Reproduction strategies and distribution of larvae and juveniles of benthic soft-bottom invertebrates in the Kara Sea (Russian Arctic)

The influence of river discharge on the structure of benthic communities: a larval approach

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Summary

Reproduction strategies strongly influence distribution patterns and abundance of marine benthic invertebrates. Most of them exhibit rather complex and diverse life cycles that are adapted to the environment the species live in. The great diversity of life history patterns found has generated intense debates among ecologists on classification of different development types and their relationship to given biotic and abiotic environments. In the light of new findings from polar seas much interest is given to the potential geographical shift in main life history traits of benthic invertebrates. However, until now little is known about the reproduction strategies of the majority of Arctic invertebrates. Most species in temperate areas reproduce with pelagic larvae, which often act as passive drifting particles in the water column. Their distribution is therefore mainly determined by local hydrographic patterns, which can either transport them away or retain them close to their spawning ground, the distribution of their adults (=place of release) and the duration of their stays in the water column. Direct development ensures that the offspring stays on approved sites where adults already survived and guarantees sufficient recruitment within the community since larvae are not endangered to be transported away by currents.

The main aims of this work are to determine the reproductive patterns of benthic invertebrates in the Kara Sea and to analyse possible adaptations of reproduction strategies to polar conditions. The structuring influence of river discharge and hydrography on the spatial distribution of larvae and settled juveniles in relation to the distribution of their adults is investigated. Given the specific characteristics of the Kara Sea, special emphasis is put on the role of the pycnocline in separating meroplankton communities. The Kara Sea is a shallow shelf sea with an average depth of 50 m located in the Russian Arctic. Besides strong fluctuations in light, temperature and ice coverage, hydrography and ecosystems are strongly affected by the immense freshwater input of the two adjacent rivers Ob and Yenisei. The outflow creates a pronounced bilayered pelagic habitat with a confined pycnocline. Analyses of zooplankton samples from three years revealed a strong structuring effect of river discharge on pelagic communities. River run off varied significantly between years. Benthic communities are clearly shaped by the influence of freshwater input but also by the deposition of imported organic material, which can be utilised as a food source.

Pelagic larvae and juveniles of marine benthic invertebrates of the Kara Sea were sampled, identified and their quantity and dispersal patterns in relation to the presence and distribution of their adults analysed. At each sampling station, three plankton samples were taken: one below the pycnocline, one across and one above it. Additionally, sediment samples were collected using a large box corer and a multicorer to monitor adult and juvenile distribution, respectively.

During the investigation period in 2000 and 2001, 44 larval and 54 juvenile species were identified. For 23 of the larval species adults were present in benthos samples. For the remaining 21 larval species, adults were reported from the adjacent Barents and Petchora Sea, indicating a strong larval supply from the neighbouring seas. Most larvae were found in all water layers, although highest abundances were present in the upper low salinity layer, revealing a high acclimatisation potential of most larvae to low salinities. Notably, the ophioplutei of the brittle star *Ophiocten sericeum*, whose adults are very sensitive to lowered salinity, showed high concentrations within low salinity meltwater plumes. No differences in meroplankton densities were found between the surface layer and the pycnocline, but surface and bottom layer differed significantly. The pycnocline seems to act as a physical barrier for most larvae. Meroplankton densities of individual species were generally <1 ind. m^{-3}, but ophioplutei of *O. sericeum* reached densities of 200 ind. m^{-3}. The hydrographical regime strongly influences larval distribution both vertically and horizontally. Generally, lowest concentrations were found in the wake of the rivers, although along a transect out of the Yenisei River local accumulation of larvae in the estuary was found. Retention is most likely caused by circulation patterns created by the strong river run off. Retention of larvae of benthic invertebrates within nursery grounds and/or the return to their parental grounds is challenging for species in areas with strong riverine output. The importance of retention in the study area was demonstrated for five exemplary species.

Most benthic species of the study area show an Arctic zoogeographic distribution, but a considerable number of Arctic-boreal, boreal and cosmopolitan species were also found. The river run off may not only foster the survival of euryhaline species but through its thermal input also creates favourable conditions for boreal species. Most invertebrate species in the Kara Sea seem to reproduce directly. This large proportion can be explained in some parts by the high share of peracarid crustaceans (Cumacea, Isopoda and Amphipoda) in the species composition. While other taxa display a huge spectrum of reproduction modes, which vary strongly between species and geographic regions, peracarids show a direct reproduction trait all over the world. Their elimination from the dataset in this study reveals for the Kara Sea a larger share of species reproducing with pelagic larvae. It is assumed that due to its variability in both biotic and abiotic factors, the environment of the Kara Sea shelf often creates unfavourable conditions for benthic species. Species with pelagic larvae or highly mobile species like most peracarid crustaceans may have an advantage in reoccupying defaunated habitats.

The numerous larval types found in this study indicate that planktonic development is important in the Kara Sea ecosystem. There is still a considerable lack of knowledge on reproductive strategies of marine invertebrates, which especially holds true for organisms of the Arctic Ocean. Better knowledge on reproduction traits and dynamics of polar benthic invertebrates is not only a fundamental aspect for understanding Arctic ecosystems, but also a prerequisite for the interpretation of their reaction to future global change.

Zusammenfassung

Reproduktionsstrategien haben einen starken Einfluss auf Abundanzen und Verbreitungsmuster mariner benthischer Evertebraten. Die meisten Evertebraten zeigen relativ komplexe und diverse Lebenszyklen, die an ihre jeweilige Umwelt angepasst sind. Die große Diversität von Entwicklungsmustern ist Anlass für rege Diskussionen zwischen Ökologen über mögliche Klassifizierungen der unterschiedlichen Entwicklungsstrategien und ihre Beziehungen zu den biotischen und abiotischen Lebensbedingungen. Angeregt durch neue Erkenntnisse aus polaren Gewässern vor allem im Hinblick auf Klimaänderungen ist das Interesse an einer möglichen geographischen Verschiebung der wichtigsten Charakteristika der Lebensgeschichte benthischer Evertebraten in den letzten Jahren gestiegen. Allerdings ist bis heute nur wenig über die Reproduktionsstrategien eines Großteils der arktischen Evertebraten bekannt.

Die meisten Arten der gemäßigten Breiten pflanzen sich über pelagische Larven fort. Diese verhalten sich meist wie passiv driftende Partikel in der Wassersäule. Ihre Verbreitung ist deshalb hauptsächlich durch lokale hydrographische Prozesse bestimmt, die sie entweder forttransportieren oder in der Nähe ihres Ursprungsgebiets halten. Für die Verbreitung der Larven spielt außer dem Vorkommen und der Verbreitung der Adulten (Ort der Reproduktion) sowie den Strömungen die Dauer des Aufenthalts im Wasser eine Rolle. Direktentwicklung dagegen garantiert, dass die Nachkommen in günstigen Gebieten bleiben, in denen sich Adulte ihrer Art bereits erfolgreich niedergelassen und fortgepflanzt haben. Da die Larven oder Jungtiere in diesem Fall nicht von Strömungen wegtransportiert werden, wird so trotz geringerer Nachkommenzahl für eine ausreichende Rekrutierung gesorgt.

Diese Arbeit hat zum Ziel, Reproduktionsmuster benthischer Evertebraten in der Karasee zu bestimmen und potentielle Anpassungen an die polaren Bedingungen zu untersuchen. Die Karasee ist ein flaches Schelfmeer in der russischen Arktis mit einer mittleren Tiefe von 50m. Neben den sehr starken saisonalen Schwankungen des Lichtregimes, der Temperatur und Eisbedeckung ist das Ökosystem stark von dem enormen Süßwassereintrag der beiden Flüsse Ob und Yenisei beeinflusst. Ihr Abfluss schafft ein deutlich geschichtetes, pelagisches Habitat mit einer ausgeprägten Pyknokline. Der strukturierende Einfluss des Flusseintrags und der Hydrographie auf die räumliche Verteilung der Larven und niedergelassenen Juvenilen wird in Abhängigkeit von der Verteilung ihrer Adulten untersucht. Dabei wird der Rolle der Pyknokline für die Abgrenzung unterschiedlicher Meroplanktongemeinschaften besondere Bedeutung beigemessen. Untersuchungen von Zooplanktonproben aus drei Jahren haben die Bedeutung der Flusseinträge bestätigt, deren Stärke allerdings zwischen den Jahren stark schwankte. Die benthischen Gemeinschaften sind ebenfalls eindeutig durch den Einfluss des Süßwassers strukturiert. Es spielt hier aber auch die Ablagerung von eingetragenem organischem Material eine wichtige Rolle, da die Tiere es offensichtlich als Futterquelle nutzen können.

Pelagische Larven und Juvenile mariner benthischer Evertebraten wurden in den Jahren 2000 und 2001 gesammelt und bestimmt. Ihre Häufigkeiten und Verbreitungsmuster in Abhängigkeit von dem Vorkommen und der Verteilung ihrer Eltern wurden analysiert. An jeder Probennahmestation wurden drei Planktonproben mit Schließnetzen genommen: eine unterhalb der Pyknokline, eine durch die Pyknokline, und die dritte oberhalb. Zusätzlich wurden Sedimentproben mit

Hilfe eines Großkastengreifers und eines Multicorers genommen, um die Verteilung der Adulten und Juvenilen zu erfassen.

Während der Probennahmezeit wurden 44 Larven- und 54 Juvenilarten gefunden. Von 23 Larvenarten wurden auch Adulte im Benthal verzeichnet. Für die übrigen 21 Larvenarten sind Adulte aus der angrenzenden Barents- und Pechorasee bekannt, was auf einen Eintrag von Larven aus den Nachbargebieten hindeutet. Die meisten Larven kamen in allen Wasserschichten vor. Die höchsten Dichten wurden jedoch in der oberen, salzarmen Schicht beobachtet, was ein hohes Anpassungsvermögen der Larven an erniedrigte Salinitäten voraussetzt. Bemerkenswerterweise zeigten z.B. die Ophioplutei des Schlangensterns *Ophiocten sericeum*, der adult sehr empfindlich auf erniedrigte Salinitäten reagiert, hohe Konzentrationen in ausgesüßten Schmelzwasserzungen an Meereisrändern. Es konnte kein Unterschied in den Meroplanktondichten zwischen der Oberflächenschicht und dem Bereich der Pyknokline gefunden werden, während sich die Oberflächen- und die Bodenschicht stark voneinander unterschieden. Die Pyknokline scheint für die meisten Larven eine physikalische Barriere darzustellen.

Die Dichten der meisten Arten lagen unter 1 Ind. m^{-3}. Eine Ausnahme waren die Larven von *O. sericeum*, die Dichten von bis zu 200 Ind. m^{-3} erreichten. Das hydrographische Regime beeinflusst die horizontale und vertikale Verbreitung der Larven. Im Allgemeinen wurden die geringsten Larvenkonzentrationen in der Flussfahne gefunden. Allerdings wurden entlang eines Transekts aus dem Yenisei lokale Ansammlungen von Larven im Ästuar festgestellt. Das Zurückhalten (die Retention) von Larven wird wahrscheinlich durch Zirkulationsmuster hervorgerufen, die durch den starken Ausfluss entstehen. Die Retention von Larven benthischer Evertebraten in ihren Brutgebieten und/oder ihre Rückkehr in die Gebiete ihrer Eltern ist für Arten in Gebieten mit starkem Flusseintrag eine Herausforderung. Die Bedeutung der Retention im Untersuchungsgebiet wird anhand von fünf exemplarischen Arten demonstriert. Die meisten benthischen Arten des Untersuchungsgebiets weisen eine arktische zoogeographische Verbreitung auf. Allerdings wurde auch eine bemerkenswerte Anzahl an Arten mit arktisch-borealer, borealer oder kosmopolitischer Verbreitung gefunden. Der Flusseintrag könnte nicht nur das Überleben von euryhalinen Arten begünstigen, sondern durch den Wärmeeintrag auch günstige Bedingungen für boreale Arten schaffen.

Die meisten Evertebratenarten in der Karasee scheinen eine Direktentwicklung aufzuweisen. Der große Anteil an Direktentwicklern kann teilweise durch den hohen Prozentsatz von peracariden Crustaceen (Cumacea, Isopoda und Amphipoda) in der Artenzusammensetzung erklärt werden. Während andere Taxa ein großes Spektrum an Reproduktionsmodi aufweisen, die zwischen den einzelnen Arten und geographischen Regionen stark variieren, zeigen die Peracariden weltweit eine Vermehrungsstrategie mit Direktentwicklung. Werden diese Arten in der vorliegenden Untersuchung aus dem Datensatz herausgenommen, so zeigt sich für die Karasee ein hoher Anteil an Arten, die sich über pelagische Larven fortpflanzen. Es wird angenommen, dass die hohe Variabilität der biotischen und abiotischen Faktoren in der Karasee oft zu ungünstigen Habitatbedingungen für benthische Arten führen. Arten mit pelagischen Larven oder hoch mobile Arten wie die meisten peracariden Crustaceen dürften bei der Wiederbesiedlung von gestörten Gebieten im Vorteil sein.

Die vielen in dieser Untersuchung gefundenen Larventypen und auch ihre Abundanzen deuten darauf hin, dass die pelagische Entwicklung für das Benthos in dem Ökosystem der Karasee

von Bedeutung ist. Nach wie vor gibt es nur unzureichende Kenntnisse über Reproduktionsstrategien mariner benthischer Evertebraten, v.a. von Arten des arktischen Ozeans. Ein besseres Verständnis der Reproduktion und Populationsdynamik polarer benthischer Evertebraten ist nicht nur eine fundamentale Voraussetzung für ein besseres Verständnis arktischer Ökosysteme, sondern auch eine Bedingung für eine Abschätzung ihrer Reaktion auf zukünftigen globalen Wandel.

1 Introduction

1.1 Life-history traits in marine invertebrates

With over 1.2 million known species invertebrates represent the largest group within the animal kingdom. About 240,000 of these are aquatic and among these around 170,000 are exclusively found in the marine environment (Thorson 1957, Tardent 1993). However, the true number is assumed to be much higher as new species are still being discovered at a high rate. Actual species diversity is a topic that is controversially discussed in the scientific world (May 1986, 1988, Grassle & Maciolek 1992, Gray 2001).

More than 70% of the invertebrate species exhibit indirect development with larvae that differ from adults in size, form, habitat, mode of feeding or ability to move (Barnes et al. 1993). Life cycles in these marine invertebrates are biphasic with a dramatic, often rapid series of morphological, behavioural and physiological changes termed as metamorphosis (Young & Eckelbarger 1994). The larvae of these species usually have a pelagic phase. A smaller number of species, however, have direct development without a pelagic phase. Young individuals of these species are born as precise miniature copies of their adults, except for the capacity to reproduce. Relative proportions of body parts may change during subsequent growth but changes are gradual (Young 2002; Fig. 1). In some species (especially Spionidae and Opisthobranchia) direct and indirect reproduction modes are not absolute. According to the environmental situation, these species may switch between direct reproduction or one with a larva (poecilogony; Chia et al. 1996, Blake & Arnofsky 1999, Duchene 2000).

While reproduction via larvae is seen as the original trait in marine species (originating from the external fertilisation of gametes), modification or suppression of the pelagic phase is interpreted as an advanced trait achieved during the evolutionary history of benthic species (Jablonski & Lutz 1983, Wray 1995). Advanced or modified reproductive features are often found in marine invertebrates living in specific environments such as the deep sea, polar regions and estuaries (Young & Eckelbarger 1994).

However, the majority of benthic invertebrates in temperate regions reproduce via pelagic larvae (Bhaud 1993, Giangrande et al. 1994, Grantham et al. 2003). Especially for sessile species this ensures a wide distribution and a good ability for exploitation of new territories (Thorson 1950, Scheltema 1989). In isolated habitat patches the supply of propagules is of critical importance for the survival of a community (Barnay et al. 2003, Dethier et al. 2003). Larval exchange between populations sustains high genetic variation within a community and may enhance overall flexibility of individuals adapting to environmental changes (Grosberg &

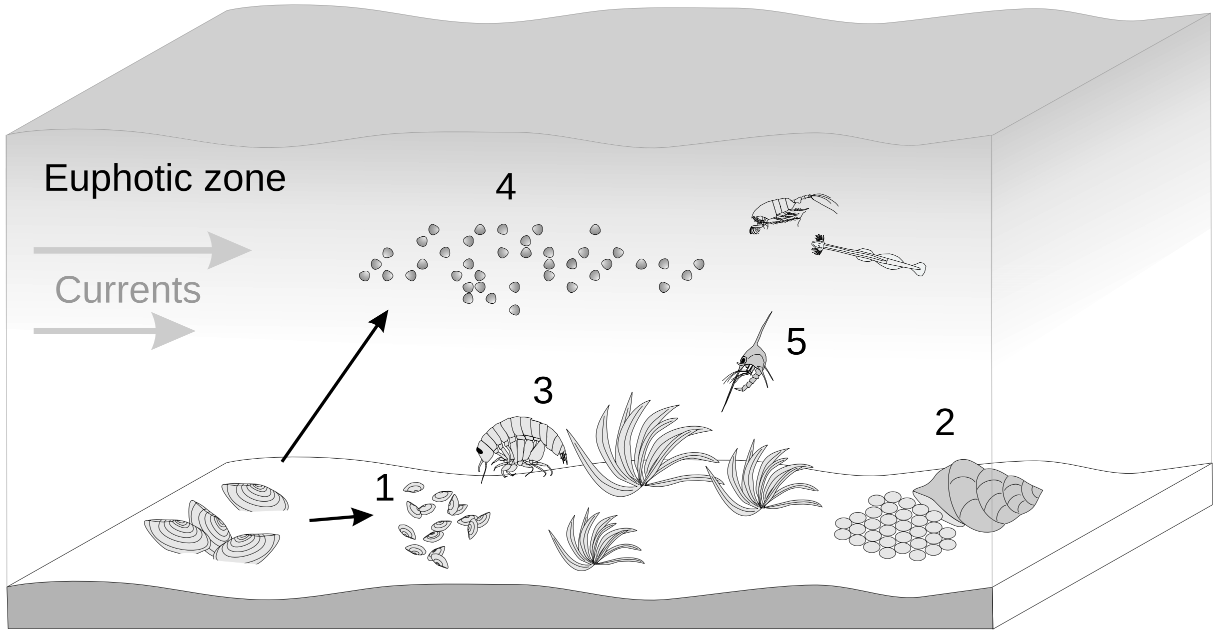


Figure 1: Examples of reproduction types. Direct development: Young individuals are released directly from the adults without a larval stage (1) or hatch from egg-capsules (2). In some species the off spring is brooded in special pouches (3) before it is set free. Indirect development: Pelagic larvae are released by the adults into the water column. Planktotrophic larvae subsequently have to feed on phytoplankton (4), while lecithotrophic larvae (5) drift in the water column until metamorphosis.

Quinn 1986, Grosberg 1987, Edmands & Potts 1997). Moreover, planktonic stages are able to enter the euphotic zone and, thus, to instantaneously utilise the primary production in the upper and warmer water layers. Such they also avoid direct food competition with their adults. On the other hand, pelagic stages strongly depend on environmental factors, which constrain their settlement success. Prevailing currents often carry them away to unfavourable sites; and they are exposed to high predation pressure by planktonic scavengers resulting in high mortality (Mileikovsky 1974, Pechenik 1999).

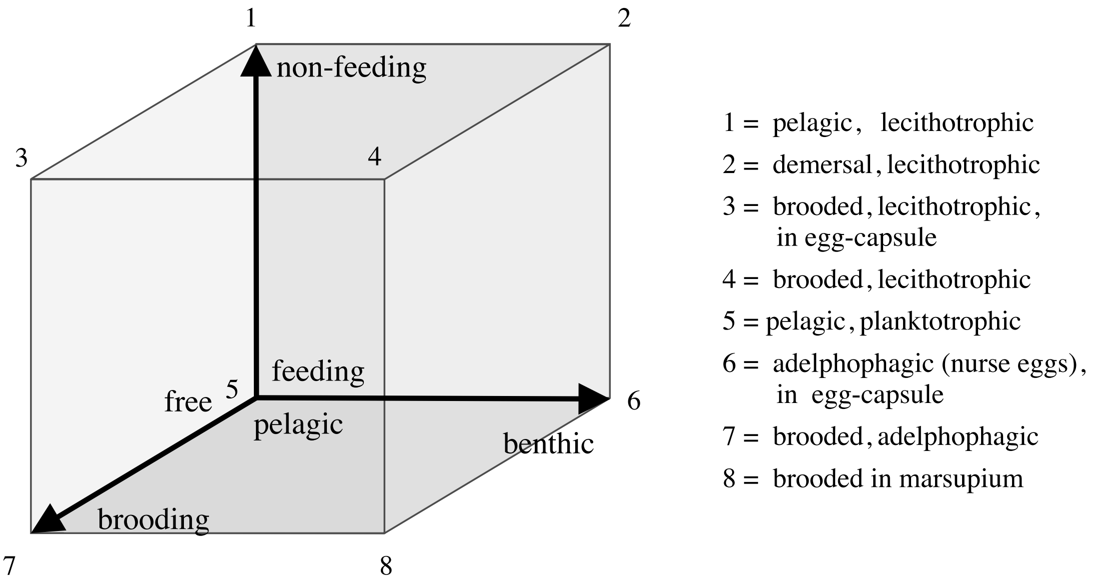
Direct development, on the other hand, ensures that juveniles settle in the vicinity of the adults and stay on approved sites where adults already survived. It guarantees sufficient recruitment of a community since larvae are not endangered to be transported away by currents. Thus, for species living in spatially restricted and/or strongly fragmented habitats direct development might be advantageous (Johst & Brandl 1997, Bhaud 1998). One consequence of direct development is that on evolutionary timescales species in isolated, sessile communities tend to higher speciation (Jablonski & Lutz 1983) since often no larval exchange with other populations occurs and, thus, revitalisation of the genetic pool is constrained (Levinton 2001).

In most species showing direct development brood protection is common. This reduces the mortality of the offspring to a minimum. Species caring for their eggs and/or offspring are often termed as ’brooders’. Since larvae of brooding species cannot feed in the plankton, these species usually provide their offspring with nutrients. Broadcasting species, on the contrary, usually spawn their eggs/larvae freely into the water column and, thus, mostly have pelagic-planktotrophic larvae (Ebert 1996).

Usually pelagic larvae are not provided with nutrients by their parents and consequently depend on an exotrophic, planktonic food source. However, many pelagic larvae do not feed but are supplied with yolk by the parental organism. The nutrients are often directly applied to the larval organism and apparent in the larvae as a yolk sack or granules. Within species producing egg capsules larvae hatch within these capsules and feed on often unfertilised, yolky eggs (adelphophagy). Since the first pelagic type depends on a planktonic food source it is termed ’planktotrophic’, the second type, which is independent of any external food supply, is known as ’lecithotrophic’ (Ockelmann 1965, Mileikovsky 1971). Subdivisions into the mentioned developmental types are often not absolute and many larvae exhibit mixed development (Barnes et al. 1993, Poulin 2001). Larvae are often lecithotrophic when hatching but subsequently have to feed on an external food source. This may buffer the mismatch between larval release and onset of primary production.

Recruitment success of species usually depends on the survival of their propagules (Cushing & Horwood 1994). Within reproducing species there is a general trade-off between the number of offspring and their individual fitness. Species producing lecithotrophic larvae and/or brooding their offspring perform a higher quantitative investment in a single larva. These larvae are energetically better equipped and usually hatch in a more developed stage than their feeding counterparts and, thus, have a higher survival potential (Begon et al. 1996). Since lecithotrophic larvae are supplied with nutrients by their parents, such species can produce only very few, but often big progenies. Specimens with planktotrophic stages, on the other hand, usually broadcast huge amounts of small larvae to compensate for larval mortality (Anger 2001). Additionally to the above described sexual propagation modes, asexual reproduction (e.g. budding, cloning, fission) of either adults or larvae has been described as an ecologically important strategy for some invertebrate species which increases their fecundity drastically (Mileikovsky 1971, Eaves & Palmer 2003).

The great diversity of life history patterns has generated intense debates on how to classify types of development. Various schemes have been proposed for different viewpoints relating to ecology, evolution and/or larval development (e.g. Thorson 1950, Mileikovsky 1971, Chia 1974, Jablonski & Lutz 1983). However, these classifications do not efficiently discriminate between development patterns. Poulin et al. (2001, 2002) suggested an ecological, multifactor classification based on the niche occupied by the larvae, such as spatial location (benthic vs. pelagic), trophic types (feeding vs. non-feeding) and degree of parental care (free vs. brooding) where all different strategies can be integrated (Fig. 2).



1 = pelagic, lecithotrophic
2 = demersal, lecithotrophic
3 = brooded, lecithotrophic, in egg-capsule
4 = brooded, lecithotrophic
5 = pelagic, planktotrophic
6 = adelphophagic (nurse eggs), in egg-capsule
7 = brooded, adelphophagic
8 = brooded in marsupium

Figure 2: Multifactor classification of development patterns in benthic marine invertebrates. The three axes display (starting from the most frequently encountered developmental type) all of the conceivable alternatives of life history traits in benthic invertebrates (redrawn after Poulin et al. (2001)).

