and *Conchocele scarlatoi* is not available; findings of *Macoma golikovi* are likely subfossill shells.

Overall number of bivalve species in Ussuriysky Bay decreases with depth from 84 in the depth range of 0–30 m to 24 species below the 61 m depth (Fig. 7). The

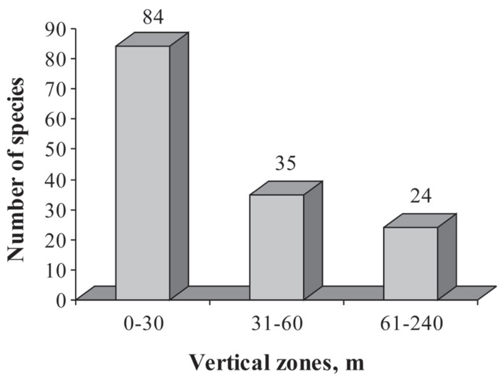

Fig. 7. The number of species of bivalve mollusks in different vertical zones of Ussuriysky Bay.

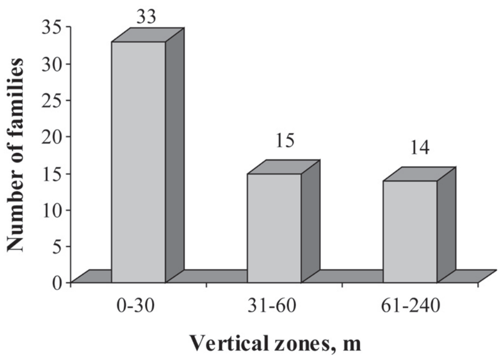

Fig. 8. The number of families of bivalve mollusks in different vertical zones of Ussuriysky Bay.

Table 5

Number of species of bivalve mollusks of different biogeographical nature in three vertical zones of Ussuriysky Bay

Zonal-geographical characteristics	0–30 m	31–60 m	61–240 m
Tropical-subtropical	4	1	0
Subtropical+subtropical-lowboreal	39	3	3
Lowboreal	20	6	4
Widely distributed boreal+circumboreal	15	11	7
Boreal-arctic	6	13	10

same trend was obtained for families of mollusks, from 33 to 14 (Fig. 8). This is similar to Amursky Bay fauna; however, twice as less species (17) are known here as compared to Ussuriysky Bay (35).

Bathymetric distribution of biogeographical complexes shows that warm-water species prefer the upper subtidal zone while cold-water species concentrate deeper (Table 5). For instance, an overwhelming majority of subtropical and subtropical-lowboreal mollusks (39) inhabits the depth range of 0–30 m but are rare below 31 m; tropical-subtropical species are not recorded deeper than 61 m. In conrast, the number of boreal-arctic species increases with depth. The same trend is observed for molluscan faunas of Possjet and Amursky Bays. The depth distribution of bivalve species of different biogeographical nature in various parts of the Sea of Japan has been discussed elsewhere [Lutaenko, 1999; 2003].

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