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Journal of Marine Systems 60 (2006) 98–114

JOURNAL OF MARINE SYSTEMS

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Effect of river run-off on the distribution of marine invertebrate larvae in the southern Kara Sea (Russian Arctic)

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Received 13 July 2004; accepted 15 November 2005
Available online 3 February 2006

Abstract

Within the generally oligotroph Arctic marine environment river outlets are favoured by many planktonic and benthic organisms due to their high input of organic carbon. The retention of pelagic larvae within nursery grounds and/or the ability to return to their parental grounds prior to settlement is one important factor for the persistence of benthic communities in such river influenced areas. The southern Kara Sea is strongly controlled by high freshwater inputs from the Ob and Yenisei Rivers, which create a pronounced bi-layered pycnocline with a warm fresh/brackish water layer on top and a cold high saline marine layer below. The dispersal of five meroplanktonic species and settled juveniles (the brittle star *Ophiocten sericeum*, and the polychaetes *Micronephtys minuta*, *Nereimyra aphroditoides*, *Phyllodoce groenlandica* and *Prionospio cirrifera*) in relation to the adult distribution patterns was investigated. For all apart from *P. cirrifera* the highest densities of larvae were found in the upper brackish water layer. To assess size-at-settlement, the body sizes of larvae and newly settled juveniles were estimated and compared. Dispersal patterns ranged from virtually no adaption to river run-off as in the common, stenohaline *O. sericeum* and *M. minuta* (7 ind. m^{-3}, 459 μm) to local retention as in *N. aphroditoides* (7 ind. m^{-3}, 541 μm) and *P. groenlandica* (0.5 ind. m^{-3}, 1121 μm) retained by horizontal eddies created by the outflow. Adults of *P. cirrifera,* which were exclusively restricted to the estuary of the Yenisei River, showed a well adapted reproductive behaviour to ensure a high retention potential of their progenies. The larvae (1.5 ind. m^{-3}, 1513 μm) were only present in the lower water layers, most probably taking advantage of the prevailing near bottom counter current retaining them within their hatching areas.

Keywords: Arctic Ocean; Russia; Kara Sea; Benthos; Juveniles; Meroplankton; River run-off; Lat 70–78°N; Lon 70–90°E

1. Introduction

Meroplanktonic organisms are generally weak swimmers and so mainly subject to passive transport processes (Pedrotti and Fenaux, 1992). Hydrography and prevailing currents are therefore often the key factors determining site specific settlement strength, and, thus, strongly influence population and community dynamics (Connolly and Roughgarden, 1998).

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doi:10.1016/j.jmarsys.2005.11.005

In the generally oligotroph Arctic oceans, river outlets are favoured by many planktonic and benthic organisms due to their high input of nutrients and organic carbon (Klages et al., 2003).

Consequently for species dwelling in river influenced areas, such reproductive strategies should be favoured which enhance the retention of their progenies within the nursery areas and/or the ability to return to their parental grounds prior to settlement. Thus pelagic reproduction traits should be avoided or abbreviated to ensure a high survival rate of the offspring. However, a great number of marine and estuarine benthic invertebrates living in or close to Arctic estuaries reproduce via meroplanktonic larvae (e.g. Smidt, 1979; Andersen, 1984; Schlüter and Rachor, 2001; Fetzer and Arntz, submitted for publication).

High river discharge usually creates strong hydrographical clines between fresh- and marine waters acting as barriers for many planktonic organisms, since small drifting animals are often not able to overcome these local density regimes (Gallager et al., 1996). Planktonic organisms are therefore mainly distributed by the physical structuring of the water column which isolate biological communities from neighbouring water masses and transported via displacement by current movements (Scheltema, 1988; Gallager et al., 1996). Entrainment of planktonic organisms within water masses has already been the subject of a number of studies (e.g. McGowan, 1967; Trinast, 1970; Wiebe et al., 1976).

In Arctic areas gradients can be even more pronounced. Here not only saline differences account for the establishment of boundaries but also the greater temperature disparities enhance hydrographical barriers. In Arctic estuaries, marine waters usually prevail throughout the year at temperatures below zero while entering riverine freshwater often originates from much warmer areas. Thus, within river influenced Arctic areas a strong bi-layered water column is usually established, in summer this is additionally enhanced by melting sea ice (Pivovarov et al., 2003).

The often extremely strong seasonal fluctuation of riverine run-off in polar realms may additionally enhance the dislocation processes affecting newly released larvae. Arctic river discharge often increases in late spring to early summer and rapidly decreases towards autumn and very little input during winter (see e.g. Pavlov and Pfirman, 1995). Therefore, the exact timing of the release of larvae is essential in particular for species restricted to the inner estuaries.

The duration of the planktonic phase and hence the distance transported depends on the specific developmental period each species requires under the given environmental conditions (see Mileikovsky, 1960, 1966 for further details). This can last from several hours in a number of spionid polychaetes (Blake and Arnofsky, 1999) to up to 6 months after hatching in ophiuroid echinoderms (Pearse, 1969). Even within a species, the length of larval life may vary widely. In many species larvae can delay settlement for several additional time periods if no suitable habitat is found (e.g. Pearse, 1969; Chia, 1974; Pearse et al., 1991).

In estuaries showing a bi-layered flow, ontogenetic changes in larval behaviour facilitates the upstream transport by compensatory currents (Moore, 1977; Thiebault et al., 1992). The release and development time of a species needs to be highly synchronised to the establishment of the compensatory current in order to ensure sufficient recruitment rates.

In this study, the distribution of five species (*Ophiocten sericeum*, *Nereimyra aphroditoides*, *Phyllodoce groenlandica*, *Micronephtys minuta* and *Prionospio cirrifera*) in relation to the hydrographic regime and spatial occurrence of their adults from the river influenced southern part of the Kara Sea (Arctic Russia) are presented. The species were chosen according to the importance of larval retention for these species in relation to the distribution of their adults and their relatively straightforward taxonomic identification of both adults and larvae.

Taxonomic descriptions of meroplankters and thus potential for identification of larvae in Arctic areas are generally rare. Good morphological descriptions are found, e.g. for the larvae common arctic brittle star *O. sericeum* (Thorson, 1934; Semenova et al., 1964). Also for the larvae of *N. aphroditoides* (formerly described by Thorson, 1946; Banse, 1955 as *Castalia punctata* (see also Andersen, 1984), for *P. groenlandica* and *P. cirrifera* fairly good morphologic descriptions are available (e.g. Thorson, 1946; Andersen, 1984) little is known about larvae of *M. minuta*. Except for a note in Hartmann-Schröder (1996) mentioning a larval reproduction trait in this species, no additional information is so far available in the literature. However, adults of *M. minuta* are very common on the Kara Sea shelf and the only species occurring within the taxon Nephtidae (Poltermann et al., 1999; Deubel, 2000; Lubin and Eckert, 2001; but see also Deubel et al., 2003). Additionally, older specimens of the larvae have many typical morphophenic traits in common with the adults. Thus, the very abundant nephtid larvae in the Kara Sea plankton must therefore resemble the larvae of *M. minuta*.

The aim of this study is to give insight on the adapted release of larvae by the benthic adults and larval behavioural capability to return to their spawning area within a strongly fluctuating hydrological Arctic habitat. For this five invertebrate species in the Kara Sea in relation the immense freshwater run-off of the Rivers Ob and Yenisei were investigated. The huge riverine freshwater discharge creates strong physical or physiological barriers for larvae. The peculiar hydrographical situation created by the high freshwater input also allow for assessment of physical transport processes of larvae. Distribution and/or retaining of larvae in certain regions influence larval distribution and, hence, also the settling of juveniles and consequently establishment and preservation of adult populations.

