

## **Siberian River run-off in the Kara Sea**

R.Stein, K. Fahl, D.K. Fütterer, E.M. Galimov and O.V. Stephanets (Editors)

Proceedings in Marine Science no. 6,

©2003 Elsevier Science B.V pp. 195-212

(submitted version)

### **Distribution of meroplankton in the southern Kara Sea in relation to local hydrographic pattern**

**Ingo Fetzer\***

Alfred Wegener Institute for Polar- and Marine Research, Bremerhaven, Germany

#### **Abstract:**

Meroplankton was sampled at 11 stations in the southern Kara Sea and the Yenisei Estuary in September 2000. Larvae of 29 benthic taxa representing 10 higher groups were identified. Meroplankton was present at almost all stations and most depth levels. The two most abundant groups were Echinodermata (68%) and Polychaeta (26%). Echinoderms dominated total meroplankton locally due to mass occurrences of Ophiopluteus larvae. The relative group composition was highly variable and seemed to depend mainly on the local hydrographic pattern. Comparison of meroplanktonic data with the distribution of the adults revealed for Spionida and Bivalvia a ‘downstream’ transport of the larvae whereas for other polychaete species and Ophiuroida ‘upstream’ transport into the estuary occurred. The distribution and concentration of the larvae within the estuary is explained by physical barriers established by hydrographic gradients, the prevailing mixing processes and the presence of a near-bottom counter current.

#### **1. Introduction**

Indirect development with a pelagic larval stage represents the most widely spread developmental mode of benthic marine invertebrates in temperate latitudes. This adaptation facilitates a wide distribution of a species and enables the quick colonization of new territories.

The lack of larvae in the first meroplankton investigations in polar waters inspired the hypothesis that many polar species reproduce without a planktonic, in particular without a planktivorous stage (Thorson 1936, 1946, 1950). New discoveries of an increasing number of pelagic larvae, especially in the Antarctic waters and the deep sea, fuelled doubts on the validity of such generalisations (Scheltema & Williams 1995). Except for the studies of Thorson (e.g. 1936, 1950, 1966) and Mileikovsky (1971), very little is known about the ecology of meroplankton in the Arctic.

On the other hand, the persistence of populations depends upon the successful recruitment of juveniles into adult habitats. Benthic communities are therefore determined by the supply of larvae, their transport and settlement success (Butman 1987). To which degree environmental factors may influence the distribution and the mortality of the planktonic stages and later juvenile stages and how far postlarval processes are responsible for creating the observed distribution pattern of the adult infauna, is almost unknown (Thorson 1966, Muus 1973, Watzin 1983, 1986). Benthic

---

\* corresponding author: ifetzer@awi-bremerhaven.de

investigations traditionally do not consider whether distinct assemblages may result from different larval recruitment processes, and often care only about the adult stages (Butman 1987, Olafson *et al.* 1994). This is surprising as it is commonly accepted that an understanding of the dynamics of benthic communities without a fair knowledge of larval and juvenile ecology is almost impossible to achieve (Scheltema 1986).

Recruitment within estuaries seems especially problematic for animals with planktonic larvae because the potential recruits are transported away by the seaward flow of estuarine surface waters. Additionally within these areas the introduced water mass undergoes massive physical changes, the environmental regime often creates physical and physiological barriers and hence restricts the distribution of meroplankters (Epifanio 1988, Scheltema 1988).

The aim of this study is to investigate the presence and distribution of the larvae of Arctic benthic invertebrates in the Yenisei Estuary and the adjacent Kara Sea in relation to their adults and with respect to the structuring effects of the freshwater influence of the river.

## 2. Material and Methods

The sampling was carried out in September 2000 as part of the joint Russian-German SIRRO (Siberian River Run-Off) project onboard the RV 'Akademik Boris Petrov' (Stein & Stephanets 2001). Sampling stations were located in the estuary of Yenisei River and the southeastern Kara Sea (Figure 1).

Larval plankton was collected with a Nansen Closing Net (NCN) at 11 stations using 55µm mesh size and an opening of 70cm diameter (Table 1). Since the water column was characterised by a pronounced halocline, two vertical net hauls were taken at each station: one from the bottom to beneath the halocline ('below') and the second through the halocline to the surface ('above'). Only at the southerly Station 22 a single net haul was conducted since no halocline was present. The water body structure was determined by instant CTD probe data, taken at each station prior to all other sampling (Stephansev & Shmelkov 2001).

In order to get information about adult-larvae interrelationships and transport processes, data from simultaneous benthic fauna investigations were included in this paper. In the present study, the distribution of the larval stages will be emphasized. More detailed studies on macrozoobenthos will be presented by Deubel *et al.* (this volume) and Denisenko *et al.* (this volume).

All samples were preserved in 4% borax buffered formalaldehyd until further treatment in the laboratory.

In the laboratory, the meroplankton was picked out using a stereomicroscope and identified to the lowest possible taxon. The data were then normalized to individuals m<sup>-3</sup> (ind. m<sup>-3</sup>) for meroplankton (Table 2) and individuals m<sup>-2</sup> (ind. m<sup>-2</sup>) for benthos (Figure 5). For better comparison of meroplankton densities with earlier investigations the meroplankton data are also given in cumulative abundances (ind. m<sup>-2</sup>; Table 1).

Larvae that could not be determined to species level due to their small size and inadequate identification literature were pooled under the name of a higher taxon. Morphologically similar specimens that could not be identified any further, were put together under a common name that either described their appearance (e.g. 'spherical trochophora') or the type of larvae (e.g. Cyphonautes) found (Table 2). The identified specimens were taxonomically grouped according to Westheide & Rieger (1996).

Although most of the adults and some larvae were identified to species level, for the larvae's distribution and the following comparison with the occurrence of the adults, both of them were pooled to order level. Prior to this, adults of those species with explicit non-pelagic reproduction modes were excluded.

For a better understanding and comparison of the larval distribution pattern in relation to their adults a longitudinal transect was drawn following the Stations 22, 13, 23, 24, 7, 5, 30, 28 out of the Yenisei River (figure 1). Although aware of constraining some of the data's horizontal information, in this way a better understanding will be gained. The gradient was chosen in agreement to the transect chosen for plankton and macrozoobenthic data (Deubel *et al.*, this volume).

As the Ophiuroida showed a very distinct distribution pattern, their occurrence will be described in more detail. To get an idea of the possible spatial distribution of both Ophiuroid larvae and adults abundance isolines, based on the data of all stations, were calculated. Since the purpose of this plot is to show distribution pattern rather than real densities, no numbers are given for the isolines. For the adult organisms all available data on adult Ophiuroida were used (Deubel *et al.*, this volume, for more details).

