Korean J. Malacol. 31(3): 221-232 2015
http://dx.doi.org/10.9710/kjm.2015.31.3.221

# Observations on seaweed attachment to bivalve shells in Peter the Great Bay (East Sea) and their taphonomic implications

**Konstantin A. Lutaenko and Irina R. Levenets**

*A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok 690041, Russia*

## ABSTRACT

Observations in beach, intertidal and upper subtidal environments in Peter the Great Bay (north-western East Sea) have shown that attached algae were found on empty shells of 13 species of epifaunal and infaunal bivalve mollusks. Thirteen algae species were identified on empty dislodged shells but more than 50 species are known to be epibiotic on living bivalves. The dislodgement of shells with attached algae takes place in semi-enclosed, low-energy areas, as well as those which are open and affected by strong wave action, indicating the large scale of this phenomenon. The significance of seaweed transportation of living mollusks and their empty shells in the coastal zone, involving both taphonomic and ecological processes, is stressed. Algae appear to be a taphonomic agent and play a similar role as compared to birds or hermit crabs, but they act passively and contribute to environmental mixing in death assemblages in coastal environments.

**Key words:** bivalve shells, attached algae, dislodgement, dispersal, taphonomy.

## INTRODUCTION

Taphonomic observations in modern coastal zones show that the transportation of molluscan shells occurs widely in intertidal and subtidal environments by various methods. Among factors of shell transportation/displacement in shallow waters, longshore currents, ice dispersal, transfer by means of birds and attached algae and also hermit crabs, draining currents in the intertidal zone, and even by wind during storms are described by many researchers (Baturin and Kolokolov, 1940; Alekseev and Naidin, 1973; Ivanova, 1973; Sultanov *et al*., 1975; Tarasov, 1997; Warme, 1971; Trewin and Welsh, 1972; Alexandrowicz, 1978; Lindberg and Kellogg, 1982; Dörjes *et al*., 1986; Staff *et al*., 1986; Frey and Dörjes, 1988a, b; Frey *et al*., 1988; Cadée, 1989; 1992; Powell *et al*., 1989; Walker, 1989; Petersen, 1990; Fürsich and Flessa, 1991; Lutaenko, 1994a, b; Avila-Serrano and Téllez-Duarte, 2000; Cintra-Buenrostro *et al*., 2002; Cadée and Wesslingh, 2005). The variety of means of molluscan shell transportation has been termed "comidological differentiation" (Lutaenko, 1992); comidology is a branch of actuopaleontology studying patterns of post-mortem transportation of remains of organisms (Richter, 1928; Lutaenko and Oleinik, 1992). Transportation of molluscan shells is an important process leading to modification of ecological information, and formation of allochtonous thanatocoenoses, breakage, sorting, and accumulation of shelly material.

The aim of this paper is to present results of observations on the phenomenon of bivalve shells and living mollusk dispersal by means of floating and wave-transported seaweed, distribution of shells with seaweed on beaches and in the intertidal zone, and to provide data on species composition of seaweed and associated mollusks in some areas of Peter the Great

Received: September 10, 2015; Revised: September 22, 2015; Accepted: September 30, 2015
Corresponding author : Konstantin A. Lutaenko
e-mail: lutaenko@mail.ru, iralevenetz@rambler.ru
1225-3480/24587

Bay (north-western East Sea/Sea of Japan). Although mollusk shells are often used as substrate by seaweeds, no attention has been paid to their associations in previous studies of macroalgae fouling communities in this area except for detailed studies of epibionts of the Japanese scallop *Mizuhopecten yessoensis* (Jay, 1857) (Levenets, 2011).

## MATERIALS AND METHODS

Bivalve shells with attached algae were collected in seven localities in Peter the Great Bay (south to north): Kanal (a channel between Elena Islet and Russky Island) (**Loc. 1**), Novik Bay, Russky Island, Shoshina Inlet (**Loc. 2**) and southern coast of Novik Bay (**Loc. 3**), Sobol Bay (**Loc. 4**), and Tri Porosenka Bay (**Loc. 5**), Telyakovskogo Bay (**Loc. 6**) and Sukhodol Bay (**Loc. 7**) during 2011-2015 (Fig. 1). Novik Bay is part of Amursky Bay, and localities 4-7 are within Ussuriysky Bay; all bays are parts of the larger Peter the Great Bay. Shells were collected in the summer season, both in beach and intertidal zones, mostly with attached fresh (living) algae, but sometimes with dried pieces of rhizoids and thalli. Shells and algae were identified and photographed, either in the field or in the laboratory. In total, 13 species of bivalves were studied. Related observations were made on beach deposits, wave action, and origins of shell thanatocoenoses.

## RESULTS

**Kanal (Loc. 1)**. In the summer of 2015, sporadic shells of *Protothaca jedoensis* (Lischke, 1874) and *Mya japonica* Jay, 1857 with attached *Ulva lactuca* Linnaeus, 1753, were collected on the beach (Fig. 2). This site is an artificial channel connecting Bosfor Vostochny Strait (between the island and continent) with Novik Bay. According to observations by Bregman *et al.* (1998) at an adjacent site in Novik Bay, in the upper subtidal zone at a depth range of 2-5 m, algal communities are dominated by *Ulva* sp. (with projected bottom cover of 90-100%) and *Codium* sp. (30-40%).