2. Materials and methods

2.1. Study area

The Kara Sea is a marginal shelf sea located in the Eurasian part of the Arctic Ocean (Fig. 1). The realm is influenced by water mass exchanges with the Arctic Ocean, the North Atlantic and the Barents Sea. However, the Kara Sea is very strongly affected by the immense freshwater inputs of the Siberian rivers Ob and Yenisei. They release about 30% of the total annual freshwater discharge into the Arctic Ocean (Harms et al., 2003).

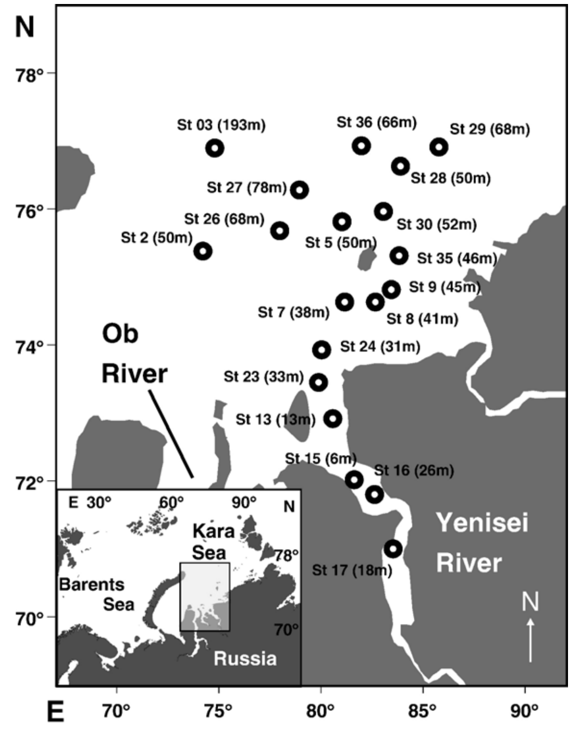

Fig. 1. Overview of the investigated area (indicated by grey box) during the expedition to the Kara Sea in 2000.

Apart from the summer months (June–August) the Kara Sea is ice covered for about 9 months of the year (Blanchet et al., 1995). Ice formation usually starts at the end of October. Break up coincides with the main river discharge of the two rivers in early to late June (Mironov et al., 1994). The large freshwater run-off and strong ice melting causes an intense bi-layered vertical stratification (Harms et al., 2000). Since the stratification is caused by both haline and thermal differences between the warm riverine freshwater and the cold marine waters a pycnocline is established. The river run-off has a strong seasonal variability with a maximum outflow from June (where 80% of the annual discharge is introduced into the Kara Sea) to September and a minimum during the winter period (Pavlov and Pfirman, 1995; Gordeev et al., 1996).

Seasonal changing wind fields are reported to have a strong effect on the general hydrography and variability of the surface currents (Harms et al., 2000). The dominating wind direction in summer is from north to northeast which forcing an anti-cyclonic circulation pattern. Towards the end of the year (autumn/winter) the prevailing wind direction changes to southwest creating a cyclonic surface circulation pattern flushing the Kara Sea water from the southwest to the northeast (Harms and Karcher, 1999; Harms et al., 2000).

2.2. Sampling

Samples were collected between 4–19 September 2000 at 15 stations during a cruise on board *R/V Akademik Boris Petrov* in the south-eastern Kara Sea (Stein and Stephanets, 2001). For meroplankton sampling a Nansen closing net was used (0.442 m^2 catching area, 55 μm mesh size, 0.5 m s^{-1} hauling speed). At each station, one haul from the bottom to below the pycnocline and a second one through the pycnocline to the surface were carried out. The location of the pycnocline was predetermined from CTD profiles. Juvenile stages were collected with a multicorer (28 cm^2 coverage area per tube). At each station parallel samples of 3–6 tubes was taken and subsequently separated into fractions of 500/250/125 μm by wet sieving.

Adult organisms were sampled with a large box corer (0.25 m^2) and animals were extracted by sieving sediments on 500 μm screens. Samples were preserved in 4% borax-buffered formalin. All adult and juvenile benthic organisms were identified to the lowest feasible taxon, counted and their body length measured individually under a stereomicroscope. Meroplanktonic larvae were separated from the plankton samples, identified and also measured. In ophioplutei the length of the lateral larval body appendages were measured. For juvenile ophiuroids disc diameter was recorded. Juvenile Ophiuroida were found both as floating individuals in the plankton samples and settled on the substratum. In addition, for polychaete larvae and juveniles the number of segments was reported.

Since it would have been beyond the scope of this study to determine the maturity state of individuals histologically, 'juveniles' (=immature specimens) were arbitrarily defined as all settled specimens smaller than 1/3 of the species adult size given in literature, ensuring their immature status.

Specimens from parallel multicorer tubes were pooled and their numbers averaged. Counted abundances were normalised to ind. m^{-3} for meroplanktonic larvae and ind. m^{-2} for adults and juveniles.

In order to obtain more detailed distribution patterns for the adults, adult data from expeditions in 1997, 1999, 2000 were added for the analysis in this study (Deubel and Poltermann, 1998; Deubel, 2000; Lubin and Eckert, 2001; but see also Deubel et al., 2003; Klages et al., 2003). This is justified since most benthic organisms in Arctic realms are relatively long living and Kara Sea communities do not show strong interannual distributional changes (Deubel et al., 2003).

To determine the range and size at settlement for the larvae the minimum, mean, and maximum size for each species was calculated. For polychaetes the same was also done for the number of segments.

To gain a better understanding of the distribution of adults, juveniles and larvae, abundance data within the

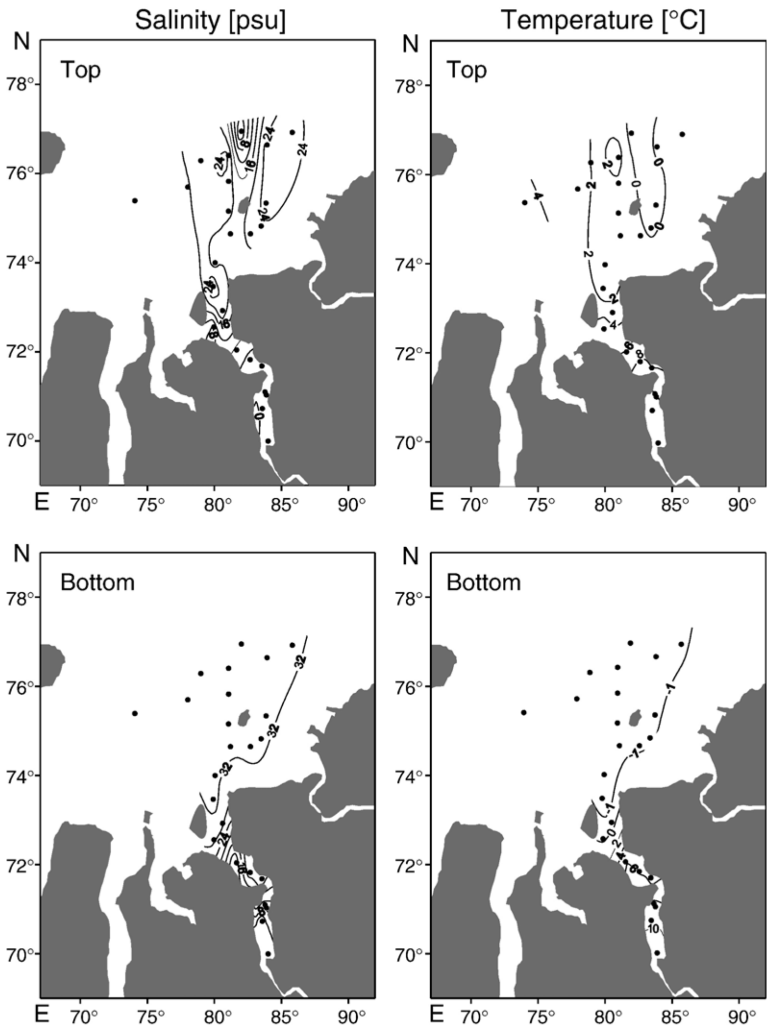

Fig. 2. Salinity and temperature distribution during the sample taking of the Kara Sea in 2000. Dots indicate the sampling stations.