### 3. Results

#### 3.1 Hydrography

In September, a pronounced halocline, derived from the high freshwater output of the Yenisei River was clearly visible in its mouth (figure 2). At the bottom, saline marine water intruded into the estuary to 71°N. Here it still showed a thickness of 5m. The brackish water plume on the other hand reached 72.5°N (Station 13) into the Kara Sea. At Stations 22, 13, 23 a prominent front is visible where strong mixing processes occurred. The extent of the frontal zone was about 100km. At Stations 23 (73°N) and 24 (73.5°N) water of >18 was found close to the surface. Between Stations 24 and 5, a water lens with <18 had apparently been separated from the river plume.

#### 3.2 Meroplankton

Larvae of 29 benthic taxa representing 10 higher taxonomic groups were identified (Table 2). Most larvae were rather big and well developed. Only the 'small Trochophora' seemed to have hatched just recently since they had not developed any body segments yet. From the unidentified groups the 'spherical Trochophora' most probably belonged to the Phyllodocida. 'Trochophora 1' occurred only at Station 7 whereas specimens of 'Trochophora 2' were exclusively present at Stations 7 and 24. They differed significantly in appearance from all other polychaete larvae found, but could not be identified any further yet.

Meroplankton was present at all but two stations and depth levels. At Station 5, however, only three polychaete trochophores were observed in the upper water layer whereas at Station 22 no larvae were found in the entire water column. Local total abundances ranged from 0.2 (Station 5) to 128 ind. m<sup>-3</sup> (Station 24). The two most dominant groups were Echinodermata (68%) and Polychaeta (26%). The echinoderms dominated meroplankton by mass occurrence of Ophiopluteus larvae. Larvae of Crustacea, Cnidaria, Mollusca, Sipunculida, Priapulida, Tentaculata, Nemertini and Tunicata were also present (6%), but only in low numbers.

About 62% of the found species were present in surface and bottom net hauls at the same station. Only rare species such as *Glycera* sp., *Eteone longa*, *Harmothoe* sp.,

*Owenia* sp., *Scoloplos* sp., the hydrozoan actinula, both sipunculid and priapulid Pelagosphera, the Nemertini Pilidium and the Tunicata tadpole larvae were present in the lower water layer exclusively. They referred to 35% of all. Of these taxa, only one or two specimens were found in all samples, as also was the case for the ‘Trochophora□’ (3%) that were present only in the upper water mass.

The abundance of larvae continuously increased northward along the transect to Station 24 and then decreased sharply at Station 5 (Figure 3). Somehow Station 5 seems exceptional since the nearby Stations 26 and 27 showed high densities (Table 1). Towards Stations 28 the abundance increased again to 40 ind. m<sup>-3</sup> (above) and 5 ind. m<sup>-3</sup> (below), respectively. The species numbers followed about this same pattern (Table 1).

Total abundances along the transect showed generally higher concentrations of larvae in the lower more saline water layer (Figure 3). Only at Station 30, did the upper water layer contain more individuals than the lower.

The relative group composition at the stations was highly variable and no general trend was detectable (Figure 4a). Below the halocline, mainly echinoderm larvae dominated. At almost all stations, they provided >60% to the meroplankton. Only the Stations 2, 5, 23, 27 and 30 were different, because here the polychaetes outnumbered the echinoderms representing >75%. At Station 2, also Crustacea, Cnidaria and Mollusca contributed much to the local inventory.

Above the halocline, the overall composition generally revealed a more equal distribution between the groups (Figure 4b). On a longitudinal transect (Stations 13, 24, 7, 26 and 28) Echinodermata larvae dominated the plankton, whereas at Stations 23, 30, 27, 2 and 5 polychaetes dominated the meroplankton. Crustacea were found in high numbers at Stations 23, 24 and 26 whereas they played only a minor role at all other stations.

In order to detect relations between the origin of some larvae and the presence of adults, both larvae above and below the halocline and data on the densities of adults were plotted (Figure 5).

While adult Spionida were solely found at the southern Stations 22 and 13, the highest numbers of larvae were present at the more northerly Stations 23, 24 and 7. Generally the lower layers contained more spionid larvae. Only at Station 7 did the number of spionid larvae in the upper water layer surpass that of the lower layer. However, in relation to the abundances of the adults only very few spionid larvae of this group were found in the water column.

The situation among the ‘other polychaetes’ was slightly different. Here the highest numbers of adults, which were exclusively determined by Phyllodocida, were found further north than the main abundance of their planktonic stages.

The density of adult bivalves was high both in the estuary (Station 13) and at Station 28 showing ~98 ind. m<sup>-3</sup>. The highest abundances of larvae were found at Stations 23, 24 and 28, but only with very few (<1 ind. m<sup>-3</sup>) specimens.

Ophiuroid larvae seem to originate from local production of adults at Station 24 since here the highest densities of adults were present. However, looking at the horizontal distribution of the adults Station 24 is only a local ‘hotspot’ with high abundances of adults, whereas the highest abundances were found in two areas further north (Figure 6c). The larvae had their main distribution in the northern area, but a larval ‘plume’ extends to the area further south into the estuary (Figure 6a). Below the halocline, the highest densities were found close to Stations 24 and 7 (Figure 6b).

## 4. Discussion

Since only a single net haul per layer and station was taken, comparison between the stations and conclusions of the distribution of meroplankton in the entire research area have to be made with caution. It should be kept in mind that the results reflect only local distribution at the moment of sampling. The lack of replicate samples also restricts the feasibility of statistical analysis.

### 4.1 Hydrography

Because meroplanktonic organisms are subject to passive transport processes, the knowledge of the hydrography of the research area is a pre-condition for the interpretation of the observed distribution patterns.

The water mass along the Yenisei transect showed a defined structure. The salinity profile indicated that the river run-off had exceeded its seasonal discharge maximum and the freshwater plume was 'retreating' into the estuary (Pavlov & Pfirman 1995). South of Station 23 strong mixing processes in the upper water masses occurred. Nevertheless, a strong halocline between 10m and 25m remained with highly saline waters (salinity >30) beneath. Harms & Karcher (1999) described salinity distribution as typical for the summer month in the Kara Sea, which is characterised by a strong thermohaline stratification caused by freshwater run-off and melting of ice, but also by strong mixing processes occurring due to increasing wind stress. Between August and September the wind regime changes from easterly to southwesterly directions, deflecting the weakening freshwater plume of the rivers from northwest to east (Harms *et al.* 2000). Wind stress may also have been responsible for the separation of a water lens visible at Station 7, where the 20 salinity isoline was deflected into greater depth. Tidal forces are unlikely to have a major effect in the Yenisei estuary (Telang *et al.* 1991, Gordeev *et al.* 1996) because the tidal amplitude is only 10cm (Harms & Karcher 1999).

### 4.2 Larval distribution

Generally the meroplankton densities for all species found in this study are within the range (311 ind. m<sup>-3</sup> which reveals to 13,000 ind. m<sup>-2</sup>) of investigations done by Thorson (1946), who reported densities of 17,500 ind. m<sup>-2</sup> for the Danish Sea. Although in some Arctic fjords peaks of >500,000 ind. m<sup>-2</sup> were observed (Thorson 1936).