**Novik Bay**. This is a narrow, semi-enclosed, shallow

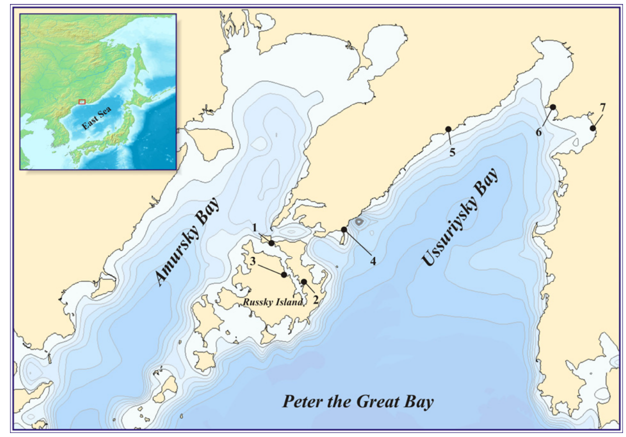


**Fig. 1**. A map of Peter the Great Bay (East Sea) showing sampling localities.

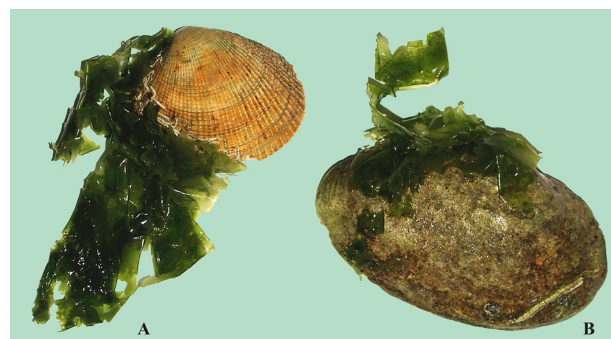


**Fig. 2**. Shells of *Protothaca jedoensis* (**A**) and *Mya japonica* (**B**) with attached *Ulva lactuca* (Loc. 1).

bay with maximum depth of about 10 m, with low salinity in the innermost part (where *Macoma balthica* (Linnaeus, 1758) abundantly occurs) and small inlets along the coast. Novik Bay opens to the larger Amursky Bay, and it is covered by ice from November to April. Water dynamics are low-energy. Beaches are mostly gravelly, narrow, with admixture of sand and remains of sea grass in the inner part; beach drift is seasonal and shell dislodgement is observed only during strong storms. The molluscan fauna is typical for semi-enclosed bays, with a predominance of *Crenomytilus grayanus* (Dunker, 1853), *Modiolus kurilensis* Bernard, 1983, *Crassostrea gigas* (Thunberg, 1793), and *M. yessoensis* (Bregman *et al.*, 1998). The mytilids *C. grayanus* and *M. kurilensis* are distributed nearly ubiquitously throughout the bay along the coasts, forming aggregations (druses) at a distance of one to three meters from each other. The Japanese

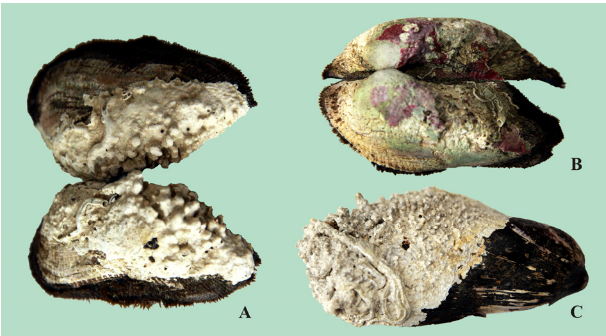


**Fig. 3**. Shells of *Arca boucardi* (**A**, **B**) and *Modiolus kurilensis* (**C**) with attached algae (Novik Bay, Loc. 2).

scallop (*M. yessoensis*) forms several local fields with a settlement density of up to 2-3 $m^2$ (*l.c.*). The inner part of Novik Bay is occupied by dense populations of the eelgrass *Zostera marina* Linnaeus, 1753 and it is replaced in deeper water by *Saccharina cichorioides* (Miyabe, 1902) (C.E. Lane, C. Mayes, Druehl et G.W. Saunders, 2006) (Bregman *et al.*, 1998). Subtidally, there are many starfish, *Asterias amurensis* Lütken, 1871 and *Patiria pectinifera* (Müller et Troschel, 1842), and the central part of the bay is dominated by pelite muds inhabited by brittle stars *Amphipholis kochii* Lütken, 1872 (*l.c.*).

The role of macroalgae in the intertidal communities in mixed and soft bottoms in Novik Bay is not as significant as in the open areas of Russky Island. In the upper horizon of the intertidal zone, red alga *Gloiopeltis furcata* (Postels et Ruprecht, 1840) J. Agardh, 1851 dominates, along with barnacles *Chthamalus dalli* Pilsbry, 1916 and littorinid gastropods (three species); in the middle horizon, perennial calcareous red alga *Corallina pilulifera* Postels et Ruprecht, 1840 forms a community (Levenets, 2008; Ivanova *et al.*, 2009).

In the summer of 2014 and 2015, in Shoshina Inlet (Loc. 2), empty shells of *Arca boucardi* Jousseaume, 1894, *Mytilus coruscus* Gould, 1861, and *M. kurilenses* were collected in the intertidal and upper subtidal zones to a depth of 0.5 m (Fig. 3). *M. kurilensis* shells were overgrown by the red calcareous algae *Lithothamnion phymatodeum* Foslie, 1902, which covered up to 82% of the total outer surface, *M. coruscus* by *Lithothamnion sonderi* Hauck, 1883, up to

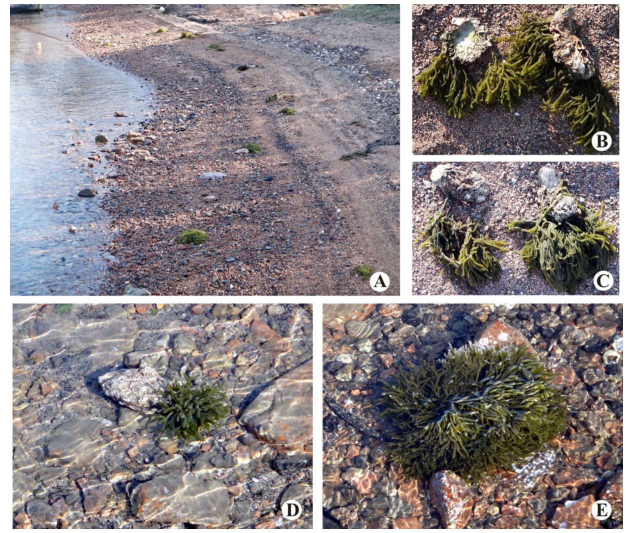


**Fig. 4**. Views of the beach (**A**) and the intertidal zone (**E**) showing numerous *Codium fragile*, including those attached to shells of *Chlamys farreri* (left, **B**), *Crassostrea gigas* (right, **B**; left, **C**; **D**), and *Modiolus kurilensis* (right, **C**) in Novik Bay (Loc. 3).

9%, and *A. boucardi* by *Clathromorphum compactum* (Kjellman, 1883) Foslie, 1898, up to 67%, *L. phymatodeum*, up to 59%, *Clathromorphum circumscriptum* (Strömfelt, 1886) Foslie, 1898, up to 12%, *Dasya sessilis* Yamada, 1928, up to 1.2%, and *Ceramium kondoi* Yendo, 1920 up to 1.2%. These seaweeds do not greatly increase the risk of shells being dislodged. However, living mollusks exhibited extensive cover by *Codium* at the same site.

