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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

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The distribution of various types of larval development among marine invertebrates has been most comprehensively discussed by Thorson (1936, 1950, 1965). The vast majority of tropical and boreal species of the bottom invertebrates inhabiting the shallow-shelf zone have the planktotrophic larval stages of varying duration in their development. In the arctic and antarctic seas characterized by low water temperature and short periods of phytoplankton production, according to the widely accepted Thorson's concept the pelagic development is nearly or totally suppressed and replaced by direct development and viviparity. Thorson postulated that less than 5% of species of high arctic bottom invertebrates have the planktotrophic larvae with a long pelagic life. Lecithotrophic larvae, originating from large yolky eggs are absent in the high arctic seas, but in all other seas 10% of the species with pelagic larvae have such type of larvae (Thorson, 1950).

Mileikovsky (1971) summarizing the literature on the problem, marked once more "the considerable scarcity or complete absence of pelagic larvae of bottom invertebrates in the plankton of highest latitudes". The pattern of regular replacement of pelagic development by direct development and viviparity with the latitude increase has been well demonstrated by Thorson (1950, 1965) for the Gastropoda Prosobranchia. However species of each group of animals have their own peculiarities of reproduction and larval development and the correlation between habitat and form of larval development is not always direct. As Mileikovsky noted, the type of larval development is not influenced by the environmental factors only, but also by the endogenous factors (genotype). E.g., in the coastal arctic regions of East Greenland the species with pelagic larvae practically absent among Prosobranchia and constitute 25% of total number of Echinodermata species inhabiting the same territories (Thorson, 1936; Einarsson, 1948). More than one third of the total number of bivalve species in the same regions have lecithotrophic larval development with a short pelagic larval stage, 15% of species develop by means of the planctonotrophic pelagic larvae and the direct development is characteristic

for about 50% of bivalve species only (cf. with more than 93% among prosobranch species) (Ockelmann, 1965). Among 14 species of shallow-water asteroids known from McMurdo Sound, Antarctica, only 3 have non-pelagic development (Pearse et al. 1991). Moreover, contrary to Thorson's opinion, lecithotrophic pelagic development turned out to be common both in arctic and in antarctic seas (Andersen, 1984; Pearse et al. 1991).

At polar latitudes the mode of development of the most bottom polychaetes is unknown. The larvae of a vast majority of antarctic and arctic polychaete species have not yet been observed and described. Only several pelagic larvae of bottom polychaetes were described from antarctic waters (Ehlers, 1913; Scheltema et al. 1997). As to the arctic regions, Thorson (1936), the first who figured a few polychaete larvae from a plankton of Northeast Greenland. Based on small number of polychaete larvae found in the Northeast Greenland plankton, Thorson (1936) supposed that several other polychaetes in the region reproduce without any pelagic larval stage. However Andersen (1984) revealed the relatively abundant meroplankton in high-arctic fiord of North Greenland. Most diverse among the meroplancters were the polychaete larvae represented 19 species from 10 families. At least 4 species of them have entirely or partly lecithotrophic pelagic development (Andersen, 1984). Recently lecithotrophic larvae of *Trochochaeta carica* (Trochochaetidae) was described from the Kara Sea (Buzhinskaja & Jorgensen, 1997).

The study of arctic plankton over the past several decades showed that pelagic larvae of bottom polychaetes occur in all arctic seas and their quantity in the upper 20-30m in spring-summer biological season may be considerable (Grainger, 1962, 1965; Chislenko, 1972a, b; Andersen, 1984; Pavshtiks, 1984, 1990, 1994; Pinchuk, 1994). Scientists who used Yuday net (vertical hauls, 0.158-0.168 mm mesh size) to collect a plankton, calculated the number of polychaete larvae per one cubic metre in different coastal arctic regions (Chislenko, 1972a, b; Pavshtiks, 1984, 1990, 1994, Pinchuk, 1994). In spring-summer season the highest density of polychaete larvae varies from 250 to 570 specimens per m^3 , that can constitute up to 20% of the total number of plankton organisms. The largest total number of the polychaete larvae in one zooplankton sample was 1375 specimens and was recorded near New Siberian Islands. In abundance polychaete larvae in high Arctic usually dominate over other larvae of bottom invertebrates and only sometimes they are surpassed by the bivalve larvae (see Andersen, 1984). The appearance of a number of polychaete larvae in a plankton at the beginning of May characterizes the pre-springs state in the Kara Sea (Chislenko, 1972 a,b).