The meroplankton was dominated by mass occurrence of Ophiopluteus larvae. Earlier investigations already reported Ophioplutei as typical for the open Kara Sea throughout the year (Fomin 1989). Casual identification of individuals from different samples and water depths showed that all larvae belonged to *Ophiocten sericeum*. Thorson (1936) regularly found *O. sericeum* larvae in samples taken in Northeast Greenland fjords during July-September. However, unlike to this study they played a subordinate role in the Greenland fjords, where bivalves generally dominated the plankton. Schlüter & Rachor (2001) reported a high abundance of *O. sericeum* larvae in the surface layer near the ice edge of the Central Barents Sea in May and June. However, planktonic investigations by Vinogradov *et al.* (1995) conducted in August-September 1994 within the Yenisei Estuary did not report any occurrence of echinoderm larvae. The maximum densities of echinoderm larvae (~75 ind. m<sup>-3</sup> at Station 27) we found were similar to observations done by Schlüter & Rachor (2001), who found maximum densities of 50 ind. m<sup>-3</sup>.

The Spionids in the region of the Yenisei River are restricted to two species *Prionospio cirrifira* and *Marenzelleria arctia* (Volkov *et al.* 1997, Deubel *et al.*, this volume). Only of *P. cirrifira* larvae have been described whereas the reproduction biology of *M. arctia* is unknown (Hartmann-Schröder 1996, Jirkov 2001).

Spionid larvae quite common for shallow Boreo-Atlantic regions (Smidt 1951, Heiber 1988, Plate 1992, Husemann 1992) are rarely described for Arctic waters (Thorson 1936, Mileikovski 1968). In warmer regions Spionids usually appear early in the year and have a long planktonic phase lasting until the end of summer (Blake & Arnofsky 1999). Some species are poecilogenous and may alternate between reproduction modes, sometimes even lacking a planktonic stage, depending on food availability and environmental conditions (Rasmussen 1973, Clarke 1992, Blake & Arnofsky 1999). The semi-Boreal conditions caused by the relatively warm river water within the estuary may promote the boreal reproduction behaviour of spionids.

Within the ‘other polychaetes’ larvae of *Phyllodoce* cf. *groenlandica* were the predominant species. All larvae of *P. groenlandica* were of the same size suggesting a single spawning event.

The low numbers of bivalve larvae might be explained by the fact that sampling took place in the mid of September. Thorson (1936) reported a larval peak in the arctic waters in late July/early August. The adult bivalve fauna consisted exclusively of *Thyasira gouldii* and *Macoma calcarea*; both are common species in Arctic waters. Thorson (1936) found only very few larvae of *T. gouldii* (*Axinus flexuosus*) in late summer (Aug.- Sept.) and he concluded that this species has either a short or no planktonic phase whereas for *M. calcarea* no larvae were found.

#### 4.3 The influence of adults on the distribution of larvae

Generally, meroplanktonic larvae are weak swimmers hence their dispersal depends on the distribution of adults and the prevailing hydrodynamics (Pedotti & Fenaux 1992). The duration of the planktonic phase and the distance transported depends on the specific developmental period each species requires under the given environmental conditions and can last from several hours in some Spionida (Blake & Arnofsky 1999) to six months after hatching in *Ophiocten sericeum* (Pearse 1969). The length of larval life even within a species varies widely – the length of the competent stage of most species studied depends on a cue for settlement; e.g. some polychaetes may become competent within a month but delay settlement for several additional months (e.g. Chia 1974, Pearse 1969, Pearse *et al.* 1991). The duration in the plankton determining the distance the larvae can be transported (Mileikovsky 1960, 1966). Currents may generally enhance larval dispersal but also create physical barriers (e.g. density gradients, mixing zones) restricting the spreading of larvae (Scheltema 1988).

Harms & Karcher (1999) postulated average current speeds of  $10\text{cm s}^{-1}$  for the Kara Sea (see also Harms *et al.* 2001, Harms & Karcher this volume). (According to this, a larva with a development time of six-month may drift approximately 1500km until metamorphosis). Within the estuary current speeds can reach much higher values during the highest discharge period in May-June (Pavlov & Pfirman 1995, Harms *et al.* 2001). The annual cyclonic pattern observed in the hydrographic simulations made by Harms & Karcher (1999) and Harms *et al.* 2001 let us hypothesise that larvae are mainly produced locally.

Comparing the presence of adults with the occurrence of larvae in the water column reveals between both the Spionida and the Bivalves that the larvae are found 'downstream' (northward) of the location of the adults in accordance with the surface run-off from the river. Since the larvae are already liberated into the upper brackish water explained their high abundance there. Probably, trapping of larvae within the water lens at Station 7 explains the high abundances of spionids in the upper water layer of this station. Larvae are often retained in the water layer where they hatched (Pearse 1994) and tend to follow density gradients along boundary layers at abrupt density discontinuities (e.g. halocline surfaces) (Banse 1955, Moore 1977). Due to continuing mixing processes and followed by a reduction of the halocline, they sink into deeper waters.

For the Bivalvia larvae the same transport processes may hold true, although here the highest densities are found below the halocline. Adult *Thyasira gouldii* were exclusively found at Stations 22 and 13. Larvae released here would drift with the outgoing currents to the more northern stations. The water lens mentioned above probably influences the absence of bivalve larvae above the halocline at Station 7.

With 'other polychaetes', the situation is different. Their larvae are found 'upstream' of their adults. Here bottom near counter currents may explain the pattern found. Counter-currents caused by outgoing surface currents are well known for estuaries (e.g. Moore 1977). The presence of a counter-current is predicted by the hydrodynamic model of Harms & Karcher (1999) for the Kara Sea. They calculated a daily mean near bottom water flow of  $15 \text{ cm s}^{-1}$  back into the estuary reaching its maximum speed in late summer. Larvae released at the northern stations will therefore be carried into the estuary. Passive upstream drift is found to be an important mechanism for the retention of larvae in estuaries (Chen *et al.* 1997). Newly hatched larvae are often unable to overcome the horizontal flow they encounter (Epifanio 1988) and are therefore frequently found in the near bottom water layers (Pearse 1994). Local accumulations of polychaete larvae in the bottom layer are also known from other areas (e.g. Wilson 1982).

Also the ophiuroid larvae are partly transported via the counter-current towards the estuary, where they are found in high densities.

The highest densities of meroplankters were found at Stations 23, 24 and 7. This may be explained by accumulating transport processes at the freshwater-seawater interface. Shear stress between the water masses forces particles into a circulation pattern and final consolidation. Marine seston transported by the counter current into the estuary hence tends to concentrate downstream of the mixing zone (see Moore 1977 for details). Larvae, as passive drifters, most probably experience the same fate.

This area of maximum meroplankton concentration corresponds with the marginal filter zone postulated by Lisitsyn (1995), which he defined for the Kara Sea Shelf at about  $73^\circ \text{ N}$ . These filters, arising on the continental margins in regions of river and seawater mixing, are relatively narrow zones of intense deposition of particles and suspended matter imported by the rivers.