In October, 2014, on the southern coast of Novik Bay (Loc. 3), shells of *C. gigas*, *Chlamys farreri* (Jones et Preston, 1904), and *M. kurilensis*, with attached *Codium fragile* (Suringar, 1867) Hariot, 1889, were observed intertidally and as washed up empty shells on the beach, with up to 8-10 algae clusters (10-20 cm long) per 5 m of beach segment (Fig. 4). Oyster and *Modiolus* shells were large adult specimens; shells of *C. farreri* were extensively overgrown by serpulids (Polychaeta). Dislodgement of shells seems to be extensive. The algae were observed to transport gravel and small rocks.

**Sobol Bay**. Sobol Bay (Loc. 4) is an open bay, with a boulder and gravel beach, sometimes with an admixture of coarse-grained sand, and rocky slabs and reefs in the upper subtidal zone. It is subject to strong wave action. The bay does not freeze in the winter, even in the most severe frosts; the shore ice covers only the intertidal zone and exposed reefs. In summer, the water warms to 20° C. Small subtidal areas with a mixture of sand, pebbles and shells are present in the most protected areas of the bay, but after each heavy storm the size and position are changed (Tarasov *et al*., 2005). The bottom is mostly rocky. At a depth of 3 to 10 m, extensive rocky reefs occur protruding from the bottom to a height of 1-1.3 m. The average depth is 5 m, with a maximum of 22 m (*l.c.*). According to previous floral studies (Skriptsova and Levenets, 2012; Kalita and Skripsova, 2014), a total of 65 macrophyte species were identified in Sobol Bay, and four macrophyte assemblages were discriminated there. An assemblage dominated by *Phyllospadix iwatensis* Makino, 1831 and *Coccophora langsdorfii* (Turner, 1811) Greville, 1830 occupied muddy-gravel bottoms in depths from 0.5 to 2 m throughout the year. An assemblage co-dominated by annual brown algae *Desmarestia viridis* (O.F. Müller, 1782) J.V. Lamouroux, 1813 and *Costaria costata* (C. Agardh, 1817) De A. Saunders, 1895 occurred at depths more than 3 m at late spring. Two other assemblages occurred on the rock and boulder bottom at 0.5-2 m depths; an assemblage co-dominated by annual laminarian algae (*Undaria pinnatifida* (Harvey, 1860) Suringar, 1873 and *C. costata*) developed at late spring and was succeeded in the autumn and winter by a *Tichocarpus crinitus* (S.G. Gmelin, 1768) Ruprecht, 1850, *U. lactuca*, *Sargassum pallidum* (Turner, 1808) C. Agardh, 1820 and *C. fragile* co-dominated assemblage.

On the beach, we collected shells of *C. grayanus* overgrown by the green algae *U. lactuca* and a red calcareous algae *L. sonderi*. *M. kurilensis* possessed attached red algae *Symphyocladia latiuscula* (Harvey, 1857) Yamada, 1941 and brown algae *Dictyopteris undulata* Holmes, 1896, with epiphytic *Ectocarpus siliculosus* (Dillwyn, 1809) Lyngbye, 1819 (Fig. 5).

Additionally in Sobol Bay, a small bivalve, *Turtonia minuta* (Fabricius, 1780) (Veneridae), about 3 mm, was repeatedly observed in the 1980-1990s in beach drift, being attached to the bushy brown and red algae *C. langsdorfii*, *Neorhodomela aculeata* (Perestenko, 1967) Masuda, 1982 and *Sargassum* sp. (Lutaenko, 2012). According to Golikov and Scarlato (1967), this bivalve is a common component of macrophyte communities in Possjet Bay, south-western Peter the Great Bay, where it lives from the intertidal to a depth of 10 m on hard substrate or attached to algae or, more rarely, to seagrass. Its population density reaches 3,000 individuals/0.1 $m^2$. *T. minuta*'s density may reach 35,000 individuals/0.1 $m^2$ on the herringbone-like algae *C. langsdorfii*. It is evident that the transportation and floating of this algae lead to wider dissemination of shells of *T. minuta*.


**Fig. 5**. Views of the gravel beach (**A**) and shells of *Crenomytilus grayanus* (**B**) and *Modiolus kurilensis* (**C**) in Sobol Bay (Loc. 4).

**Tri Porosenka Bay** (Loc. 5) is a small inlet on the western coast of Ussuriysky Bay. We collected shells of *M. kurilensis*, *M. yessoensis* and *Protothaca adamsii* (Reeve, 1863) with rhizoids of *Sacharina* cf. *japonica* (Areschoug, 1851) C.E. Lane, C. Mayes, Druehl et G.W. Saunders, 2006 on the beach (Fig. 6).

**Telyakovskogo Bay** (Loc. 6). This is an open bay located in the inner part of Ussuriysky Bay. The beach is mostly sandy-gravel in the middle of the bay, or

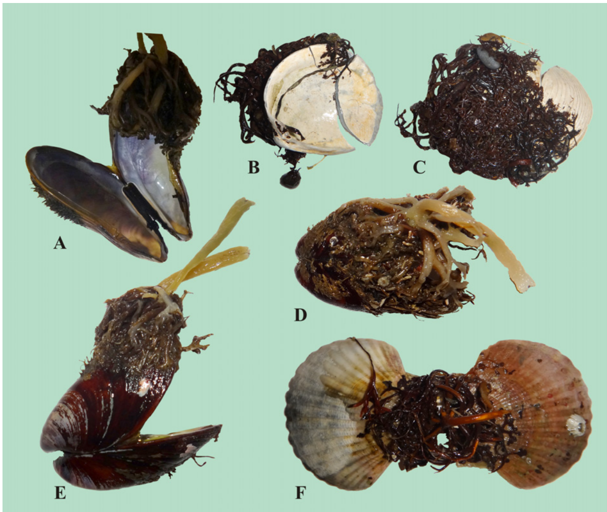


**Fig. 6**. Shells of *Modiolus kurilensis* (**A**, **D**, **E**), *Protothaca adamsii* (**B**, **C**) and *Mizuhopecten yessoensis* (**F**) with attached algae in Tri Porosenka Bay (Loc. 5).

gravel with breakstones in the northern part, with a significant admixture of shells.