sample area was interpolated by statistical gridding method using the surface mapping software SURFER, which is commonly used in visualisation of water mass distribution in oceanography and geographic chart making. Gridding is the process of using original data in an XYZ data file to generate calculated data points on a regularly spaced grid. Interpolation schemes estimate the value at locations where no original data exists, based on known data values. For this a grid of 80 × 100 points was placed on the map of the investigation area such that the XY values of the grid resembles the metric Lat/Lon data of the area. As an appropriate interpolation model the 'kriging' technique was applied on the data. In relation to other gridding techniques which depend on more spacial homogeneous data points, this method is most adequate for spatially irregularly distributed data (Abramowitz and Stegun, 1972; Isaaks and Srivastava, 1989). Kriging interpolates data on weighted mean basis, but additionally tries to detect trends between and across data points. Finally, based on the achieved grid data values isopleth lines were drawn by the software.

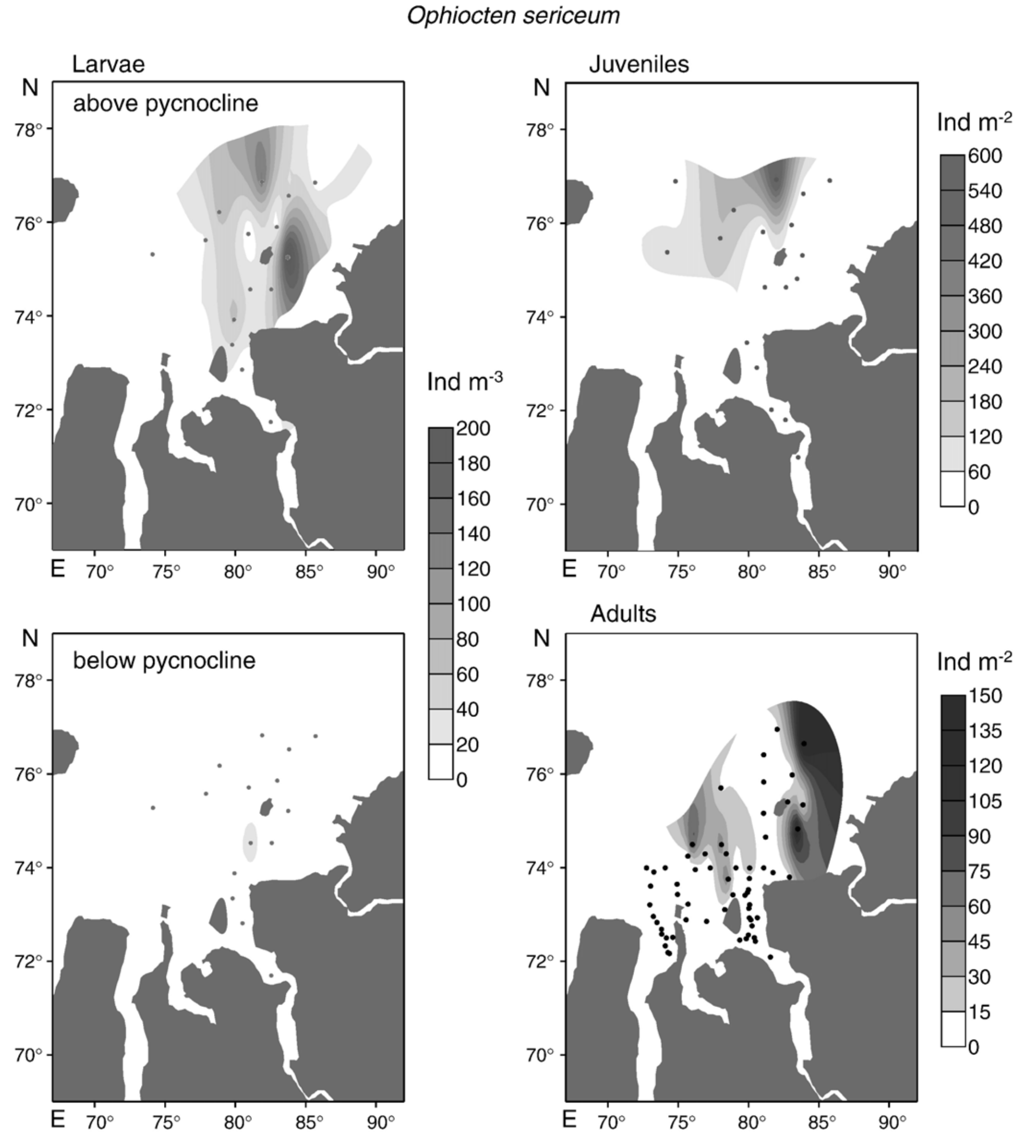

Fig. 3. Distribution of larvae above and below the pycnocline and juveniles and adults of the brittle star *Ophiocten sericeum* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3} and juveniles and adults as ind. m^{-2}. Dots indicate the sampling stations.

3. Results

3.1. Topography and hydrography

The depth of the investigated areas in the southeastern Kara Sea varied from 6m in the estuary of the Yenisei River (Station 15) to 193 m at the northwestern rim of the area (Station 3; Fig. 1). At most stations average depth did not exceed 30–50 m. During the sampling period prevailing strong easterly winds occurred. In the northeastern part between 75°N and 85°E ice floes prevented further sampling.

The hydrographical regime during the sampling period revealed a pronounced bi-layered structure with a warm fresh/brackish water layer on top (further referred to as 'top layer') and a cold high saline (>30 psu) marine layer below (further referred to as 'bottom layer') (Fig. 2). The average thickness of the top layer was about 20 m, becoming slightly deeper as mixing processes proceeded towards the northern shelf. The top layer increased in salinity from 0 to >25 psu from south to north while temperature decreased from 11 °C to <2 °C (Fig. 2). In the northern part, the top water masses became less saline and cooler again due the cold freshwater input from melting ice floes. Saline cold bottom waters penetrated to 71°N into the river (for more details see Stephantsev and Shmelkov, 2001).

3.2. Size ranges

The length of the postero-lateral rod in ophioplutei of *O. sericeum* ranged from 550 μm to 1950 μm (mean = 1229 μm). In addition, the highest number of individuals was measured for this species (*N* = 1114 ind.). For the floating juveniles a disk diameter of between 280 and 680 μm (mean = 456 μm) was recorded. However, only 13 specimens were found in all samples. For the found 808 metatrochopore individuals of *M. minuta* the larval size varied between 120 and 990 μm (*N* = 808 ind., mean = 459 μm) in size and contained 0–11 segments. The larvae of *N. aphroditoides* had a slightly bigger size range (180–810 μm with 3–10 segments, *N* = 473 ind., mean = 541 μm) compared to *M. minuta*. In *P. groenlandica* the larvae had sizes of 117–1420 μm (*N* = 117 ind., mean = 1121 μm, 5–15 segments). With between 9 and 26 segments larvae of *P. cirrifera* had the highest number of chaetigers found in all the investigated species (*N* = 59 ind., mean = 1513 μm, size range of 450–2700 μm).

For settled juvenile *O. sericeum*, disk diameters varied between 310 and 950 μm (*N* = 110 ind., mean = 585 μm). The size of the juveniles of *M. minuta* fluctuated between 420–4000 μm and 7–26 segments (*N* = 348 ind., mean = 2235 μm). For *N. aphroditoides* juvenile sizes ranged between 300–4700 μm (*N* = 113 ind., mean = 1054 μm, 6–26 segments), although mean size of *N. aphroditoides* was only half of *M. minuta*. Juveniles of *P. groenlandica* showed the biggest size spectrum. Here juveniles in a range of 350 μm and 8800 μm were recorded (*N* = 100 ind., mean = 2002 μm, size range of 350–8800 μm, 4–44 segments). For the spionid *P. cirrifera* no settled juveniles were found.