The present study shows the relevance of the distribution of adults together with local current pattern for the retention of larvae within the estuary for the Bivalvia and

Spionida. However, the question arises as to the fate of stenohaline species such as Ophiuroida because their larvae are also retained in the estuary by the same forces. It is unlikely that neither the larvae nor, after metamorphosis, the juveniles will survive in an environment of varying salinity as the Yenisei Estuary.

Clearly more detailed studies on the recruitment of juveniles and interactions between the larvae and adults are necessary. In addition, a better long-term, understanding of the hydrography within the area would give an improved explanation for the present distribution patterns found.

Improved knowledge on larval supply either by currents or through local production, and on life strategies of polar species is necessary to assess the significance of planktonic development for benthic communities in polar waters, and to gain a more comprehensive knowledge of Arctic benthos dynamics.

### **Acknowledgements**

We thank the crew and the Russian scientists onboard RV 'Akademik Boris Petrov' for their help and the good company during the expedition in 2000. Especially Victor Khorshev and Alexandr Latko helped during sampling. Also Leonid Stephantsev, Boris Shmelkov and the Vernadsky Institut have to be mentioned for providing the CTD records, and Hendrik Deubel for making his benthos data available to us. This work was supported by BMBF 03G0539A1, Project Siberian River Run-Off (SIRRO).

### **References**

- Banse K., 1955. Über das Verhalten von meroplanktischen Larven in geschichtetem Wasser. *Kieler Meeresforschung*. 11, 188-199.
- Blake J.A., Arnofsky P.L., 1999. Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. *Hydrobiologia*. 402, 57-106.
- Butman C.A., 1987. Larval settlement of soft-sediment invertebrates, the spatial scales of pattern explained by active habitat selection and the emerging rôle of hydrodynamical processes. *Oceanogr. Mar. Biol. Ann. Rev.* 25, 113-165.
- Chen Y.H., Shaw P.-T., Wolcott T.G., 1997. Enhancing estuarine retention of planktonic larvae by tidal currents. *Estuar. Coastal Shelf Sci.* 45, 525-533.
- Chia F.S., 1974. Classification and adaptive significance of developmental pattern in marine invertebrates. *Thalassia Jugoslavica* 10, 121-130.
- Clarke A., 1992. Reproduction in the cold: Thorson revisited. *Invertebr. Reprod. Dev.* 22, 175-184.
- Denisenko N.V., Rachor E., Denisenko S.G., 2002. Benthic fauna in the southern part of the Kara Sea. *Proceedings in Marine Science*. this volume.
- Deubel H., Fetzer I., Gagaev S., Hirche H.-J., Lubin P., Lubina O., Nöthig E.M.,

- Otkolotkov J., 2002. The southern Kara Sea ecosystem, phytoplankton, zooplankton and benthos communities influenced by river run-off. Proceedings in Marine Science. this volume.
- Epifanio C.E., 1988. Transport of invertebrate larvae between estuaries and the continental shelf. Am. Fish. Soc. Symp. 3, 104-115.
- Fomin O.K., 1989. Some characteristic structures of the zooplankton . ('Nekatorije strukturnije kharakteristiki zooplanktona'). In: Matishov G.G. (Ed.), The ecology and Bioresources of the Kara Sea ('Ekologia i Bioresurci Karskovo Moria'). Murmansk Marine Biological Institute. Akademia Nauk SSSR. Apatiti, pp 65-85 [in Russian]
- Gordeev V.V., Martin J.M., Sodorov I.S., Sidorova M.V., 1996. A reassessment of the Eurasian river input of water, sediment, major elements and nutrients to the Arctic Ocean. Amer. J. Sci. 296, 664-691.
- Harms I.H., Karcher M.J., 1999. Modeling the seasonal variability of hydrography and circulation in the Kara Sea. J. Geophys. Res. 104, 13431-13448.
- Harms I.H., Karcher K.J., Dethleff D., 2000. Modeling Siberian river runoff - implications for contaminant transport in the Arctic Ocean. J. Mar. Sys. 27, 95-115.
- Harms I.H., Hübner U., Backhaus J.O., Janssen F., 2001 Applications of the Hamburg Ocean Model (HAMSOM/VOM) to the Kara Sea – ESTABLISH-Report to the European Commission, Center for Marine and Climate Research, University of Hamburg
- Hartmann-Schröder G., 1996. Annelida, Borstenwürmer, Polychaeta, Die Tierwelt Deutschlands und der angrenzenden Meeresteile, 58. Teil. Gustav Fischer Verlag, Jena.
- Heiber W., 1988. Die Faunengemeinschaft einer großen Stromrinne des Wurster Wattengebietes , Deutsche Bucht., PhD Thesis, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany. [in German]
- Husemann E., 1992. Bestandsaufnahme und Larvenentwicklung der im Helgoländer Plankton auftretenden Polychaeten und Polychaetenlarven. PhD Thesis, Ruhr-Universität Bochum, Germany. [in German]
- Jirkov I.A., 2001. Polychaeta of the Arctic Ocean. Yanus-K, Moscow.
- Lisitsyn A.P., 1995. The marginal filter of the ocean. Oceanology. 34, 671-682.
- Mileikovsky S.A., 1960. On the distance of dispersal with marine currents of pelagic larvae of bottom invertebrates on the example of *Limapontia capitata* Müller , Gastropoda, Opisthobranchia. from the Norwegian and Barents Seas. Dokladi Akademik Nauka SSSR. 135, 965-967. [in Russian]

- Mileikovsky S.A., 1966. The range of dispersal of the pelagic larvae of bottom invertebrates by ocean currents and its distributional role on the example of Gastropoda and Lamellibranchia. *Okeanologia* 6, 482-492.
- Mileikovsky S.A., 1968. Distribution of pelagic larvae of bottom invertebrates of the Norwegian and Barents Sea. *Mar. Biol.* 1, 161-167.
- Mileikovsky S.A., 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance, a re-evaluation. *Marine Biology* 10, 193-213.
- Moore P.G., 1977. Inorganic particulate suspensions in the sea and their effect on marine animals. *Oceanogr. Mar. Ann. Rev.* 15, 225-363.
- Muus K., 1973. Settling, growth and mortality of young bivalves in the Øresund. *Ophelia* 12, 79-116.
- Olafsson E.B., Peterson C.H., Ambrose H.G. Jr., 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments, the relative significance of pre- and post-settlement processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32, 65-109.
- Pavlov V.K., Pfirman S.L., 1995. Hydrographic structure and variability of the Kara Sea, Implications for pollutant distribution. *Deep-Sea Res.* 42, 1369-1390.
- Pearse J.S., 1969. Slow developing demersal embryos and larvae of the Antarctic sea star *Odontaster validus*. *Mar. Biol.* 3, 110-116.
- Pearse J.S., 1994. Cold-water echinoderms break 'Thorson's Rule'. In: Young C.M., Eckelbarger K.J. (Eds.), *Reproduction, Larval biology and Recruitment of the Deep-Sea Benthos*. Colorado University Press, New York, pp. 26-43.
- Pearse J.S., McClintock J.B., Bosch I., 1991. Reproduction of Antarctic benthic marine invertebrates, tempos, modes and timing. *Am. Zool.* 31, 65-80.
- Pedrotti M.L., Fenaux L., 1992. Dispersal of echinoderm larvae in a geographical area marked by upwelling, Ligurian Sea, NW Mediterranean. *Mar. Ecol. Prog. Ser.* 86, 217-227.
- Plate S., 1992. Untersuchung zum zeitlichen Auftreten, zur Abundanz und Entwicklung meroplanktischer Polychaetenlarven im Gebiet Helgoland Reede. PhD Thesis, Ruhr-Universität Bochum, Germany. [in German]
- Rasmussen E., 1973. Isefjord fauna, general remarks. *Ophelia* 11, 441-450.
- Scheltema R.S., 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bull. Mar. Sci.* 39, 290-322.
- Scheltema R.S., 1988. Initial evidence for the transport of teleplanic larvae of benthic invertebrates across the East Pacific barrier. *Biol. Bull.* 174, 145-152.

