Proc. Zool. Inst. Russ. Acad. Sci., 310, 2006: 25-34

Ecology of reproduction of shallow water benthic polychaetes in high latitude Arctic seas

Galina N. Buzhinskaja

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab., 1, St.Petersburg, 199034, Russia

Studies of ecology of reproduction of marine benthic invertebrates in the high latitudes of the Arctic were undertaken for the first time by G. Thorson in the 1930s. Among the larvae of invertebrates discovered by him as a result of year round investigations into plankton of fjords of Eastern Greenland there were only three different types of larvae belonging to polychaetes (Thorson, 1936). Identification of these larvae was not performed, however it can be asserted from the drawings made by Thorson that those were larvae of Hesionidae, Sphaerodoridae and Spionidae. At that time in the coastal waters of north-eastern Greenland 73 species of benthic polychaetes were recorded, the majority of those being species widespread in both arctic and boreal waters. Thorson assumed that boreal-arctic species having pelagic larva in temperate waters, e.g. *Harmothoe imbricata* and *Spio filicornis*, pass over to direct development and even viviparity in the high latitudes. He rejected a possibility of lecitotrophic larval development in plankton in the high latitudes and believed that only approximately 5% of benthic invertebrates of high latitudes have a larva with a relatively long-term pelagic development. Thorson (1950) wrote: "*In order to survive in high arctic areas a planktotrophic pelagic larva has to complete its development from hatching to metamorphosis within 1-1.5 months (i.e. the period during which phytoplankton production takes place) at a temperature below 2-4 °C. Most larvae, that is in 95% of the species, are unable to do so and have a non-pelagic development.*"

In 1971 S.A. Mileikovsky having generalized the literature on the problem noted that plankton samples collected over several decades from 1931 through 1969 showed exceptional rarity or total absence of pelagic larvae of benthic invertebrates in plankton of the highest latitudes as compared to the occurrence of such larvae in subarctic and subantarctic regions. At that time a possibility of a wide distribution of different types of larval development was admitted, particularly for polychaetes, in local populations of one and the same species inhabiting e.g. temperate and arctic waters (Mileikovsky, 1971, review).

It is noteworthy that during many years plankton in the high latitudes was collected from time to time using different catchment methods and different gear, often with too large mesh size, which did not catch larvae. Nevertheless, some investigations of neritic plankton of Siberian seas using Juday nets (sieve mesh size 0.158-0.168 mm) showed that polychaete larvae in the spring–summer biological season sometimes comprise 20% of the total number of organisms of the arctic plankton in the upper 20-30 m (Buzhinskaja, 1998, review).

A large number of pelagic larvae of benthic invertebrates (42 species) were discovered by Andersen (1984) in Jørgen Brønlund Fjord of North Greenland where plankton was collected from 3 June through 12 August 1968 by net with diameter of 30 cm and 0.08 mm mesh nets. Among those there were larvae of 19 polychaete species belonging to 12 families. Of them 6 species had mostly lecitotrophic pelagic development, which in Thorson's opinion is absent in the high latitudes. That was the only attempt to identify polychaete larvae found in the highest Arctic latitudes to a species, genus or family.

It is known that in the seas of the high latitudes the major factor restricting plankton development is the light, limiting primary production, rather than temperature. The same is true also for pelagic larvae of benthic polychaetes occurring near surface at temperatures close to 0 °C or lower in both arctic and boreal waters (Grainger, 1962; Chislenko, 1972a; Prygunkova, 1974; Smidt, 1979; Vyshkvartsev, 1979; Andersen, 1994, and others). In the Possjet Bay (the Sea of Japan) where winters are sunny with little snow and growth of planktonic algae continues the year round (Konovalova, 1979), abundance of polychaete larvae in the surface plankton beneath the ice of the Novgorodskaya Inlet in December 1970 and February 1971 attained approximately 10.000 specimens per m^3 (Vyshkvartsev *et al.*, 1979). The authors assume that those were larvae of boreal-arctic species inhabiting the Possjet Bay. It is noteworthy that 10 liter bathometer and 0.94 mm mesh size sieve were used for plankton collecting. Larvae of 12 species of polychaetes were reported in the Amursky Bay of the Sea of Japan above the depth of 7 m at low water temperature (0 °C) and lower from December through March (Omelyanenko & Kulikova, 2002). Schmidt (1979) found larvae of 11 polychaete species at temperature that was below 0 °C or close to zero near west Greenland coast.