1.2 Definition of ’larva’

The term ’larva’ has been used by biologists in a number of different ways. Disagreement about the definition arises in part from diverse invertebrate life histories and in part from various differing perspectives of researchers. For example Gastropoda often reproduce via encapsulated stages that include veliger or trochophora like larvae rotating within their egg-capsules but hatch as morphological juvenile form of their adults. An evolutionary scientist would refer to those encapsulated stages as larvae because the species’ life cycle incorporates a larval stage. A geneticist would also clearly certify a larval phase for the species since larval gene expression occurs within the species. However, somebody interested in life history strategies or dispersal would refer to this species as functionally equivalent to direct development since the species does not release dispersing offspring. A morphologist would probably not call metatrochophora stages of polychaetes larvae since they functionally add segments while growing and do not undergo metamorphosis (Young 2002).

There is no generally accepted definition of a ’larva’ comprising all the above given criteria (Stanwell-Smith 1999). Definitions of larvae depend on whether the focus is on structure, evolution, life history, development sequences or ecological attributes. Nevertheless a comprehensive description is given by McEdward (1995) and Young (2002), which satisfactorily defines a larva for the purposes of the present study, although it does not include aspects of dispersal, feeding or habitat selection:

> “A larva is the post embryonic stage in the life cycle which is eliminated by the metamorphic transition to the juvenile and is capable of independent locomotion.”

1.3 Historical background

The study of invertebrate reproduction and larval biology has initially not drawn the attention of many biologists. Due to their temporary limited appearance in the water column, their small size and difficulties in identification meroplankton organisms generally have never received much attention in plankton surveys (Thorson 1946, Plate & Husemann 1994). Benthic 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, Olafsson et al. 1994). Therefore first descriptions of meroplankters have for the most part been made at random and identities of many of the found larval forms were not known. In many cases the species of larvae could not be ascertained and larvae have been given provisional names, which later often led to false conclusions concerning species identity (Hannerz 1956).

The first known meroplanktonic records in literature were produced by Martinius Slabber (1778), a Dutch microscopist. Since then pioneer work of e.g. Lovén (1846), Thomson (1828, 1830), Ehrenberg (1834), Milne-Edwards (1842), Müller (1846, 1847, 1850), MacDonald (1858), Sars (1844) on the development of invertebrate larvae has attracted the interest of many scientists (Young 2002).

The relatively incomplete, until then mostly descriptive work was compiled for the first time in the first half of the 20th century by Thorson (1936, 1946, 1950, 1964) and put into an environmental context. Thorson’s reviews established the broad outlines for the discipline of larval ecology (Mileikovsky 1971, Young 2002).

Since then much research has been done on larval ecology, the impact of the environment on meroplanktonic larvae and their effects on benthic communities. Several aspects of meroplankton ecology have been suggested as potential mechanisms in regulating marine populations (Morgan 2001, Eckert 2003).

Already in early investigations mortality was observed to play an important role in the recruitment success of benthic species (e.g. Muus 1973, Jackson & Strathmann 1981, Jørgensen 1981, Hines 1986, Hughes 1990, Gosselin & Qian 1996, 1997, Hamamoto & Mukai 1999). Thorson (1950, 1966) emphasised the importance of larval mortality in regulating populations and benthic communities. Behaviour and larval habitat selection were found to be key factors for the maintenance of community structures. Larval habitat selection was believed to be a critical factor enhancing the survival and reproduction success of the many sessile species and sedentary organisms that have little or no capabilities of adjusting their position after metamorphosing into juveniles (e.g. Jägersten 1940, Wilson 1952, Cameron & Schroeter 1980, Chia 1978, Strathmann 1978, Todd & Doyle 1981, Grant & Williamson 1985, Butman 1987, Butman et al. 1988, Günther 1991, 1992, Giangrande et al. 1994, Basch & Pearse 1996, Gosselin & Qian 1996, Miller & Emlet 1997, Qian 1999). Larval survival and their subsequent recruitment was shown to be constraining for the establishment of initial distributions and abundances of benthic invertebrates inhabiting rocky bottom as well as soft bottom habitats (e.g. Thorson 1966, Cameron & Schroeter 1980, Santos & Simon 1980, Cazaux 1985, Yoshioka 1986, Mullin 1988, Boicourt 1988, Roughgarden et al. 1988, Bosselmann 1989, Hughes 1990, Pedrotti 1993, Bhaud 1993, Olafsson et al. 1994, Giangrande et al. 1994, Günther 1992, Günther 1994, Gosselin & Qian 1996, Ambrose & Renaud 1997, Archambault & Bourget 1999, Grantham et al. 2003, Jaklin 2003).

Especially in recolonisation of devastated habitats and spreading of a species the dispersal potential of larvae has been found to be an important factor (e.g. Mileikovsky 1960, 1966, 1968, Roff 1975, Hansen 1980, Olson 1985, Scheltema 1986, 1989, Grosberg 1987, McConaugh 1992, Pedrotti & Fenaux 1992, Giangrande et al. 1994, Kim et al. 1994, Bhaud & Duchene 1995, Petersen & Svane 1995, Young 1995, Tylor & Young 1999, Marsh et al. 2001, Lefebvre et al. 2003), especially with regard to the reproduction modes related to zoogeography (e.g. Thorson 1936, Mileikovsky 1968, Raymont 1983, Scheltema 1986, Giangrande et al. 1994). Nevertheless, how far pre- and post-larval processes structure populations and communities of macroinvertebrates is still little known (Olafsson et al. 1994, Heuers & Jaklin 1999, Jaklin 2003). The orthodox view that pelagic larvae are the only dispersing life stage of benthic species has been rejected because several studies revealed that many species may have a second phase of dispersal as postlarvae and juveniles (Günther 1992, Armonies 1994, Jaklin & Günther 1996).

1.4 'Thorson's rule'

Until today an assumption posed by Thorson (1936) based on his first meroplankton observations in Greenlandic fjords is one of the most debated topics in meroplankton research. From the scarcity of larvae he found, Thorson concluded that many polar species reproduce without a planktonic stage. He explained this as a mismatch in the prolonged development time and short periods of food availability in polar areas apparently constraining species with indirect life history.

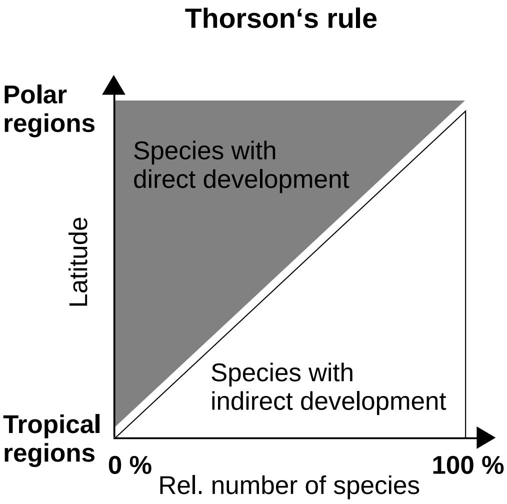


Figure 3: Scheme of Thorson's rule.

His hypothesis was confirmed by observations indicating that many species at higher latitudes tend to produce larger yolk-rich eggs than their counterparts of lower latitudes. Comparative studies of life history patterns of benthic invertebrates throughout the world's oceans revealed a latitudinal trend in the proportion of indirect development for most species from high numbers in the tropics to almost none in polar regions (Fig. 3; Thorson 1950, 1966, Ockelmann 1965, Mileikovsky 1971, Curtis 1975). The term 'Thorson's rule' was later created by Mileikovsky (1971) to describe this geographical shift in life history traits of benthic animals. Numerous groups such as Echinodermata, Crustacea, Mollusca, Annelida and Porifera were cited as examples supporting this general increase in non-planktonic development with increasing latitudes (Thorson 1935, 1936, 1950, Mortensen 1936, Ockelmann 1958, 1965, Thurston 1972, Curtis 1977).

However, findings of increasing numbers of pelagic larvae from surveys in Arctic and Antarctic waters imposed doubts on the general validity of this rule (e.g. Pearse 1969, 1994, Clarke 1992, 1996, Scheltema & Williams 1995, Stanwell-Smith et al. 1997, 1999, Buzhinskaja & Jørgensen 1997). Various ecological studies, that have been conducted in the Arctic and Antarctic either support or reject this paradigm (e.g. Hines 1986, Scheltema 1989, Grebmeier & Barry 1991, Hain & Arnaud 1992, Clarke 1992, Pearse 1994, Gallardo & Penchaszadeh 2001, Thatje et al. 2003).

Today Thorson's paradigm, which distinguishes planktonic from benthic development, has been partly replaced by one in which latitudinal shifts are observed in the proportions of planktotrophy and lecithotrophy among planktonic larvae (Clarke 1992, Pearse 1994, Poulin & Féral 1998).

Since Thorson's first meroplankton investigations in the Arctic most recent work has been carried out in Antarctic waters (e.g. Pearse & Llano 1965, Pearse 1969, Pearse & Bosch 1986, Olson et al. 1987, Bosch & Pearse 1990, Berkman et al. 1991, Pearse et al. 1991, Clarke 1992, Hain & Arnaud 1992, Klages 1993, Shreeve & Peck 1995, Poulin & Féral 1996, Alvà et al. 1997, McClintock & Baker 1997, Scheltema et al. 1995, 1997, Stanwell-Smith & Barnes 1997, Stanwell-Smith et al. 1997, Stanwell-Smith & Peck 1998, Marsh et al. 1999, Gambi et al. 2001, Orejas et al. 2002, Chiantore et al. 2002, 2002, Poulin et al. 2002, Thatje & Fuentes 2003, for review see Arntz & Gili 2001). There, a larger number of pelagic larvae than anticipated was found in shallow waters, with quite a number of planktotrophs among the dominant species (Hain & Arnaud 1992, Poulin et al. 2001). However, the percentage of species with indirect development appears low taking into account the large number of benthic species in these waters, and their abundance is much lower than at lower latitudes. Larval abundances are estimated to be 2-6 times of magnitude lower than peaks in comparable data from temperate and tropical zones. The low abundances (mean 2.6 ind. m^{-3} for the Antarctic realm) are interpreted to reflect both slow development rates, and, thus, spreading of the larvae over larger distances, and high dilution of larvae due to reduced spawning synchrony (Stanwell-Smith et al. 1999). Nothing is known about deep Antarctic waters except the fact that a very high percentage of species are brooders or produce pelagic-lecithotrophic larvae (Arntz et al. 1994). Investigations in deep waters revealed that meroplanktonic larvae are scarce during the Antarctic spring (Thatje pers. comm.).

Except for the studies of Thorson (1934, 1936, 1950, 1966), Chia (1970), Mileikovsky (1959, 1960, 1966, 1967, 1968, 1971), Smidt (1979), Lacalli (1980), Andersen (1984), Coyle & Paul (1990), Buzhinskaja & Jørgensen (1997), Clough et al. (1997), Schlüter & Rachor (2001) little is known about the ecology of meroplankton in the Arctic. Knowledge on meroplanktonic larvae has been achieved mainly through plankton surveys (e.g. Ockelmann 1958, Smidt 1979, Andersen 1984). As in the Antarctic, the number of described larvae rose, but feeding types of most of the larvae from the Arctic region are still not known. Except for Thorson's initial studies on egg-sizes of adult benthos in Greenlandic fjords (Thorson 1936), hardly any knowledge on the reproduction biology of adult benthic organisms has been added by verifying reproduction strategies through direct observations of animals and/or experiments.

1.5 Ecological implications of reproduction modes

> “The breeding seasons are normally the critical stages - "eye of the needle"- during the whole life of most marine bottom invertebrates and the conditions prevailing in a particular locality during the ripening and spawning and during the development of the larvae will normally be decisive for the occurrence or non-occurrence of each species within the locality”
>
> Thorson (1946, page 8)

The formation of benthic communities depends very much on specific recruitment success (Barnes et al. 1993, Levin & Bridges 1995), since only recurrent supply by new recruits ensures the survival of a population (Butman 1987, Olafsson et al. 1994, Heuers & Jaklin 1999, Jaklin 2003).

Retention of larvae of benthic invertebrates within nursery grounds and/or the return to their parental grounds prior to final settlement are important for the persistence of communities. This especially applies for species in current dominated regions and estuaries (e.g. Blake & Woodwick 1975, Cronin & Forward 1986, Boicourt 1988, McConaugh 1992, DeVries et al. 1994, Anger et al. 1994, Anger 1995, Chen et al. 1997, Dautov 1997, Bilton et al. 2002). Here the larvae are exposed to special challenges, since the net seaward flow typical of most estuaries would tend to flush larvae out. Larval vertical migration adapted to the estuarine flow field determines whether the larvae will be retained or enter an estuarine realm (Banse 1964, Sulkin 1984). It was shown that many larvae of estuarine crab species undertake endogenously controlled tidal vertical migrations, upward during high-tide and downward during ebb-tide to counteract net seaward transport (e.g. Cronin & Forward 1986, Grabemann & Krause 1989, 1994, Tankersley & Forward 1994). In estuaries showing a bi-layered flow, ontogenetic changes in larval behaviour facilitate upstream transport by compensatory currents (e.g. Moore 1977, Thiébaut et al. 1992). Currents may generally enhance larval dispersal but also create physical barriers (e.g. density gradients, mixing zones) restricting the spreading of larvae (Scheltema 1988). Hydrodynamic processes alone can passively accumulate small planktonic larvae that may not be able to overcome local flow or density regimes (Banse 1955, 1964, Gallager et al. 1996). Particularly a strong, clearly defined density layer may act as a barrier for accumulation of phototactically positive larvae or concentrate geotactically positive, competent larvae at the interphase between fresh and marine water masses (Young & Chia 1987, Vázquez & Young 1996, Gallager et al. 1996). The asymmetry of the tidal flow field during ebb and flood within the estuary may cause retention or even net upstream transport of inactive particles (Chen et al. 1997). Hence, even passive larvae might be retained if they sink toward the bottom during ebb tides and are resuspended during more energetic flood tides (Hannan 1984, DeVries et al. 1994, Chen et al. 1997). Physical structuring of the water column can cause redistribution of planktonic organisms through mixing, or it can isolate biological communities from neighbouring water masses. Entrainment of plankton organisms within mesoscale eddies has been demonstrated in a number of studies (e.g. Trinast 1970, McGowan 1967, Wiebe et al. 1976). Thus, larvae can be dislocated from their spawning area into unsuitable habitats. This is even more evident in freshwater influenced areas where well defined hydrographical pressure gradients between fresh and marine waters act as barriers for larvae. In the Arctic, gradients may be even more pronounced between riverine and marine water masses. Here boundaries are not only established due to differences in salinity but also temperature. Arctic marine waters stay all year round at temperatures below zero, while the freshwater encountered in estuaries, especially during summer, usually originate from much warmer areas of the continent's interior. Hence, strong hydrographical clines can be established.

1.6 Aims of the study and hypotheses

In order to understand what are the main reproductive traits and life history patterns of Arctic benthic invertebrates field research in a remote Arctic region, the Kara Sea, was conducted. During two Arctic summer periods expeditions were undertaken into the southern and central part of the Kara Sea, where meroplankton and benthos samples for adults and juveniles were taken and investigated. Since the Kara Sea is not only shaped by Arctic conditions, but additionally strongly influenced by two large rivers discharging into the region, hydrography plays a major role for both the adult benthos and drifting larvae. This may have strong consequences for the general distribution pattern of benthic species as well as the horizontal and vertical distribution of pelagic larvae of indirectly reproducing species. A more holistic approach including the pelagic and benthic system is necessary to evaluate how far reproduction modes, dispersal processes of larvae and hydrology influence the presence and distribution of benthic species in the Kara Sea.

Since there is only very limited knowledge on benthic reproduction and larval ecology for the area of study available, the main part of this work will focus on general reproduction traits of Arctic benthos, the abundance of meroplanktonic larvae and the influence of the abiotic regime on planktonic and benthic communities.

Starting from information on the study region (mainly from previous expeditions) three major hypotheses were worked out:

(i) Reproduction modes of benthic invertebrate species are adapted to the Arctic environment.

(ii) The hydrographic regime is the main influencing factor confining benthic community patterns of indirectly developing species by retaining larvae and determining juvenile settlement areas.

(iii) Distribution of larvae and later settlement areas of juveniles are controlled by water column structure and mixing processes; in particular, the strong pycnocline in the study area has an influence on meroplankton distribution and may separate single communities.

Although there are many factors influencing larval life stages in the water column as well as the settlement success of a species, only a few can be dealt with in this study. Most factors such as, e.g. mortality, settlement success, time of release, drifting etc. require prolonged time series of sampling, which could not be obtained within the period of study. Proceeding from the above given hypotheses this thesis has the following objectives:

(i) to investigate reproductive patterns of benthic species in the Kara Sea and compare found life history traits with results from literature.

(ii) to analyse a possible adaptation of reproductive strategies to polar areas.

(iii) to identify the influence of river discharge and hydrography on the spatial distribution of larvae and settled juveniles in relation to other (biologically relevant) restricting factors.

(iv) to investigate the role of the pycnocline in separating meroplankton communities.

Summary of the Introduction:

- More than 70% of marine benthic invertebrate species in temperate regions reproduce via larvae (indirect development).
- There is no general definition of a ’larva’. The definition depends on the perspective of the researcher.
- While morphological studies have been conducted already in the 18th century, first comprehensive ecological studies of invertebrate reproduction and larval biology have started in the first half of the 20th century. Benthic assemblages were for a long time explained as a result of the biotic and abiotic environment, without considering larval processes.
- Thorson (1936, 1946, 1950, 1964) was the first to put knowledge on meroplankton into an environmental context.
- The first meroplankton investigations by Thorson (1936) formed the basis for the paradigm later known as ’Thorson’s rule’ (Mileikovsky 1971). This paradigm has recently experienced differentiation (e.g. Poulin et al. 2001).
- Formation of benthic communities depends very much on species’ reproduction modes. Retention of larvae is important for the persistence of communities, especially in estuarine areas.
- Hydrology may create unfavourable conditions for drifting larvae, but also contribute to retention of meroplankton in spawning areas.

2 Material and Methods

2.1 Study area - environmental conditions

The Kara Sea is one of the shallow Siberian shelf seas (883,000 km^2 total area; Fig. 4). Approximately 80% of the Kara Sea has depths of less than 200 m (Fig. 6). The central part has an average depth of 50 m (Zenkevitch 1963). In its northern part the Kara Sea has an open boundary with the Arctic Basin. The western part is framed by the Novaya Semlya trough, which stretches along the east coast of Novaya Semlya to the shelf break. Severnaya Semlya and Taymyr Peninsula separate the Kara Sea plateau from the Laptev Sea in the east. The two large Siberian rivers Ob and Yenisei discharge into its southern part.

The Kara Sea is ice covered about 9 months of the year (Blanchet et al. 1995). Ice begins to break up in June and formation of new ice usually starts in October (Mironov et al. 1994). According to its high latitudinal position the area is also characterised by strong fluctuations in sun radiation and temperature. Mean air temperature ranges from 5°C in summer to -33°C in winter (ECMWF, Blanchet et al. 1995).

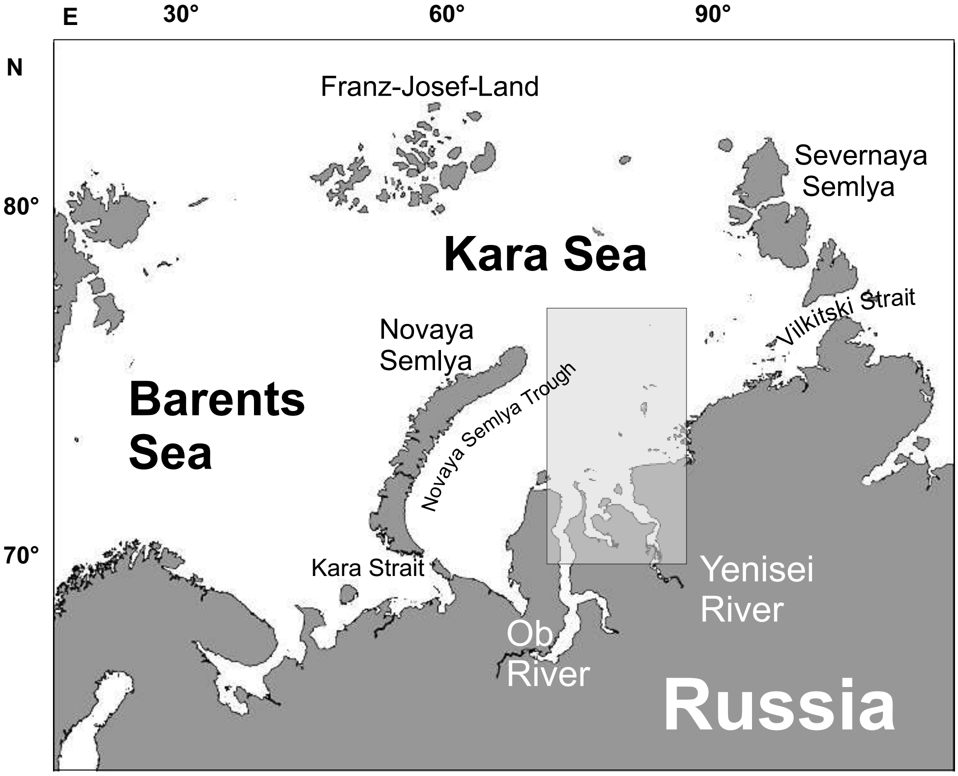


Figure 4: Overview of the study area (indicated by grey box).

A large riverine outflow is one of the most significant features of the Kara Sea, in addition to the strong seasonality of the light regime and the sea ice coverage. The southern part of the Kara Sea is strongly influenced by immense freshwater discharge of the two adjacent river systems, Ob and Yenisei (Gordeev et al. 1996; Fig. 5). They release about 30% of the total annual fresh water discharge into the Arctic Ocean. The freshwater volume of both rivers is about 1,160 km^3 a^{-1} (Aagaard & Carmack 1989, Pavlov & Pfirman 1995, Gordeev et al. 1996, Johnson et al. 1997). More than 75% of the annual river runoff from Ob and Yenisei are discharged during the spring-summer flood in June (Mironov et al. 1994, Pavlov & Pfirman 1995). Surface waters of the Kara Sea, thus, undergo significant seasonal fluctuations in temperature and salinity (Harms & Karcher 1999, Harms et al. 2000, 2001). At the time of our sampling the fresh water discharge of Ob and Yenisei had already passed its maximum and had formed a salinity gradient, which spread out northward from the estuaries to the central Kara Sea and created a bilayered structure visible throughout the Kara Sea (Pivovarov et al. 2003).

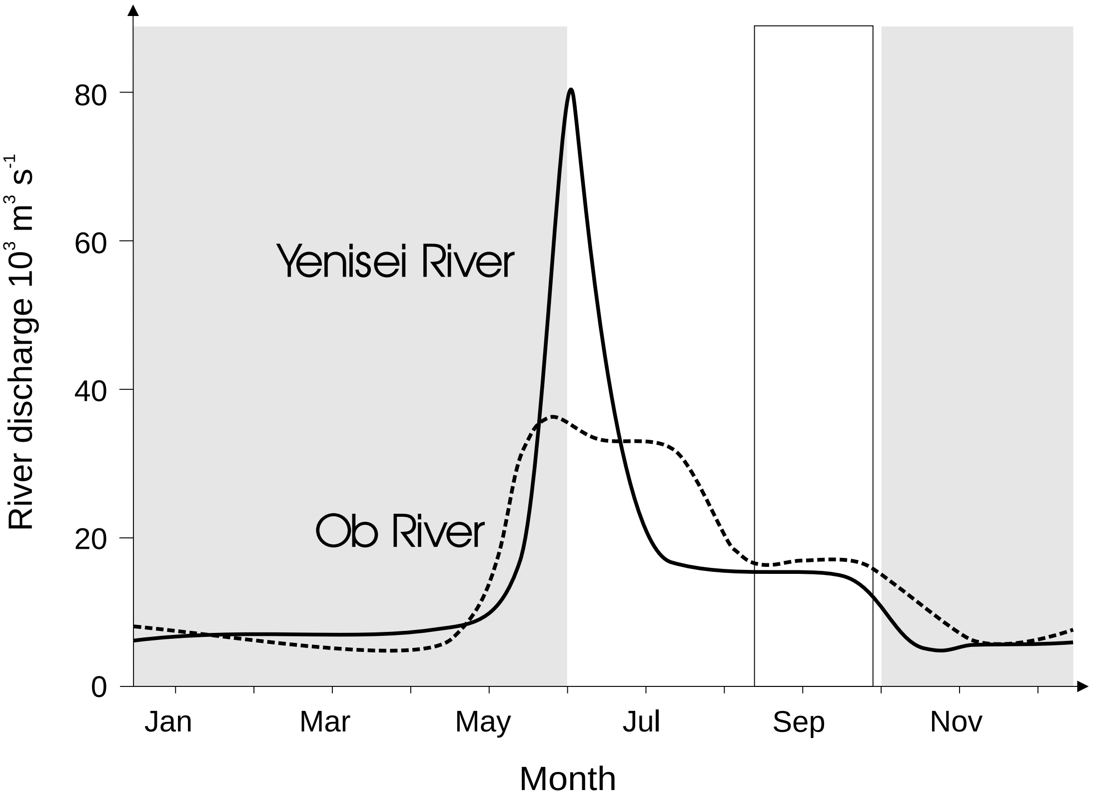


Figure 5: Monthly mean river discharge of the rivers Ob (broken line) and Yenisei (straight line). Duration of ice covering of the Kara Sea is indicated by the grey box, the framed box indexes the period of the expeditions (River discharge data from SAGE).