In this bay, we observed numerous shells of *Anadara broughtonii* (Schrenck, 1867), *C. grayanus*, *M. kurilensis*, *M. coruscus*, *C. gigas*, *Callista brevisiphonata* (Carpenter, 1864) with attached dried remnants of rhizoids of *Saccharina* sp., most likely, *S. japonica* or *S. japonica* f. *longipes* (Miyabe, 1902) Selivanova, Zhigadlova et G.I.Hansen, 2007 (Figs. 7, 8). Many mussels and oysters were collected in clusters, and they were washed ashore as living animals because they still had remnants of dried soft tissue. This means that shell dislodgement occurs massively during storms while in other seasons the bay experiences low-energy conditions and shell transportation is limited. The shells with attached algae are very abundant (Fig. 7), showing the scale of the phenomenon.

**Sukhodol Bay** (Loc. 7). In July 2011, abundant transportation of bivalve shells with attached algae was observed in the coastal zone (Lutaenko, 2012). In the center of the bay between the mouths of Sukhodol and Petrovka rivers, on a wide sandy beach with local admixtures of mud, in the muddy and sandy intertidal zone, and partly in the upper subtidal zone, to a depth of 0.5 m, abundant empty shells of *A. broughtonii*, *Spisula sachalinensis* (Schrenck, 1861) (Mactridae),


**Fig. 7**. Views of the shelly-gravelly beach (**A**, **B**) and shells of *Anadara broughtonii* (**C**, **D**, **E**), clusters of *Modiolus kurilensis* + *Crenomytilus grayanus* (**F**, **G**) and *M. kurilensis* (**H**) with attached algae in Telyakovskogo Bay (Loc. 6).

and *M. japonica* were found, with attached algae belonging to the genus *Ulva* (*Ulva prolifera* O.F.Müller, 1778, or *Ulva linza* Linnaeus, 1753) (Figs. 9, 10).

The algae were attached along the anterior and ventral margins of *M. japonica* and along the dorsal margin or throughout the entire surface of *S. sachalinensis*: these observations provide evidence that algae settled on shells after the death of mollusks. Intertidally and in the upper subtidal area, shells with attached seaweeds were located in a belt-like formation (Fig. 10). Inside nearly all large shells, males of the crabs *Hemigrapsus* cf. *penicillatus* (de Haan, 1835) were found.

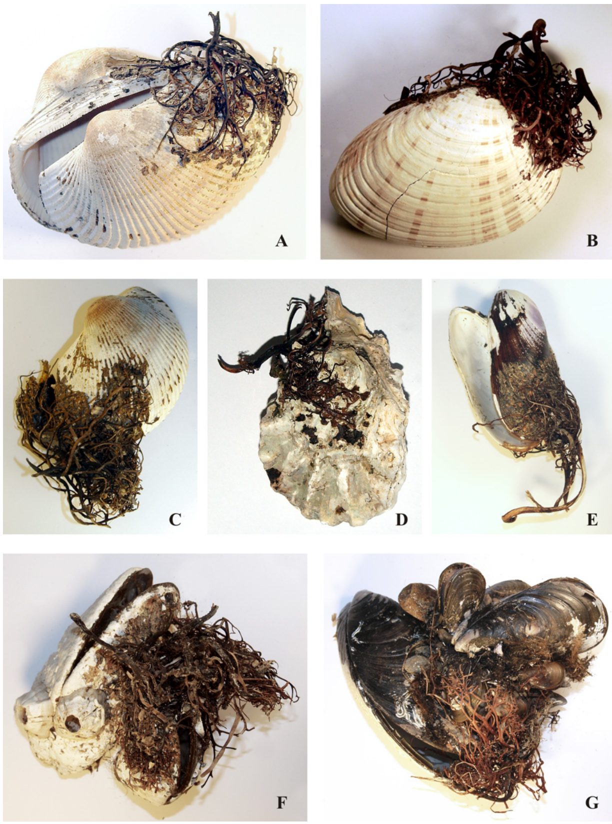

**Fig. 8**. Shells of *Anadara broughtonii* (**A**, **C**), *Callista brevisiphonata* (**B**), *Crassostrea gigas* (**D**), *Modiolus kurilensis* (**E**, **F**) and *Crenomytilus grayanus* (**G**) with attached algae collected on the beach of Telyakovskogo Bay (Loc. 6).

Species belonging to the genus *Ulva* have a simple structure, short life cycles, and wide distributional ranges. A multizonal species *U. prolifera* lives in all Russian Far Eastern seas and survives a wide range of salinity and temperature fluctuations. Boreal-notal *U. linza* occurs in the Bering, Okhotsk, and East seas, inhabiting both the inner parts of bays and open bay coasts. However, *U. linza* is limited by bays; it withstands a slight salinity decrease and flourishes in organic-enriched waters (Vinogradova, 1979). In Peter the Great Bay, this species grows in summer with two generations: June-early July, and the end of July-August, and it is very abundant in protected, euthrophic environments (Perestenko, 1980). The vegetation period of *U. prolifera* is more extended, from February to November, with several generations developing (Vinogradova, 1974).

**Fig. 9**. Views of the sandy beach (**A**) and shells of *Spisula sachalinensis* (**B**, **D**) and *Mya japonica* (**C**) with attached Ulva sp. in Sukhodol Bay (Loc. 7).

The depth of burrowing of bivalves has little influence on the post-mortem settling of algae on molluscan shells. For instance, *M. japonica* has long siphons and burrows into bottom deposits to a depth of 30 cm (Kondo, 1987; 1989). However, siphons of anadarines and mactrids are very short and these clams burrow to a depth of several centimeters. Nevertheless, even in low-energy tidal flats, transport of empty shells of *Mya* is observed (Tanabe and Arimura, 1987), and they can be overgrown by algae after death.