Chislenko (1972) who took plankton samples from the Dickson Bay (Kara Sea), by Juday net (diameter 20 cm, 0.158 mm mesh size) observed in 1955 and 1956 an abrupt increase in the numbers of polychaete larvae in May at water temperature below 0 °C. He characterized state of plankton at that period as pre-spring and explained this phenomenon by formation of polynia (patch of open water in ice) off the Dickson Island and by stimulating action of solar radiation or chemical substances released by algae. During 5 months from May through September larvae occurred in the Dickson Bay, their density being 115 to 412 specimens per m^3, and even single individuals were reported in winter time. Pre-spring was reported by Chislenko (1972b) also in the Yenisei Bay of the Kara Sea in the middle of May 1956, when the bay was covered by ice, but the ice cover was slightly disturbed. The plankton was characterized by absence of algae and appearance of large numbers of polychaete larvae, on the average 260 per m^3. Larvae were present in plankton from April through early October.

Andersen (1994) noted pre-spring in Jørgen Brønlund Fjord in the first half of June 1968, when beneath 2.5 m ice numerous larvae of invertebrates occurred. In the number of species (12) polychaete larvae were predominant; in the abundance larvae of polychaetes (up to 5458 specimens per 10 hauls) and larvae of *Hiatella striata* (Bivalvia) were predominant. There was no coincidence of maximum abundance of polychaete larvae (June) and the main phytoplankton "bloom", observed in middle August. During the entire period of research larvae of 6 species of polychaetes occurred, whereas larvae of 5 species occurred in June only (Andersen, 1994).

Thus, pelagic larval development of species of benthic invertebrates, of polychaetes in particular, in the high Arctic is not always completed in 1-1.5 months, as Thorson assumed, but can continue for at least 2.5 months as in Jørgen Brønlund Fjord and even 5 months as was recorded in the Kara Sea off the Dickson Island. Growth of planktonic algae in Jørgen Brønlund Fjord was observed throughout the entire research period. The vegetative period of microalgae in plankton of the Kara Sea continues on the average 4 months (Usachev, 1968). In the Chaun Bay of the East Siberian Sea growth of plankton algae in 1989 began in the second half of April when ice thickness was approximately 2 m and completed nearly at the end of October (Galkina *et al.*, 1994). It is known that growth of algae on the ice upper surface begins long before ice melting. Already with the appearance of wet snow, crevices and caverns in the ice green algae attain their maximum development (Melnikov, 1980). Moreover, microalgae (mostly diatoms), inhabit on the lower surface and in the interior of the ice (lower layer) attaching to ice crystals or in interstitial water between them (Melnikov, 1989). More than 300 species comprising flora of Arctic ices were recorded (Horner, 1989). Intensification of light triggers growth of ice algae. Entry of organic matter synthesized by algae into water stimulates development of colourless flagellates, infusoria, multicellular microzooplankton. Horner and Alexander (1972) who studied flora and fauna of seasonal ices off Barrow Cape in the Chuckchi Sea noted that in some samples polychaete larvae were quite common. The ice algae would be an important food source early in spring when little or no primary production occurs in the water column and the ice algae are concentrated at the ice water interface (Horner, 1989). Ice meiofauna can also be food for larvae. During ice melting ice flora becomes a part of plankton. Thus the growth of abundance of polychaete larvae in plankton of the high latitudes in pre-spring period is related more to increase of light and growth of microalgae than to water temperature rise, in any case this concerns planktotrophic larvae.