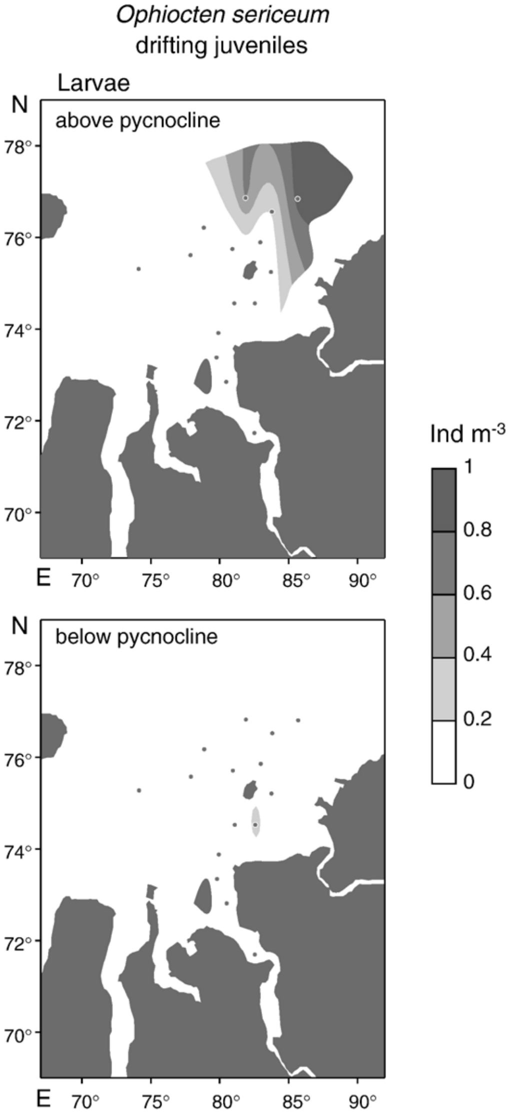

Fig. 4. Distribution of floating juveniles above and below the pycnocline of the brittle star *Ophiocten sericeum* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3}. Dots indicate the sampling stations.

3.3. Species distribution

All larvae, except those of *P. cirrifera* were found at highest abundances in the upper water column where salinity did not exceed 25 psu (Figs. 2 and 3).

As regards larvae and adults the most abundant species was the brittle star *O. sericeum*. Larvae of this species were found mainly in the upper water masses in almost all net samples except for those in the inner estuary (Fig. 3). Densities of up to 200 ind. m^{-3} (Station 35) were found. Generally, there was a trend towards higher abundances from the southern estuarine part to the northern region. With exception of a few specimens at station 7 no animals were present below the pycnocline.

Adults of *O. sericeum* were generally distributed in the northeastern part, reaching maximum values of 150 ind. m^{-2}. A few animals were also found in the northwestern part, between the wake of the two rivers. Floating juveniles of *O. sericeum* occurred exclusively in the upper waters in the northeastern part of the investigated area (Fig. 4). At two northeastern stations abundances of 1 ind. m^{-3} were found in the plankton hauls. In the lower waters only very few (<1 ind. m^{-3}) specimens were detected.

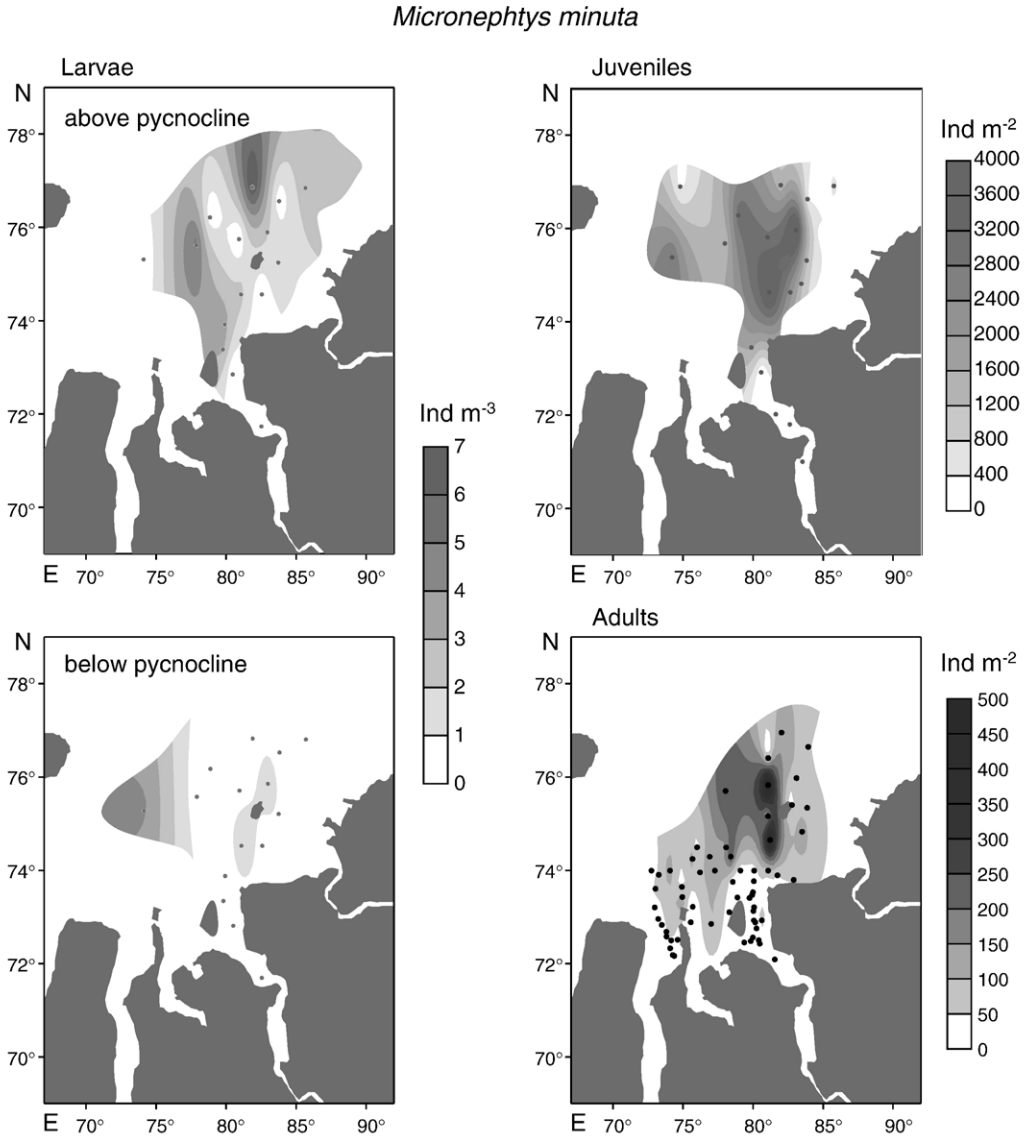

Fig. 5. Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Micronephtys minuta* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3} and juveniles and adults as ind. m^{-2}. Dots indicate the sampling stations.

The distribution of juveniles revealed a different picture. Newly settled animals were also exclusively found in the northern area at up to 600 ind. m^{-2} in contrary to the adults were populations were more established in the western part.

The larvae of *M. minuta* were concentrated mainly in the northern and western part (Fig. 5). The highest concentrations were found in the upper water column at the two stations 36 and 26, reaching 7 and 5 ind. m^{-3}, respectively. Below the pycnocline only at station 2 were 4 ind. m^{-3} found. Juveniles of this species were present in very high abundances (4000 ind. m^{-2}), and were also equally distributed on all stations of the investigated area. This was the highest density with respect to settled juveniles found for the five investigated species.