## DISCUSSION

Witman and Suchanek (1984) showed that the mussels (*Mytilus edulis* L., 1758 and *M. californianus* Conrad, 1837, Mytilidae), overgrown by the kelp (*Laminaria saccharina* (Linnaeus, 1753) J. V. Lamouroux, 1813, modern name *Saccharina latissima*


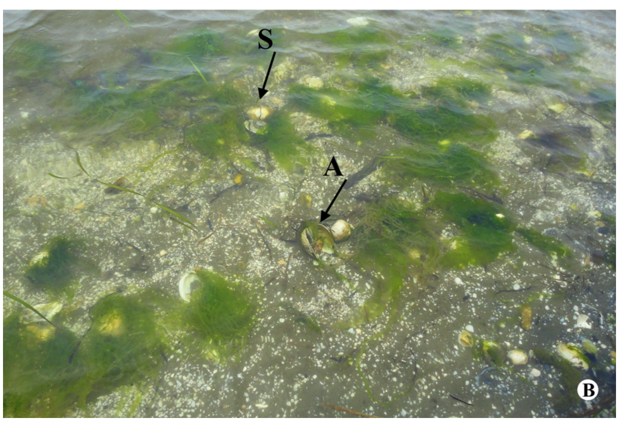


**Fig. 10**. Views of the intertidal zone (**A**, **B**) of Sukhodol Bay (Loc. 7) with concentrations of shells with attached Ulva sp. (arrows point to S-*Spisula sachalinensis*, A-*Anadara broughtonii*).

(Linnaeus, 1753) C.E. Lane, C. Mayes, Druehl et G.W. Saunders, 2006), encountered flow-induced forces that were two to six times greater than flow forces on the mussels alone. Attachment strength increased with shell area, and was influenced by the location of the mussel within the aggregation, and by the exposure of the habitat. In both species, significantly greater force was required to dislodge mussels at the edge of the mussel bed than at the center. The mean attachment strength of *M. edulis* was 15 times greater in exposed habitats than in protected habitats. Flow force data and surveys of dislodged mussels at an exposed beach indicate that epizoans increase the risk of mussel dislodgement, which has important implications for intertidal mussel beds impacted by disturbance events and for taphonomic processes: shells and living mollusks can be transported to a different environment. Direct observation of the transport behaviour of pebbles with attached algae, purposely laid out in the nearshore zone, showed that they can be easily transported by oscillatory water movements, if the ratio (weight of pebble/wet weight of algae) is less than or equal to about 3 (Kudrass, 1974). Moreover, fouling algae slow growth and reproduction of the mussels *M. californianus* (Dittman and Robles, 1991). In other words, seaweeds deteriorate the environment where mollusks exist, and facilitate mollusks dislogement and transportation in the coastal zone, thus influencing bottom communities and leading to death of mollusks. Distribution of empty shells finally leads to environmental mixing in modern death assemblages (*e.g.*, Powell *et al.*, 1989; Parsons and Brett, 1991).

Macroalgae prefer to settle on hard or mixed substrata. With the settling of spores on the shells of mollusks, algae can exist on soft bottoms. If a shell is empty or poorly secured to bottom, the thalli of macrophytes may be washed up ashore during storms with the substrate, i.e., molluscan shells. If shells are attached firmly to the bottom, the algae have a chance to survive storms and to reach the stage of sporulation (reproduction).

Sporulation of the perennial laminarian algae, including species of *Saccharina*, are accompanied by a considerable destruction of thalli of the second and subsequent years of algae life and, consequently, by a decrease in biomass of seaweed populations. After reaching its maximum size in the second year of its life-cycle, fertile *Saccharina*, due to sailing potential and mobility of bottom deposits, are easily washed ashore by storms or drift to underwater bottom depressions (Gail, 1936). In Peter the Great Bay, at depths of 20 to 30-50 m, individuals of *Saccharina* with long stalks, up to 0.5 m, form dense, unattached clusters with intertwined thalli. In such clusters, algae continue to grow and reproduce (Kashenko and Levenets, 2000). Beach drifted *Saccharina* specimens, dislodged by storms, consist mostly of old thalli.

The Japanese long-stalk kelp, *S. japonica*, or the deep-water form of this species, grows in open coast environments in the East Sea at a depth of 8-30 m on pebbly bottoms. Its stalk length reaches 0.4 m, the plate of thallus -12 m. The species forms monospecific settlements occupying large areas of the bottom. Active linear growth of thalli occurs in spring and early summer, and the breeding season falls at the end of summer and autumn (Dzizyurov *et al*., 2008). In Peter the Great Bay, at this time, the summer monsoon changes to the winter one, which is accompanied by active surge phenomena, enhancing the surf level in open areas, *e.g.* in Sobol Bay.

There are other examples of bivalve dislodgements by algae in Peter the Great Bay. Fouling of molluscan shells by algae is well documented in the Japanese scallop, *M. yessoensis* (Silina and Ovsyannikova, 1995; Levenets *et al*., 2005; 2010; Levenets, 2011). Fifty-seven species of macrophytes have been identified on living scallops, with red algae being most diverse and brown algae with the least number of species. Chlorophyta are the dominant biomass in the epibiotic flora of *M. yessoensis*, with a prevalence of bushy and filamentous algae. The seaweed often form a continuous cover on the upper valves of the scallop (Levenets *et al*., 2005). While the Japanese scallop is a mobile bivalve, it is clear that the presence of the attached algae increases the risk of the scallop dislodgement during stormy weather. Beach driftage of living scallops sometimes occurs on a massive scale leading to the washing ashore of tens of thousands of mollusks, especially after typhoons (Kalashnikov, 1984; Lebedev and Vyshkvartsev, 2013).

In Peter the Great Bay, there are also “*Ahnfeltia* fields”, unattached, intertwining concentrations of the red alga *Ahnfeltia tobuchiensis* (Kanno et Matsubara, 1932) Makienko, 1979, populated by various animals and plants (Ivanova *et al*., 1994). They form floating clusters of 5 to 100 cm thick, quite movable, at a depth of 1-30 m, and may include up to 130 species of plants and animals, among them 20 species of bivalves (*l.c.*). Density of settlement of bivalves *Vilasina pillula* Scarlato, 1960 (Mytilidae) and *Hiatella arctica* (L., 1767) (Hiatellidae) reaches 523 individials/m$^2$ and 30 individuals/m$^2$, respectively. *Ahnfeltia* communities, including associated animals, are subjected to intense water movement (a drain current from Amursky Bay, at the entrance of Stark Strait). Three epibiotic species of bivalves were found on the cultured seaweed *Gracilaria* in Possjet Bay (Zvyagintsev and Kozmenko, 1995).