Data on ecology of reproduction of polychaetes in the high latitudes of the Russian Arctic are very scanty. Information on sizes of mature eggs of 12 species and findings of epitokous individuals of 3 species of *Autolytus* from the region of the Franz Josef Land and sizes of mature eggs of 9 polychaete species from the Laptev Sea and one species from the East Siberian Sea were published by Averincev (1977, 1989, 1990). On the basis of these data we can speak about absence of pelagic development of *Sphaerosyllis* aff. *erinaceus*, because diameter of eggs on the dorsal side of the worms was 100-150 μm, and species of this genus with egg size of 90 μm develop with bottom larva (Thorson, 1946; Cazaux, 1972). *Nicolea zostericola* (egg diameter up to 250 μm) apparently has bottom larva in the Laptev Sea as well as in temperate waters when egg size is 240-300 μm (Thorson, 1946; Eckelbarger, 1974). Direct development can only be presumed for small species with large eggs, i.e. *Sphaerodoropsis minuta* (diameter of eggs up to 300 μm) and for *Dysponetus pygmaeus* with eggs up to 250 μm. At least 4 species with relatively small egg size most probably develop with planktonic larva: *Phyllodoce groenlandica* (egg diameter less than 100 μm, Franz Josef Land), *Micronephtys minuta* (100 μm, Laptev Sea), *Ophelina cylindricaudatus* (100-120 μm, Laptev Sea), *Artacama proboscidea* (approximately 200 μm, Laptev Sea). *Ph. groenlandica* in the Danish waters and in the White Sea has pelagic larva, and egg sizes being similar (Thorson, 1946; Chivilev *et al.*, 1991). *M. minuta* in the White Sea has diameter of mature eggs of 85-90 μm and is characterized by complete pelagic larval development (Lvova, 1981). Development of *A. proboscidea* (diameter of disc-shaped eggs is 170-180 μm) in the Oresund Straight occurs with pelagic lecitotrophic larva (Thorson, 1946).

In the Yenisei Bay of the Kara Sea in a sample of 12.08.1993 in layer 9-0 m, were found planktotrophic nectochaetes Spionidae possibly belonging to *Marenzelleria arctia* (see Buzhinskaja, 1998, Fig. 1, *A*).

In maternal tubes of arctic species *Trochochaeta carica*, collected in the Ob' Bay of the Kara Sea on 15.08.1993 at water temperature of 0.05 °C very large larvae 1.7-1.8 mm in length were found (Buzhinskaja & Jorgensen, 1997). Larvae were lecitotrophic, mouth not formed, supplied with long provisory setae, which suggested that they spent some time in plankton. Eggs rich in yolk in body cavity of females attained sizes of 500-564 μm and 405-650 μm. Those are the largest eggs so far discovered in polychaetes of the high Arctic latitudes. This finding evidences that not always species producing even as large eggs as *T. carica* have direct development.

Females of interstitial species *Protodrilus* sp. carrying eggs on body surface covered by mucus were found in the Kara Sea off the Nansen Island (near the Taimyr Peninsula) at a depth of 4 m (Fig. 1). Each egg had an elongated part in the form of a long strand going out of the genital pore. The eggs formed clusters of 4-26 eggs that were reminiscent of bunches of balloons. Egg size was from 42.6×37.3 μm to 53×42.6 μm, i.e. eggs were very small, pelagic larvae evidently developing from them.

I examined 5 planktonic samples collected near the Bunge Land on August 1, 1973 and September 1-3, 1973 by Juday nets (diameter 37 cm, 160-170 μm mesh nets). Larvae of 8 species of polychaetes on different developmental stages were found (Buzhinskaja, 2006). Of the family Polynoidae larvae of 4 species were found: lecitotrophic metatrochophore and nectochaetes of *Gattyana cirrhosa?*, *Harmothoe imbricata*, and Harmothoinae gen. sp. 1 and planktotrophic nectochaetae of Harmothoinae gen. sp. 2. Early metatrochophora of Nephtydidae, planktotrophic nectochaetae of two species of Spionidae were also found (of these *Pygospio elegans* was identified); many planktotrophic larvae of *Trochochaeta multisetosa* (Trochochaetidae) on different stages from early metatrochophore to late nectochaeta were also found. The number of polychaete larvae in the beginning of September approached maximally 1375 specimens per one plankton sample (Pavshtiks, 1990). Larvae of *T. multisetosa* were predominant. Surface water temperature in the region of the Bunge Land in summer does not rise above 2 °C.