Preliminary examination of only several plankton samples, collected from Bunge Land (New Siberian Islands), Chaun Bay (East Siberian Sea) and from Enisei Gulf (Kara Sea) allowed to found the polychaete larvae belonging to different families, namely Polynoidae

(several species), Nephtyidae (2 species), Hesionidae (1 species), Spionidae (several species), Trochochaetidae (1 species), Pectinariidae (1 species) (Fig. 1-3). The most of the species develop by means of entirely or partly planktotrophic larvae. Early pelagic larvae of Polynoidae gen. sp. 2 and *Nephtys* sp. are lecithotrophic (Fig. 2, C,E). The pelagic development of Polynoidae gen. sp. 1 is evidently entirely lecithotrophic (Fig. 2). Thus the pelagic larvae of bottom polychaetes are not so rare in the high arctic seas as hitherto believed. In high arctic seas the different polychaete species belonging to at least 13 families have the pelagic larvae in their development. Both planktotrophic and lecithotrophic larval development takes place in the high Arctic. It is possible that the pelagic larval development is more wide-spread among polychaetes, than among other groups of bottom invertebrates inhabiting the high Arctic.

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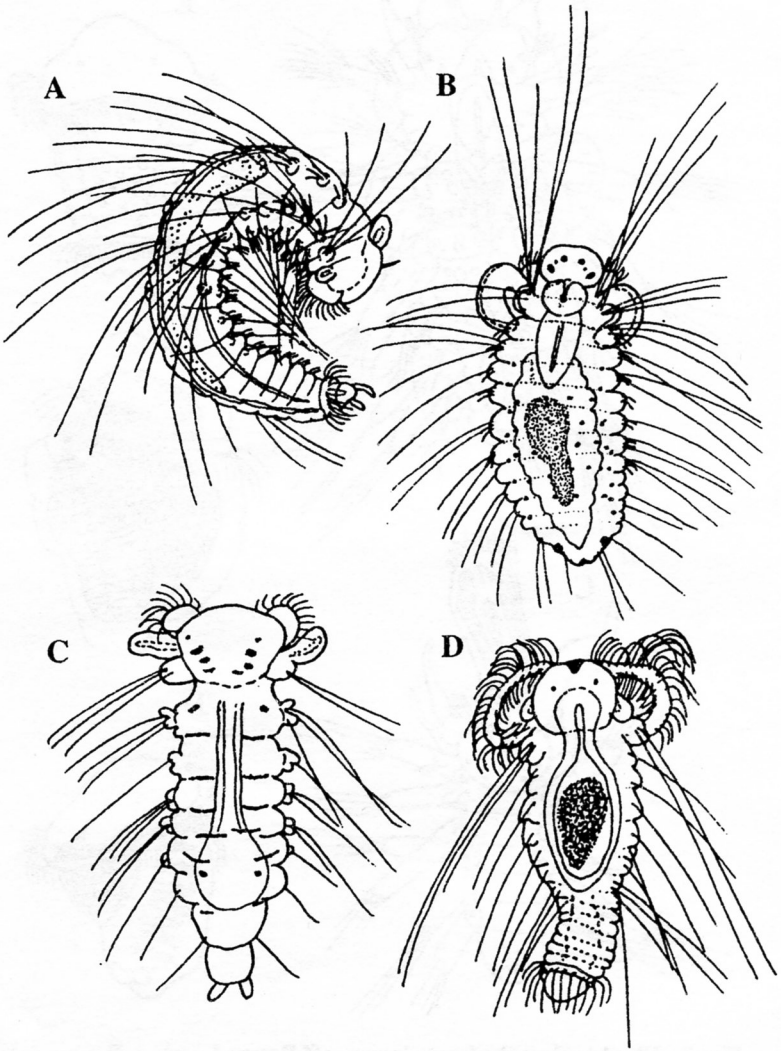

Fig. 1. Planktotrophic polychaete larvae of Spionidae (A-C) and Trochochaetidae (D):
A - from Enisei Gulf, B-D - from plankton off Bunge Land