Observations in various regions of the World Ocean show the wide occurrence of transportation of empty shells as well as living bivalve mollusks by means of seaweeds. Vallentin (1895) observed dispersal of infaunal *Cardium edule* L., 1758 (= *Cerastoderma edule* (L., 1758)) and epifaunal *M. edulis* and *Ostrea edulis* L., 1758 with rhizoids of *Chorda filum* (Linnaeus, 1753) Stackhouse, 1797 on the coast of Great Britain, a mile from land. Similar observations are known from the Caspian Sea (Tarasov, 1997; Tarasov and Kazantseva, 1994), White Sea (Ivanova, 1973; Khalaman and Berger, 2006), Scotland (Ansell *et al*., 1988), the Netherlands (Cadée and Wesselingh, 2005), Brazil (Oliveira *et al*., 1979), Iceland (Ingólfsson, 1995), Belgium (Vandendriessche *et al*., 2006). Distances of dispersal of mollusks and shells by seaweeds may reach up to several hundred kilometers.

Our observations in Peter the Great Bay have shown that attached algae and their debris were found on empty shells of 13 species of bivalves, both epifaunal and infaunal. At least, 13 algae species were detected (Table 1) but this is a preliminary estimate, as more than 50 algae species are known to be epobiotic on living bivalves. The dislodgement of shells with attached algae takes place in both semi-enclosed, low-energy and open, surf-influenced areas and it indicates the wide scale of this phenomenon.

Thus, the significance of seaweed transportation of living mollusks and their empty shells in the coastal zone, as a factor influencing taphonomic and ecological processes, should not be underestimated. Algae appear to be a taphonomic agent and play a similar role as compared to birds or hermit crabs, but they are acting passively and may dislodge large amounts of shell debris and contribute to environmental mixing in death shell assemblages in beach, intertidal, and subtidal depositional environments. Post-mortem assemblages of shells and other remains of organisms in the subtidal zone represent mixocoenoses, where

**Table 1**. Algae attached to empty shells of bivalve mollusks collected in beach/intertidal thanatocoenoses of Peter the Great Bay, north-western East Sea (Sea of Japan)

| Species of bivalves | Novik Bay (Locs. 1-3) | Sobol Bay (Loc. 4) | Tri PorosenkaBay (Loc. 5) | Telyakovskogo Bay (Loc. 6) | Sukhodol Bay (Loc. 7) |
|---|---|---|---|---|---|
| *Arca boucardi* | *Clathromorphum compactum, Lithothamnion phymatodeum, Clathromorphum circumscriptum, Dasya sessilis, Ceramium kondoi* | | | | |
| *Anadara broughtonii* | | | | *Saccharina* cf. *japonica* | *Ulva* spp. |
| *Chlamys farreri* | *Codium fragile* | | | | |
| *Mizuhopecten yessoensis* | | | *Saccharina* cf. *japonica* | | |
| *Mytilus coruscus* | *Lithothamnion sonderi* | | | *Saccharina* cf. *japonica* | |
| *Crenomytilus grayanus* | | *Ulva lactuca, Lithothamnion sonderi* | | *Saccharina* cf. *japonica* | |
| *Modiolus kurilensis* | *Codium fragile, Lithothamnion phymatodeum* | *Symphyocladia latiuscula, Dictyopteris undulata with epiphytic Ectocarpus siliculosus* | *Saccharina* cf. *japonica* | *Saccharina* cf. *japonica* | |
| *Crassostrea gigas* | *Codium fragile* | | | *Saccharina* cf. *japonica* | |
| *Callista brevisiphonata* | | | | *Saccharina* cf. *japonica* | |
| *Protothaca jedoensis* | *Ulva lactuca* | | | | |
| *Protothaca adamsii* | | | *Saccharina* cf. *japonica* | | |
| *Spisula sachalinensis* | | | | | *Ulva* spp. |
| *Mya japonica* | *Ulva lactuca* | | | | *Ulva* spp. |

autochthonous and allochthonous elements are mixed, whereas beach thanatocoenoses contain a significant admixture of subautochtonous shells. Thus, according to our classification (Lutaenko, 1993), 1st, 3rd and 4th types of thanato-areas are formed in the case of transport of empty shells, depending on their places of death and burial.

## ACKNOWLEDGMENTS

We are very grateful to Mrs. Irina E. Volvenko, Zoological Museum, Far Eastern Federal University, Vladivostok, for preparation of illustrations. R.G. Noseworthy polished the English text.

## REFERENCES

Alexandrowicz, S.W. (1978) A quantitative study of the origin of *Dreissena polymorpha* shell accumulations in Szczecin Bay, Baltic Sea. *Bulletin de l'Académie*

*Polonaise des Sciences. Série des Sciences de la Terre*, **25**: 75-82.

Alexeev, A.S. and Naydin, D.P. (1973) Observations on the conditions of transport and burial of shells of some bivalve mollusks in the intertidal zone of a tidal sea. *Integrated Studies of the Ocean Nature* (Moscow), **4**: 155-164. [In Russian].

Ansell, A.D., Robb, L. and Powell, H.T. 1988. Algal-induced dislodgement as a cause of bivalve mortality on some Scottish beaches. *Journal of the Marine Biological Associations of the United Kingdom*, **68**: 219-233.

Avila-Serrano, G.E. and Téllez-Duarte, M.A. (2000) Taphonomic processes in Recent thanatocoenoses at Playa El Pelícano, Baja California. *Ciencias Marinas*, **26**: 677-694.

Baturin, V.N. and Kolokolov, A.A. (1940) Shell thanatocoenoses in eastern part of the middle Caspian Sea. *Reports (Doklady) of the USSR Academy of Sciences*, **26**: 213-216.

Bregman, Yu.E., Sedova, L.G., Manuylov, V.A., Petrenko, V.S., Kovekovdova, L.T., Borisenko, G.S., Shulgina, L.V., Simokon, M.V and Sukhotskaya, L.Yu. (1998) A complex investigation of environments and bottom biota of Novik Bay (Russian Island, the Japan Sea). *Proceedings of the Pacific Research Center (Vladivostok)*, **124**: 320-343. [In Russian with English abstract].

Cadée, G.C. (1989) Size-selective transport of shells by birds and its palaeoecological implications. *Palaeontology*, **32**: 429-437.

Cadée, G.C. (1992) Eolian transport and left/right sorting of *Mya* shells (Mollusca, Bivalvia). *Palaios*, **7**: 198-202.

Cadée, G.C. and Wesselingh, F. (2005) From living mollusc to fossil shell: taphonomy of shells from Dutch beaches. *Spirula*, **343**: 36-52. [In Dutch with English abstract].

Cintra-Buenrostro, C.E., Foster, M.S. and Meldahl, K.H. (2002) Response of nearshore marine assemblages to global change: a comparison of molluscan assemblages in Pleistocene and modern rhodolith beds in the southwestern Gulf of California, México. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183**: 299-320.