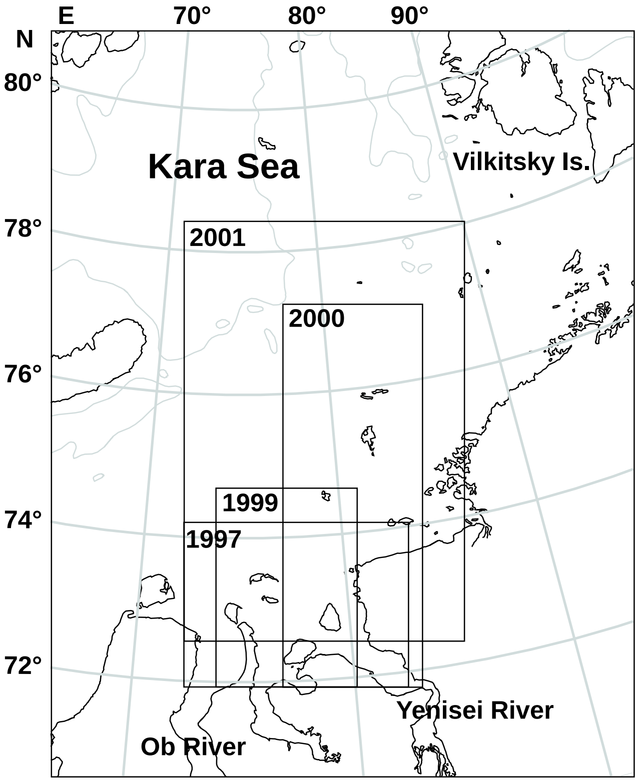


Figure 6: Study areas in the Kara Sea. Boxes specify the sampling regions of different years. The grey line indicates the 200 m isobath.

Layering of water masses is enhanced by the strong temperature gradient caused by the input of relatively warm freshwater. While near bottom temperatures stay below zero throughout the year, the surface layer may reach temperatures of up to 10°C (Pavlov & Pfirman 1995, Harms & Karcher 1999). Since layering is caused by both temperature and salinity, the interphase between the upper and lower layers is referred to as pycnocline (for details see Churun & Ivanov 1998, Stephantsev & Shmelkov 2000, Stephantsev & Shmelkov 2001, Shmelkov et al. 2002, Stanovoy & Shmelkov 2002).

General water temperature characteristics of the Kara Sea are intermediate between those of the Laptev and Barents Seas. While the latter is referred to as rather temperate due to the influence of the Transatlantic Current, the Laptev Sea is clearly high-Arctic (Volkov et al. 1997, Løset et al. 1999).

Water exchange with the adjacent Barents Sea occurs via the Kara Strait or around the northern tip of Novaya Semlya during wind induced flushing events in autumn and winter. To the east water is exchanged with the Laptev Sea through the Vilkitsky Strait (Harms & Karcher 1999, but see also publications I + II). Spreading of freshwater from the rivers is mainly governed by prevailing wind fields. In spring and summer north-easterly winds predominate, pushing river-derived water into the central Kara Sea. Autumn and winter are characterised by strong south-westerly winds pushing water flow in an eastward direction along the Yamal coast toward the Vilkitsky Islands, establishing the so-called Yamal current (Budgen et al. 1982, Pavlov & Pfirman 1995, Burenkov & Vasilkov 1995, Harms & Karcher 1999). In late summer and early autumn a close bottom counter flow, transporting highly saline marine water deep into the estuaries, is observed (Pivovarov et al. 2003). This counter flow is a compensatory current established by shear stress of the outflowing surface waters with underlying water masses (Moore 1977). Occurrence of this current has also been shown by high-resolution models made by Harms & Karcher (1999).

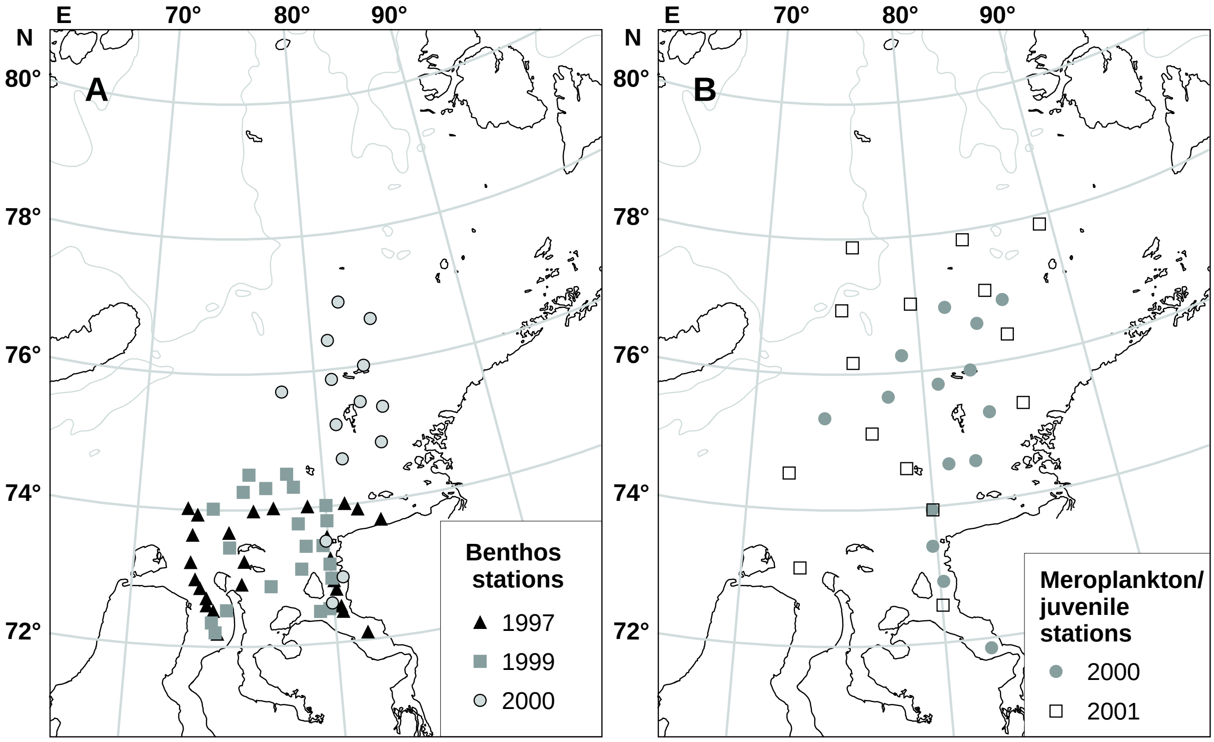


Figure 7: Sampling stations of A) benthos stations and B) meroplankton and juvenile stations from several year of RV 'Akademik Boris Petrov'. The grey line indicates the 200 m isobath.

Besides the freshwater discharge the rivers carry high loads of organic material into the Kara Sea. This input enhances the abundances and biomasses of the pelagic and benthic ecosystems of the Kara Sea (Makkaveev 1995). It is suggested that some pelagic species directly utilise river-borne detritus as a food source (Roman 1984, Tackx et al. 1995), although Vinogradov et al. (1995) suggested that the bulk of detritus sinks to the bottom in the Kara Sea and is not used by zooplankton. Imported carbon is partly utilised by benthic organisms (Klages et al. 2003), incorporated into sediments or resuspended and exported into the Arctic Ocean (Romankevich & Vetrov 2001, Stein et al. 2003). Due to rapid changes of the hydro-chemical regime, most of the imported substances accumulate in the contact zone of fresh and marine water. Highest sedimentation rates of particles occur in the river outlets between 72° - 74°N, which Lisitsyn (1995) termed as the 'marginal filter zone' of the rivers. Primary production is generally low, due to high turbulence in the mixing zones and high clastic input of the rivers, although nutrients are provided in sufficient quantities by river import (Nöthig & Kattner 1999, Nöthig et al. 2003).

2.2 Sampling areas

This study presents results based on biological material of several cruises onboard the Russian RV 'Akademik Boris Petrov'. For each expedition the sampling area depended on the permission of the Russian authorities, thus, sampling areas varied significantly between years (Fig. 6). For the study of adult benthic communities, material of 61 samples from cruises in 1997 (estuaries of rivers Ob and Yenisei; Deubel & Poltermann 1998, Poltermann et al. 1999), 1999 (estuaries of rivers Ob and Yenisei and Kara Sea, Deubel 2000) and 2000 (northern and eastern Kara Sea and Yenisei River; Lubin & Eckert 2001) were included (Fig. 7A). For the study of meroplankton assemblages and the distribution of juvenile benthic organisms plankton and sediment samples of 30 localities obtained during the cruises in 2000 (northern and eastern Kara Seas; Fetzer 2001) and 2001 (whole Kara Sea; Fetzer 2002) were analysed (Fig. 7B).

2.3 Sampling gear and treatment of samples

Benthos samples were taken with a large box corer (0.25 m^2 coverage area). Sediments were gently washed over a 500μm sieve and the remaining animals preserved in 6% borax-buffered formaldehyde.

Juveniles were sampled by means of a multicorer (28 cm^2 coverage area). At each station 3-6 tubes were obtained, to account for mesoscale patchiness in distribution of juveniles. Sediments were subsequently screened over a sieve set of 500/250/125μm mesh size. The minimum screen size was set by observations that no animals were found in fractions <125μm. Resulting sediment fractions and organisms were then stored in 4% borax-buffered formaldehyde until further treatment.

Sampling of plankton was performed with a Nansen closing net (0.442 m^2 catching area; 55 μm mesh size; 0.5 m s^{-1} hauling speed). According to the bi-layered water column structure of the study area, and under the assumption of possible accumulations of meroplankters within the pycnocline, at each station three net hauls, one below (haul I), one axross the pycnocline (haul II) and one above the pycnocline to the surface (haul III) were performed (Fig. 8). Prior to each haul the depth of the pycnocline was determined by a CTD probe.

The layers are further referred to as BELOW (haul I), PYCNOCLINE (haul II) and ABOVE (haul III). PYCNOCLINE and ABOVE were later combined into a new data set (for explanation see section 3.1). Meroplankters were sorted alive onboard as far as possible. Sorted animals and plankton samples were preserved in 4% borax-buffered formaldehyde. Since shell-bearing meroplankters (Bivalvia and Gastropoda) are very sensitive to pH<7, Carriker solution (a sugar-formaldehyde-seawater mixture buffered with Na_2CO_3) or 70% ethanol was used for their preservation.

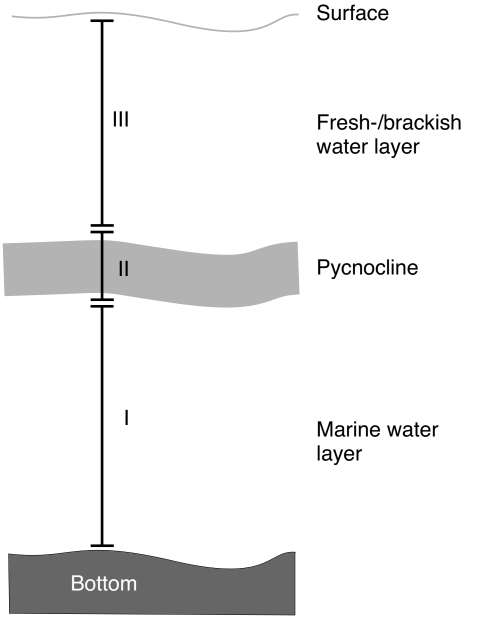


Figure 8: Sampling scheme for meroplankton investigations: haul I (BELOW) = bottom to pycnocline, haul II (PYCNOCLINE) = across pycnocline, and haul III (ABOVE) = above pycnocline to surface.

In the laboratory all benthic animals were separated from sediments and identified under a stereo-microscope to the lowest feasible taxon. Net samples were screened for meroplankton and animals classified. Comparison of identified, newly settled individuals and meroplankters significantly supported the identification process of larvae. Total body length of all larvae and juveniles was measured to ±10 μm using a micro-scale mounted on a microscope (Fig. 9). In Bivalvia and Gastropoda shell lengths were measured, whereas in juvenile Asteroidea and Ophiuroidea disk diameter was noted. In ophioplutei the length of the posterio-lateral rod was measured. In Polychaeta additionally the number of chaetigers was counted. Only apparently intact animals were measured. All animals from the multicorer samples of less than $^1/_3$ adult size reported in the literature were referred to as juveniles. All other specimens found in the multicorer samples were determined as adults and excluded.

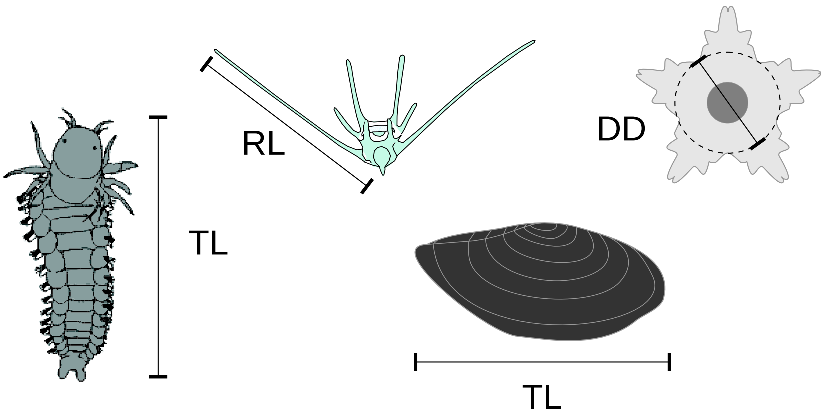


Figure 9: Size measurements of larvae and juveniles. TL = total length, RL = rod length, DD = disk diameter. Note: Sketches are not to scale.

2.4 Data handling

Life history traits and zoogeographical affiliation

Life history traits and zoogeographical distribution of the adult benthos organisms were taken from the literature. According to their main distribution, species were attributed to have Arctic, Arctic-boreal, boreal or cosmopolitan affiliation.

For the Arctic realm knowledge of most life cycles of species mainly was determined by plankton surveys (e.g. Rasmussen 1973, Smidt 1979, Lacalli 1980, Andersen 1984). Contrary to Antarctic regions (e.g. Bosch & Pearse 1990, Hain & Arnaud 1992, Clarke 1992, Chiantore et al. 2002) hardly any information on parental care (brooding - free) or adults' nutrient supply to their larvae (planktotrophic - lecithotrophic) is existent. Most information on whether species have a direct development and/or short pelagic/demersal development is mainly determined from egg size of the captured, ripe animals done by the first investigations of Thorson (1936). Time of spawning, presence of eggs and/or ripe females, as well as known duration of the pelagic stages in the water column in Arctic areas were taken from literature. Due to the very limited knowledge of Arctic meroplankton ecology and based on the given literature, reproduction types have been classified into the following groups according to the spatial occurrence of their larvae (Poulin et al. 2001). This, however, allows to make predictions on the amount of direct and indirect reproduction traits of benthic animals for the investigation area and the adjacent Arctic seas and to help estimate the species' potential ability to disperse:

• pelagic	species with a definite pelagic larval stage (≙ indirect development)
• pelagic?	species with a presumably pelagic larval stage
• demersal	species with a short pelagic phase or demersal larvae
• direct	species lacking a pelagic phase (≙ direct development)
• direct?	species with presumably non-pelagic reproduction mode
• unknown	species with undetermined reproduction mode

In most cases a characterisation by feeding type (planktotrophic - lecithotrophic) has not been possible due to lack of information.

Densities

For determination of densities all juvenile specimens from parallel multicorer samples were pooled and averaged. Adults, obtained from the large box corer samples, and juveniles from multicorer samples, were then normalised to individuals m^{-2}. The number of meroplanktonic larvae was estimated to individuals m^{-3}. For better comparison with earlier investigations, meroplankton data were also calculated to cumulative abundances (individuals m^{-2}).

Minimum, maximum and average body sizes were calculated to determine the range and size for larvae at settlement. In polychaetes additionally the number of segments for minimum, maximum and average body size were estimated.

Statistics

In order to depict the spatial distribution of the adults, juveniles and larvae at the time of sampling in the investigated area, kriging, a statistical gridding method, was used. This method interpolates station density information on a weighted mean basis and, thus, allows to draw conclusions on general distribution patterns in the observed area. In contrast to traditional gridding methods (e.g. nearest neighbourhood, minimum curvature, Shepard's method etc.), which expect spatially equally distributed sample stations, this method is useful for the connection of irregularly distributed information points (see Abramowitz & Stegun 1972, Isaaks & Srivastava 1989). Optimisation of interpolation between irregular data points is achieved through the method's capability to find trends between data points, so that interpolated overall results best integrate with found field data. Resulting isopleths illustrate densities of animals within the sampling area. Computing of isopleths was performed with the surface mapping software package Surfer™.

The distribution of adults, juveniles and larvae below and above the pycnocline for the five most common species, the brittle star *Ophiocten sericeum,* the polychaetes *Micronephtys minuta,* *Nereimyra aphroditoides, Phyllodoce groenlandica* and *Prionospio cirrifera*, was calculated.

For the analysis of the plankton and benthos communities of the Kara Sea the hierarchical agglomerative cluster method (cluster analysis) and multi-dimensional scaling (MDS) were applied. Both methods were based on the Bray-Curtis similarity calculated from transformed species abundances for each station (Clarke & Gorley 2001). The applied transformation methods depended on the range of species abundance of each investigation and are described in more detail in the publications (publications I + II).

Statistical differences between depth layers were tested by means of a 1-way ANOSIM (Analysis of Similarities). ANOSIM is roughly an analogue to a 1-way ANOVA, but is based on a ranked Bray-Curtis similarity matrix, which is suited much better for complex biological sample characteristics (Clarke & Warwick 1994, Clarke & Gorley 2001). The method provides a way to statistically test whether there is a significance for differences between two or more groups of sample units. Prior to testing the samples therefore need to be classified into specific groupings. The test is based on the assumption that if two groups of sampling units are really different in their species composition, then the compositional similarities between the groups ought to be greater than those within the groups. The test is comprised of two parts i) a global test (testing of differences between all samples) and ii) a pairwise test (testing of differences between sample groups). Under the assumption of the null hypothesis ('No differences between sites'), random permutations of sample labels are performed. This should have little effect if the null hypothesis is true. In the case that the null hypothesis must be rejected, subsequently a pairwise test between the groups is performed similar to the global test.

For the ANOSIM all samples of ABOVE, BELOW and PYCNOCLINE were *a priori* grouped and pairwise tested.

CLUSTER, MDS and ANOSIM are part of the PRIMER (Plymouth Routines in Multivariate Ecological Research) software package developed at the Plymouth Marine Laboratory, United Kingdom.

Summary of Material and Methods:

- Study area: the Kara Sea is one of the very shallow Siberian seas (~80% have depths of less than 200 m).
- Beside strong annual fluctuations in light, temperature and ice coverage, the Kara Sea is influenced by strong river discharge from the rivers Ob and Yenisei.
- The large river runoff creates a distinct pycnocline in the observed area. River discharge additionally imports huge amounts of organic carbon and nutrients into the southern Kara Sea part. Most of the imported material accumulates in the mixing area of fresh and marine water ('marginal filter zone').
- Samples were taken with Nansen closing net (zoo-/meroplankton), multicorer (juvenile benthos) and large box corer (adult benthos).
- Presence and abundance of larvae, juveniles and adults were determined and distributions estimated.
- Life history traits and zoogeographical distribution of benthos organisms were taken from literature and compared with field data.
- Kriging, a statistical gridding method, was used to depict the spatial distributions of larvae, juvenile stages and adults. Density distribution of the five most common species (the brittle star *Ophiocten sericeum* and the polychaetes *Micronephtys minuta, Nereimyra aphroditoides, Phyllodoce groenlandica, Prionospio cirrifera*) was calculated.
- For the analysis of the plankton and benthos communities, the hierarchical agglomerative cluster method and multi-dimensional scaling were applied.
- To test the importance of the pycnocline for the distribution of meroplankton, a 1-way Analysis of Similarities (ANOSIM) was performed.

3 Results and Discussion

3.1 Sampling

The different investigation areas of the expeditions generally made comparison of results between years difficult (Fig. 6 on page 25). During the expeditions in 1997 and 1999 sampling areas were limited to the Ob and Yenisei estuaries. In 2000, the area was extended up to 77° N, but it was confined to the eastern part, excluding the region north of the Ob river. In 2001, the investigated area was extended to a maximum, allowing intensive sampling across a large domain north of the Ob and Yenisei rivers and in the central Kara Sea. Except for (mero-)plankton and water characteristics, the main objectives of the expeditions were measurements of static features (e.g. distribution of sediments, their organic carbon contents etc.), which do not change much between years and, hence, do not need re-sampling in the same area. For this reason, all sites visited in 2000 were excluded during the expedition in 2001 (Fig. 7 on page 26).

One of the main objectives of this work was to describe the distribution of invertebrate larvae, juveniles and adults. Meroplankton and juvenile benthos samples for this study could only be obtained during the expeditions in 2000 and 2001. Intensive investigations of the benthos community had been carried out during the expeditions in 1997, 1999 and 2000. Benthos samples taken during the expedition in 2001 were not available for this study. Since no data points are available that cover both, the areas of 2000 and 2001, comparisons of meroplankton dynamics and species composition between these two expeditions are hardly possible. Direct comparison of adult benthos and larval distributions were therefore only realistic for the situation in 2000.

For the study of the dispersal of larvae and juveniles in relation to adult benthos distribution accumulated data of the adult benthos achieved during the expeditions in 1997, 1999 and 2000 were used. This seems acceptable, as analyses of the benthos communities in the Kara Sea between years have shown that communities are stable and do not exhibit strong interannual fluctuations in species composition and abundances (publication II). Benthic animals in Arctic regions are found to be relatively long living. Additionally, the constant environment of Arctic realms usually averts strong interannual changes. However, it has been shown that events such as strong river run off and heavy ice scouring may drastically accelerate adult benthos mortality (see publication V).

Planktonic assemblages, on the contrary, are continuously shaped by the prevailing hydrological regime. Observed distributions are therefore only of temporary character and describe the situation present at the time of sampling.

3.2 Kara Sea ecology

3.2.1 Zoobenthos

The Kara Sea bottom fauna is dominated by polychaetes (51%), crustaceans (28%) and molluscs (15%), which are tolerant to low salinities. Since echinoderms are generally very sensitive to changes in salinity only 6% belong to this group (publication II + V). This is in accordance with findings of Sirenko (2001). Of approximately 290 adult benthic species found in the Kara Sea (see publication II) only 88 species contribute with >4% to total abundance (publication V). The benthic species assemblages found are not exclusively specific to the Kara Sea. The majority of the species is widely distributed on the adjacent Arctic shelf areas (Dahle et al. 1998, Gukov et al. 1999, Petryashov et al. 1999).

Concerning zoogeographic affiliation, 47% of the species are of Arctic origin, 32% Arctic-boreal, 4% boreal and 13% are cosmopolitans. These findings very well reflect observations by Denisenko et al. (1998). The zoogeographical distribution pattern reveals a continuous decrease from Arctic and Arctic-boreal to boreal species reflecting the influence of boreal water masses within the region. The imported warm river waters may also contribute to an elevated survival rate of boreal species. Cosmopolitans were exclusively composed of polychaetes, while no taxon in the other groups showed a definite preference. Species belonging to this group as the polychaetes *Capitella capitata*, *Maldane sarsi*, *Scoloplos armiger* (see publication V; Tab. 15) are well known to be found in a wide range of different soft-bottom habitats (Hartmann-Schröder 1996).

Structure and composition of the macrozoobenthic assemblages changed along the freshwater gradient from the estuaries to the central Kara Sea (Filatova & Zenkevitch 1957, Cochrane et al. 1997, Jørgensen et al. 1999, Denisenko et al. 2003, publication II). While in the estuaries extremely freshwater tolerant species such as *Marenzelleria arctia* and *Prionospio cirrifera* dominated, the strong river outflow prevented the penetration of stenohaline species such as echinoderms into the riverine environments (Jørgensen et al. 1999). Echinoderms, which generally have a wide distribution on the Arctic shelf (Piepenburg & Schmid 1996, 1997, Anisimova et al. 1996, publication V), but are sensitive to strong salinity changes, were restricted to the northern uninfluenced deeper parts (Denisenko et al. 2003, publication IV). Anisimova (1989) reported high diversities of echinoderms for the Kara Sea between 150 - 200m depth.