Adults of *M. minuta* were distributed mainly in the central northern part showing highest abundances of up to 550 ind. m^2 just west of the 'Island of the Arctic Institute'.

Larvae of *N. aphroditoides* had their main distribution on both sides of the river outflow with >8 ind. m^{-3} (Fig. 6). Below the pycnocline only single specimens were occasionally found in the nets. Contrary to the adults juveniles were present at high abundances of up

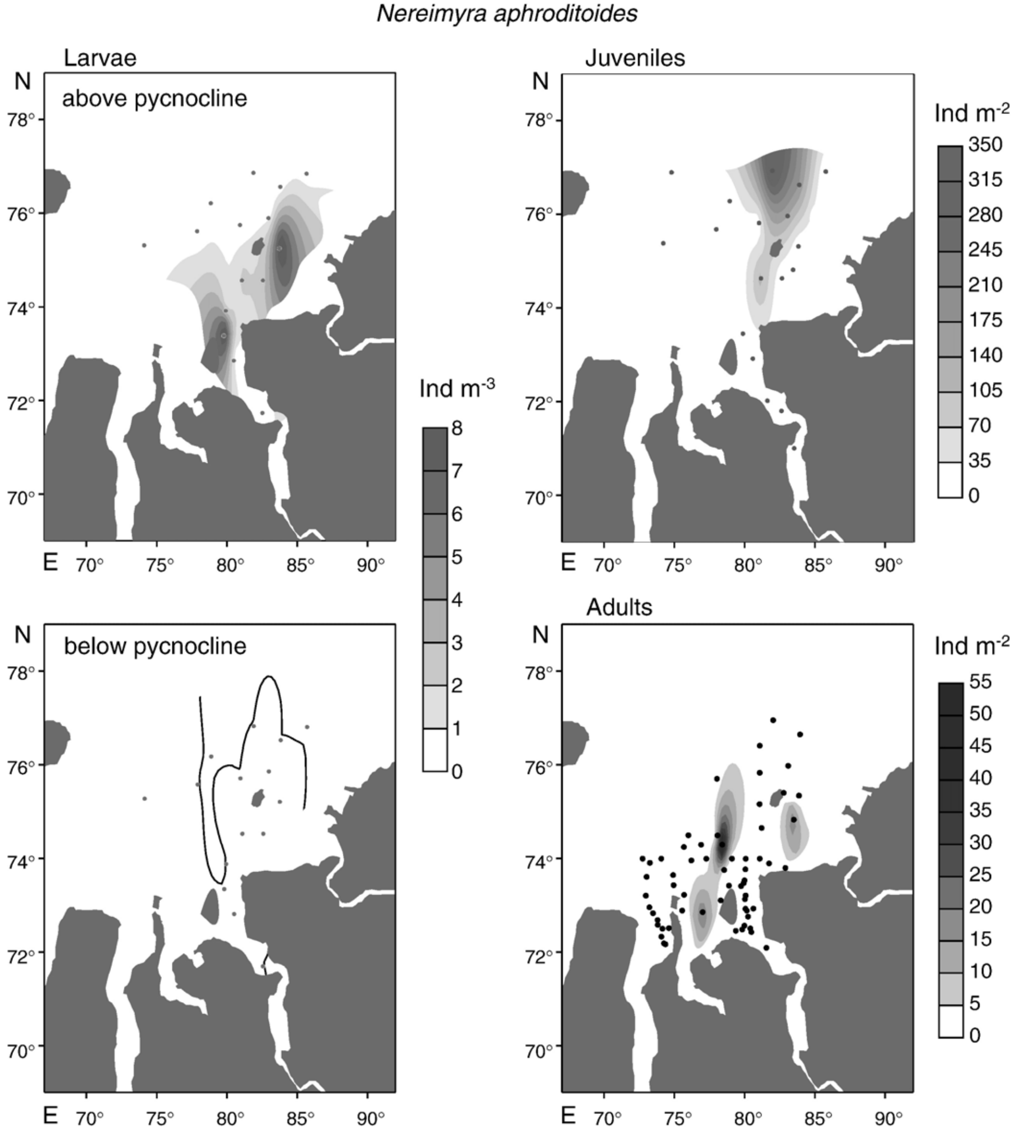

Fig. 6. Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Nereimyra aphroditoides* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3} and juveniles and adults as ind. m^{-2}. Dots indicate the sampling stations.

to 350 ind. m^{-2} in the northern region of the area, with decreasing abundances to the south.

Most of the adults of *N. aphroditoides* were found approximately in the same region as their larvae. Highest occurrences of about 55 ind. m^{-2} were found at stations in the western and northeastern parts off the Yenisei River transect.

A similar distribution pattern was found among larvae of *P. groenlandica* (Fig. 7). Up to 0.6 ind. m^{-3} were found in the northeastern part of the investigated area in the upper water column. A few larvae (0.2 ind. m^{-3}) also occurred south of the river transect at station 23. Below the pycnocline, abundances of 0.3 ind. m^{-3} were found.

While larvae of *P. groenlandica* were only present east and west of the north-going river transect, adults aggregated in single patches around the openings of both rivers, with a maximum of 70 ind. m^{-2} in the area between the estuaries. Juveniles of *P. groenlandica* were found in the northern part, with maximum abundances of 150 ind. m^2, settling at about the same locality as juveniles of *N. aphroditoides*.