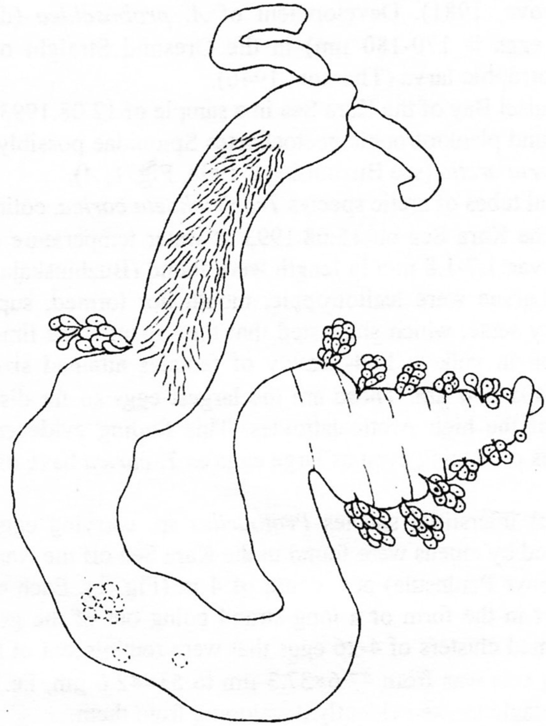

Fig. 1. *Protodrilus* sp.: female with eggs

In the Chaun Bay of the East Siberian Sea the hydrological conditions are somewhat different. In late August through early September water temperature in the upper 10 m layer usually reaches 4-5 °C, then it declines. Plankton was collected by an expedition of the Zoological Institute of the Russian Academy of Sciences from August 10 through August 27, 1986 in 10 localities of the area, 2 samples per station at different depths from 17 to 0 m. Juday net (diameter 0.75 m, 168 μm mesh size) was used. In spite of the relative large mesh size, trochophores and metatrochophores of polychaetes for different families occurred relatively frequently (Fig. 2). Moreover planktotrophic larvae of *Nereimyra aphroditoides* and *Nephtys ciliata* (see Buzhinskaja, 1998) on different developmental stages and nectochaetes of *Cistenides granulata* (see Buzhinskaja, 1998) and *Polydora* sp. were found. The largest number of larvae, 247 specimens per m^3, was observed in layer 12.0 m on 26 August (calculated from Pinchuk, 1994). It is noteworthy that Thorson (1936) observed small eggs of 70 μm in specimens of *C. granulata* from fjords of North-Eastern Greenland, but in spite of this he surmised that this species laid a mucous clutch and developed without a pelagic larva. However with such size of mature eggs polychaetes normally have a free-swimming planktotrophic larva.

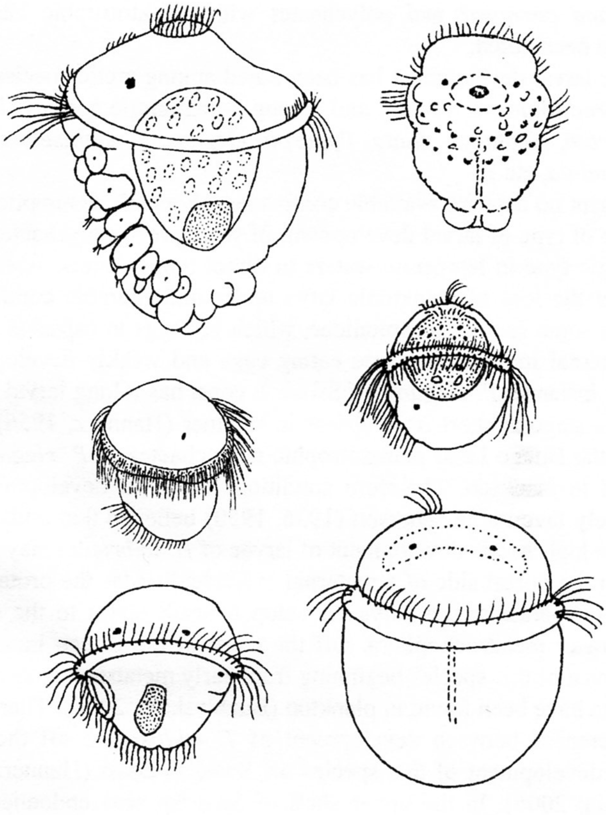

Fig. 2. Early stages of polychaete larvae from Chaun Bay

Pelagic larvae of 11 species from the Eastern Arctic were found for the first time in the high Arctic seas, among them representatives of the families Trochochaetidae and Pectinariidae. Thus, it can be stated with regard to data of Thorson and Andersen for the Greenland Sea, that in the coastal plankton of high latitudes there occur larvae of at least 30 species from 15 polychaete families. Four above-listed species with small sizes of mature eggs, which in all probability develop with a pelagic larva, should be added.