Besides high fluctuations in salinity animals living in the river mouths additionally have to tolerate high rates of sedimentation (Lisitsyn 1995). Especially small, epibenthic, sessile suspension feeders are found to be most vulnerable to high sedimentation loads and only mobile species may survive in highly turbid areas (Moore 1977, Farrow et al. 1983, Fetzer et al. 2002). Food availability is another factor that determines the presence of species. Highest biomasses are found in the mixing zones of the rivers where most of the imported carbon is deposited (Lisitsyn 1995, Chin et al. 1998). The strong import of organic matter facilitates a rich bottom fauna with high benthic biomass (publication II, Klages et al. 2003). Grebmeier & McRoy (1989) and Grebmeier (1993) recorded that macrobenthic biomass is well correlated with food availability recorded as organic carbon present in the overlying water masses. High carbon input may explain the large number of polychaetes present in the Kara Sea, since most of them are detritivorous. Molluscs, mainly bivalves, also thrive well on the rich carbon input by the rivers, as well as the very abundant amphipods, cumaceans and isopods (see publications II + V).

3.2.2 Juveniles

During the investigation period juvenile stages of 54 benthic species were present (Tab. 1; publication V). While adults often showed only low to moderate abundances, juveniles of some species reached multiple higher densities (publication IV). The most extreme was the polychaete *Micronephtys minuta*. While adults showed maximum abundances of up to 550 ind. m^{-2}, juvenile stages of this species were found in abundances of up to 4000 ind. m^{-2} equally distributed on all stations of the investigated area. Conversely no juvenile stages of the very abundant estuarine spionid *Prionospio cirrifera* were found, although pelagic stages of this species were present. This implies that *P. cirrifera* has a very sharp reproduction window and its pelagic stages had not settled yet, while those of *M. minuta* released their larvae over a long period and many specimens had already settled while larvae were still present in the water column. The great size ranges found in most juveniles supported the assumption of a long reproduction window (Tab. 2).

Most of the juveniles were distributed in almost the same regions and patterns as their adults. Secondary dispersal of the already settled post-larvae and juveniles may occur but seems of less importance for the Kara Sea. Jaklin (2003) found that secondary dispersal is of great significance and there is a high turn-over rate among settled individuals on tidal flats in the North Sea. Settling stages often colonise different regions than the adults to avoid food competition and predation by the adults (Mileikovsky 1974). On the other hand, in some species the settlement of larvae is facilitated by the presence of the adults (Heuers et al. 1998, Heuers & Jaklin 1999).

3.2.3 Meroplankton

During the sampling period in 2000 and 2001, 44 larval types were identified in the net samples (see Fig. 10, 11, 12). A detailed overview is given in Tab. 3 and publication V. For 23 of them

Table 1: List of juvenile stages found in the Kara Sea during the investigation period 2000 and 2001.

Juveniles

Group	Species	Group	Species
Polychaeta	*Aphaelochaeta* aff. *multibranchis*	**Mollusca**	*Astarte borealis*
	Aricidea nolani		*Axinulus ferruginosus*
	Aricidea cf. *suecia*		*Cylichna* cf. *acculta*
	Artacama proboscidea		*Macoma calcarea*
	Capitella capitata		*Nucula bellotii*
	Chaetozone setosa		*Pandora glacialis*
	Chone duneri		*Portlandia arctica*
	Cossura longicirrata		*Yoldiella nana*
	Eteone barbata		*Yoldiella solidula*
	Exogone naida	**Echinodermata**	*Asterias* sp.
	Gattyana cf. *cirrosa*		*Ctenodiscus crispatus*
	Levinsenia gracilis		*Eupyrgus scaber*
	Lumbrineris minuta		*Myriotrochus eurycyclus*
	Lysippe labiata		*Myriotrochus rinki*
	Marenzelleria artica		*Ophiocten sericeum*
	Micronephtys minuta	**Crustacea**	*Aceroides latipes*
	Nephtys ciliata		*Eudorella emarginata*
	Nereimyra aphroditoides		*Haploops laevis*
	Nereis zonata		*Leucon acutirostris*
	Ophelina acuminata		*Leucon fulvus*
	Ophelina cylindricaudata		*Leucon nasica typicus*
	Owenia fusiformis		*Leucon nathorsti*
	Pholoe minuta		*Saduria sibirica*
	Phyllodoce groenlandica		
	Praxillella praetermissa		**N=54**
	Sabellides borealis		
	Scalibregma inflatum		
	Scoloplos armiger		
	Sphaerodorum flavum		
	Spio limicola (arctica)		
	Terebellides stroemi		

adults were present in the benthos. For the remaining 21 larval species, adults were reported from the adjacent Barents and Petchora seas. The presence of these larvae may account for transport processes with prevailing currents. Planktotrophic larvae in boreal areas typically spend 2-6 weeks in the water column until settlement (Day & McEdward 1984). The duration of the planktonic phase and, thus, the travelled distance depend on the specific development time of each species under the given environmental conditions (Mileikovsky 1966, 1968). It may last from several hours in some spionids (Blake & Arnofsky 1999) to six months in the common

Table 2: Number of measured specimens (N), mean, minimum and maximum body size and (in polychaetes) number of body segments of A) larvae and drifting juveniles and B) settled juveniles of *Ophiocten sericeum* and larvae of *Micronephtys minuta*, *Nereimyra aphroditoides*, *Phyllodoce groenlandica* and *Prionospio cirrifera*.

A) Larvae

Species	N	Mean size [µm]	Min size [µm]	# seg	Max size [µm]	# seg
Ophiocten sericeum[*1]	1114	1229	550		1950	
***Ophiocten sericeum* juveniles**[*2]	13	456	280		680	
Micronephty minuta	808	459	120	0	990	11
Nereimyra aphroditoides	473	541	180	3	810	10
Phylodoce groenlandica	117	1121	780	5	1420	15
Prionospio cirrifera	59	1513	450	9	2700	26

B) Juveniles

Species	N	Mean size [µm]	Min size [µm]	# seg	Max size [µm]	# seg
***Ophiocten sericeum* juveniles**[*2]	110	585	310		950	
Micronephtys minuta	348	2235	430	7	4000	26
Nereimyra aphroditoides	113	1054	300	6	4700	26
Phyllodoce groenlandica	100	2002	350	4	8800	44
Prionospio cirrifera[*3]	--	--	--	--	--	--

[*1] length of postero-lateral rod [*2] disk diameter [*3] no juveniles found

Arctic brittle star *Ophiocten sericeum* (Pearse 1969). The period until settlement may even vary strongly within species since metamorphosis in most species is determinated by environmental triggers (e.g., temperature changes, substratum etc.) and many species may become competent (ready to settle) within a month but may delay settlement for several additional months (Chia 1974, Pearse 1969, Pearse et al. 1991). Mileikovsky (1968) demonstrated that currents along the Norwegian coast can transport larvae and juveniles from the shallow shelf areas over a distance of 200-600 nm. The relatively high number of larvae from the adjacent Barents Sea display the potential of larval supply from the neighbouring seas. This may also explain the relatively high amount of boreal species in the Kara Sea (see publication V). Thus, although the Kara Sea is mainly dominated by Arctic species, exchange with the Arctic-boreal Barents Sea fosters the immigration of Arctic-boreal and boreal species.

Meroplankton larvae were found at all stations and depth levels. 62% of all species were discovered in all water depths. Only larvae of rare species were restricted to one single water layer (publication III). Highest densities of meroplankters were found in the upper water lay-

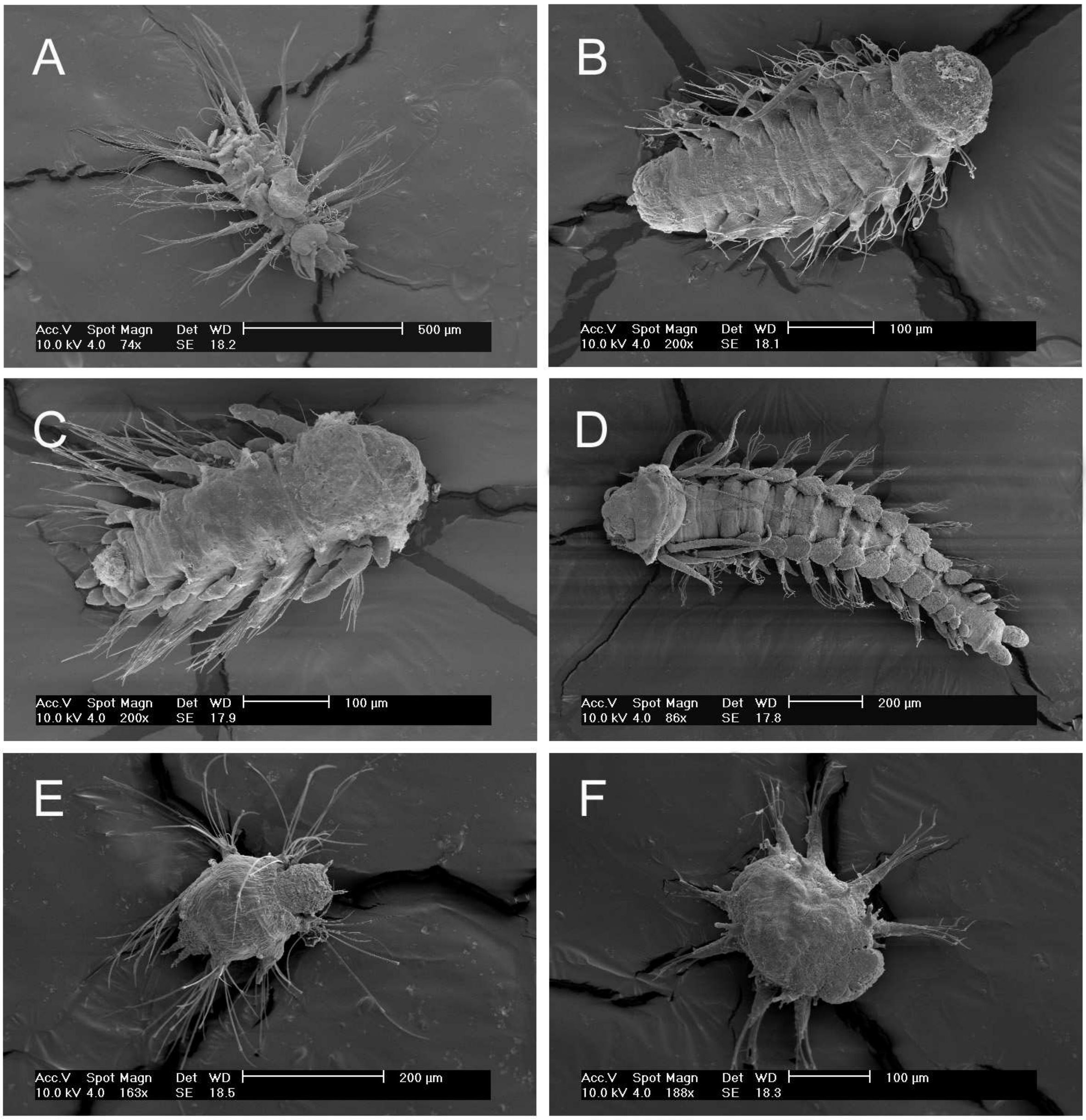


Figure 10: Scanning electron microscope pictures of some of the most abundant Polychaeta metatrochophorae present in the Kara Sea 2000/2001. A) *Gattyana* cf. *cirrosa* B) *Micronepthys* cf. *minuta* C) *Nereimyra aphroditoides* D) *Phyllodoce groenlandica* E) *Nereis* cf. *pelagica* F) *Nereis diversicolor*.

Table 3: List of meroplankton species found in the Kara Sea during the investigation period 2000 and 2001. Species with present adults are underlined.

Meroplankton

Group	Species	Group	Species
Polychaeta	*Capitella capitata*	**Mollusca**	Bivalvia type A (cf. *Arctica islandica*)*
	Chone duneri		Bivalvia type B (cf. *Portlandia arctica*)*
	Cistenides hyperborea		*Coryphella* sp.
	Eteone barbata		cf. *Cratena* sp.
	Eteone longa		cf. *Dendronotus* sp.
	Gattyana cf. *cirrosa*		*Diaphana minuta*
	Harmothoe sarsi		cf. *Trichotopis conica*
	Laonice cirrata	**Echinodermata**	*Asterias* sp.
	Micronephtys minuta		*Ophiura minor*
	Nephtys ciliata		*Ophiura robusta*
	Nereimyra aphroditoides		*Ophiura sarsi*
	Nereis diversicolor		*Eupyrgus scaber*
	Nereis pelagica		*Myriotrochus eurycyclus*
	Ophelina cylindricaudata		*Myriotrochus rinki*
	Owenia fusiformis		*Ophiocten sericeum*
	Pholoe minuta	**Ectoprocta**	cf. *Electra* sp.
	Phyllodoce groenlandica	**Cnidaria**	*Cerinathus loydii*
	Polydora coeca	**Nemertina**	*Nemertini* sp.
	Polydora quadrilobata	**Crustacea**	*Balanus* sp.
	Prionospio cirrifera		
	Prionospio malmgreni		
	Pygospio sp.		
	Scolelepsis metsugae		
	Scoloplos armiger		
	Spio limicola (arctica)		

N=44

*although adults present, affiliation of larvae to species uncertain

ers where salinity did not exceed 25 psu (publication III + IV). Only the abundant larvae of *Prionospio cirrifera* showed a higher preference for the lower water layers. Both adults and larvae of this species were restricted to the mouth of the Yenisei River (publication IV). Most of the meroplankters belonged to echinoderms (68%) caused by mass occurrence of larvae of the brittle star *Ophiocten sericeum* (publication III + IV). During the investigations in 2000 and 2001 ophioplutei of *O. sericeum* reached maximum densities of 200 ind. m^{-3}, while most other meroplankters showed only densities of <1 ind. m^{-3} (publication IV). Polychaete larvae were the second important group concerning abundances (26%) but showed the highest species richness with a contribution of 43% of the total (publication V).

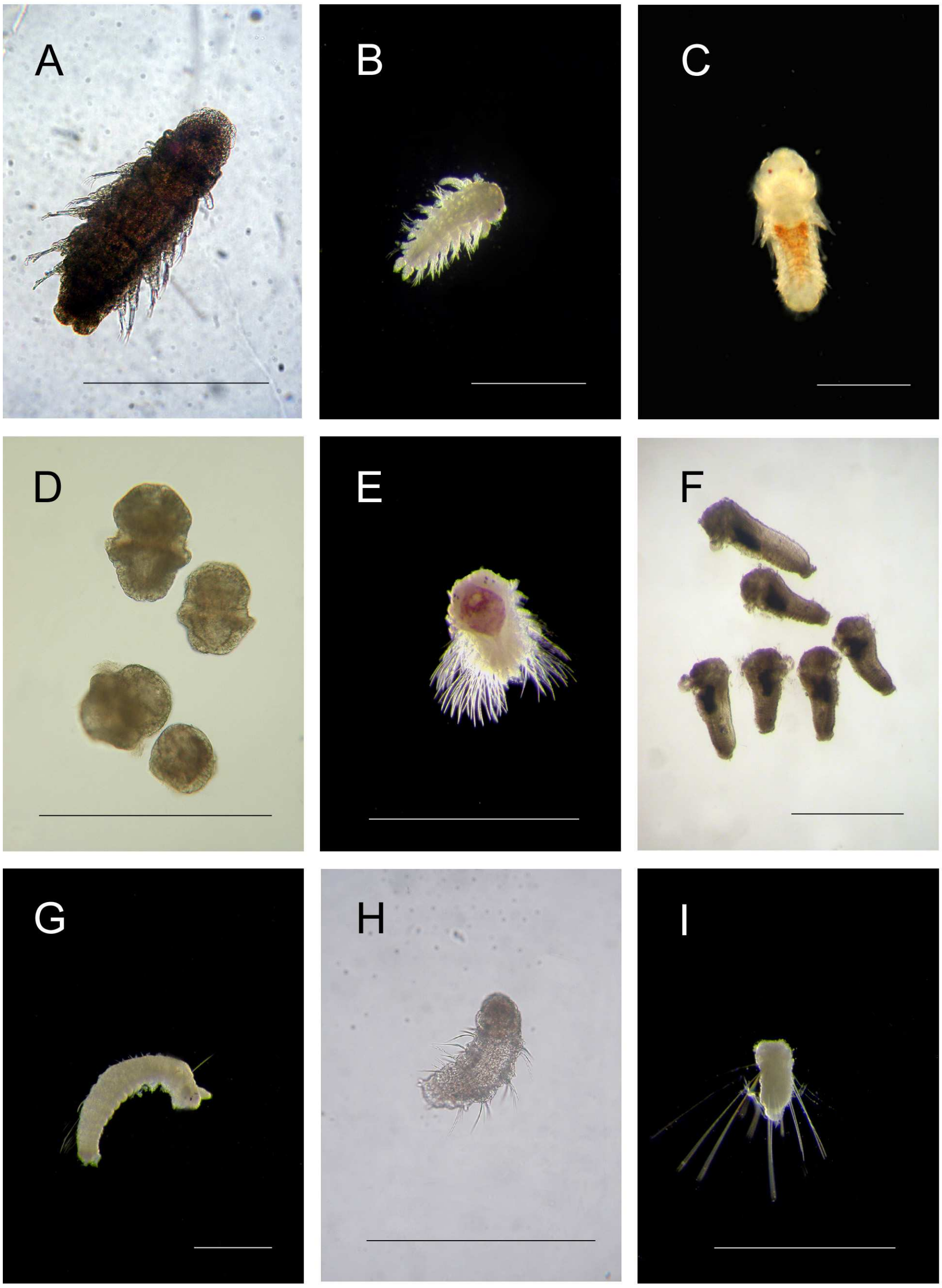


Figure 11: Light microscope photographs of polychaete larvae from the Kara Sea 2000/2001: A) *Eteone longa* B) *Nereimyra aphroditoides* C) *Phyllodoce groenlandica* D) cf. *Micronepthys minuta* E) *Gattyana* cf. *cirrosa* F) cf. *Cistenides hyperborea* G) *Prionospio cirrifera* H) *Prionospio malmgreni* I) *Spionidae* gen. sp. in egg membrane. The scale indicates 500μm.

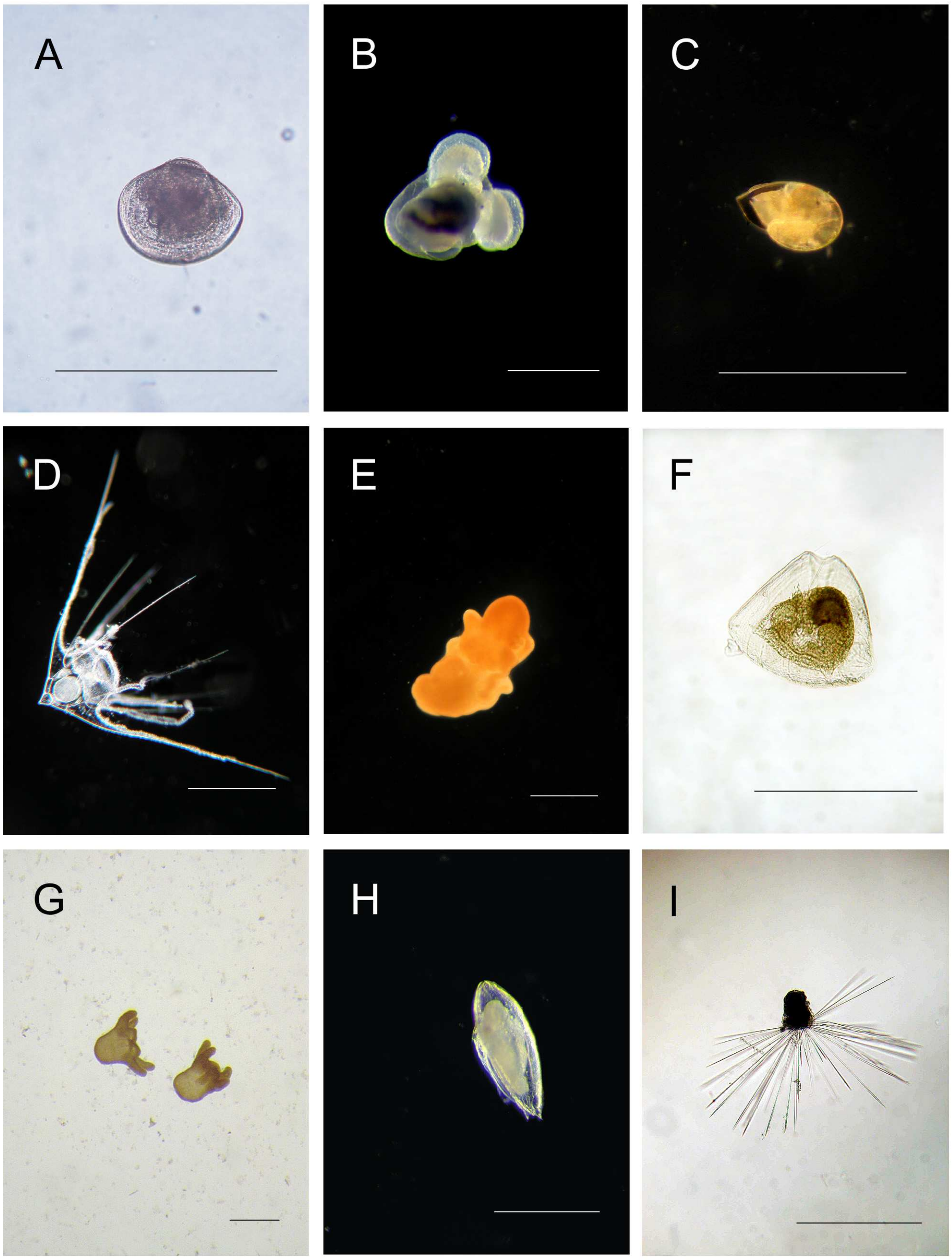


Figure 12: Light microscope photographs of various meroplankton species from the Kara Sea: A) Bivalvia 'Type B' veliger (*Portlandia arctica* ?) (Bivalvia) B) cf. *Trichotopis conica* veliger (Prosobranchia) C) cf. *Dendronotus* sp. veliger (Nudibranchia) D) *Ophiocten sericeum* ophiopluteus (Echinodermata) E) *Asterias* sp. bipinnaria (Echinodermata) F) cf. *Electra* sp. cyphonautes (Ectoprocta) G) *Cerianthus loydii* juv. (Anthozoa) H) *Balanus* sp. cypris (Crustacea) I) cf. *Owenia fusiformis* mitraria (Polychaeta). The scale indicates 500μm.

3.3 Influence of river discharge

The freshwater discharge of the two rivers shows not only a strong seasonal variation but also differs significantly between years. Plankton communities of the southern Kara Sea differed enormously between years during the expeditions in 1997, 1999 and 2000, although they took place in the same period of the year (see publication I + II).

To confirm the hypotheses (see section 1.6) that the hydrographical regime is the main influencing factor confining benthic communities, and controls the distribution of larvae and later settlement areas of juveniles, first the influence of river discharge on plankton and benthos will be discussed. Finally the possible influence of hydrography on the distribution of larvae will be reviewed, as well as the influence of the pycnocline on the meroplankton distribution. The importance of retention by the hydrography in the given study area will be demonstrated for five exemplary species.

3.3.1 Influence of river discharge on plankton and benthos

Freshwater discharge in 1997 and 2000 was considerably stronger than in 1999, creating a larger potential distribution area for riverine species (Churun & Ivanov 1998, Stephantsev & Shmelkov 2000, Stephantsev & Shmelkov 2001). Animal concentrations were higher in 1999, but the species inventory was more diverse in 1997 and 2000. The presence of meroplankton species mainly accounted for this higher species richness in 1997. In 2000 an enormous amount of brittle star larvae was present. They were totally absent in 1999 and very rare in 1997 (publication I + IV). Generally, the successional stage of the plankton community was more advanced in the cruises in 1997 and 2000 than in 1999 (publication I + II). While in 1997 all developmental stages of most zooplankton species were found, in 1999 mainly adult zooplankton dominated the net samples. This may also explain the absence of meroplanktonic species, because the adults may not yet have spawned (a detailed species list of plankton species is given in publication I). The generally earlier stage of the plankton succession in 1999 was also supported by phytoplankton and nutrient data (Nöthig et al. 2003, Nöthig & Kattner 1999).

Community analysis of plankton distribution clearly demonstrated the effect of hydrographic factors. The pattern found agreed well with watermass allocation and the general circulation pattern. Cluster analysis and MDS divided the zooplankton community into five distinctive groups reflecting the impact of freshwater, following the freshwater and temperature gradients from the rivers to the open sea (see publication I + II). The zooplankton assemblages showed low species numbers in the estuaries, moderate numbers in the marine environment and a maximum in the mixing area. In 1997 the estuarine, brackish and marine stations were less clearly separated by

MDS probably due to a less pronounced water stratification and more intensive mixing processes.

Highest numbers of zooplankton were present in the upper water layers. Despite the sharp salinity and temperature gradient most zooplankton species did not show a clear preference for a certain water layer, which points to a wide salinity tolerance in many species (publication I + II, Hirche et al. 2003).

Stability of the layers may be responsible for the higher concentration of phytoplankton in the upper water masses. Import of freshwater algae from the rivers may be the cause for high chlorophyll values in the upper water masses. Nöthig et al. (2003) showed that, as with zooplankton, gradual change of species occurred as mixing processes proceeded (see also publication II). Nutrient import by river waters together with higher light attenuation enhance primary production in the upper water masses (Nöthig et al. 2003).