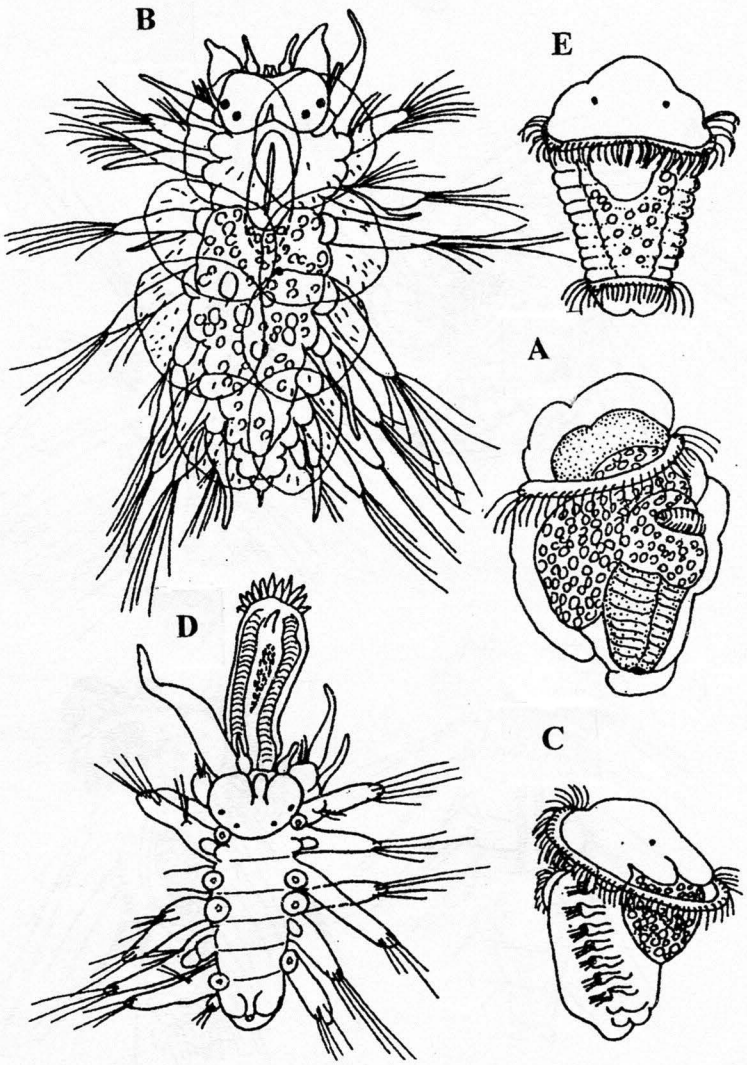

Fig. 2. Planktonic polychaete larvae off Bunge Land:
A,B - Polynoidae gen.sp. 1
(A - lecithotrophic metatrochophora, B - lecithotrophic nectochaeta); C,D - Polynoidae gen.sp.2 (C - lecithotrophic metatrochophora, D - planktotrophic nectochaeta); E - lecithotrophic metatrochophora of *Nephtys* sp. (Nephtyidae)

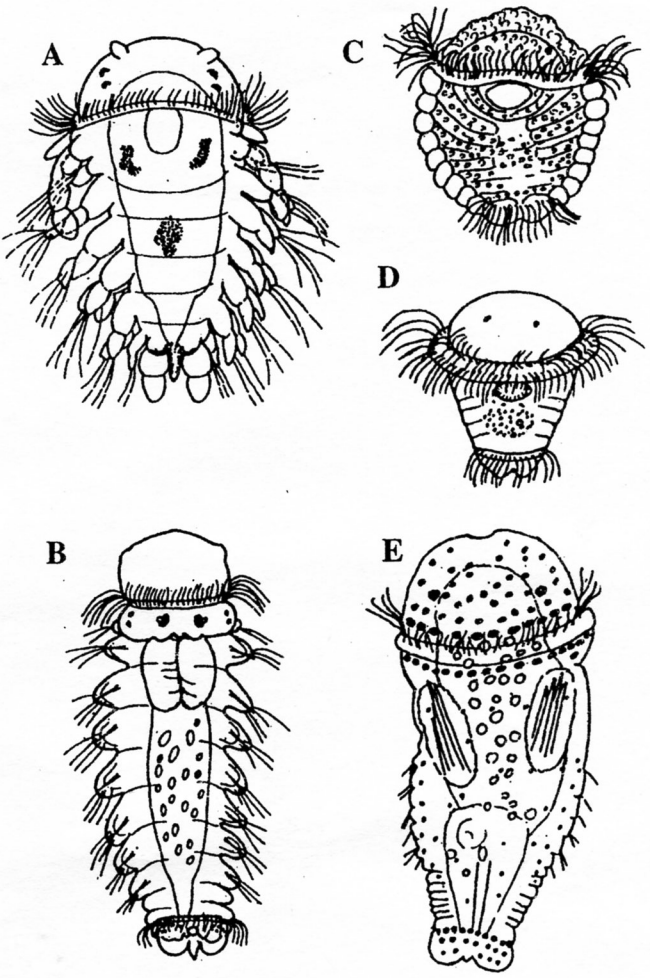

Fig. 3. Some polychaete larvae from Chaun Bay:
A -planktotrophic nectochaeta of *Nereimyra aphroditoides* (Hesionidae); B - nectochaeta of *Nephtys ciliata* (Nephtyidae); C - planktotrophic metatrochophora (family unknown); D - planktotrophic metatrochophora of Nephtyidae; E - lecithotrophic nectochaeta of *Cistenides granulata* (Pectinariidae)