Dittman, D. and Robles, C. (1991) Effect of algal epiphytes on the mussel *Mytilus californianus*. *Ecology*, **72**: 286-296.

Dörjes, J., Frey, R.W. and Howard, J.D. (1986) Origins of, and mechanisms for, mollusk shell accumulations on Geogria beaches. *Senckenbergiana Maritima*, **18**: 1-43.

Dzizyurov, V.D., Kulepanov, V.N., Shaposhnikova, T.V., Sukhoveeva, M.V., Gusarova, I.S. and Ivanova, N.V. (2008) Atlas of Common Species of Algae and Seagrass of the Russian Far East. 327 pp. TINRO-center, Vladivostok. [In Russian].

Frey, R.W. and Dörjes, J. (1988a) Fair- and foul-weather shell accumulations on a Georgia beach. *Palaios*, **3**: 561-576.

Frey, R.W. and Dörjes, J. (1988b) Carbonate skeletal remains in beach-to-offshore sediments, Pensacola, Florida. *Senckenbergiana Maritima*, **20**: 31-57.

Frey, R.W., Hong, J.-S. and Hayes, W.B. (1988) Physical and biological aspects of shell accumulation on a modern macrotidal flat, Inchon, Korea. *Netherlands Journal of Sea Research*, **22**: 267-278.

Fürsich, F.T. and Flessa, K.W. (1991) The origin and interpretation of Bahia la Choya (northern Gulf of California) taphocoenoses: implications for paleoenvironmental analysis. *Zitteliana*, **18**: 165-169.

Gail, G.I. (1936) Laminarian algae of the Far Eastern seas. *Bulletin of the Far Eastern Branch, USSR Academy of Sciences*, **19**: 31-65. [In Russian].

Golikov, A.N. and Scarlato O.A. (1967) Molluscs of the Possjet Bay (the Sea of Japan) and their ecology. *Proceedings of the Zoological Institute, USSR Academy of Sciences*, **42**: 5-154. [In Russian].

Guiry, M.D. in Guiry, M.D. and Guiry, G.M. (2015) AlgaeBase. http://www.algaebase.org (accesed on August 25, 2015).

Ingólfsson, A. (1995) Floating clumps of seaweed around Iceland: natural microcosm and a means of dispersal for shore fauna. *Marine Biology*, **122**: 13-21.

Ivanova, I.-N.V. (1973) Bivalve Molluscs and Sedimentation Conditions (Actualistic and Lithologo-Paleoecological Analysis of Late Paleozoic Coal-Bearing Deposits of South-West Siberia and Some Sea of the USSR). 164 pp. Nauka, Moscow. [In Russian].

Ivanova, M.B., Novozhilov, A.V. and Tzurpalo, A.P. (1994) Environment and some features of flora and fauna composition of the *Ahnfeltia tobuchiensis* exploited natural fields at Stark Strait (Peter the Great Bay, Sea of Japan) and Ismena Bay (Kunashir Island, Kuril Islands). *Proceedings of the Pacific Research Institute of Fisheries and Oceanography (Vladivostok)*, **113**: 83-99. [In Russian with English abstract].

Ivanova, M.B., Belogurova, L.S. and Tsurpalo, A.P. (2009) Composition and distribution of benthos in the intertidal zone of Russky Island (Peter the Great Bay, Sea of Japan). ***In***: Ecological Studies and the State of the Ecosystem of Amursky Bay and the Estuarine Zone of the Razdolnaya River (Sea of Japan) Vol. 2 (ed. by Lutaenko, K.A. and Vaschenko, M.A). Dalnauka, Vladivostok. P. 87-146.

Kalashnikov, V.Z. (1984) Effect of the wind-induced typhoon "Ellis" on the population of the Yezo scallop *Patinopecten yessoensis* in Posyet Bay. *Soviet Journal of Marine Biology*, **10**: 51-54.

Kalita, T.L. and Skriptsova, A.V. (2014) The current state of subtidal macrophyte communities of Ussuriysky and Amursky Bays, Sea of Japan. *Russian Journal of Marine Biology*, **40**: 418-425.

Kashenko, N.V. and Levenets, I.R. (2000) The first finding of the unattached form of *Laminaria gurjanovae* in Pos'eta Bay, Sea of Japan. *Russian Journal of Marine Biology*, **26**: 46-47.

Khalaman, V.V. and Berger, V.Ya. (2006) Floating seaweeds and associated fauna in the White Sea. *Oceanology*, **46**: 827-833.

Kondo, Y. (1987) Burrowing depth of infaunal bivalves - observation of living species and its relation to shell morphology. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **148**: 306-323.

Kondo, Y. (1989) A method of analyzing mode of occurrence of bivalve fossils - comparison of position and orientation of living and fossil bivalves. *Benthos Research*, **37**: 73-82. [In Japanese with English abstract].

Kudrass, H.-R. (1974) Experimental study of nearshore transportation of pebbles with attached algae. *Marine Geology*, **16**: 9-12.

Lebedev, E.B. and Vyshkvartsev, D.I. (2013) The impact of the typhoon "Bolaven" on the benthos of the Far Eastern Marine Biosphere Reserve FEB RAS. ***In***: 10th Far Eastern Conference on Wildness Protection, Blagoveschensk, September 25-27, 2013: Materials of the Conference. BGPU Publ., Blagoveschensk. P. 194-195. [In Russian].

Levenets, I.R. (2008) Intertidal flora of Russky Island, Peter the Great Bay. ***In***: Modern State of Water Bioresources: Materials of the Scientific Conference Dedicated to the 70th Anniversary of S.M. Konovalov, March 25-27, 2008, Vladivostok. TINRO-center, Vladivostok. P. 148-151. [In Russian].

Levenets, I.R. (2011) Macroalgae of Fouling Communities in Shallow Waters of Southern Primorye. 187 pp. Dalnauka, Vladivostok. [In Russian].

Levenets, I.R., Ovsyannikova, I.I. and Lebedev, E.B. (2005) Composition of macroepibiosis of the scallop *Mizuhopecten yessoensis* in Peter the Great Bay, Sea of Japan. *Bulletin of the Russian Far East Malacological Society*, **9**: 155-168. [In Russian with English abstract].

Levenets, I.R., Ovsyannikova, I.I. and Lebedev, E.B. (2010) Epibiotic macroalgae on the scallop *Mizuhopecten yessoensis* in Peter the Great Bay, Sea of Japan. *Russian Journal of Marine Biology*, **36**: 340-349.