While a direct connection between food availability and biomass was detected for benthic animals, the pelagic fauna is obviously decoupled from phytoplankton abundance, suggesting rather factors such as hydrography control their distribution (publication II).

3.3.2 Influence of hydrography on the distribution of larvae

Recruitment of benthic species with pelagic larvae may be problematic within the Kara Sea since released offspring is transported away by the seaward flow of the estuarine surface waters. This seems especially challenging for species recruiting within the estuaries of Ob and Yenisei.

Highest aggregations of larvae were exclusively found outside the wake of the Yenisei River (publication IV). Dilution effects of the river discharge most probably account for the fewer larvae in the plume. Along a transect in the Yenisei river, following the fresh water plume, highest densities of meroplankters were found in the mixing zone at about 74°N. Within estuaries concentrations of passively drifting particles are forced into a vertical circulation pattern caused by the tides and the shear stress of outflowing surface waters and near bottom counter flow (Moore 1977). Larvae, as most passive drifters, may as well concentrate within the area as a consequence of the same effect (Fig. 13; Hanan 1984). The presence of a counter-current was assumed by observations of salinity distributions in the Yenisei estuary (Pivovarov et al. 2003). Additionally, results of the hydrodynamic model of Harms & Karcher (1999) for the Kara Sea affirmed the existence of a near bottom counter-current. They estimated a daily mean bottom counter flow of 15 cm s^{-1} reaching its maximum speed in late summer/early autumn. Within the transect ophioplutei of the brittle star *Ophiocten sericeum* were most abundant in water masses below the pycnocline (publication III). These specimens were probably transported into the estuary by the near bottom counter current. Retention of these larvae in the mixing zone is crucial for ophiuroids since, after metamorphosis, they may not be able to survive in this area (Weslawski & Legezynska 1998, Weslawski et al. 2000).

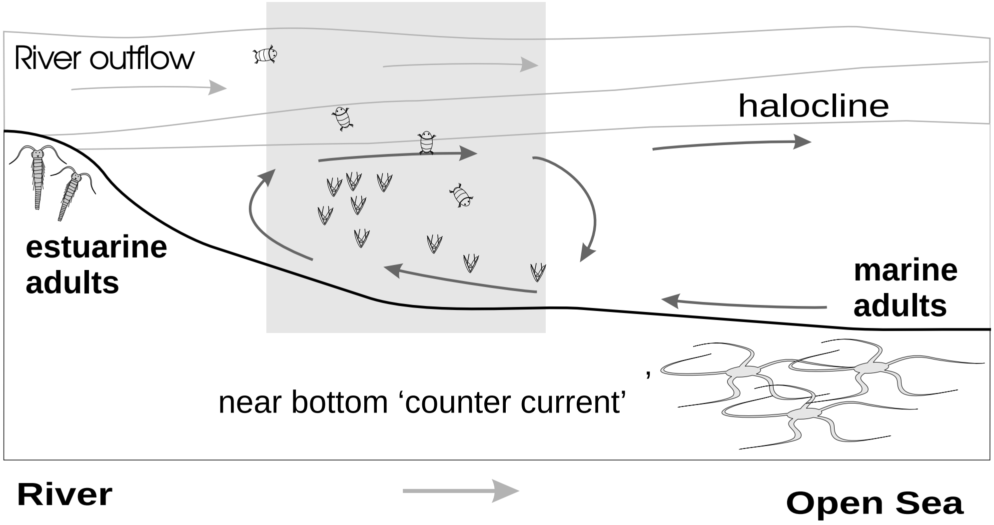


Figure 13: A near bottom counter current is established by strong river run off. The resulting hydrographic flow pattern concentrates larvae in the mixing zone

Effects of water stratification

At the boundary of the comparatively warm and low saline river water and the underlying cold high saline marine water masses strong hydrological pressure gradients are formed. It was assumed that these discontinuity layers (pycnoclines) create not only physiological restrictions for meroplanktonic organisms but also act as a direct physical barrier for the larvae (Epifano 1988, Scheltema 1988).

Discontinuity layers, whether they are haloclines, thermoclines or both, are often places where larvae accumulate (Banse 1955, 1964, Young & Chia 1987, Gallager et al. 1996). It has been demonstrated that when larvae enter the pycnocline from below, they show low kinesis, stop swimming and sink for a short distance before they resume upward swimming (Young 1995). In the Seine estuary vertical distributions of mitraria larvae varied depending on the level of water column stratification. In absence of a pycnocline the larvae mostly reached the surface (Thiébaut et al. 1992). Although accumulation of meroplanktonic larvae at layer interphases is often the result of passive processes, behaviour of larvae adds to maintain high concentrations at or near density layers (Gallager et al. 1996).

The original assumption in this study about the influence of the pycnocline on plankton communities and hence, on meroplanktonic larvae was derived from observations during the expeditions in 1997 and 1999 (see publication I). In both years a high stability of the surface layer with little mixing processes was observed. However, separation of the layers was apparently more pronounced in 1997 than in 1999 due to higher freshwater discharge.

Statistical analyses of species abundances of the meroplankton samples were performed to test differences between the two layers and the pycnocline from the sampling period in 2000. It was assumed that the spatial diversity in abundance and species richness would be smaller within than between layers. ANOSIM resulted in rejection of the global Null-hypothesis (H_0= there are no differences between layers) at a significance level of 0.025 ($R_{Global} = 0.156$), thus, confirming differences between layers. The following ANOSIM pairwise test between the layers revealed differences between BELOW and ABOVE ($R_{BELOW/ABOVE} = 0.194$), BELOW and PYCNOCLINE ($R_{BELOW/PYCNO} = 0.271$) but no differences between ABOVE and PYCNOCLINE ($R_{ABOVE/PYCNO} = 0.015$).

Within the pycnocline, the expected accumulation of meroplankters resulting from upward swimming larvae from underlying marine water masses or of sinking organisms from the upper brackish surface layers could therefore not be confirmed. Despite the presence of a distinct pycnocline at 6-10 m depth (∼2-5m thickness) during the expeditions in 2000 and 2001 (see Stephantsev & Shmelkov 2001, Shmelkov et al. 2002) the observed strong north-easterly winds, present especially during the expedition in 2000 (Stein & Stephanets 2001), may have enhanced mixing processes of the upper water layers. Harms et al. (2000) suggested that strong north-easterly winds are highly responsible for destabilisation of the water layers in the Kara Sea. They enforce mixing processes because the winds counteract the general flow direction of the rivers (Harms et al. 2000). Tidal forces are unlikely to have great influence on mixing processes in the Kara Sea because the tidal amplitude is only 10-20 cm (Telang et al. 1991, Gordeev et al. 1996, Harms & Karcher 1999), although they can be a strong mixing agent in the very shallow near coast areas off the Ob estuary (Harms et al. 2001). Low meroplankton densities (often <20 ind. m^{-3} per catch) may further counteract a statistically clear separation of the layers. However, investigations of larvae in the northern Mediterranean Sea by Pedrotti & Fenaux (1992) also showed no tendency of larvae to concentrate at prevailing fronts as predicted by the above mentioned reasons. Therefore, for further analysis of the distribution of meroplankters the sample sets of ABOVE and PYCNOCLINE were merged into a new data set used for distribution of meroplankton in upper water masses (see publication III + IV).

Effects of hydrographic conditions on five exemplary species

Comparing the occurrence of larvae, settlement area of juveniles and presence of adults within the sampling area reveals a clear effect of river runoff on the distribution of larvae. Outflowing currents determine the distribution of larvae and the settling area of juveniles. The effect is differently pronounced for the individual species and will be discussed in the following for the distribution patterns of the five most abundant larval species in the Kara Sea in relation to their adults:

(1) Although larvae of the brittle star *Ophiocten sericeum* were present at almost all stations and depth intervals, its larvae and juveniles had their main distribution in the northern Kara Sea part. This is the main distribution area of the adults and, thus, the region where the larvae were released (publication II + IV). Since ophioplutei are weak swimmers (∼0.1mm s^{-1}; Konstantinova 1966, Mileikovsky 1973, Emlet 1983) their dispersal depends almost exclusively on the place of release (=the distribution of adults) and the prevailing hydrodynamics (Pedrotti & Fenaux 1992).

Larvae of *O. sericeum* had a strong preference for the upper water layer, which may be explained by observations that released ophiuroid eggs and developing larvae are strongly positive buoyant (Hendler 1991, Westheide & Rieger 1996). Hatching in the upper, food-rich water layers should be of advantage for feeding of the slow swimming larvae. Highest concentrations of larvae were even found in melt water plumes at ice edges where salinity was <20psu (publication IV). Schlüter & Rachor (2001) reported the same phenomenon from investigations of meroplankton in the Barents Sea. Gallager et al. (1996) found aggregations of ophioplutei at physical interfaces between water masses. With their slow swimming capabilities ophioplutei may not be able to overcome physical boundaries by active swimming. Aggregations of larvae of other slow swimming larval groups at such interfaces were also reported by Young (1995), which he explained by a sensitivity of larvae to salinity gradients rather than by physical trapping.

Occurrence of ophioplutei of *O. sericeum* in the upper, less saline water masses is in contrast to a conclusion made by Thorson (1946). He stated that echinoderm larvae are more sensitive to changes in temperature and salinity than other meroplanktonic larvae. Contrarily, Kashenko (2000) showed that the early larval stages of the sea cucumber *Apostichopus japonicus*, after a period of acclimatisation, can be very resistant to changes in salinity and even tolerate low salinities, where their adults do not survive.

This may also explain that ophioplutei were even more tolerant to low salinities than their adults, which due to the river runoff were restricted to the northern part of the investigation area (see 3.2.1, publication IV).

During the expedition in 2000 ophioplutei larvae had a plume-like distribution entering the investigation area from the north and diluting towards the southern part (publication IV, Fig. 38). This may be explained by the strong north-easterly winds, which characterised the region that year (see publication IV). Such winds are typical of the summer season in the Kara Sea (Harms & Karcher 1999). Drifting larvae in surface waters are most probably pushed by the winds from the northern region into the southern parts of the investigation area. Additional mixing processes, caused by interaction of wind fields and river run off would explain the presence of larvae in small densities at all depth levels and stations. Hinrichsen et al. (2001) described wind-driven retention and dispersal as one of the key processes for recruitment success of fish larvae in the Baltic Sea. Wind driven distribution may also explain the absence of ophioplutei during the investigations in 1997 and 1999, although samples were obtained in the same period of the year (see publication I). Vinogradov et al. (1995) did not report the presence of any echinoderm larvae within the Yenisei estuary during planktonic investigations conducted in August-September 1994, supporting this assumption.

(2) Larvae of the polychaete *Micronepthys minuta*, in comparison, are found evenly distributed within the investigation area. The same dispersal pattern was found for their adults. The wide size range of larvae found indicates a permanent release of larvae into the water column. Additionally, the small size difference between mean larval size and the first settled juveniles indicates a short presence in the plankton. This implies that hydrography has only very little effect on dislocating the larvae.

(3, 4) This seems different with larvae of the polychaetes *Phyllodoce groenlandica* and *Nereimyra aphroditoides*: Adults of these two species had their two main distribution areas east and west of the main outflow of the Yenisei River. Their larvae were also concentrated in these areas. Intensive river run off most probably forms local eddies, which trap larvae not far from their hatching areas. Banse (1964) observed that larvae, which are released by adults, are often retained in the water masses where they are hatched. Entrainment of plankton organisms within eddies has been demonstrated in a number of studies (McGowan 1967, Trinast 1970, Wiebe et al. 1976). However, juveniles of both species settled exclusively north of the hatching area, following the wake of the run off.

(5) Retention of larvae is even more extreme with larvae of the spionid *Prionospio cirrifera*. Their adults occur exclusively in the inner parts of the Yenisei estuary. Contrary to all other larval types, larvae of *P. cirrifera* were mainly present below the pycnocline in the Yenisei estuary. After release of the larvae from their parents they run the risk of being transported away by the river run off. For successful reproduction the released larvae have to return to their spawning areas. Either ontogenetically induced geotactic swimming behaviour or passive sinking of the larvae brings about their accumulation in the deeper water layers. Here they encounter an 'upstream' near bottom counter-current transporting the larvae back into their hatching areas (see Fig. 13). To guarantee an adequate reproduction success, timing of release seems extremely important for this species. Retention of larvae within spawning areas especially applies to many estuarine species in freshwater influenced areas (Laprise & Dodson 1994, Bilton et al. 2002). Besides hydrography, larval behaviour has been found to be one of the major factors leading to a return of the recruits to the habitats of their parents (Thiébaut et al. 1992, Anger et al. 1994).

Notable is the fact that adults of *P. cirrifera* were found in the Yenisei estuary, but not in the Ob estuary. The shallow and broad shape of the Ob outlet may be responsible for the lack of a counter current that would transport larvae into the estuary.

In contrast to the other four meroplanktonic species, larvae of *P. cirrifera* were comparatively well developed with many segments. Buzhinskaja & Jørgensen (1997) observed only large larvae of the spionid *Trochochaeta carica*, which is also common in the Kara Sea, in their net samples. Closer investigations revealed that larvae of up to 21 segments are brooded in the parental tubes before they are released. Those well-developed larvae have only a short pelagic phase and as such reduce the risk to be carried away by prevailing currents. Brooding of larvae within the tubes of the adults of *P. cirrifera* has not been reported yet.

Retention of larvae within their parental settling habitats seems of different importance for the five observed species. Ophioplutei of *O. sericeum* have a relatively long development time (Pearse 1969) and, hence, can be dislocated over great distances (Mileikovsky 1966, 1968), which most probably account for their wide distribution on the Arctic shelf (Piepenburg & Schmidt 1996, 1997). Stocks living in the shelf region therefore rather belong to a metapopulation, supplying each other with new recruits. Larvae of *O. sericeum* do not have to be retained in certain areas and release of larvae within a certain period of the year seems not important for this species. This is also reflected in the obviously permanent release of larvae during the year (Thorson 1936, Semenova et al. 1964, Geiger 1964, Andersen 1984, Smidt 1979). On the other hand, a long drifting period also enhances the probability of the larvae to be drifted into unfavourable sites such as freshwater influenced areas, as are the shallow parts of the Kara Sea (see above). The same is true for larvae of *Micronepthys minuta*, which do not necessarily need to be retained in a certain area since their adults tolerate a wide spectrum of salinities. Nevertheless, they are restricted to the shallow, low saline areas such as the Kara Sea shelf. These larvae, therefore, have a moderate to short pelagic phase, together with a prolonged reproduction period of the adults as found in *O. sericeum*. For *Nereimyra aphroditoides* and *Phyllodoce groenlandica* a synchronised release seems more important, since larvae need to be retained within the eddies created by the river run off. A rather short pelagic phase is assumed for them as well. The most extreme example is the release of larvae in *Prionospio cirrifera*. As mentioned above timing of release is fundamental for a successful retainment of recruits within the spawning area.

3.4 Reproduction modes and zoogeographic affiliation

Among the 88 most abundant macrozoobenthos species in the Kara Sea direct development obviously dominates. According to data taken from literature 33% reproduce directly without pelagic larvae. For another 11% direct development is presumed. Only 25% have a pelagic stage. Additionally 11% seem to have a short pelagic phase. In 1% the reproduction mode is unproven but a pelagic phase is strongly assumed. For 19% of the species reproduction modes are unknown. Crustaceans contribute with 28% to the overall species composition, representing the second abundant group after polychaetes (51%). Several of their main orders are distinguished from the other groups by a direct reproduction strategy (see publication V). The group Crustacea was exclusively composed of Peracarida (Cumacea, Isopoda and Amphipoda), while, except some rare findings of the brooding shrimp *Sclerocrangon boreas*, Decapoda were absent in all of our samples (see publication II).

The Arctic environment, especially the high river discharge should select for species with short pelagic or with direct development, since according to Thorson (1936), reproduction in directly reproducing species is not constrained physiologically by low temperatures and short food availability, and the larvae of these species are less likely to be dislocated by river run off.

It may be questioned if direct reproduction makes many crustaceans more successful in cold environments than other taxa. Comparison with the taxa composition of the German Bight, a temperate area similar to the Kara Sea shelf in terms of freshwater influence, carbon content of the sediment and depth, reveals a similar distribution. As in the Kara Sea, Peracarida are very abundant (Salzwedel et al. 1985). However, other factors might be more important in determining the success of these taxa. Contrary to most other adult benthic groups, most peracarids are highly mobile, which is an advantage for the fast occupation of new territories, exploitation of food sources and avoidance of unfavourable habitats (Santos & Simon 1980).

Peracarid crustaceans reproduce directly all over the world, mostly brooding their progenies (Curtis 1975). Other taxa, on the contrary, display a huge spectrum of reproduction modes, which vary strongly between species and the regions they inhabit. Because of the independence of pericarid development modes from environmental conditions they should be excluded from the present analysis. When crustaceans are excluded, species with indirect development become significantly more important on the Kara Sea shelf. Especially in Arctic-boreal species, reproduction via larvae becomes the main reproductive trait (publication V).

Contrary to the findings in this study, Thorson (1950) reported that only 5% of Arctic marine invertebrates in the fjords of East Greenland reproduce via larvae (a value which has been regarded far too low by many authors (see Arntz & Gili 2001 for review)). In contrast to the Greenland shelf the Kara Sea shelf is a comparatively unstable environment. The shallow parts of the Kara Sea are characterised by strong ice scouring and events of abnormal high fresh water discharge (Makkaveev & Stunzhas 1994, Pavlov & Pfirman 1995, Volkov 2002), which probably periodically have a strong effect on benthos communities. Instability of the regime may therefore promote fast re-colonising species with planktonic larvae and highly mobile species such as amphipods, isopods and cumaceans (Mileikovsky 1971, Santos & Simon 1980, Burkovsky et al. 1997).

Short pelagic development is a very important reproduction strategy among many species on the Kara Sea Shelf (see publication V). Clarke (1992) assumed that demersal reproduction is of great importance among Arctic species.

Independently of reproduction modes and zoogeographic affiliation most species reproduce during the ice-free summer months (see publication V; Tab. 15). In temperate regions reproduction is tightly coupled to primary production in the upper water masses, since phytoplankton serves as initial food source for new recruits (Cushing 1990). Also, zooplankton reproduction and abundances are strongly enhanced at ice edges with elevated primary production (Hirche et al. 1994). Release of planktotrophic larvae should therefore occur mainly at the time of high primary production. Nonetheless, species such as the brittle star *Ophiocten sericeum*, the polychaete *Eteone longa*, and the cirriped *Balanus* sp., which reproduce continuously throughout the year at high latitudes (Groom 1894, Hoek 1907, Thorson 1936, 1946, Geiger 1964, Semenova et al. 1964, Petersen 1966, Rasmussen 1973, Smidt 1979, Andersen 1984, Korn & Kulikova 1995, Hartmann-Schröder 1996). Observations of Formin (1989) support these findings, since he reported larvae of *O. sericeum* as typical in the plankton of the Kara Sea throughout the year. A prolonged reproduction period for *O. sericeum* has also been reported from other Arctic regions (Thorson 1936, Semenova et al. 1964, Geiger 1964, Andersen 1984, Smidt 1979). Also for many bivalve species continuous reproduction seems a common trait (Thorson 1936, Ockelmann 1958, Hain & Arnaut 1992).

Uncoupling from the short primary production period is likely to be advantageous in polar regions. Especially in Antarctic regions continuous reproduction that is detached from the phytoplankton bloom in summer seems to be widespread among many benthic animals (Pearse et al. 1991, Clarke 1992). This may be facilitated through the utilisation of alternative food sources. Rivkin et al. (1991) and Chiantore et al. (2002) mentioned that ophioplutei seem to be able to take up bacteria, detritus and dissolved amino acids (Welborn & Manahan 1991, Rivkin et al. 1991, Chiantore et al. 2001). Absorption of dissolved nutrients from the surrounding water seems also likely for some larvae (Chia 1970). Lecithotrophy is another well known trait among many meroplanktonic organisms, especially in Antarctic waters (Poulin 2001). In these cases the energy demand of the larvae is totally covered by nutrients provided by their parents, mainly yolk, which is gradually fed by the larva. Adults may accumulate energy at any time during the year when food is available to them and transfer it directly into the egg. Thus, larvae still maintain their spreading features but do not depend on a (only temporarily available) external food source. Wray (1995) noted that lecithotrophs may also have an advantage over planktotrophs re-occupying devastated areas during mass extinctions (e.g. by ice scouring). Lecithotrophy is found to be common in many demersal larval types, especially in the Antarctic (Clarke 1992, Pearse 1994). This may explain the general trend to fewer larvae in polar waters. Many species may continuously release their larvae and, thus larvae are more diluted in the water column. Species with demersal larvae are difficult to obtain with traditional net sampling methods. For them diver-towed, near-bottom nets (Stanwell-Smith et al. 1999) and autonomous plankton suctors (Thadje pers. comm.) are more appropriate. Additionally, many species may reproduce during winter time when it is almost impossible to access polar regions. Curtis (1973) reported 36 species found off west Greenland that produce lecithotrophic eggs. The majority of them apparently spawn during autumn and winter. The same holds true for a vast amount of species from Antarctic regions (Pearse & Bosch 1986, Pearse et al. 1991, Pearse 1994). Benthic investigations during the expedition ANTARKTIS XVII/3 (EASIZ III) of RV ’Polarstern’ in the Antarctic autumn revealed that many organisms were in a very advanced reproductive state, ready to release their larvae and juveniles (Arntz & Brey 2001).

However, even those species in the Kara Sea, which apparently do not depend on the short phytoplankton bloom have their main reproducive period during the Arctic summer months (see publication V). Probably not only food availability may play an important role, but increased temperatures may accelerate metamorphosis, and, thus, shorten the time the larvae are exposed to pelagic predators or are displaced by currents.

Summary of Results and Discussion:

- The different size and position of the investigation areas between expeditions in 1997 - 2001 made comparison of meroplankton and juveniles distribution in relation to their adults between years difficult.
- Comparison of the dispersal of larvae and juveniles in relation to adult benthos was only realistic for data of the expedition in 2000.
- Fresh water discharge of the rivers was higher in 1997 and 2000 than in 1999, creating a larger potential distribution area for riverine plankton species.
- While zooplankton abundance was higher in 1999 the species inventory was more diverse in 1997 and 2000, which is accounted for mainly by higher numbers of meroplankton species.
- Direct connection between food availability and biomass was detected for benthic animals, but the pelagic fauna is obviously decoupled from phytoplankton abundance. Zooplankton abundances closely followed the hydrological regime, suggesting that pelagic communities are mainly shaped by the high freshwater discharge.
- The Kara Sea benthic fauna is dominated by polychaetes (51%), crustaceans (28%) and molluscs (15%).
- The benthic inventory of the Kara Sea is not specific to the area. Most species are also common in the adjacent Laptev and Barents seas as well as in the Arctic Basin. However, prevailing species are vastly superior in their tolerance to low salinities.
- 47% of the benthic species have an Arctic affiliation, 37% are Arctic-boreal, 4% boreal and 13% cosmopolitan.
- During the sampling periods in 2000 and 2001, 44 larval types were identified. For 23 of them adults were present in the benthos. For the remainig 21 larval species, adults were reported from the adjacent Barents and Petchora Sea. These findings display the strong species input from the neigbouring seas by larvae.
- Most larval species (62%) were found in all water masses, although highest abundances were present in the upper water layers where salinities were $<$25 psu.
- no differences of meroplankton densities were found for the surface layer and the pycnocline, but surface and bottom layer differed significantly. The pycnocline seems to act as a physical barrier for most larvae.
- Meroplankton species densities were generally very low ($<$1 ind. m^{-3}) but ophioplutei of the brittle star *Ophiocten sericeum* reached densities of 200 ind. m^{-3}.

Summary of Results and Discussion: (continued)

- Within the Yenisei transect highest concentration of larvae was found in the mixing zone of fresh and marine water masses. Larvae concentrate within the area as a result of the circular current pattern created by the shear stress of the outflowing surface waters and the near bottom counter flow.

- Larvae of the brittle star *Ophiocten sericeum* are mainly distributed in the northern part of the Kara Sea, close to the main distribution areas of their adults. Since the larvae were mainly found in the surface layers higher tolerance to low saline water than their adults is suggested. The distribution of ophioplutei is mainly shaped by hydrographical barriers and windfields. The long drifting period (>6 months) suggests an inter-community supply of larvae between different stocks.

- Larvae and adults of the polychaete *Micronepthys minuta* are distributed evenly within the investigation area. Distribution pattern implies that hydrography has seemingly only little influence on their dislocation.

- Adults of *Phyllodoce groenlandica* and *Nereimyra aphroditoides* were restricted to two regions east and west of the main outflow of the Yenisei River. Also the larvae were restricted to these two areas, probably trapped in local eddies formed by the intensive river runoff. Juveniles of this species settle exclusively north of the hatching area, following the wake of the run off.

- Retention of larvae was even more extreme with larvae of the spionid *Prionospio cirrifera*. Adults were exclusively found in the Yenisei estuary which was also the main distribution area of the larvae. Contrary to other species larvae of *P. cirrifera* were present below the pycnocline and mainly well developed. This suggested brooding, a timed release of the larvae, and larvae to have only a short pelagic period.