In the high latitudes of the Eastern Arctic polychaetes with completely planktotrophic larval development (except possibly the most initial stages), e.g. *Nephtys ciliata*, *Nereimyra aphroditoides*, and *Trochochaeta multisetosa*, polychaetes with a completely lecitotrophic development, e.g. *T. carica, Gattyana cirrhosa?* and polychaetes with planktotrophic late larval stages have been noted.

Pelagic larval development has been noted among arctic species (*Nereimyra aphroditoides*, *T. carica*) and among boreal-arctic species (*Harmothoe imbricata, Nephthys ciliata, Pygospio elegans, T. multisetosa, Pectinaria granulata*, etc.).

At present no data are available confirming Thorson's assumption about the change of type of larval development of widespread polychaete species from pelagic type in temperate waters to direct type in arctic waters. It is known that the loss of planktonic larva under unfavourable conditions is possible in some species of Spionidae, which lay eggs in capsules in tubes of the maternal individual, larvae eating eggs and weakly developed embryos. For instance, *P. elegans* off Swedish coast has a long larval stage in spring, this stage is short or is absent in summer (Hannerz, 1956). In the region of the Bunge Land planktotrophic nectochaetes of *P. elegans* were discovered in plankton. Therefore conditions of larval development here are relatively favourable. Thorson (1936, 1950) believed that under conditions of the high Arctic development of larvae of *H. imbricata* may proceed entirely on the dorsal side of a maternal individual under the protection of elytra. In temperate waters larvae develop beneath elytra to the stage of trochophora or metatrochophora. Off the coast of the Bunge Land lecitotrophic larvae of this species beginning from early metatrochophore up to a nectochaeta have been found in plankton (Buzhinskaja, 2006). There are no basic differences between development of *T. multisetosa* off the Bunge Land and development of this species off Swedish coast (Hannerz, 1956; Buzhinskaja, 2006). In the upper shelf of Siberian seas endemics of the Arctic among polychaetes comprise not more than 15%, other species are relatively widely spread in temperate waters. It would be logical to assume that those of the latter who have free-swimming larvae in temperate waters have them in high latitudes.

It should be noted in conclusion that neritic meroplankton of high latitudes is apparently much richer than it has been represented in published results of our coastal expeditions, taking into consideration the small number of samples collected and investigated and too large mesh size of nets. Moreover specialized methods and technique for collecting meroplankton has not been used.

References

Andersen, O.G.N. 1984. Meroplankton in Jørgen Brønlund Fjord, North Greenland. *Medd. Grønland. Biosci.* 12: 3-25.

Averincev, V.G. 1977. Polychaetes of the Franz Josef Land shelf. *Issled. Fauny Morey* 14 (22): 140-184. (In Russian).

Averincev, V.G. 1989. *Seasonal dynamics of polychaetes of the high arctic marine ecosystems of Franz Joseph Land (Errantia)*. Apatity. 78 pp. (In Russian).

Averincev, V.G. 1990. The polychaetous fauna of the Laptev sea. *Issled. Fauny Morey* 37 (45): 186. (In Russian).

Buzhinskaja, G.N. 1998. Modern data on pelagic larvae of bottom polychaetes from high arctic seas and Thorson's hypothesis about suppression of pelagic development in bottom marine invertebrates at polar latitudes. *Proc. Zool. Inst. RAS* 276: 53-59.

Buzhinskaja, G.N. 2006. Planktonic larvae of bottom polychaetes at Bunge Land (East Siberian Sea). *Issled. Fauny Morey* 56 (64): 79-92. (In Russian).

Buzhinskaja, G.N. & L.L. Jørgensen. 1997. Redescription of *Trochochaeta carica* (Birula, 1897) (Polychaeta, Trochochaetidae) with notes on reproductive biology and larva. *Sarsia* 82: 69-75.

Cazaux, C. 1972. Développement larvaire d'annélides polychètes (Bassin d'Arcachon). *Arch. Zool .Exp. Gén.* 113: 71-108.

Chislenko, L.L. 1972a. Zooplankton of the Dikson Bay (Kara Sea). *Issled. Fauny Morey* 12 (20): 228-238.