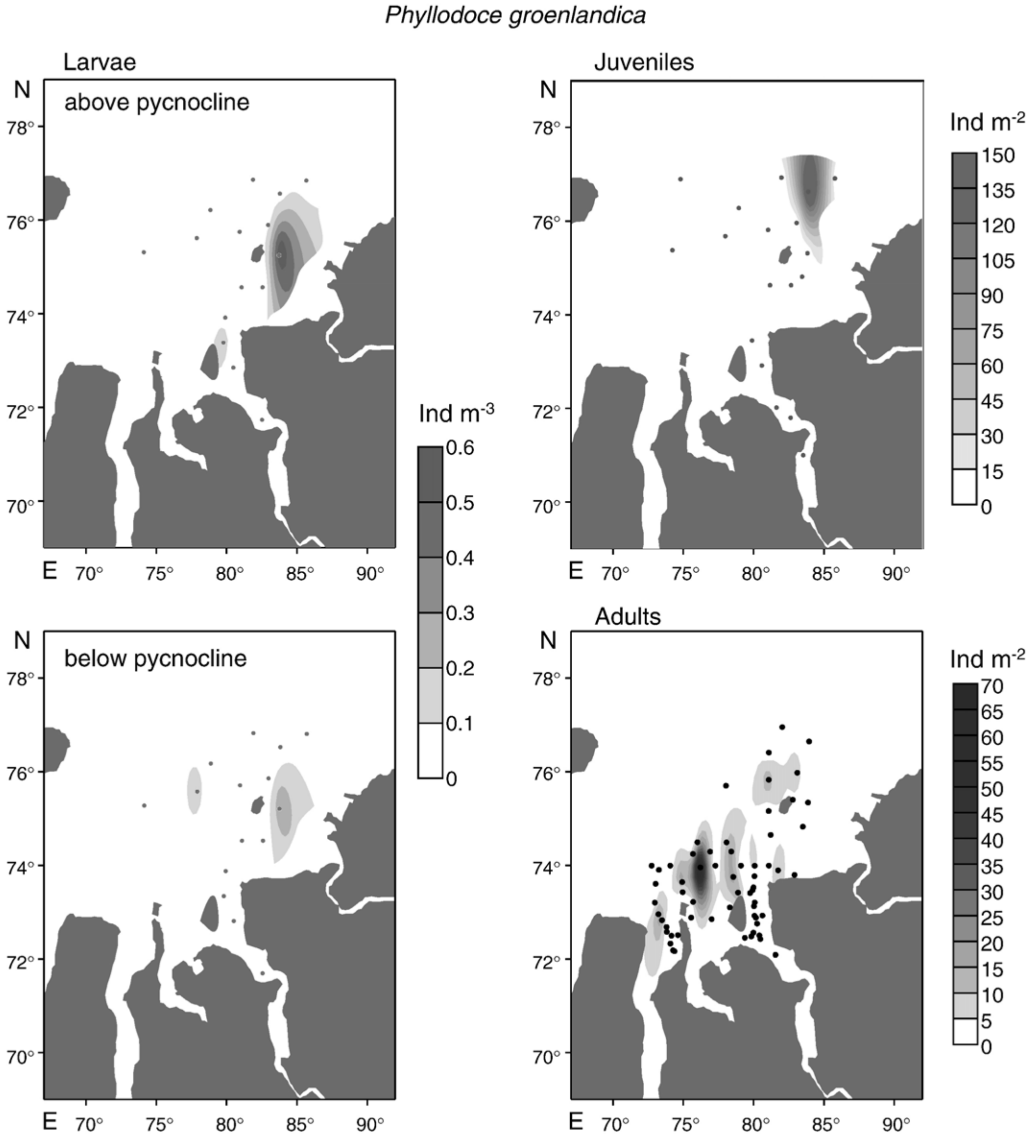

Fig. 7. Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Phyllodoce groenlandica* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3} and juveniles and adults as ind. m^{-2}. Dots indicate the sampling stations.

The only species occurring with higher abundances below the pycnocline were the larvae of the spionid *P. cirrifera* (Fig. 8). The larvae resided in moderate numbers with up 1.5 ind. m^{-3} at all stations north of the river outflow. Highest numbers occurred in the lower waters of the river outflow. No settled juveniles of this species were found in the Multicorer samples.

Adults of *P. cirrifera* were present exclusively within the estuary of the Yenisei River reaching densities of up to 800 ind. m^{-2}.

4. Discussion

Interpolation provides a useful tool for the interpretation of large scale patterns and the distribution for spatially limited datasets. The kriging method applied to the dataset is known to be an exact interpolator (exact interpolators honour data points exactly when the point coincides with the grid node being interpolated) but it interprets trends for areas where no data are available and thus may create results, which are higher to the found values in the fields. However, a cross-

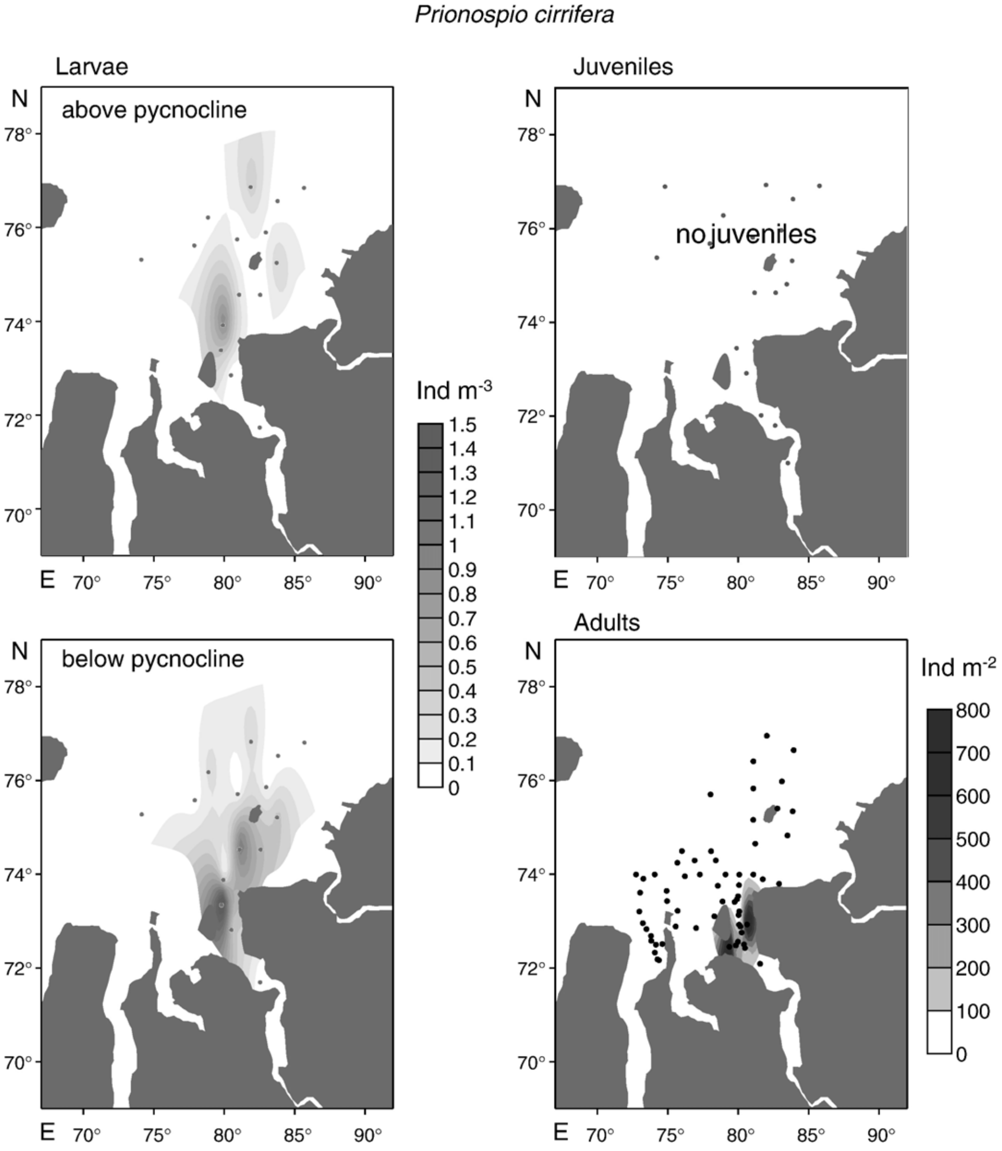

Fig. 8. Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Prionospio cirrifera* in the investigation area during the expedition to the Kara Sea in 2000. Larvae are calculated as ind. m^{-3} and juveniles and adults as ind. m^{-2}. Dots indicate the sampling stations.

check of the field and calculated data showed that this was not the case in this study. Moreover, since the data points were classified into defined classes, sometimes the interpolation even resulted in slightly lower estimates than those found in the field.

4.1. Physical conditions

The observed salinity and temperature distribution in the area showed a typical late summer situation with a pronounced warm brackish water layer on the surface and a cold high saline bottom layer, following the general patterns as described by Harms and Karcher (1999). The meteorological regime with prevailing strong easterly winds also represented the typical summer situation (Stein and Stephanets, 2001; Harms et al., 2001). The outflow of the Yenisei River was already deflected to the east indicating that the river run-off had already passed its maximum discharge (Pavlov and Pfirman, 1995; Harms et al., 2000).

In contrast to many other rivers in the northern hemisphere, which are redirected to the right at their mouth by the Coriolis effect, the Yenisei shows a strong discharge flowing straight into the Central Kara Sea. Harms and Karcher (1999) explained this feature by the prevailing northeasterly wind fields causing an Ekman deflection of the currents to the west, in conjunction with the narrow and deep opening of the Yenisei estuary, which results in a straight run-off (Pavlov and Pfirman, 1995).