- Of the 88 most abundant benthic species 33% have direct development, 11% presumably develop directly, 25% have a pelagic phase, 11% demersal larvae or a short pelagic phase, and for 1% a pelagic phase is assumed. However, removing peracarids, as obligatory direct developers, species with indirect development become the main reproduction mode on the Kara Sea shelf.

- Irrespectively of their reproduction modes >90% of the species reproduce during the summer months. Except for higher food availability also the increased water temperature is assumed to be advantageous for decreasing larval development times.

- For many species continuous reproduction seems common. Here other food sources than primary production are assumed or larvae are lecithotrophic.

4 Conclusion and future perspectives

The high number of larval types found in this study indicates that planktonic development is important in the Kara Sea ecosystem. More studies are needed to understand the significance of life history strategies in this polar realm.

There is still considerable lack of knowledge on reproductive strategies of marine invertebrates, which especially holds true for organisms of the Arctic Ocean. Since the first ecological approaches on benthic animal reproduction our knowledge about life history traits of benthic animals in polar regions is increasing slowly. Today it is still controversial whether and how reproduction patterns evolved along latitudinal gradients.

The importance of reproduction strategies for benthic community dynamics has often been underestimated (Eckert 2003). In part this can be explained by the fact that reproduction, dispersal and final survival of each larva is influenced by many complex factors and until now not well understood. Today we begin to understand some of these complex rules and may apply them to build a more complete picture.

Expected temperature rise of the world oceans will have a strong effect on water mass transports and hence, on local benthos communities in polar regions. Future changes to these areas, within the context of global warming, are very uncertain and unknown. Particularly strong environmentally controlled areas such as the shelf regions of the Kara Sea may undergo profound changes. Next to a shift in water exchange with the adjacent Barents and Laptev Seas there might be an enhanced fresh water input by the rivers, due to increased ice-melting processes of the continental permafrost areas, and sea level rise.

In the following, I will propose some future research needs:

- More autecological studies of invertebrate reproduction traits from all taxa are required to reduce the general lack of information on invertebrate reproduction from Arctic regions. This should permit a better identification of larvae and allow improved conclusions on species' ecology.

- Detailed studies on the recruitment of juveniles, the timing of larval release and the distribution of adults are necessary to understand life-cycle strategies of polar species. This will allow to assess the significance of planktonic development for benthic communities in polar waters and to gain a more comprehensive understanding of Arctic benthos dynamics.

- For several Arctic species reproduction in winter is proposed. To gain a better insight in the reproduction strategies of invertebrates, an increased number of samples from winter expeditions is urgently required for ecological work. Besides land bases or icebreakers, autonomous underwater vehicles with sampling devices, (moored) plankton pumps or deployment of artificial colonisation substrates may be used as scientific platforms and instruments.

- Coupled biologic-oceanographic simulation models of dispersal should be applied on pelagic larvae to explain species distribution and ecology. This would help to improve the understanding of the importance of dispersing versus non-dispersing reproduction modes.
- Study of feeding types should be emphasised in future research of Arctic meroplankton, since this allows conclusions on the general ecological capacity of a species.
- New sampling methods for demersal larvae should be applied. Until now demersal reproduction is only anticipated for many Arctic species, but very few larvae have been found.
- Next to autecological studies of species, genetic tools can be applied to increase identification success for both larvae and adults. Larval identification through the use of genetic markers or molecular probes has already been successfully used for meroplanktonic species (e.g. Baldwin et al. 1996, Claxton et al. 1997, Claxton & Boulding 1998, Frischer et al. 1995). Genetic identification of Arctic species may also help to explain evolutionary pathways and the origin of species in Arctic waters. Additionally, increased insight is gained on the importance of speciation in Arctic and Antarctic regions.
- Physiological responses of early life stages of invertebrates to the Arctic environment need to be studied in more detail. For this aspect investigations are necessary not only of a larva's tolerance to a changing environment but also of the physiological changes in tolerance of larvae vs. adults. E.g., in this study it was shown that echinoderm larvae apparently tolerate a wider range of salinity changes than their adults.

5 Publications

Below, the publications included in this thesis are listed and my contribution to each study is explained.

Publication I

I. Fetzer, H.-J. Hirche, E.G. Kolosova

The influence of freshwater discharge on the distribution of zooplankton in the southern Kara Sea

Polar Biology (2002) 25:404-415

Zooplankton sampling was done by me in the pilot phase of the SIRRO project into the Kara Sea in 1999. I also developed the concept of the work and did statistical analyses and interpretation of the data. Sorting and identification was done by the third author. The manuscript was mainly written by me with conceptional contribution by the second author. I also did the interpretation of the hydrographical data and the connection to the biotic information.

Publication II

H. Deubel, M. Engel, **I. Fetzer**, S. Gagaev, H.-J. Hirche, M. Klages, V. Larionov, P. Lubin, O. Lubina, E.-M. Nöthig, Y. Odkolodkov, E. Rachor

The Kara Sea ecosystem: phytoplankton, zooplankton and benthos communities influenced by river run-off

in: R. Stein, K. Fahl, D.K. Fütterer, E.M. Galimov, O.V. Stephanets (Editors)
Siberian river run-off in the Kara Sea: Characterisation, quantification, variability and environmental significance.

Proceedings in Marine Science (2003) No. 6,
Elsevier Science B.V. pp. 237-266

The paper represents a joint outcome of the result from benthos, zoo- and phytoplankton during the expeditions in 1997, 1999, 2000 and 2001 in the Kara Sea within the SIRRO project. Taxonomic work was mainly done by S. Gagaev, V. Larionov, P. Lubin, O. Lubina and Y. Odkolodkov. H. Deubel, M. Engel, I. Fetzer, H.-J. Hirche, M. Klages, E.-M. Nöthig and P. Lubin contributed to data analysis and interpretation of biotic and abiotic data. Concept and manuscript were done in joint cooperation with all authors.

Publication III

I. Fetzer

Distribution of meroplankton in the southern Kara Sea in relation to local hydrographic data

in: R. Stein, K. Fahl, D.K. Fütterer, E.M. Galimov, O.V. Stephanets (Editors)
Siberian river run-off in the Kara Sea: Characterisation, quantification, variability and environmental significance.

Proceedings in Marine Science (2003) No. 6,
Elsevier Science B.V. pp. 195-212

Sampling, sorting and identification of the samples was done by me, as well as interpretation of data and manuscript writing.

Publication IV

I. Fetzer, H. Deubel

Effect of river run-off on the distribution of marine invertebrate larvae in Arctic shelf seas

submitted to: Journal of Marine Systems

I developed the scientific idea, sorted the samples and did all the larval identification. I also did data processing and manuscript writing. The manuscript was improved in cooperation with the co-author.

Publication V

I. Fetzer, W.E. Arntz

Life-history traits of benthic invertebrates in the Central and Southern Kara Sea (Arctic Ocean) - indications for adapted reproduction modes in cold regions?

submitted to: Marine Ecology Progress Series

Designing of the concept for this study, sampling and laboratory work was done by me. I wrote the manuscript. The final version was achieved considering the revisions by the co-author.

Further publications written during working on the PhD thesis:

H.-J. Hirche, **I. Fetzer**, M. Graeve, G. Kattner

Limnocalanus macrurus **in the Kara Sea (Arctic Ocean): an opportunistic copepod as evident from distribution and lipid patterns**

Polar Biology (2003) 26: 720-726

I did the sampling and designed the experimental work on board. At home I did the data processing and compilation of most figures and diagrams. Lipid analysis was done by the third and the last author, while the manuscript was mainly written by the first and the last author. The third author and myself did major improvements on the final manuscript.

5.1 Publication I

published in: Polar Biology (2002) 25: 404-415

The influence of freshwater discharge on the distribution of zooplankton in the southern Kara Sea

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Abstract

Zooplankton was collected on two cruises to the southern Kara Sea to study the effect of the freshwater outflow of the rivers Ob and Yenisej on plankton distribution. Calanoid copepods dominated the composition with more than 75% of all specimens collected in both years, *Drepanopus bungei* was the most abundant species. Species composition showed a wide spectrum from freshwater to marine species. The abundance and community composition of the zooplankton communities followed closely the hydrographic pattern along a gradient from the inner to the outer estuaries, as revealed by Cluster analysis and Multi Dimensional Scaling. There were also differences in species composition and abundance between the two rivers. The stable brackish surface layer created a large distribution area for riverine species, while in the underlying marine water masses oceanic species penetrated far into the estuaries. In 1997 this area was considerably larger, probably due to a higher freshwater discharge. During the 1999 cruise, which took place 3 weeks earlier, salinities were generally higher. Both species composition and overall abundances were higher in 1999 than in 1997, due to especially the enormous increase of *Limnocalanus marcrurus* and *Pseudocalanus major*

Keywords: Kara Sea, zooplankton distribution, estuarine, Ob, Yenisej

1 Introduction

In the Arctic marginal seas plankton communities are shaped by the strong seasonality of light intensity, ice cover and fresh water supply by large rivers. These regions are of great importance for the formation of water masses and sea ice (Lisitsyn & Vinogradov 1995), and additionally are of great significance for zooplankton with respect to growth and reproduction (Kosobokova & Hirche 2000).

The Kara Sea covers an area of 883 000 km^2 and is one of the very shallow Siberian shelf seas, which in its central part hardly exceeds a depth of 40 to 50m. It is separated from the influence of the Barents Sea by Novaya Semlya to the West and by the Vilkitsky Archipelago from the Laptev Sea to the East (Cherkis et al. 1991), while to the North it opens into the Arctic Ocean (Fig. 14).

The hydrographic characteristics of the Kara Sea are intermediate between the Laptev and Barents Seas. While the latter is referred to as rather temperate due to the influence of the Transatlantic Current, the Laptev Sea is clearly high arctic (Volkov et al. 1997, Løset et al. 1999). The biogeographical data available (Vinogradov et al. 1995b) all support the intermediate status of the Kara Sea.

In its southern part the Kara Sea is strongly influenced by the immense freshwater discharge of the two river systems Ob and Yenisej (Gordeev et al. 1996), which provide one-third of the total freshwater entering the Arctic Ocean and about 55% (1290 km^3 year^{-1}) of the total continental river run-off to the entire Siberian Arctic (e.g. Pavlov & Pfirman 1995). The two rivers contribute about 80% of the run-off to the Kara Sea. While the Ob has the largest length and drainage area, the Yenisej has with 620 km^3 year^{-1} the greatest discharge volume of all the Siberian rivers (Telang et al. 1991, Gordeev et al. 1996). The river run-off shows a strong seasonal and interannual variability with a maximum in June when the coastal zone is still ice covered (Gordeev et al. 1996).

Little is known of the influence of the large fresh water discharge on the pelagic fauna of the Kara Sea. The freshwater signal is assumed to be the main structuring factor for the marine fauna in the estuaries through rapid changes in salinity and temperature. Thus during the Russian Mendeelev-Expedition to the southern part of the Kara Sea up to 76°N three types of zooplankton communities were identified (Vinogradov et al. 1995b): 1) one adapted to the eddy of the south-western part of the sea, which was dominated by copepodite stage V (CV) *Calanus finmarchicus* s.l. (57% biomass); 2) a community of the coastal areas of the Yamal peninsula and Baidara Bay consisting of chaetognata and small plankters such as *Oithona similis*, *Pseudocalanus minutus* and *P. acuspes* (20-77% biomass); and 3) one associated with the detritus rich brackish waters in the eastern regions. There the biomass was relatively high and consisted >50% of *C. finmarchicus*. The highest concentrations were found in the bottom layers and in the salinity mixing front. The communities within the estuaries of Ob and Yenisej showed strong differences, with the Ob Bay much richer both in abundance and species number (Vinogradov et al. 1995a).

The rivers also affect food distribution. According to observations during the Mendeleev-Expedition (Lisitsyn & Vinogradov 1995, Vinogradov et al. 1995b), and work conducted in the inner estuaries (Vinogradov et al. 1995a), it seems that the central Kara Sea is characterised by a strong oligotrophy (Lisitsyn et al. 1995). The rivers, in contrary, supply the estuaries with nutrients (Telang et al. 1991, Lisitsyn 1995), which may enhance primary production (Verdernikov et al. 1995). Furthermore, the input of high loads of organic material should promote or constrain the presence of some pelagic species (Makkaveev 1995). Thus it is assumed that some species can directly utilise river-borne detritus as a food source (Roman 1984, Tackx et al. 1995), although Vinogradov et al. (1995a) suggested that the bulk of the detritus in the Kara Sea sinks to the bottom and is not used by zooplankton. The large amount of bacteria and protozoans, which are driving on the detritus (Mitskevich & Namsaraev 1995) may serve as an alternative food source for zooplankton.

The aim of the present study is to analyse characteristics of the mesoplankton distribution in the stuaries of Ob and Yenisej in relation to hydrographic features in the years 1997 and 1999. The data were collected during two expeditions of RV Akademic Boris Petrov as part of the joint Russian-German project "Siberian River Run-off" (SIRRO) which emphasizes on the transformation processes of organic matter in the Siberian Seas.

2 Materials and Methods

The data were collected during two cruises of R/V Akademik Boris Petrov from September 13 to 25, 1997, and from August 26 to September 9, 1999, between 72° and 74°N and 72° and 83°E. During the expeditions 20 (1997) and 24 (1999) stations were visited, respectively. Zooplankton samples were collected with a Nansen closing net (0.442 m2 catching area, 150μm mesh size; 0.5m s^{-1} hauling speed). Four net samples were taken at each station: two below and two above the pycnocline, which was determined from a CTD profile before sampling. At shallow stations (<10m depth) the Nansen net frame was mounted with a non-closing, short net of 1m length. Since the short net could not be closed only two samples of the whole water column were landed per station. The samples were preserved in 4% borax-buffered formaline. All specimens were counted and measured under a stereo microscope and identified to species

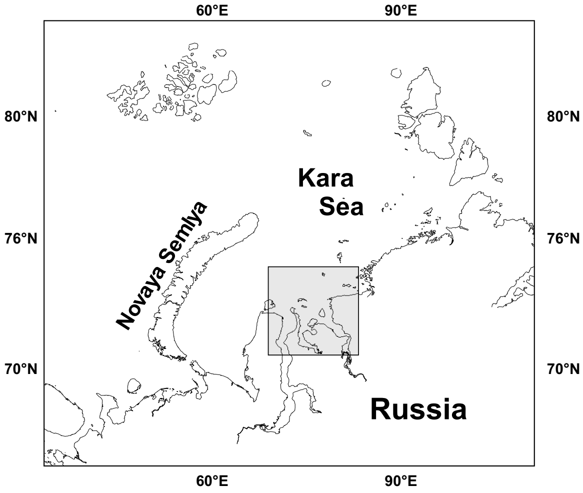

Figure 14: Sampling area

level if possible. Copepodite stages of calanoid copepods were also identified and counted. Prosome length was used to distinguish copepodites and adult females of the two closely related copepods *Calanus finmarchicus* and *C. glacialis* according to Hirche et al. (1994). Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment.

Overall distribution and community analysis (hierarchical, agglomerative cluster analysis and non-metrical Multi Dimensional Scaling (MDS)) in relation to abiotic data was performed using the PRIMER package (Clarke 1993, Clarke & Warwick 1994). To reduce the emphasis of abundant species, data were double square root transformed. When clustering the date of the two depth layers produced always pair clusters of the stations the data from the nets hauls were pooled. In order to archive the characteristic species assemblages responsible for each cluster, the number of species was first reduced, retaining only those that accounted for >4% of the total abundance at any one site, and then the single stations were grouped according to the results of the cluster analysis. Afterwards the species were sorted according to occurrence and abundance (also referred to as Shade matrix). The species principally responsible for the sample grouping in the cluster analysis (e.g. the one with the highest abundances) were then highlighted. This simple but informative approach was chosen to concentrate on the species similarities, rather then reverse cluster analysis (or species clustering) which is found to be more delineated (Clarke & Warwick 1994).

3 Results

3.1 Sea ice and river discharge

The Kara Sea is usually covered by ice for about 9 months of the year (Blanchet et al. 1995). Ice formation starts in the end of September or beginning of October; the break-up begins in early to late June (Mironov et al. 1994). River run-off exhibits a large seasonal variation with most of the discharge occurring during June to September (Pavlov & Pfirman 1995). During our expeditions the southern Kara Sea was completely ice free and the hydrography was strongly influenced by the two river systems.

3.2 1997

3.2.1 Hydrography

In 1997, the depth range of the 20 stations varied between 40m off the Taymyr Peninsula (sta. 21) and 10m within the Yenisej Estuary (sta. 32; Tab. 4). The hydrography was described in detail by Churun & Ivanov (1998). Salinity and temperature distribution at 2m depth together with north to south transects in the two rivers are presented in Fig. 15. (Fig. 16 gives the salinity and temperature distribution in 1999). Both salinity and temperature showed a sharp gradient from the innermost parts of the estuaries to the outer parts, with a strong gradient in an east to west direction in the Ob and in a south to north direction in the Yenisej. Salinity in the upper layer increased from 1 in the Yenisej and 4 in the Ob to 21 at the outermost stations while temperature decreased from 8°C in the Yenisej and from 6°C in the Ob to 4°C further north (Tab. 14). In the south a pronounced pycnocline was established at around 10m depth, which on the Ob transect flattened out through progressive mixing towards the northern parts. The pycnocline was deeper on the Yenisej transect than on the Ob transect, suggesting a higher discharge of freshwater in the former. Below the pycnocline, a tongue of high saline water reached far into the estuaries. In the Ob at the southernmost sta. 10 salinities >25 were registered near the bottom; in the Yenisej salinities were around 15. The deeper layer had temperatures between 0° and -1°C except at the shallow stations (30, 32) in the Yenisej, where temperatures up to 5.8°C were measured. In depressions, cold winter water of -1.5°C and a salinity of 32 were found (Churun & Ivanov 1998).

Table 4: Station data on the expedition “Boris Petrov” 1997 and 1999. Station marked with * were excluded in the transect (see text for further explanations)(# indicates no lower layer available or too shallow)

1997	Station	Date	Latitude (N)	Longitude (E)	Depth [m]	Salinity surface/ bottom	Temp. [°C] surface/ bottom	No. of Species [N]	Abundance upper layer [Ind m^{-2}]	Abundance lower layer [Ind m^{-2}]
Ob transect	10	14. Sep	72°30'	74°04´	19	4.5/25.2	6.3/-0.2	18	795	5029
	47	22. Sep	72°35´	73°44´	18	19.3/29.5	4.1/0.5	23	2943	4639
	48	22. Sep	72°57´	73°00´	28	13.9/31.1	4.5/-1.3	30	342	1773
	49	23. Sep	73°12´	72°53´	29	16.6/31.5	4.3/-1.5	30	302	599
	50	23. Sep	73°36´	72°57´	29	21.0/31.8	4.2/-0.7	28	729	556
	1	13. Sep	73°54'	73°10'	28	13.0/32.0	5.3/-1.9	26	73	1080
	52	24. Sep	74°00´	72°39´	29	18.1/32.0	4.2/-0.3	27	651	717
Yensisej transect	32	19. Sep	72°05´	81°28´	10	1.0/15.0	8.3/5.8	10	241	#
	30	18. Sep	72°30´	80°20´	13	4.3/13.1	7.2/5.0	14	285	#
	27	18. Sep	72°53´	80°05´	19	4.8/30.3	6.5/-0.1	24	749	985
	38	20. Sep	73°12´	80°00´	31	7.2/31.3	6.4/-0.9	23	552	558
	24	17. Sep	73°32´	79°55´	39	11.3/31.4	6.0/-1.7	27	588	2128
	21	17. Sep	74°00´	81°00´	40	14.8/32.0	5.9/-1.8	30	930	1717
Middle transect	56	25. Sep	72°53´	75°28´	14	9.1/16.3	4.5/-0.1	12	694	#
	55	24. Sep	73°13´	75°37´	14	9.8/17.9	4.4/-0.2	16	538	#
	58	25. Sep	73°39´	74°50´	21	9.0/30.7	6.3/-0.1	27	499	1131
	18	16. Sep	73°57´	76°08´	31	---/---	---/---	27	841	2438
	46	21. Sep	73°59´	77°12´	27	12.4/32.0	6.4/-1.4	25	274	820
	42*	20. Sep	73°53´	81°40´	30	15.1/32.0	5.9/-1.8	29	221	1983
	43*	20. Sep	73°42´	82°48´	31	11.2/21.4	6.0/0.5	27	523	279
1999										
Ob transect	19	1. Sep	72°11'	74°11'	14	1.9/11.0	2.5/0.6	15	1649	#
	18	1. Sep	72°19'	74°00'	15	1.7/26.0	4.0/-0.4	29	760	690
	20	2. Sep	72°30'	74°43'	16	2.8/27.0	3.9/0.1	29	1017	#
	17	31. Aug	72°51'	73°56'	19	5.3/29.9	3.6/-1.2	32	1444	2270
	21	3. Sep	73°14'	74°02'	16	7.0/23.5	3.5/-1.4	20	550	2314
	25	4. Sep	74°00'	73°59'	26	8.9/32.0	3.4/0.1	26	277	575
	37	8. Sep	74°18'	74°20'	30	9.8/32.3	2.9/-1	27	416	665
Yenisej transect	6	28. Aug	72°17'	80°01'	7	2.6/3.0	6.6/6.6	16	1386	#
	31	6. Sep	72°29'	79°45'	17	4.4/29.6	5.8/-1.1	14	1139	#
	8	28. Aug	72°55'	79°59'	22	4.7/29.0	5.9/-1.3	21	1630	2617
	32	7. Sep	73°08'	79°57'	27	5.9/31.1	5.3/-1.5	18	480	1353
	28	5. Sep	73°25'	78°48'	23	8.8/28.0	3.3/-1.4	17	191	554
	11	29. Aug	73°46'	79°59'	36	7.0/33.2	3.1/-1.5	26	2005	357
	12	29. Aug	73°45'	78°28'	25	4.6/31.5	4.5/-1.3	27	1876	451
	35	7. Sep	74°18'	78°20'	34	12.1/33.3	2.9/-1.3	28	911	421
	13	30. Aug	74°29'	78°00'	36	8.8/33.1	4.4/-0.6	23	732	131
Middle transect	24	3. Sep	73°26'	74°52'	20	6.4/29.5	3.6/-1.4	15	927	1856
	38	8. Sep	74°15'	75°36'	30	11.1/32.2	3.1/-0.3	24	560	509
	39	9. Sep	74°17'	76°49'	38	10.6/33.0	2.9/-0.8	22	74	523
	2	26. Aug	74°30'	75°55'	30	5.5/29.3	4.1/-1.9	25	2151	545
	1*	26. Aug	73°59'	74°30'	27	6.0/31.0	3.9/-1.8	31	2747	479
	3*	27. Aug	73°48'	79°59'	32	5.9/30.6	3.7/-1.7	23	1703	604
	29*	5. Sep	73°05'	78°30'	17	8.7/26.9	3.4/-1.0	18	454	4000
	30*	6. Sep	72°27'	79°17'	14	5.3/13.0	5.5/3.9	12	937	#

3.2.2 Zooplankton composition

A total of 59 species were identified with 25 species of copepoda (20 calanoida, 1 harpacticoida and 4 cyclopoida), 6 gelatinous species, 3 amphipoda, 2 cladocera, 2 rotatoria, 2 pteropoda, 2

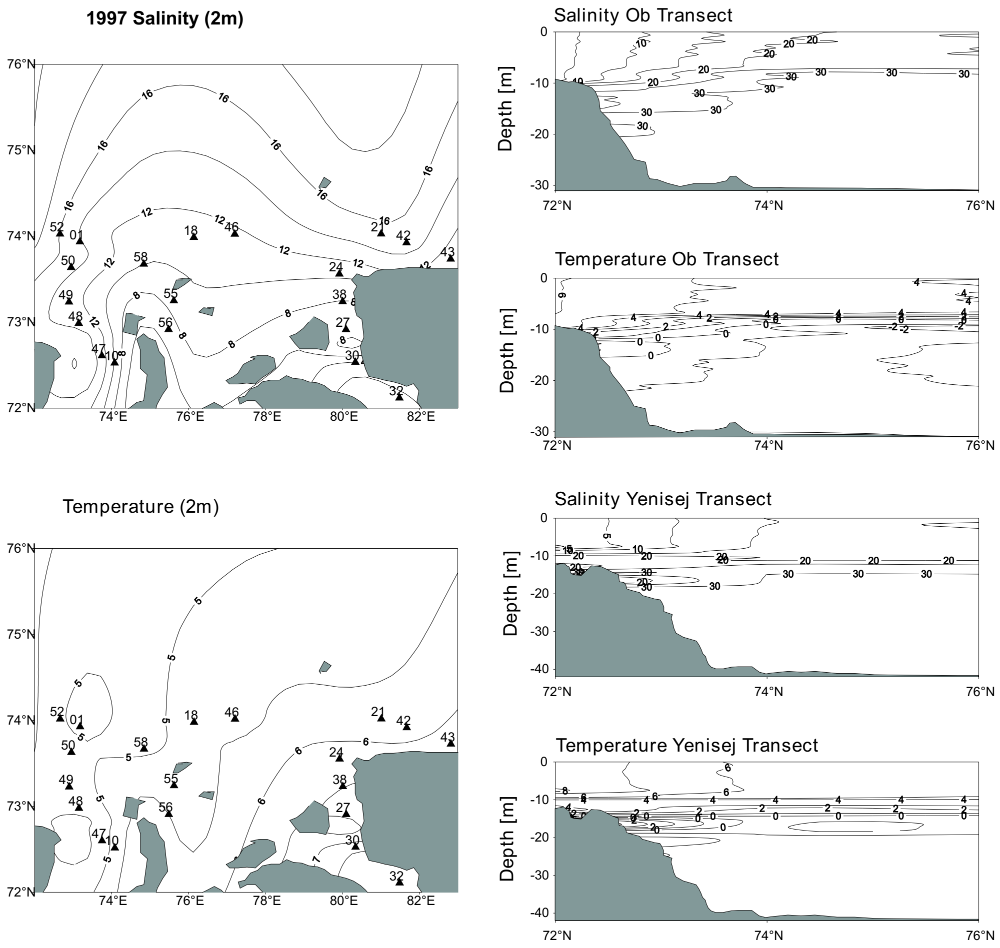

Figure 15: 1997: salinity and temperature at 2 m along the transects based on 59 CTD stations. Station numbers indicate biological stations.