- Scheltema R.S., Williams I.P., 1995. Observations on the meroplankton of Antarctic waters. In: Grassle J.P., Kelsey A., Oates E., Snelgrove P.V. (Eds.), 23. Benthic ecology meeting, Rutgers-State-University, New Brunswick.
- Schlüter M., Rachor E., 2001. Meroplankton distribution in the central Barents Sea in relation to local oceanographic pattern. *Polar Biol.* 24, 582-592.
- Smidt E.L.B., 1951. Animal Production in the Danish Wadden Sea, C.A. Reitzel Forlag, København, Danm. Fisk- og Sjøundersøgelser Serie Fiskeri Nr. 6 Bnd. XI, pp 90-109.
- Stein R., Stepanets O.V., 2001. The German-Russian project on Siberian River Run-off (SIRRO), Scientific cruise report of the Kara Sea expedition 'SIRRO 2000' of RV 'Akademik Boris Petrov' and first results. *Ber. Polarforschung* 393, 1-287
- Stephantsev L., Shmelkov B., 2001. Some peculiarities of the hydrological structure on a meridional section Kara Sea - Yenisei Estuary - Yenisei River, in Stein R. Stephanets O.V. (Eds.), The German-Russian project on Siberian River Run-off , SIRRO., Scientific cruise report of the Kara Sea Expedition 'SIRRO 2000' of RV 'Akademik Boris Petrov' and first results. *Ber. Polarforschung* 393, 6-14.
- Telang S.A., Pocklington R., Naidu A.S., Romankevich E.A., Gitelson I.I., Gladyshev M.I., 1991. Carbon and mineral transport in major North American, Russian Arctic and Siberian rivers, The St. Lawrence, the Mackenzie, the Arctic Alaskan rivers, the Arctic Basin rivers in the Soviet Union and the Yenisei. In: Degens E.T., Kempe S., Richey J.E. (Eds.), Biogeochemistry of Major World Rivers. Wiley and Son, New York, SCOPE 42, pp 74-104.
- Thorson G., 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. *Medd. Gron.* 100, 1-155.
- Thorson G., 1946. Reproduction and larval development of Danish marine invertebrates, with special reference to the planktonic larvae in the Sound , Øresund. *Medd. K. Omm. Dan. Fisk. Havunder. Ser. Plankton.* 4.
- Thorson G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25, 1-45.
- Thorson G., 1966. Some factors influencing the recruitment and establishment of marine benthic communities. *J. Sea Res.* 3, 267-293.
- Vinogradov M.E., Shuskina E.A., Lebedeva L.P., Gagarin V.I. , 1995. Mesoplankton in the east Kara Sea and the Ob and Yenisei River Estuaries. *Oceanology* 34, 646-652.
- Volkov V., Kosheleva G.J., Smolyanitsky V., Vinje T., 1997. Natural Conditions of the Kara and Barents Seas. *Proceedings of the Russian-Norwegian Workshop-95*, 97, 1-470.

- Watzin M.C., 1983. The effect of meiofauna on settling macrofauna, meiofauna may structure macrofaunal communities. *Oecologia* 59, 163-166.
- Watzin M.C., 1986. Larval settlement into marine soft-sediment systems, interaction with the meiofauna. *J. Exp. Mar. Biol. Ecol.* 98, 65-113.
- Westheide W., Rieger R. , 1996. *Spezielle Zoologie – Teil 1, Einzeller und Wirbellose Tiere*. Gustav Fischer Verlag, Stuttgart, Jena, New York.
- Wilson S.R., 1982. Horizontal and vertical density distribution of polychaete and cirripede larvae over an inshore rock platform off Northumberland. *J. Mar. Biol. Assoc. UK.* 62, 907-917.

**Table captions:**

**Table 1:** Station number, position, depth, depth of halocline, meroplankton abundances (ind m<sup>-3</sup>) and number of species sampled in the Kara Sea in September 2000 during the expedition on RV 'Akademik Boris Petrov'. The stations are ordered according to a South-North transect from the inner Yenisei Estuary to the central Kara Sea. The last three stations (below the line) are not included in the transect.

**Table 2:** List of species/types of larvae found in the study area during in the Kara Sea in September 2000. Relative abundance over all stations, minimum and maximum densities, occurrences of species in different water layers (a = above / b = below halocline) are given. For species with only single occurrence one density value is presented. For comparison with adult abundances larvae of other polychaetes were pooled into one group (pooled groups).

**Figure captions:**

**Figure 1:** Map of the study area with all meroplankton stations in the central Kara Sea. The investigated transect out of the inner Yenisei Estuary to the central Kara Sea is highlighted. The isolines on the map represent 50m and 100m depth lines, respectively.

**Figure 2:** Latitudinal salinity profile of the transect from the inner Yenisei Estuary to the central Kara Sea showing the depth and the positions of stations.

**Figure 3:** Total meroplankton abundances (ind m<sup>-3</sup>) on the stations above and below the halocline of the transect from the inner Yenisei Estuary to the central Kara Sea.

**Figure 4:** Relative group abundances a) above and b) below the halocline of all meroplankton stations.

**Figure 5:** Distribution of absolute abundances of larvae (ind m<sup>-3</sup>) above/below the halocline and adults (ind m<sup>-2</sup>) of Spionida, 'other polychaetes', Bivalvia and Ophiuorida along the transect from the inner Yenisei Estuary to the central Kara Sea.

**Figure 6:** Spatial distribution of Ophiuroida larvae a) above and b) below the halocline and c) adults in the study area. Iso-lines show areas of equal densities. No values are given since the plot is only intended to reveal trends.