The horizontal transition zone between the freshwater and brackish water in the Yenisei, as observed in summer 2000, was located between 71°30′ and 72°N which is in accordance to earlier observations (Antonov, 1962; Antonov and Maslaeva, 1965; Stanovoy and Nøst, submitted for publication). Penetration of high saline water deep into the Yenisei Estuary is mainly the result of a near bottom counter flow created by the strong river run-off (Ivanova, 1984; Stanovoy, 1984; Ivanov and Sviyatsky, 1987; Harms and Karcher, 1999). Harms et al. (2003) estimated velocities of 5–10 cm s^{-1} for this counter flow. According to Harms and Karcher (1999) it follows the Siberian shores into the Yenisei estuary is most developed at the time of sampling.

Tidal forces in the realm can be neglected since they are weak and are superimposed by the river discharge (Harms and Karcher, 1999).

4.2. Distribution of larvae, juveniles and adults

4.2.1. *O. sericeum*

The larvae of *O. sericeum* revealed the highest abundances for all the found larvae. Plankton investigations done by Formin (1989) reported ophioplutei in the Kara Sea to be present throughout the year. The found larval densities of up to 200 ind. m^{-3} much higher than those reported from studies from other polar regions. Schlüter and Rachor (2001) found a maximum of only 50 ind. m^{-3} in the upper water masses of the Barents Sea.

The highest abundances in this study were found close to melting drifting ice encountered at the northernmost station, as indicated by the less saline and cooler surface waters (Fig. 2). Since no correlation with higher food sources (e.g. phytoplankton (Makarevich and Larionov, 2001; Deubel et al., 2003) could be detected, passive accumulation of drifting larvae in the less saline water masses is suggested. Gallager et al. (1996) observed that passive drifting ophioplutei, which are usually randomly distributed in uniform water bodies, tend to accumulate at interfaces between water masses and are not able to pass through them.

The generally significant higher abundances in the northern areas correlates well with the genera distribution patterns of the adults which are exclusively found in the northern parts of the Kara Sea on the shallow shelf areas north and east of the Taymyr peninsula and the Vilkitsky Strait. Lubin and Eckert (2001) found local densities of adult brittle stars of 200 ind. m^{-2} for the northern region of the examined area. Even higher densities (566 ind. m^{-2}) were reported for the adjacent Laptev Sea (Piepenburg and Schmid, 1997).

Adult Ophiuroida are known to be very stenohaline and thus avoid areas with unstable salinities (as for example in the mouth of the rivers were the freshwater of the rivers may reach the bottom during flushing events (Piepenburg and Schmid, 1997). Investigations by Deubel et al. (2003) and Denisenko et al. (2003) reported occurrences of *O. sericeum* not further south than 74°N. The same holds true for our observation of settling juveniles. However, this seems not the case for larvae and drifting juveniles. Larvae seem to tolerate salinities of even less than 15 psu, although the highest abundances were found together with their drifting juvenile counterparts mainly in surface waters of <25 psu. This stands in contrast to the observations of Thorson (1946), which suggested that echinoderm larvae are more sensitive to low salinities than other meroplanktonic larvae. Since they passively drift within water masses they probably successfully adapt to lower salinities and may not experience strong salinity and temperature changes within their water mass.

The high presence of ophiuroid larvae in the upper water column (see also Fetzer, 2003) may be explained by the fact that ophiuroid eggs and developing larvae are highly positively buoyant due to their high lipid contents (Hendler, 1991; Westheide and Rieger, 1996), which concentrates the animals in the surface waters. After spawning and hatching on the northern shelf areas the passive drifting larvae are most probably driven into the Kara Sea by the prevailing north-eastern wind which also causes the thinning plume of larvae to the south and west.

Although ophiuroids have a developmental time of about 2–3 weeks in temperate waters, Pearse (1969) presumes a developmental time of six month for the arctic ophiuroid *O. sericeum*. Harms and Karcher (1999) calculated an average current speed of 10cm s^{-1} for the Kara Sea. According to this a larvae may drift more than 1500 km until metamorphosis. Currents may even be enhanced in ice-free wind-driven areas. Thus, due to high potential larval exchange, communities of *O. sericeum* may not belong to single isolated populations but rather form a metapopulation (see Botsford et al., 1994) spreading over the whole Siberian Arctic shelf area (Piepenburg and Schmid, 1996, 1997). The high amount of drifting juveniles found in the water column show that even after metamorphosis animals may even extend the drifting period (Fig. 4).

The continuous reproduction of *O. sericeum* coupled with a high reproductional output does not restrict this species to a certain reproductive window where environmental factors maximize laval survival and hence the reproductive output. Since this species is present on all shelf areas where salinities are stable, all larvae encountered in the southern part of the Kara Sea are probably accidentally drifted into the area. Settled animals will most probably die after colonising the area.

The fact that all found juveniles were rather small (mean size disk diameter = 456 μm) and possessing only rudimentary podia indicates a recent metamorphosis.

4.2.2. *M. minuta*

The larvae of *M. minuta* were the second abundant species concerning larvae in the Kara Sea and reached densities of up to 7 ind. m^{-3} (Fig. 5). Larvae of *M. minuta* appeared at almost all stations in the upper water column except at Station 2 in the west. Here, larvae were found only in the deeper layers. Intrusions of freshwater from the river Ob from the west overlaid brackish waters and pushed larvae to greater depths (Stephantsev and Shmelkov, 2001). As with the ophioplutei, the larvae of *M. minuta* had a local maximum at Station 36 but were more or less evenly distributed over the whole area. This agrees with the homogenous distribution pattern of the adults in the area.

Juveniles also do not seem to have preferential colonising regions since they showed the same distribution as adults and larvae. The local maximum abundances of 4000 ind. m^{-2} were the highest densities found among the settled juveniles for the five species described in this study. The high densities of already settled juveniles lead to the conclusion that *M. minuta* starts reproducing rather early in the year since for many of the species the descendants have already passed the larval stage and settled.

According to the large size range of larvae found in the water column, ranging from newly hatched trochophores to old individuals of 980 μm body size and 11 segments, *M. minuta* obviously continuously release larvae into the water instead of having a single spawning event as is known from many other benthic invertebrates (e.g. Günther et al., 1998). Interestingly, even small settled juveniles with a minimum body size of 430 μm and seven segments were found. This may lead to the assumption that this species gets competent for settling at a size of 430 μm but may be able to prolong their planktonic life period to grow up to a size of 990 μm reaching 11 segments. Since large larvae were exclusively found in the upper water layers, the resuspension of larvae can be excluded. A second explanation would be an additional direct developing mode of this species. This is known from many spionids, which are able to switch between direct and indirect development modes, releasing much smaller offspring from their parents lacking a planktonic phase. A detailed description of the reproduction and development is generally missing in the literature (see Jirkov, 2001).

Adults were more predominant in the wake of the Yenisei estuary than the Ob River. In the mixing area of marine and fresh water, the so-called marginal filter zone, large amounts of dissolved and particulate matter is transformed and sinks to the sea floor (Lisitsyn, 1995). It is most likely extensively utilised by the deposit feeding *M. minuta*. The shape of the Yenisei estuary probably promotes higher accumulation rates of transformed matter (Lisitsyn et al., 1995; Jørgensen et al., 1999; see also Klages et al., 2003). Probably, food availability rather than hydrography determine the presence of the adults since both the adults and larvae are able to tolerate high salinity and temperature changes. Jirkov (2001) describes this species as typical for the shallow Arctic shelf areas characterised by low annual average temperatures and low salinities. *M. minuta* seems to be restricted to the shelf area of Siberia since it is not reported from other shallow Arctic areas as e.g. Greenland Shelf were the genus (*Micro*-)*nephtys* is represented by *Nephtys cilliata* (Smidt, 1979; Lacalli, 1980; Andersen, 1984).