chaetognatha, 2 appendicularia and 1 mysidacea and euphausiacea. Meroplanktonic larvae of cirripedia, polycheata, bivalvia, gastropoda, echinodermata, bryozoa and nauplii of copepods, euphausidacea and ostracoda present, were counted but not determined to species level (Tab. 5). Of all animals collected 84.9% belonged to the copepoda, with 74.3% calanoida, and 10.6% harpacticoida and cyclopoida. Within the calanoida, *Drepanopus bungei* (58.7%) was by far the most abundant species and dominated the zooplankton communities at all stations (Tab. 6). Other species showed much lower abundances such as *Calanus glacialis* (1.4%), *Microcalanus pygmaeus* (1.4%), *Pseudocalanus acuspes* (3.5%), *P. major* (3.5%) and within the cyclopoida *Cyclops strenuus* (3%) and *Oithona similis* 6.2%. The next biggest group were that of the copepode nauplii (13.6%). All other groups contributed with <1% to the total (Tab. 5). Dominant copepodit stages within the calanoida were CIII to CV, which made up 72%. This stage compo-

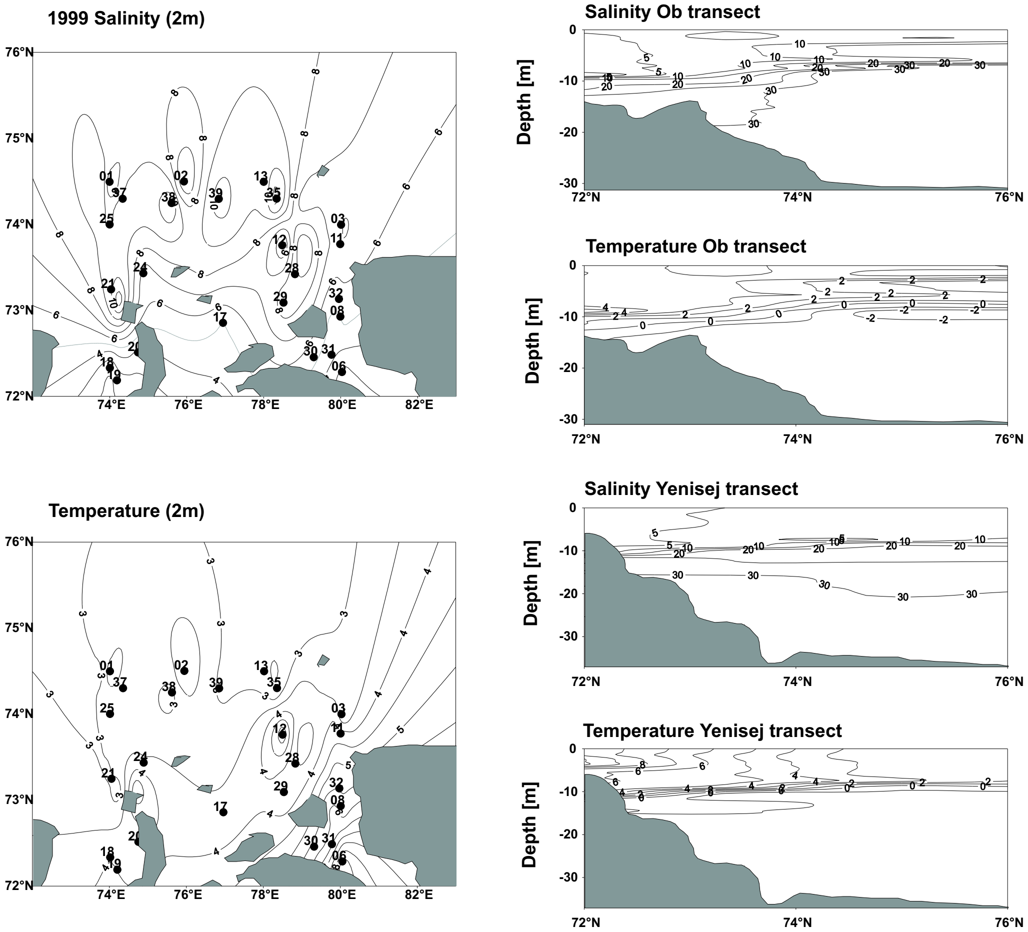

Figure 16: 1999: salinity and temperature at 2 m along the transects based on 37 CTD stations. Station numbers indicate biological stations.

sition was characteristic of most families. Early copepodites were mostly found in *Drepanopus bungei* and *Pseudocalanus* spp., while *Limnocalanus macrurus* was dominated by adults.

3.2.3 Regional distribution:

An overall mean of 1960 ±412 individuals m^{-3} was calculated for all stations. However, there was a strong regional variability both in abundance and species number between the two river systems and along a south to north gradient (Tabs. 4 and 6). In the Ob Estuary, the highest abundances (stas. 10, 47 and 48) and the highest number of species (stas. 30, 48 and 49) were found. Along a transect from the inner Ob Estuary to the north (Tab. 4) species numbers first increased from 18 species at sta. 10 to 30 species at stas. 48 and 49), then slowly decreased to

26 species at the northernmost sta. 52. In the Yenisej River, both abundance and species number were much lower than in the Ob Bay, but increases towards the north to high abundances at stas. 21, 24 and 42 at the northeast of the Taymyr Peninsula (Tab. 4). The distribution of dominant species is presented in Tab. 6. It shows clearly that high zooplankton abundances were mostly due to mass occurrences of the copepod *Drepanopus bungei*, which was found at all stations.

Vertical distribution showed strong differences between the two depth layers sampled (Tab. 4). Generally the lower layers showed 2-4 times higher abundances and slightly higher species numbers than the upper layers. Several species were more frequent in the lower layers such as *Calanus glacialis*, *Jaschovia tolli*, *Microcalanus pygmaeus*, *Pseudocalanus major* and *Oncaea borealis*. Only at the innermost sta. 10 in the Ob were more speciments present in the surface layer. There *Drepanopus bungei* dominated the bulk. This species was generally less abundant in the marine waters below the pycnocline

Cluster analysis resulted in five distinctive groups identified as "Yenisej River", "Ob River", "Estuarine", "Brackish" and "Marine" (Fig. 17a). The species that mainly characterised the clusters were *Diaptomus spp.* and *Cyclops strenuus* in the "Yenisej River", *Cyclops strenuus* in the "Ob River", the combination of *Eurytemora* sp. and *Oithona similis* in the "Estuarine, *Pseudocalanus major*, *Oithona similis*, *Pseudocalanus* spp, *Calanus glacialis* and juvenile Asterioida in the "Brackish". The "Marine" stations where mainly characterised by *Microcalanus pygmaeus*, *Pseudocalanus major, Oithona similis*, *Pseudocalanus acuspes*, *Calanus glacialis* and *Oncea borealis*. Copepod nauplii occurred in all groups except in "Brackish". The regional distribution of the clusters (Fig. 18a) reflects closely the surface pattern of salinity and temperature (Fig. 15).

Community analysis using MDS based on species assemblage and abundance showed a strong gradient from the inner estuaries to the outer more marine areas, but the distinction between brackish and marine stations was less clear (Fig. 17b). Differences between the zooplankton assemblage of the "Yenisej estuary" and the "Ob estuary" showed up in both the cluster analysis and MDS. On the latter the stations are aligned in a south to north direction, which probably reflects the salinity gradient. The large statistical distance between the neighbouring stas. 30/27 and 10/47 indicates pronounced hydrographic fronts between these stations, but only minor differences further to the north along the transect. Differences between the two rivers are probably reflecting their different salinity regimes (Fig. 15).

Table 5: Species list and relative abundance (% of total abundance per station) during the expeditions “Boris Petrov” 1997 and 1999. Species with $\geq$1% rel. abundance in **bold** type

Group		**1997**	**1999**
Calanoida	*Acartia longiremis*	0.1	--
	Calanus finmarchicus	0.1	0.1
	Calanus glacialis	**1.4**	**2.3**
	Calanus hyperboreus	<0.1	<0.1
	Centropages hamatus	<0.1	--
	Diaptomus gracilis	<0.1	--
	Diaptomus sp.	0.4	0.9
	Drepanopus bungei	**58.7**	**44.7**
	Eurytemora sp.	0.2	<0.1
	Heterocope appendiculata	--	<0.1
	Jaschnovia c.f *brevis*	0.3	0.8
	Jaschnovia tolli	0.5	**1.7**
	Limnocalanus macrurus	0.5	**10.6**
	Metridia longa	0.1	<0.1
	Microcalanus pygmaeus	**1.4**	0.6
	Neoscolecithrix farrani	--	<0.1
	Pareuchaeta glacialis	<0.1	<0.1
	Pareuchaeta norvegica	<0.1	--
	Pseudocalanus acuspes	**3.5**	**3.5**
	Pseudocalanus major	**3.5**	**12.6**
	Pseudocalanus spp.	**3.6**	--
	Temora longicornis	<0.1	--
Harpacticoida	*Harpacticoida* spp.	<0.1	0.2
Cyclopoida	*Cyclops strenuus*	**3.0**	**4.3**
	Microsetella norvegica	<0.1	<0.1
	Oithona similis	**6.2**	**7.3**
Poecilostomatoi	*Oncaea borealis*	0.9	0.4
Cladocera	*Bosmina longirostis*	--	<0.1
	Bosmina sp.	0.1	0.4
	Daphnia sp.	<0.1	0.1
Nauplii	Nauplii Copepoda	**13.6**	**7.7**
	Nauplii Euphausiacea	<0.1	--
Cirripedia	Cypris larvea	<0.1	--
Amphipoda	*Acanthostepheia malmgreni*	<0.1	--
	Hyperia galba	<0.1	<0.1
	Gammarida gen. sp.	<0.1	0.1
	Themisto libellula	--	<0.1
Ostracoda	*Ostracoda* spp.	<0.1	<0.1
Mysidacea	*Mysis oculata*	<0.1	0.2
Euphausiacea	*Thysanoessa rashii*	<0.1	--
Hydromedusa	*Aeginopsis laurentii*	<0.1	<0.1
	Eumedusa birulai	<0.1	<0.1
	Euphysa flammea	<0.1	<0.1
	Halitholus yoldia-arcticae	<0.1	<0.1
	Obelia sp.	<0.1	--
Ctenophora	*Ctenophora* spp.	<0.1	--
	Beroe cucumis	--	<0.1
Foraminifera	*Foraminifera* spp.	--	<0.1
Tintinnida	*Tintinnopsis beroidea*	--	<0.1
	Tintinnopsis fimbriata	--	<0.1
Rotatoria	*Brachionus guadridentata*	--	0.1
	Keratella cochlearis	<0.1	0.1
	Keratella guadrata	--	0.6
	Sychaeta sp.	<0.1	<0.1
Nematoda	*Nematoda* spp.	--	0.1
Polychaeta	Polychaeta larvae	0.5	0.1
	Polychaeta pelagobia	--	<0.1
	Polychaeta spp. juv.	<0.1	0.1
Pteropoda	*Limacina* sp.	0.1	<0.1
	Clione limacina	0.2	<0.1
Bivalvia	Bivalvia larvae	0.1	--
Gastropoda	Gastropoda larvae	<0.1	--
Chaetognata	*Eukrohnia hamata*	<0.1	--
	Sagitta elegans	0.2	0.2
Appendicularia	*Fritillaria borealis*	0.1	<0.1
	Oikopleura vanhoeffeni	0.1	0.1
Echinodermata	Asteroida/Ophiuroida spp. juv.	0.3	--
	Echinodermata sp. juv.	0.1	<0.1
	Plutei spp.	0.1	--
Bryozoa	Bryozoa larvae	<0.1	--
Number of species		**$\Sigma = 58$**	**$\Sigma = 51$**

Table 6: Abundance (individuals m^{-3}) of dominant zooplankton species during the expeditions “Boris Petrov” 1997 and 1999. Stations are sorted according to clusters (Fig. 17 a, c)

1997	Copepod nauplii	Drepanopus bungei	Oithona similis	Cyclops strenuus	Pseudocalanus major	Pseudocalanus acuspes	Calanus glacialis	Limnocalanus macrurus	Microcalanus pygmaeus	Oncaea borealis	Diaptomus gracilis	Eurytemora sp.	Asteroida/Ophiuroida
Sta 30	82.6	83.9	0.2	89.4	0.4	--	--	--	--	--	22.1	1.5	--
Sta 32	51.7	31.3	--	94.3	--	--	--	--	--	--	39.6	1.1	--
Sta 10	383.9	1097.3	3.0	256.6	0.2	0.6	--	31.3	--	2.3	7.0	0.2	--
Sta 55	88.9	422.9	7.4	4.9	3.1	--	2.1	5.3	1.6	0.2	--	--	0.2
Sta 56	66.6	601.4	--	1.0	14.2	2.1	1.4	2.9	--	--	0.2	--	--
Sta 27	145.1	478.5	18.9	62.2	10.2	5.1	16.3	5.1	2.5	2.0	2.3	34.9	0.1
Sta 38	115.9	328.1	27.5	14.2	5.1	8.1	15.6	2.2	4.0	0.4	0.8	8.5	--
Sta 43	91.8	318.8	13.2	--	13.7	2.9	8.7	0.3	1.1	0.5	--	0.1	--
Sta 58	137.9	431.1	54.3	11.2	1.7	10.8	3.5	1.3	10.1	0.8	--	--	0.1
Sta 18	107.4	1359.0	22.6	45.8	107.1	18.4	10.3	2.9	4.6	8.7	0.4	0.1	0.1
Sta 21	33.9	694.5	272.0	--	140.9	52.8	60.6	0.5	31.9	12.4	--	--	64.6
Sta 24	36.7	1077.5	90.8	0.6	173.6	17.0	15.8	50.3	12.9	4.8	--	--	0.3
Sta 47	855.5	2318.1	59.1	--	33.2	80.5	40.9	29.1	19.3	4.2	--	--	--
Sta 1	7.1	309.2	85.3	--	27.7	37.4	4.9	--	53.7	2.7	--	--	0.6
Sta 42	52.6	485.9	231.6	--	2.8	14.8	12.9	--	40.8	89.7	--	--	0.2
Sta 46	20.3	461.6	21.3	--	23.4	20.8	11.6	0.2	5.3	1.3	--	--	0.1
Sta 48	248.0	552.9	68.0	1.5	20.1	58.7	9.4	8.1	49.6	14.5	--	0.2	--
Sta 49	48.9	172.0	51.0	--	25.1	76.3	10.0	0.3	11.1	10.8	--	--	0.3
Sta 50	69.6	158.6	42.8	--	28.0	152.8	31.1	0.2	13.2	12.3	--	--	0.2
Sta 52	26.8	156.1	142.7	--	51.5	131.0	23.8	--	13.9	7.7	--	--	1.4

1999	Copepod nauplii	Drepanopus bungei	Oithona similis	Cyclops strenuus	Pseudocalanus major	Pseudocalanus acuspes	Calanus glacialis	Limnocalanus macrurus	Microcalanus pygmaeus	Jaschnovia tolli	Jaschnovia brevis	Diaptomus sp.	Keratella quadrata
Sta 6	124.9	52.5	45.2	558.4	4.5	--	1.8	10.4	--	0.5	--	343.9	--
Sta 30	5.6	719.1	--	4.2	13.6	--	0.2	172.6	--	5.9	8.7	1.7	--
Sta 31	102.6	514.0	1.8	171.9	13.3	2.4	--	249.8	--	28.7	0.5	45.9	--
Sta 19	807.2	30.3	--	201.4	--	0.5	--	108.1	--	--	359.7	0.2	76.9
Sta 17	371.4	1120.9	624.6	478.2	331.5	371.2	55.3	142.8	44.1	22.3	20.7	4.8	6.9
Sta 18	288.5	544.1	18.9	279.4	14.4	29.1	19.5	53.3	1.1	6.4	3.7	0.6	88.2
Sta 20	232.9	264.3	30.2	190.0	6.3	73.6	3.0	21.6	0.3	6.5	1.7	0.8	113.4
Sta 8	89.1	2022.7	115.4	85.0	927.8	32.8	31.0	745.3	5.4	150.8	--	6.4	--
Sta 21	50.0	1214.4	41.4	28.3	793.2	79.6	18.3	614.0	--	14.3	0.8	--	--
Sta 24	425.6	1742.1	32.3	20.9	157.7	1.7	10.4	380.7	--	2.9	--	0.2	--
Sta 29	78.7	1964.3	15.3	--	1546.8	28.3	18.8	520.4	0.2	268.1	--	--	--
Sta 32	36.9	1324.2	25.9	--	176.9	37.2	6.9	170.2	0.5	37.2	0.1	6.7	--
Sta 1	139.8	1892.8	589.2	--	124.0	97.6	98.4	34.9	17.8	61.6	--	--	--
Sta 2	98.0	762.4	525.6	--	121.0	305.8	379.1	384.8	21.9	16.8	--	--	--
Sta 3	66.0	1055.1	204.0	0.6	359.4	211.2	135.1	163.8	43.4	30.9	--	--	--
Sta 11	170.9	1322.9	182.2	1.1	241.6	45.6	37.2	300.3	30.0	5.3	--	0.8	--
Sta 12	61.2	1542.1	119.2	1.8	328.7	34.4	24.4	89.3	13.0	88.2	0.2	0.6	--
Sta 13	21.9	297.5	29.0	--	61.5	51.1	111.1	266.3	4.8	6.6	--	0.2	--
Sta 25	18.0	358.7	259.7	--	60.8	28.1	16.1	76.3	11.1	2.1	--	--	--
Sta 28	80.8	374.4	46.6	0.6	157.9	8.8	10.1	36.9	5.6	13.7	--	--	--
Sta 35	12.8	813.0	105.7	--	255.2	32.6	22.9	36.6	16.5	4.9	--	--	--
Sta 37	207.7	395.2	160.2	--	106.8	89.5	20.1	54.4	15.4	2.0	--	--	--
Sta 38	83.3	447.3	101.3	--	43.5	30.5	22.1	316.7	6.9	0.4	--	--	--
Sta 39	7.9	219.1	141.5	--	57.4	37.8	33.9	47.5	37.2	0.3	--	--	--

3.3 1999

3.3.1 Hydrography

In 1999, the station positions were slightly different. In the west the working area was limited to 74°E, in the north to 74.5°N. The depth range of the 24 stations visited in 1999 varied from a maximum of 38m (sta. 39) in the central part of the Kara Sea to 5m (sta. 6) in the inner estuary of the Yenisej River. Details of the hydrogaphic situation are described by Stephansev & Shmelkkov 2000) and Amon & Köhler (2000). Both surface salinity and temperature in the study area were generally lower in 1999. The distribution pattern of surface salinity was similar to 1997 (Fig. 16), differences in the distribution pattern of surface salinity in the south-western part were at least partly due to the shift of several stations on the Ob transect to the east in 1999. The 1999 data showed a strong east to west gradient there. Both rivers showed differences in their surface salinity (Fig. 16). While the inner parts of the Ob Bay showed a minimum salinity value of about 2, which slowly increased to about 10 towards the outer parts, in the southernmost station in the Yenisej river surface salinity was with 2.7 slightly higher. Surface temperature ranged between 3.5° to 7°C in both rivers and their estuaries. At the northernmost stations, where the influence of the cooler marine water masses became more prominent, the surface temperature decreased to 2.9°C. As in 1997, the bottom temperatures showed constant values between 0° to -1.9°C, but the bottom salinity was with 33 slightly higher than two years before. The pycnocline was deepest at the southernmost stations with 13m and flattened to 10m towards the north, where the marine water masses became more important. As in 1997, high saline waters reached far into the rivers (Figs. 15 and 16) below the pycnocline.

3.3.2 Zooplankton composition

In 1999 only 52 species were identified (Tab. 5). Again the largest share belonged to the copepoda with 21 species (16 calanoida, 1 harpacticoida, 4 cyclopoida). In addition 3 cladocera species, 3 amphipoda, 1 mysidacea, 4 hydromedusa, 1 ctenophora, 2 tintinnida, 4 rotatoria, 2 pteropoda, 1 chaetognata, and 2 appendicularia species were found. Furthermore, ostracoda as well as larvae and juveniles of polychaeta, echinodermata and nematoda were observed, which were not determined to species level. Some of the meroplanktonic groups as bivalvia, gastropoda, cirripedia and bryozoa larvae were missing this year. Although copepod nauplii were present, no nauplii of euphausiids were found in the samples. In addition several species common in 1997 such as the calanoids *Acartia longiremis, Centrophages hamatus, Diaptomus gracilis, Pseudocalanus minutus, Temora longicornis*, the amphipod *Acanthostepheia malmgreni*, the hydromedusea *Aglantha digitale, Obelia* sp. and *Ctenophora* spp. were absent. In contrast, other species as the calanoids *Heterocopte appendicularia* and *Neoscolethrix farrani*, the amphipod *Themisto libellula*, the ctenophore *Beroe curcuma*, pelagic foraminifera and tintinnida, the rotatoria *Brachionus guadridentata* and *Keratella guadrata*, the Nematoda and juvenile *Polychaeta pelagobia* were new in the samples (Tab. 5).

Copepods again dominated abundance with 89.9% (Tab. 5). 12% of the total were represented by cyclopoida, 0.2% by harpacticoida and 77.7% by calanoida. The most common calanoid copepods were *Drepanopus bungei* (44.7%) followed by *Pseudocalanus major* (12.6%) and *Limnocalanus macrurus* (10.6%). Other quite common species of this group were *Calanus glacialis* (2.3%), *Jaschnovia tolli* (1.7%) and *Pseudocalanus acuspes* (3.5%). Copepoda nauplii (7.7%) were also rather common. Within the Cyclopoida again *Oithona similis* (7.3%) and *Cyclops strenuus* (4.3%) were the most important. In contrast to 1997, many copepod species were represented by all copepodite stages. Only *Limnocalanus macrurus* was dominated by adults, earlier copepodites were only found at the two southernmost stations in Ob Bay.

3.3.3 Regional distribution

An overall mean of 1955 ±232 individuals m^{-3} was calculated for all stations, which is very similar to 1997. One of the biggest differences was the much higher density of animals in the upper water layers in 1999 (1084 ±142 individuals m^{-3}) than in 1997 (638 ±132 individuals m^{-3}). In contrast, the lower layers showed less individuals in 1999 (1101 ±210 individuals m^{-3}) than in 1997 (1652 ±313 individuals m^{-3}). In 1999 the highest densities occurred in the central parts (Tab. 4) while the number of specimens in the inner estuaries of Ob and Yenisej were only moderate. The highest concentration was found at sta. 29 (4000 individuals m^{-3}) in the south-eastern Kara Sea. The species richness showed a slight tendency to higher values further outside. Both along the Yenisej and at the inner stations of the Middle Transect 15 species were caught. This number increased to 25 species at the outer marine parts. Along the Ob Transect (Tab. 4) a sharp increase from 15 species (sta. 19) to 29 (sta. 18) was observed within a short distance. As on the other transect the number of species finally decreased to 27 species at the northernmost sta. 37.

Most species were found in both depth layers sampled; exceptions were *Oncaea borealis* and *Microcalanus pygmaeus*, which were mainly restricted to the deeper layer. In all other species there was no clear preference for water depth.