**Table 1**

<b>Station</b>	<b>Date</b>	<b>Lat</b>	<b>Lon</b>	<b>Depth</b>	<b>Depth of</b>	<b>Abundances</b>	<b>Number of</b>
<b>label</b>	<b>day/ month</b>	<b>N</b>	<b>E</b>	<b>[m]</b>	<b>Halocline</b>	<b>ind. m<sup>-3</sup></b>	<b>Species</b>
					<b>[m]</b>		<b>[S]</b>
22	13/09	72° 33	79° 54	11	--	0	0
13	08/09	72° 56	80° 33	13	6	11.3	6
23	13/09	73° 28	79° 51	33	17	73.2	22
24	13/09	74° 00	79° 59	31	18	128.2	18
07	06/09	74° 39	81° 08	38	23	106.2	20
05	05/09	75° 50	81° 00	50	24	0.2	1
30	16/09	75° 56	83° 02	52	23	20.1	14
28	15/09	76° 39	83° 52	50	20	45.8	10
02	03/09	75° 24	74° 11	50	22	6.4	8
26	14/09	75° 42	77° 57	68	28	34.6	13
27	14/09	76° 18	78° 55	78	29	80.4	13

Table 2

Taxa	pooled groups			Rel	Min	Max	occurring layer
				Abundance			
				%	ind. m <sup>-3</sup>	ind. m <sup>-3</sup>	
Cnidaria	Hydrozoa		Actinula larvae	0.3	0.1	0.6	b
	Anthozoa		<i>Cerianthus cf. loydii</i>	2.3	0.1	6.3	a/b
Nemertini			Pilidium larvae	0.2	0.1	0.6	b
Mollusca	Gastropoda		Gastropoda Veliger	0.3	0.2	0.4	a/b
			Nudibranchia Veliger	0.8	0.1	2.2	a/b
	Bivalvia	Bivalvia	Bivalve Veliger	0.7	0.1	0.8	a/b
Sipuncula			Pelagosphera	0.1	0.1	0.3	b
Annelida	Polychaeta	Spionida	Spionid larvae	3.6	0.1	3.7	a/b
		other polychaetes	<i>Eteone longa</i>	<0.1	*	0.1	b
			<i>Gattyana</i> sp.	1.4	0.4	3.8	a/b
			<i>Glycera</i> sp.	<0.1	*	0.2	b
			<i>Harmothoe</i> sp.	<0.1	*	0.2	b
			<i>Nephtys</i> sp.	2.1	0.1	3.4	a/b
			<i>Nereis</i> sp.	0.3	0.1	0.7	a/b
			<i>Pholoe cf. minuta</i>	1.4	0.1	5.2	a/b
			<i>Phyllodoce cf. groenlandica</i>	5.3	0.1	9.9	a/b
			spherical Trochophora	4.6	0.3	7.1	a/b
			<i>Scoloplos</i> sp.	<0.1	*	0.2	b
			Owenia Mitraria	<0.1	*	0.1	b
			unidentified Polychaeta larvae	1.2	0.1	2.0	a/b
			small Trochophora	5.9	0.1	7.8	a/b
			Trochophora 1	0.1	*	0.8	a
			Trochophora 2	0.2	0.4	0.7	a/b
			Arthropoda	Crustacea		Cirripedia Cypris larvae	0.4
Nemathelminthes	Priapulida		Pelagosphera larvae	0.1	*	0.6	b
Bryozoa			Cyphonautes larvae	0.2	0.1	0.3	a/b
Echinodermata	Ophiuroida	Ophiuroida	Ophiopluteus larvae	67.8	0.2	74.7	a/b
	Asterioida		Bipinnaria larvae	0.3	0.1	0.7	a/b
Chordata	Tunicata		tadpole larvae	0.3	1.6	1.6	b