Chislenko, L.L. 1972b. Specific composition and distribution of ecological complexes of zooplankton in the Yenisei Gulf. *Issled. Fauny Morey* 12 (20): 239-260.

Chivilev, S.M., Shilin, M.B. & V.K. Lebsky. 1991. Pelagic polychaete larvae from the Chupa Inlet (White Sea). *Proc. Zool. Inst. RAS* 233: 58-78. (In Russian).

Eckelbarger, K.J. 1974. Population biology and larval development of the terebellid polychaete *Nicolea zostericola. Marine Biol.* 27: 101-113.

Galkina, V.N., Rura, A.D. & S.Y. Gagaev. 1994. Phytoplankton and its production in the Chaun Bay of the East Siberian Sea. *Issled. Fauny Morey* 47 (55): 112-120. (In Russian).

Grainger, E.N. 1962. Zooplankton of Fox Basin in the Canadian Arctic. *J. Fish. Res. Board Canada* 19 (3): 377-400.

Hannerz, L. 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). *Zool. Bidrag Uppsala* 31: 1-204.

Horner, R.A. 1989. Arctic sea-ice biota. In: Herman, Y. (Ed.). *The Arctic Seas. Climatology, Oceanography, Geology, and Biology*. pp.123-146. New York: Van Nostrand Reinhold Company.

Horner, R. & V. Alexander. 1972. Algal populations in Arctic sea ice: An investigation of heterotrophy. *Limnology and Oceanography* 17:454-458.

Konovalova, G.V. 1979. Species composition and phytoplankton abundance in Possjet Bay (the Sea of Japan). In: Kussakin, O.G. (Ed.). *Investigations of pelagic and bottom organisms from the Far Eastern Seas*. pp. 5-16. Vladivostok: FESC AS USSR. (In Russian).

Lvova, T.G. 1981. Life cycle and salinity adaptations of *Micronephtys minuta* Théel (Nephthydidae, Polychaeta) in the White Sea. Leningrad: Zoological Institute AS USSR. 20 pp. (In Russian).

Melnikov, I.A. 1980. Ecosystem of arctic drifting ice. In: Vinogradov, M.E. & I.A. Melnikov (Eds.). Biology of the Central Arctic Basin. pp. 61-97. Moskow: Nauka. (In Russian)

Melnikov, I.A. 1989. Ecosystem of the Arctic sea ice. Moskow: Izd. AN SSSR. 191 pp. (In Russian).

Mileikovsky, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: re-evaluation. Marine Biol. 10: 193-213.

Omelyanenko, V.A. & V.A. Kulikova. 2002. Composition, seasonal dynamics and interannual changes in abundance of polychaete larvae in Amursky Bay (Peter the Great Bay, Sea of Japan). Biologia morya 28 (5): 348-355. (In Russian).

Pavshtiks, E.A. 1990. Composition and quantitative distribution of the zooplankton near New Siberian Islands. Issled. Fauny Morey 37 (45): 89-104. (In Russian).

Pinchuk, A.I. 1994. On the zooplankton of the Chaun Bay. Issled. Fauny Morey 47 (55): 121-127. (In Russian).

Prygunkova, R.V. Certain pecularities in the seasonal development of zooplankton in the Chupa Inlet of the White Sea. Issled. Fauny Morey 13 (21): 4-52. (In Russian).

Smidt, E.L. 1979. Annual cycles of primary production and of zooplankton of Southwest Greenland. Greenland Bioscience 1: 3-51.

Thorson, G. 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. *Medd. Grønland.* 100 (6): 1-155.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with species reference to the planctonic larvae in the Sound (Øresund). *Medd. Komm. Danmarks Fisk. Havunders.*, Ser. Plancton 4 (1): 1-523.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Review* 25: 1-45.

Usachev, P.I. 1968. Phytoplankton of the Kara Sea. In: *Plankton of Pacific Ocean.* pp. 6-28. Moskow: Nauka.

Vyshkvartsev, D.I., Kruchkova, G.A. & T.Sh. Karapetyan. 1979. Studies of zooplankton in shallow inlets of Possjet Bay. In: Kussakin, O.G. (Ed.). *Investigations of pelagic and bottom organisms from the Far Eastern Seas.* pp.17-29. Vladivostok: FESC AS USSR. (In Russian).