4.2.3. *N. aphroditoides*

The densities and distribution of the larvae of *N. aphroditoides* are almost equivalent to those of *M. minuta*, although their larvae are found in more southernly regions and are restricted to two localities to the west and east of the Yenisei outflow (Fig. 6). The hydrographic patterns may play an important role in restraining the larvae in the two areas. Both areas are situated away the direct influence of the river outflow and are characterised by relatively calm waters. Additionally, local eddies driven by the intense river run-off at the interface between the moving water and the calm shore-zone may stabilise the location of the larvae. However, the eastern part may be flushed as run-off ceases towards the end of the season and river run-off is deflected towards the coast (see Harms and Karcher, 1999). Adults were roughly restricted to the same areas as the larvae, which suggests that the area is the species-spawning site. This does not seem to be the case for the juvenile stages, since they were found in the northern plume of the Yenisei River. Such behaviour is known from juvenile settlers of the lugworm *Arenicola maritima* for example, where juveniles settle closer onshore and later migrate into deeper waters to the settling grounds of the adults (Flach and Beukema, 1994). It is assumed that this way juveniles avoid (i) intraspecific food competition and (ii) circumvent cannibalism from the carnivourous adults (Hartmann-Schröder, 1996; Jirkov, 2001).

In *N. aphroditoides* a wide range in body size of both larvae and juveniles was found. This suggests a prolonged reproduction window and, hence a continuous settlement of the larvae. Although juveniles of *N. aphroditoides* had almost the same size range as juveniles found for *M. minuta*, the mean body size of the juveniles was only half of that of *M. minuta* indicating a much earlier successive settlement state for *N. aphroditoides*.

4.2.4. *P. groenlandica*

The larvae of *P. groenlandica* were restricted to two areas of the study site at very low frequencies of 0.55 ind. m^{-3} (Fig. 7). Although most of the larvae were found in the upper water column, a comparatively high amount was found below the pycnocline. These larvae were mainly advanced nectochaeta stages with many segments. The first settled animals were actually smaller and showed fewer segments than the smallest specimens near the surface. In contrary to the larvae of *M. minuta* the larvae of *P. groenlandica* may settle but are also capable to return into swimming mode again. Thorson (1946) describes that *P. groenlandica* reproduces in Øresund (Denmark) in spring and early summer. The relatively big trochophores have a quite long pelagic period and settle at a size of around 3000 μm (26 segments). This agrees with our findings.

In this survey large numbers of undeveloped phyllodocid larvae were present, reaching maximum values of 7 ind. m^{-3} (personal observation, see also Fetzer, 2003). All were still trochophores with no segments visible. Since *P. groenlandica* was the only adult phyllodocid polychaete in measurable amounts in the area, the larvae most probably belong to this species. Trochophores appeared in the same area as the identified larvae, but in contrast at highest amounts below the pycnocline. It remains unclear whether these trochophores belong to a second spawning event.

The adults were very patchily distributed all over the sampling area, with a tendency towards the river mouths. *P. groenlandica* is known to inhabit a wide range of habitats and tolerates low salinities. As a carnivore, it most probably feeds on organisms utilising the depositing organic matter in the marginal filter zones of the rivers (Hartmann-Schröder, 1996).

4.2.5. *P. cirrifera*

In contrast to all the other observed larvae, the larvae of *P. cirrifera* were distributed mainly below the pycnocline (Fig. 8). Most larvae were large (mean body size = 1513 μm) and well developed. According to their size and horizontal distribution, these larvae were about to settle shortly. This agrees with the findings of Schlüter and Rachor (2001), which also found trochophores of *Prionospio* spp. in the lower water masses on the Barents Seas Shelf in June. Hannerz (1956) and Plate and Husemann (1994) mentioned size at metamorphosis of 1200 μm, which accounts to 15–19 chaetigers. The mean body size of the larvae found in this study was 1513 μm, although the biggest planktonic larvae we encountered had a size of 2700 μm and 26 segments. Interestingly, no juveniles of this species were present. However, this may be explained by the very few sampling stations in the estuary. The larvae were present all over the investigated area but with higher densities in the mouth of the Yenisei estuary. Since high concentrations of adult *P. cirrifera* are exclusively found in the estuary of the Yenisei River, retention and/or returning of the larvae into the estuary is of major importance for this species. Since outflow currents of the river are quite high, it is unclear how far those larvae released in the river mouth are washed out into the northern region. Since larvae are not capable of overcoming water currents by swimming, larval behaviour may play a significant role. Newly hatched larvae are liberated into the water column and most probably flushed out of the estuary into the northern region. As they grow and start sinking, they most probably enter the bottom near counter current to return into the estuary (Hannan, 1984). Release and development time needs to be synchronised to a high degree with the seasonality of the outflow to ensure high recruitment rates. Hannerz (1961) noted that the first larvae appear quite late in the year during the middle and later part of the summer. Blake and Arnofsky (1999 and citations therein) found that the release of many Spionids is triggered by temperature and salinity. In many spionidiforms peaks of reproduction appear during periods when the water temperature is highest. Additional stimuli such as low salinity may enhance the precision of the release. In June, at times of maxima water discharge both temperature and salinity changed drastically in the estuary most probably serving as the stimulus to spawn.

4.3. Biotic factors

One general pattern, which was observed in all species was the lowest abundances in the area directly influenced by the river. This observation may be explained by the fact that this area with the strongest water movement is also an area where water masses undergo the widest changes in both temperature and salinity. Many (mero-) planktonic organisms are quite adaptable to a wide range of hydrographic conditions, but are intolerant to rapid temporal changes.

In addition abiotic factors restricting the allocation of meroplanktonic organisms, predators may also cause strong reductions in abundances and hence determine the found distribution patterns. Planktonic carnivores such as cnidarians may heavily prey on planktonic animals (Schneider and Behrends, 1998). Additional mesozooplanktons investigation done in the same period (see Suck, 2001; Deubel et al., 2003) revealed the presence of hydromedusa reaching 4 ind. m^{-3} in the mixing zone. Schneider and Behrends (1998) found that even concentrations of 0.004 ind. m^{-3} may have a significant effect on pelagic systems in the Baltic Sea. Other possible scavengers such as chaetognaths showing densities of 24 ind. m^{-3} in the northern region, may also affect the present meroplanktonic composition. Other predators were of less or no significance in the Kara Sea system (personal observation).

4.4. Conclusions

Despite the high river output, remarkably large number of larvae were retained within the distribution areas of their adults. It still remains unclear to what degress a benthic community is determined just by local accumulation of drifting larvae or whether active spawning strategies by adults and larval behaviour define the composition of an assemblage. The first would imply, however, that benthic communities are exclusively shaped by the hydrology.

Nevertheless, as shown the hydrography changes immensely during the season and nothing is known about how future hydrographical patterns may influence the distribution of larvae. Changes of the prevailing current pattern due to general global warming may have a crucial effect on the reproductive success of species (Cushing, 1990). Determining the actual causes of the distribution pattern of meroplankton is difficult because of the complexity of the underlying processes. The distribution of the larvae in the area is the result of many interacting factors such as the physical processes, larval behaviour, the distribution of adults and probably predation. Miscellaneous small-scale processes may also have strong effects on larval distribution.

Improved insights into the life strategies of benthic species and larval ecology such as the timing of larval release, duration of lavae in the water column and larval behaviour would help to understand how species may actively influence the distribution of their larvae in the water column via adult reproductive strategies and larval behaviour in comparison to the passive influence of hydrological forces.

Acknowledgements

We thank the officers and crew members of *R/V Akademik Boris Petrov*, as well as the participants of the cruise in 2000 for their help and the excellent company during the expedition. We would especially thank Inken Suck (AWI) for her assistance during the sampling as well Victor Khorshev and Alexandr Latko (ships' technical staff) for their help with the gear onboard. Also many thanks to Kilian Smith (UFZ) for his comments improving this MS. This work was supported by BMBF 03G0539A1, Project Siberian River Run-Off (SIRRO).

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