**Figure 1**

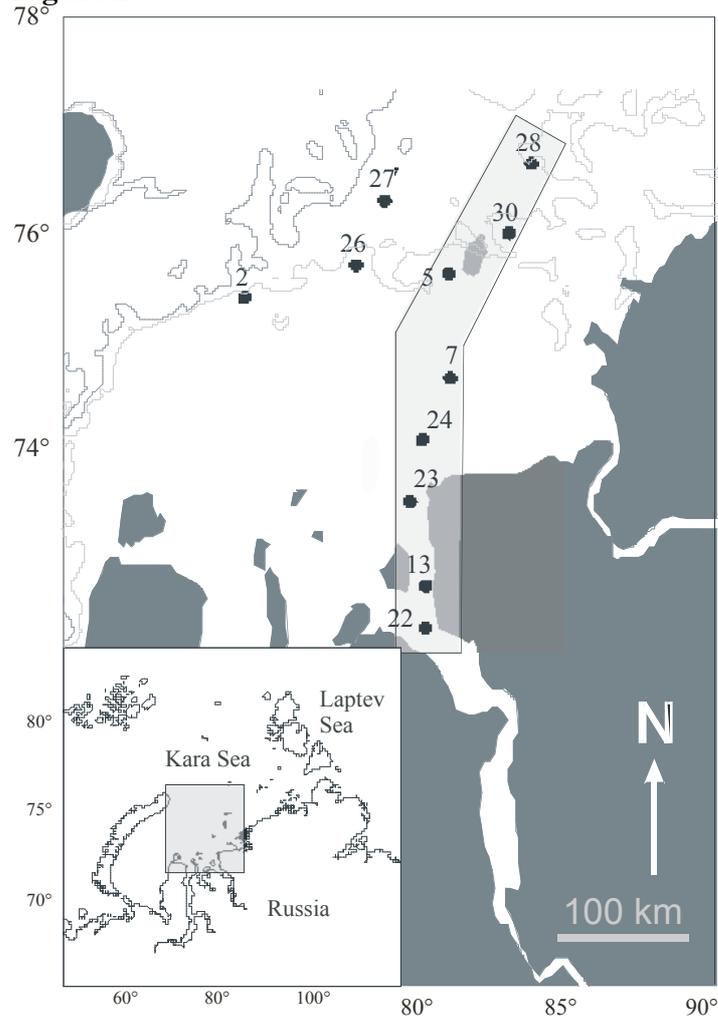


Figure 2

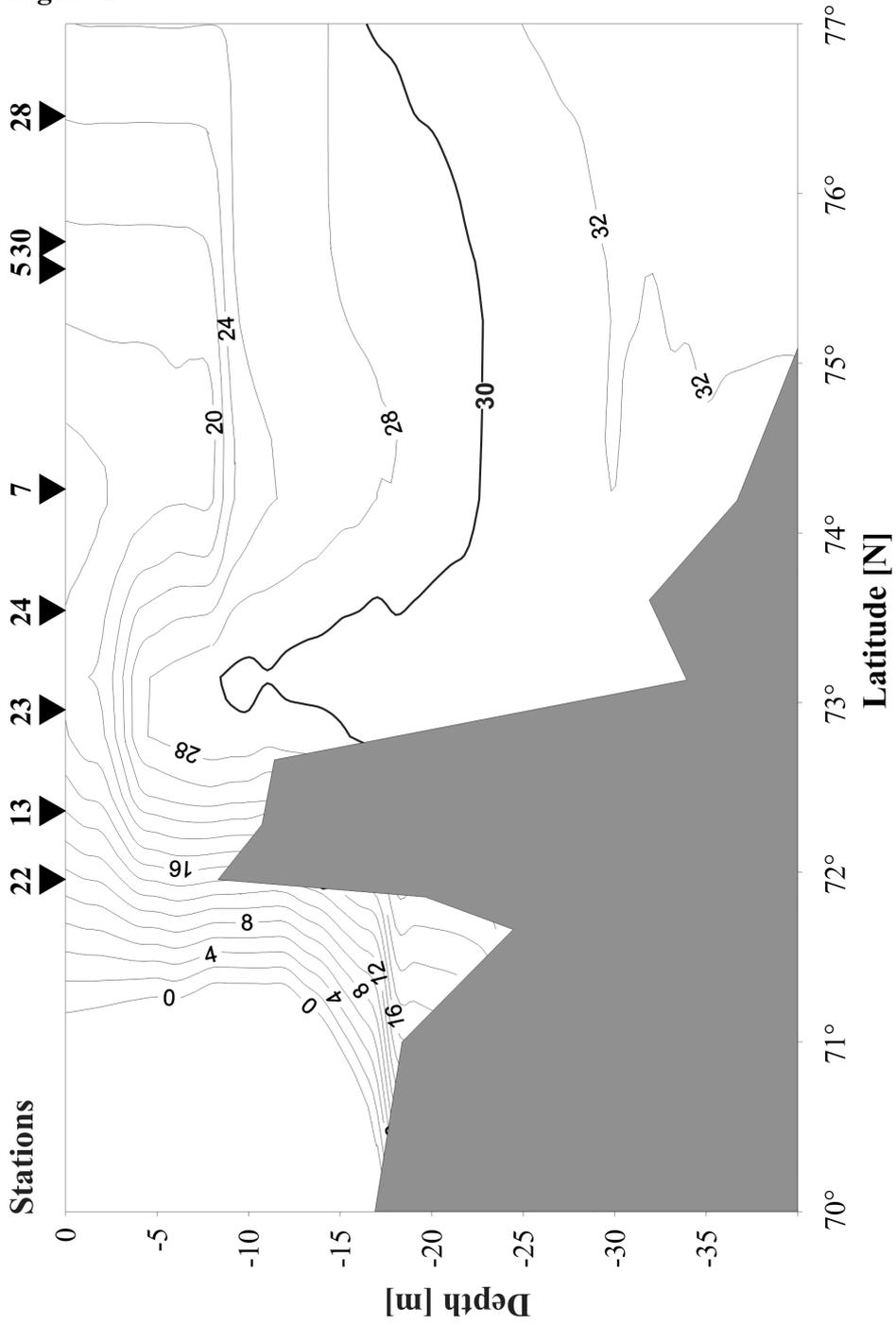


Figure 3

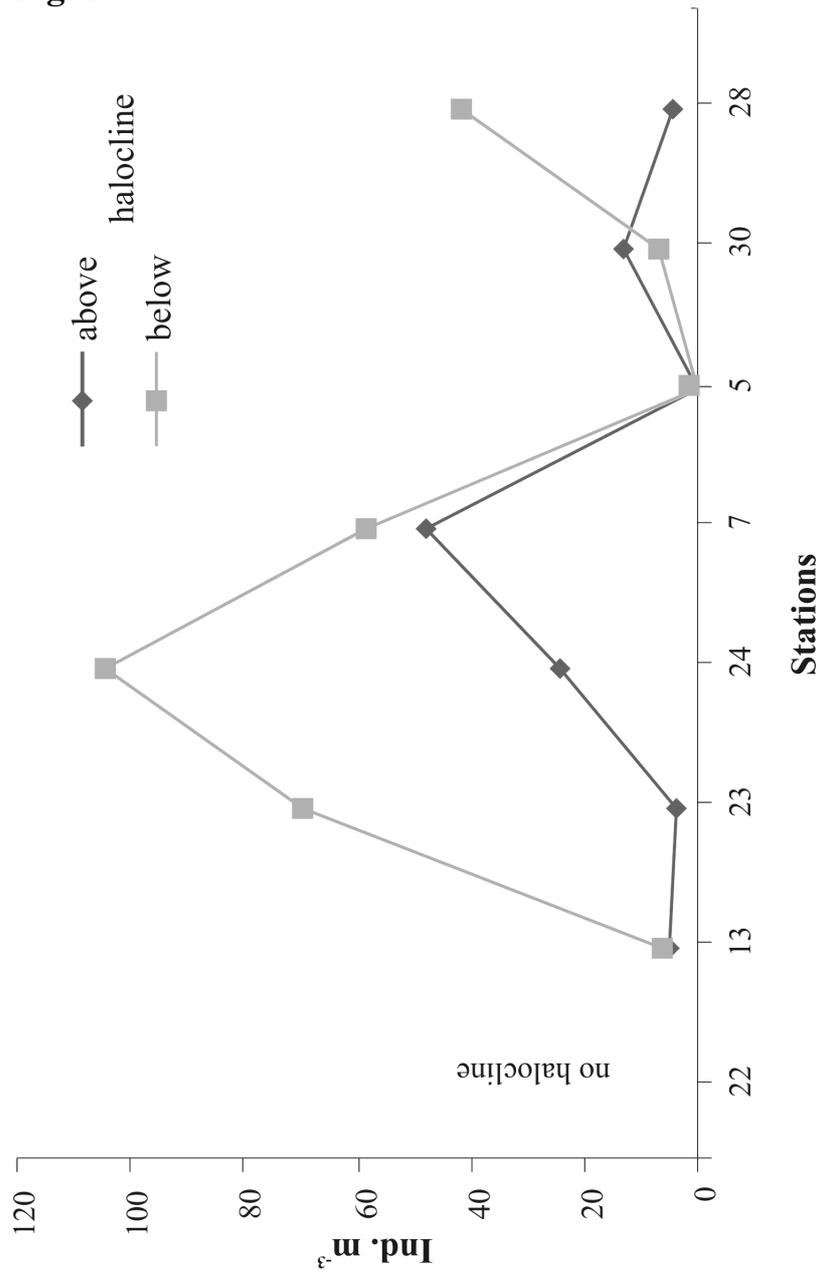