Lindberg, D.R. and Kellogg, M.G. (1982) Bathymetric anomalies in the Neogene fossil record: the role of diving marine birds. *Paleobiology*, **8**: 402-407.

Lutaenko, K.A. (1992) Comidological differentiation of heterochronous shell material in the coastal zone of the sea. *Paleontological Journal*, **26**: 79-82.

Lutaenko, K.A. and Oleynik, A.E. (1992) Actuopaleontology and formation of fossil record incompleteness. *Proceedings of the Academy of Sciences [Moscow], Series Biological*, **4**: 582-589. [In Russian with English abstract].

Lutaenko, K.A. (1993) Thanato-areas of benthic invertebrates in the sea coastal zone. *Russian Journal of Marine Biology*, **19**: 48-52.

Lutaenko, K.A. (1994a) An actuopaleontological study of beach thanatocoenoses of bivalved mollusks on the Sea of Japan. *Paleontological Journal*, **28**: 21-33.

Lutaenko, K.A. (1994b) Beach molluscan thanatocoenoses in Possjet Bay, Sea of Japan: comparison between open and sheltered beaches. *Benthos Research*, **47**: 1-12.

Lutaenko, K.A. (2012) Transportation of bivalve shells with attached algae in Ussuriysky Bay (Sea of Japan). *Bulletin of the Russian Far East Malacological Society*, **15/16**: 154-164. [In Russian with English abstract].

Oliveira, E.C., de, Ugadim, Y. and Paula, E.J., de. (1979) Associated epibiota on Sargassum floating on the waters of the Brazilian Current - biogeographical remarks. *Boletim do Botanica, Universidade de Sao Paulo*, **7**: 5-9.

Parsons, K.M. and Brett, C.E. (1991) Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation. ***In***: The Processes of Fossilization (ed. by Donovan, S.K.). Columbia University Press, New York. P. 22-65.

Perestenko L.N. (1980) Seaweeds of Peter the Great Bay. 232 pp. Nauka, Leningrad. [In Russian].

Petersen, D.W. (1990) Assessing environmental parameters and transport from the spatial distribution of a mollusc-dominated modern shell concentration in a restricted subtropical lagoon, Long Key Lake, Florida Keys, USA. *Compass Sigma Gamma Epsilon*, **67**: 15-29.

Powell, E.N., Staff, G.M., Davies, D.J. and Callender, W.R. (1989) Macrobenthic death assemblages in modern marine environments: formation, interpretation, and application. *Critical Reviews in Aquatic Sciences*, **1**: 555-589.

Richter, R. (1928) Aktuopälaontologie und Paläobiologie, eine Abgrenzung. *Senckerbergiana*, **10**: 285-292. [In German].

Silina, A.V. and Ovsyannikova, I.I. (1995) Long-term changes in a community of Japanese scallop and its epibionts in the polluted area of Amurskii Bay, Sea of Japan. *Russian Journal of Marine Biology*, **21**: 54-60.

Skriptsova, A.V. and Levenets, I.R. (2012) Seasonal dynamics of subtidal macrophyte assemblages in Sobol Bay (Peter the Great Bay, Sea of Japan) in relation to depth. *Journal of the Marine Biological Association of the United Kingdom*, **92**: 429-437.

Staff, G.M., Stanton, R.J., Powell, E.N. and Cummins, H. (1986) Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geological Society of America Bulletin*, **97**: 428-443.

Sultanov, K.M., Isaev, S.A. and Efendiev, H.M. (1975) Thanatocoenoses of bivalve mollusks in modern deposits of the continental shelf of the southern Caspian Sea. *Paleontological Journal [Moscow]*, **1**: 32-40. [In Russian].

Tanabe, K. and Arimura, E. (1987) Ecology of four infaunal bivalve species in the Recent intertidal zone, Shikoku, Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **60**: 219-230.

Tarasov, A.G. (1997) Transboundary transport of molluscan shells: errors of interpretation and the importance in paleoecological studies. *Proceedings of the Academy of Sciences [Moscow], Series Biological*, **2**: 224-227. [In Russian with English abstract].

Tarasov, A.G. and Kazantseva, S.Z. (1994) Post-mortem transport of freshwater mollusc shells in the northern Caspian Sea: a cautionary note on the implications for palaeoecological reconstructions. *International Journal of Salt Lake Research*, **3**: 49-52.

Tarasov, V.G., Kasyanov, V.L., Adrianov, A.V., Chernyshev, A.V., Shulkin, V.M., and Semykina, G.I. (2005) The ecological state and bottom communities in the Patrokl Bight and Sobol Bight (Peter the Great Bay, Sea of Japan): the past and the present. *Bulletin of the Far Eastern Branch, Russian Academy of Sciences*, **1**: 3-18. [In Russian with English abstract].

Trewin, N.H. and Welsh, W. (1972) Transport, breakage and sorting of the bivalve *Mactra corallina* on Aberdeen beach, Scotland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **12**: 193-204.

Vallentin, R. (1895) Some remarks on the dispersal of marine animals by means of seaweeds. *Annals and Magazine of Natural History*, **16**: 418-423.

Vandendriessche, S., Vincx, M. and Degraer, S. (2006) Floating seaweed in the neustonic environment: a case study from Belgian coastal waters. *Journal of Sea Research*, **55**: 103-112.

Vinogradova K.L. (1974) The Sea Lettuce Algae (Chlorophyta) of the USSR Seas. 166 pp. Nauka, Leningrad. [In Russian].

Vinogradova K.L. (1979) Identification Guide-Book of the Algae of the USSR Far Eastern Seas. 147 pp. Nauka, Leningrad. [In Russian].

Walker, S.E. (1989) Hermit crabs as taphonomic agents. *Palaios*, **4**: 439-452.

Warme, J.E. (1971) Paleoecological aspects of a modern coastal lagoon. *University of California Publications in Geology*, **87**: 1-133.

Witman, J.D. and Suchanek, T.H. (1984) Mussels in flow: drag and dislodgement by epizoans. *Marine Ecology Progress Series*, **16**: 259-268.

Zvyagintsev, A.Yu. and Kozmenko, V.B. (1995) Fouling of aquacultural installations and epiphyton of Gracilaria in Posyeta Bay, Sea of Japan. *Russian Journal of Marine Biology*, **21**: 12-16.