Figure 4

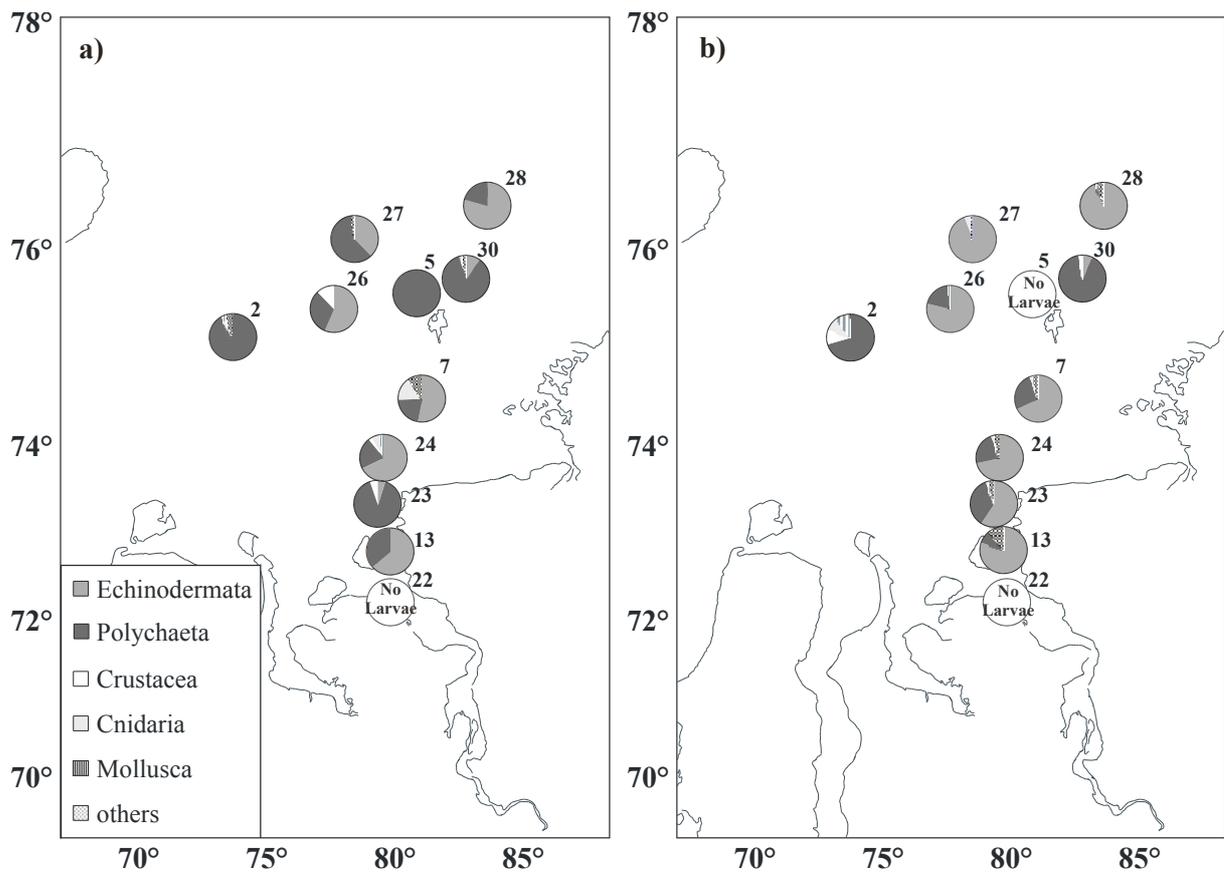
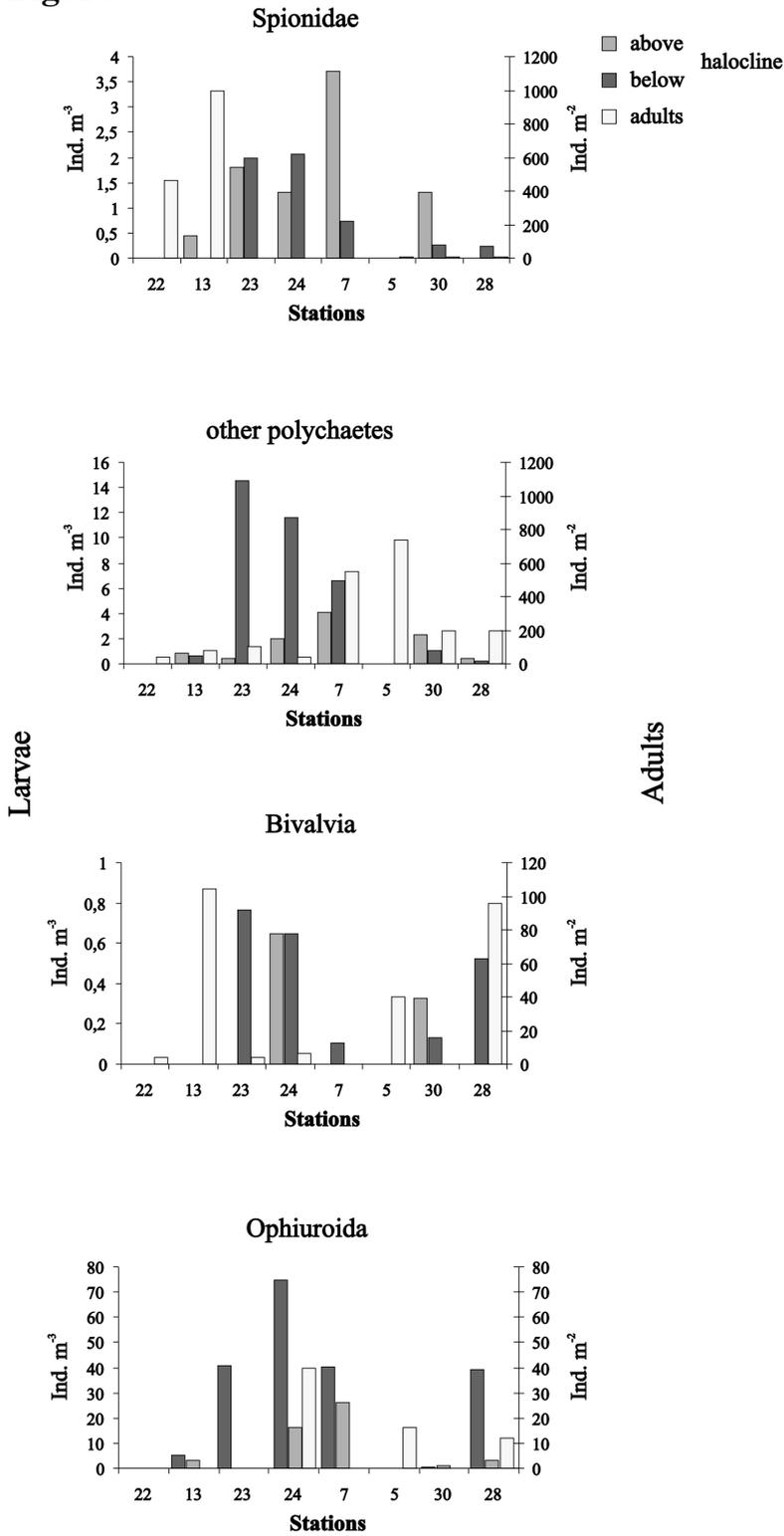


Figure 5



Larvae

Adults

Figure 6