The characteristic changes in species number and abundance along the transect described above are clearly expressed in the community analysis. Cluster analysis produced six groups

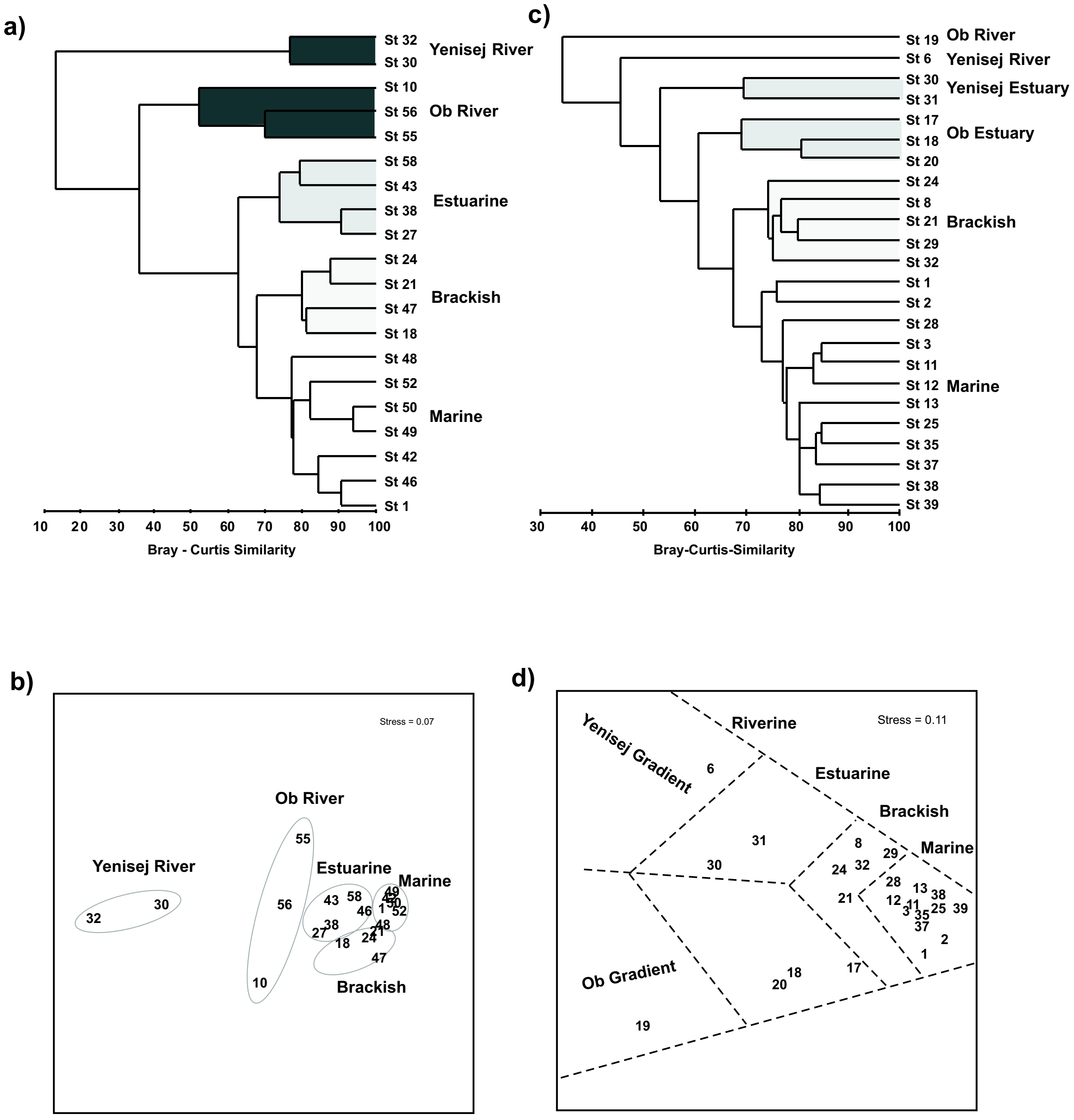

Figure 17: 1997: Cluster dendrogram (a), MDS plot (b). 1999: Cluster dendrogram (c), MDS plot (d)

named "Ob River", "Yenisej River", "Yenisej-Estuary", "Ob Estuary", "Brackish" and "Marine" (Fig. 17c). The MDS plot (Fig. 17d) shows the gradual change from different community types in both rivers that converge to a rather homogenous marine community with increasing marine conditions. The most important species for the cluster "Ob River" were *Jaschnovia brevis*, *Cyclops strenuus* and *Keratella quadrata*, for the "Yenisej River" *Diaptomus* spp. and *Cyclops strenuus*, for the "Ob Estuary" *Pseudocalanus acuspes*, *Pseudocalanus major*, *Cyclops strenuus*, *Oithona similis* and *Keratella quadrata*. The copepods *Diaptomus* spp. and *Cyclops strenuus* were the characteristic species combination of the "Yenisej Estuary". The presence of *Pseudocalanus major* and *Jaschnovia tolli* mainly structured the group "Brackish", while *Oithona similis*, *Calanus glacialis*, *Pseudocalanus acuspes*, *Pseudocalanus major* and *Microcalanus pygmaeus* contributed to the "Marine" cluster. The regional distribution of the clusters (Fig. 18b) was very similar to 1997 (Fig. 18a), given the differing station locations between these years.

4 Discussion

Our species inventory of the southern Kara Sea agrees well with earlier observations in this area (Timofeev 1989, Vinogradov et al 1995a), which reported *Pseudocalanus major* as one of the most abundant species in the marine layers beside *Calanus finmarchicus* s.l., while *Drepanopus bungei* and *Limnocalanus macrurus* were the typical species for the freshwater layers. During this study, *D. bungei* dominated the bulk and was present at almost all stations. Similarly, *L. macrurus* was quite common in the lower layers within the estuaries where the salinity did not exceed 28. This species was originally described as a relict freshwater species (Sars 1903), but it seems to have a wide range of osmotic tolerance. It is reported from many cold and deep freshwater lakes of the northern hemisphere, but is also quite common in the coastal waters of Canada, Siberia and Alaska (Bowman & Long 1973, Roff & Carter 1972, Løvik 1979, Vanderploeg et al. 1998). Single populations are also found in the Baltic and Caspian Sea (Holmquist 1970).

The zooplankton communities found here match with more than 75% of all species described by Kosobokova et al. (1998) for the shallow parts of the Laptev Sea Shelf, although there salinity was much higher. Only freshwater species as *Diaptomus* spp. and the Cladocerans *Daphnia* sp. and *Bosmina* sp. as well as some of the harpacticoid and amphipod species were missing in the Laptev Sea. The great importance of crustaceans and especially the calanoid copepods seems to be typical for Arctic Seas (Timofeev 1989, Kosobokova et al. 1998, Kosobokova & Hirche 2000).

For many species all life stages were found, suggesting successful breeding within the estu-

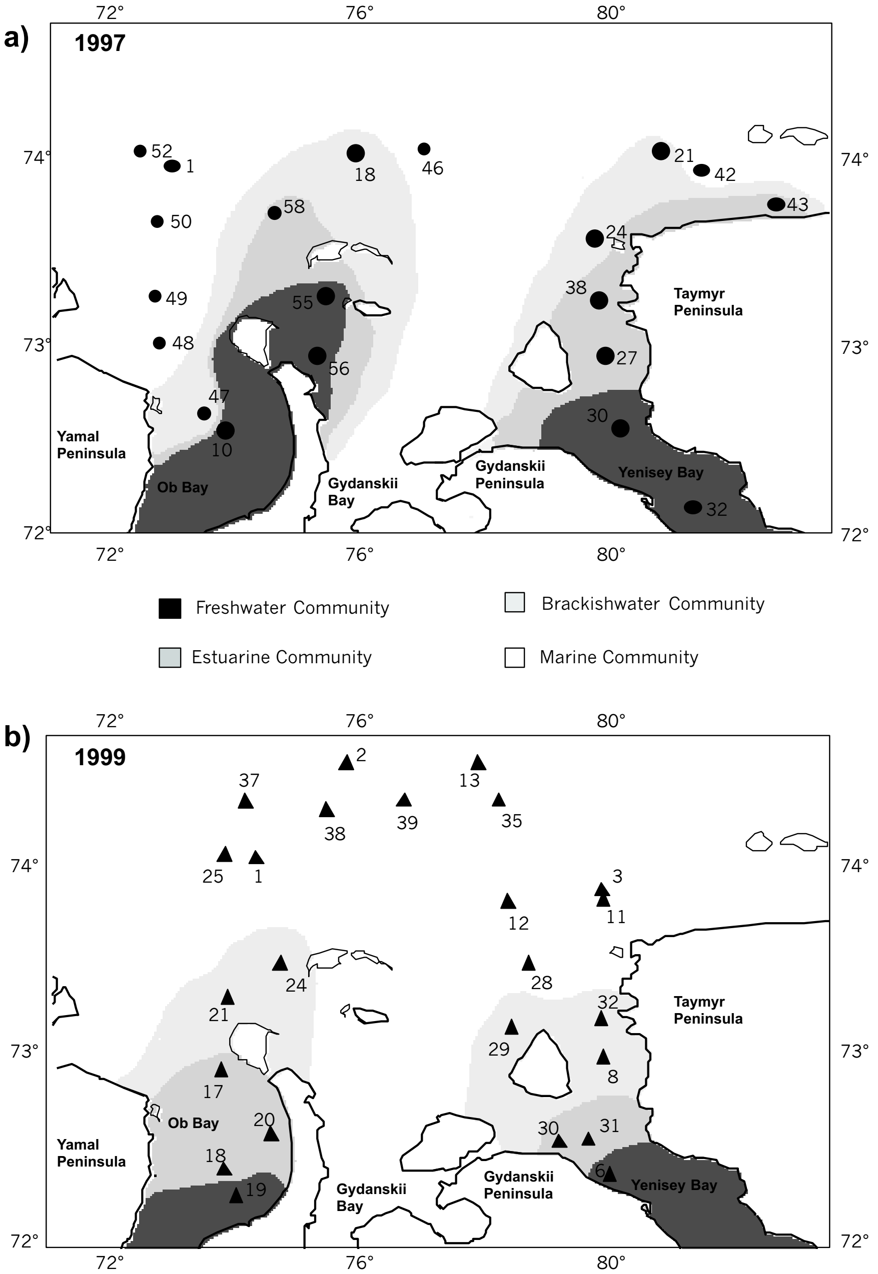

Figure 18: Regional distribution of 1997 clusters from Fig. 17a (a); regional distribution of 1999 clusters from Fig. 17c (b)

aries. This was also observed by Vinogradov et al. (1995a). In contrast, stenohaline marine and freshwater species may not hatch in the estuaries and may be advected by the estuarine circulation. It is noteworthy that life history stages of the abundant copepod *Limnocalanus macrurus* were almost exclusively adult. Evidently this species had already completed its life cycle, as Sars (1903) described it as reproducing during the late winter and early spring.

Community analysis demonstrated clearly the effect of hydrographic conditions on zooplankton distribution, which agreed with water mass distribution and the general circulation patterns. Zooplankton assemblages showed a characteristic change from a low number of freshwater species at the innermost stations of the estuaries to a maximum number in the mixing region where brackish water overlay marine water masses and hence inhabitants of both systems were present. Finally the northern regions with the strongest marine characteristics were inhabited by slightly less species. Surprisingly, despite large salinity differences, there was no effect of the two different depth layers on cluster analysis. We assume that our sampling method did not effectively separate the communities inhabiting the two depth layers. As the pycnocline is a transition zone, the nets may always have sampled parts of the other layer and in addition, some of the euryhaline species may be able to migrate through the pycnocline.

Both cluster analysis and MDS showed differences between the communities of Ob and Yenisej in both years studied, pointing to general differences between the plankton communities. Several factors may account for this:

- While the Ob is a typical river of the plains flowing through the taiga forest and tundra zones, the Yenisej drains the upper and middle mountain areas of the Ural (Telang et al 1991). It therefore may transport more mineral components and less organic material, thus creating a different food environment. Nöthig & Kattner (1999) reported the highest silicate concentrations during the 1997 cruise for the mouth of the Yenisej river, reflecting the rivers rocky origin (Sukhoruk & Tokarev 2000). This is also supported from samples taken during the expedition that high contents of lithogenic clastics were observed (Unger et al. 2000).

- In contrast to the Ob, the Yenisej has a rather narrow but deep opening into the Kara Sea, which may result in different mixing processes. This in turn may affect, directly or via phytoplankton development, the structure of zooplankton communities.

- Different nutrient regimes and mixing dynamics may lead to a different spring bloom dynamics. Thus in 1997 highest chlorophyll concentrations were measured in the Yenisej

> estuary (Nöthig & Kattner 1999). In 1999 a strong phytoplankton bloom was observed in the Ob estuary, but not in the Yenisej Estuary (Larionov & Kodina 2000).

The regional distribution patterns of the clusters especially in 1997 (Figs. 18a and 18b) mirror the spreading of freshwater from rivers in a north-eastern direction, along the eastern shorelines according to the general circulation patterns of the Yamal Current in the southern Kara Sea (Budgen et al. 1982, Pavlov & Pfirman 1995, Burenkov & Vasilkov 1995). This causes the hydrographic and biological gradients at least in the southern Kara Sea to run in a southeast-northwest direction rather than south to north. Recent modelling studies modified the current view of the circulation in the Kara Sea and showed a strong seasonality of the circulation patterns in the southern region (Harms et al 2000). They suggest that the circulation patterns and hence the zooplankton distribution described here are typical only for the fall/winter period. A seasonal change of the currents, together with the interannual variability of the freshwater supply by the rivers, should strongly affect the zooplankton distribution and should be considered in future studies. Of special interest is the fate of the brackish water fauna, which is spread over a large area in summer. The models also predict seasonal variability of the trajectories of particle exported by the two rivers.

Interannual comparison of the two cruises is difficult due different timing and different station position, specially at the southernmost riverine stations, where the freshwater and the brackish-water communities are separated by steep fronts (e.g. in 1997 stas. 10 and 47 in Fig. 18a). The cruise in 1997, which started 3 weeks later than in 1999, met warmer water temperatures, but also higher salinities. Nevertheless, the general distribution patterns of the zooplankton communities were very similar, but there were marked differences in species composition and abundance. Less species were found in 1999, mainly due to the absence of most meroplanktic and several copepod species (Tab. 5). Evidently the pelagic larvae were not yet released. On the other hand, Fomin (1989) reported that e.g. Polychaeta and Bivalvia are commonly found in the Kara Sea throughout the year.

A striking difference between the two years was the much higher abundance in the upper water layers in 1999 (Tab. 4). The highest overall concentrations were found in the central parts of the Kara Sea while the highest number of species were found in the two estuaries. In 1997, in contrast, both the highest densities and the highest number of species were found in the estuaries. The difference in abundance is mainly due to the enormous increase of *Limnocalanus macrurus* and *Pseudocalanus major* (Tab. 6). The total number of *L. macrurus* increased by a factor of 21, maximum abundance at one station was 8 times higher in 1999. Also its distribution was more widespread. While it occupied (>1% of individuals present at each station) only 50% of all stations in 1997, it was present at 96% in 1999. Its spatial distribution patterns covaried with those of the copepod *Drepanopus bungei*, with the main occurrence in Ob Bay in 1997 (stas. 10 and 47) and in the outer brackish water region of both rivers (stas. 21, 24, 8, 29) in 1999. The abundance of *Pseudocalanus major* increased by a factor of 5 and its distribution also changed between cruises, but in the opposite way to *L. macrurus*. While its main centre of distribution was at the north-eastern edge in the study area in 1997, it had shifted south into the Yenisej Estuary in 1999. In contrast, the number of calanoid nauplii were more prominent in 1997. Similarly to the meroplanktic species the copepods may not yet have spawned before the 1999 cruise.

These differences in zooplankton composition and abundance between two years point to large variability of the pelagic system of the southern Kara Sea. The factors controlling mass occurrences of on or the other species are not understood, partly because there is little knowledge of the life cycles of these species.

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5.2 Publication II

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The Kara Sea ecosystem: phytoplankton, zooplankton and benthos communities influenced by river run-off

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Abstract

Phytoplankton, zooplankton and macro-zoobenthos in the estuaries of Ob and Yenisei and the adjacent southern Kara Sea were investigated during three expeditions with RV "Akademik Boris Petrov" in August/September 1997, 1999 and 2000. Plankton and macrobenthic community structures were distinguished by cluster analysis and multidimensional scaling. Differences in species number, abundance and biomass as well as the zonation pattern of biological assemblages reflected the continental outflow from the rivers Ob and Yenisei along a salinity gradient from south to north. Additionally, strong regional variability in species composition between the two river systems Ob and Yenisei was obvious. The spatial biomass distribution of phytoplankton, zooplankton and macro-zoobenthos along a transect from the inner Yenisei to the open Kara Sea was related to the influence of different water masses.

1 Introduction

Approximately 80% of the Kara Sea (883.000km^2) constitute a shelf zone with depth less than 200 m (Zenkevitch 1963). Especially the estuaries of Ob and Yenisei rivers and the adjacent southern and eastern coastal zone are very shallow, less than 50 m, and build-up a large area where mixing of freshwater and sea water occurs. Ob and Yenisei, two of the largest rivers draining in the Siberian Arctic, discharge about 30% of the total annual river run-off into the Arctic Ocean. The volume of both river inflows into the Kara Sea is about 1.160 km^3 (Aagard & Carmack 1989). In addition to the strong seasonality of the light regime and the sea ice cover a large continental outflow is one of the most significant features of the Kara Sea. More than 75% of the annual river run-off from Ob and Yenisei is discharged during the spring-summer flood from May to September. Therefore the surface waters have significant seasonal fluctuations in temperature and salinity. The fresh water discharge of Ob and Yenisei forms a salinity-gradient, which spreads out northward from the estuaries to the central Kara Sea. Together with the fresh water large amounts of dissolved and particulate material are advected towards the central Kara Sea. The strong signals of fresh water and organic matter during spring and summer control the distribution of the fauna and flora in the Kara Sea as well as their productivity and consumption.

Investigations of the fauna and flora of the Kara Sea were initiated with the expedition of Nordenskjøld in 1875. Zenkevitch (1963) summarized the historic expeditions and gave a general overview. More recent observations were published by Vedernikov et al.. (1995) for phytoplankton, Vinogradov et al.. (1995) for zooplankton and Jørgensen et al. (1999) for benthos.

Here we present results of three summer cruises (1997, 1999, 2000) to the southern Kara Sea within the framework of the German-Russian project "Siberian river run-off" (SIRRO). Our aim was to combine observations on the distribution of species and biomass of phytoplankton, zooplankton and macrozoobenthos and relate it to the hydrographic regime.

2 Material and Methods

2.1 Phytoplankton biomass and species composition

Water samples for estimating phytoplankton biomass and species composition were collected with a Niskin Rosette sampling system. During all three cruises subsamples were taken from 3 to 4 different water depths according to different water masses determined by the CTD profiles. In most cases, samples were taken at the surface, just above and below the pycnocline, and close to the bottom. For the chlorophyll a determination 250-500 ml of water were filtered through Whatman GF/F glasfibre filter and stored at -18°C and analyzed at AWI. The filters were extracted in 90% acetone and analyzed with a spectrophotometer for higher values and with a Turner-Design fluorometer for lower values according to the methods described in Edler (1979) and Evans & OReily (1984). The values from the fluorometer were calibrated with the values obtained with the spectrophotometer. Phyto- and protozooplankton samples obtained with the water bottles were preserved in hexaminebuffered formalin (final concentration of ca. 0.5%). In aliquots of 10 or 50 ml settled for 48 hours, a 4 minimum of 50-100 cells of the dominant species or groups were counted with an inverted microscope at four different magnifications using phase contrast (Utermöhl, 1958).

2.2 Zooplankton biomass and species composition

For zooplankton sampling a Nansen closing net was used (0.442 m^2 catching area, 150 μm mesh size; 0.5 ms^{-1} hauling speed) from close to the bottom to the pycnocline, which was determined from a CTD profile before sampling, and from the pycnocline to the surface. At shallow stations (<10 m depth) the net frame was mounted with a non-closing, short net of 1 m length. The samples were preserved in 4% borax-buffered formaline. All specimens were counted and measured under a stereo microscope and identified to species level if possible. Copepodite stages of calanoid copepods were also identified and counted. Prosome length was used to distinguish copepodites and adult females of the two closely related copepods *Calanus finmarchicus* and *C. glacialis* according to Hirche et al. (1994). Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment. Dry weight was calculated for copepods only using material collected during the cruises and literature data. Live copepods of the species *Calanus glacialis* (adult females (AF), adult males (AM), copepodit stage V (CV)), *Limnocalanus macrurus* (AF, AM, CV), *Drepanopus bungei* (AF, AM) were shortly rinsed in distilled water and stored at 20°C in pre-weighed aluminum trays. In the laboratory they were dried at 60°C for 24 h and weighed on a microbalance. For other stages and species data from Peters (2001) and Kosobokova et al. (1998) were applied.

2.3 Macrofauna collection

Macrofauna was collected at a total of 61 stations during the three expeditions with 52 Okean grabs (0,25 m^2) and 58 Large Box Corers (0,25 m^2) from water depth between 10 to 70 m. The partition of animals was gently separated from sediment by sieving over 500 μm screens. All samples were preserved and stored in buffered 7% formalin. Biomass was determined using wet weight and later recalculated in ash-free dry weights (AFDW) according to Rumohr et al. (1987). For comparison, abundance and biomass data was calculated for 1 m^2.

2.4 Statistics

Overall distribution and community analysis of zooplankton and macrofauna [hierarchical, agglomerative cluster analysis and non-metrical Multi Dimensional Scaling (MDS)] in connection with the abiotic data from the CTD was performed using the PRIMER v5 package (Clarke & Gorley 2001). The analysis was based on the Bray-Curtis Similarity Index. To level the significance of each species, the input data were double square root transformed. This transformation mode was confirmed by a simple test recommended by Clarke & Warwick (1994).

For zooplankton analysis, the data from the two nets hauls were pooled, since the different depth layers at each station produced no different results for the community analysis. In order to archive the characteristic species assemblages responsible for each cluster, the number of species was first reduced, using only those that accounted for >4% of the total abundance at any one site, and then the single stations were grouped according to the results of the cluster analysis. Afterwards the species were sorted according to occurrence and abundance. The species principally responsible for the sample grouping in the cluster analysis were then highlighted.

For the macrofauna analysis, at first all species were removed, which occurred in >80% of the stations. Supplementary Field et al. (1982) suggested also to exclude all taxa occurred on single stations, since the species were randomly distributed. Classification (hierarchical agglomerative, complete linkage) was carried out for all selected stations and taxa. A modified Bray-Curtis index was used to identify the discriminator taxa for the different benthic assemblages. Species diversity analysis was used to assess whether there has been a significant change in benthic community structure. The diversity was estimated by Shannon-Wiener diversity index H' (Shannon & Weaver 1964) and the evenness by Pilou J (Pilou 1977). The Shannon index is sensitive to evenness and richness components of diversity.

3 Results

3.1 Sea ice, topography and hydrography

Sea ice and river discharge The Kara Sea is usually covered by ice for about 9 months of the year (Blanchet et al. 1995). Ice formation starts in the end of September or beginning of October; the break-up begins in early to late June (Mironov et al. 1994). During our expeditions the southern Kara Sea was completely icefree.

The stations studied during three expeditions are shown in Fig. 19. In 1997, the depth range of the 20 stations varied between 40m off the Taymyr Peninsula (sta. 21) and 10m within the Yenisei Estuary (sta. 32). In 1999, the station positions were slightly different. In the west the working area was limited to 74°E, in the north to 74.5°N. The depth range of the 24 stations visited in 1999 varied from a maximum of 38 m (sta. 39) in the central part of the Kara Sea to 5 m (sta. 6) in the inner estuary of the Yenisei River. In 2000 the working area was restricted to the Yenisei in the south, but was extended further to the north than the previous cruises. Sampling depth varied between 6 m in the southern Yenisei to 78 m. More detailed analysis of biological data will be shown on a transect following a salinity gradient from the inner Yenisei Estuary to the open Kara Sea (Fig. 19, Fig. 30).

River run-off exhibits a large seasonal variation with most of the discharge occurring during June to September (Pavlov & Pfirman 1995). During this study the hydrography was strongly influenced by the two river systems. Details on the three cruises were published Churun & Ivanov (1998) for 1997, by Stephansev & Shmelkov (2000) and Amon & Köhler (2000) for 1999 and by Stephansev & Shmelkov (2001) and Köhler & Simstich (2001) for 2000. Interannual comparison of the hydrographic regime is presented by Harms et al. (this volume). Therefore hydrography is only briefly described here. Maps for the distribution of salinity on the surface and near bottom for the three expeditions are presented in Fig. 20.

In 1997 both salinity and temperature showed a sharp gradient from the innermost parts of the estuaries to the outer parts, with a strong gradient in an east to west direction in the Ob and in a south to north direction in the Yenisei. Salinity in the upper layer increased from 1 in the Yenisei and 4 in the Ob to 21 at the outermost stations while temperature decreased from 8°C in the Yenisei and from 6°C in the Ob to 4°C further north. In the south a pronounced pycnocline was established at around 10m depth, which on the Ob transect flattened out through progressive mixing towards the northern parts. The pycnocline was deeper on the Yenisei transect than on the Ob transect, suggesting a higher discharge of freshwater in the former. Below the pycnocline, a tongue of high saline water reached far into the estuaries. In the Ob at the southernmost sta. 10 salinities >25 were registered near the bottom; in the Yenisei salinities were around 15. The deeper layer had temperatures between 0° and 1°C except at the shallow stations (30, 32) in the Yenisei, where temperatures up to 5.8°C were measured.

Both surface salinity and temperature in the study area were generally lower in 1999. The distribution pattern of surface salinity was similar to 1997. Both rivers showed differences in

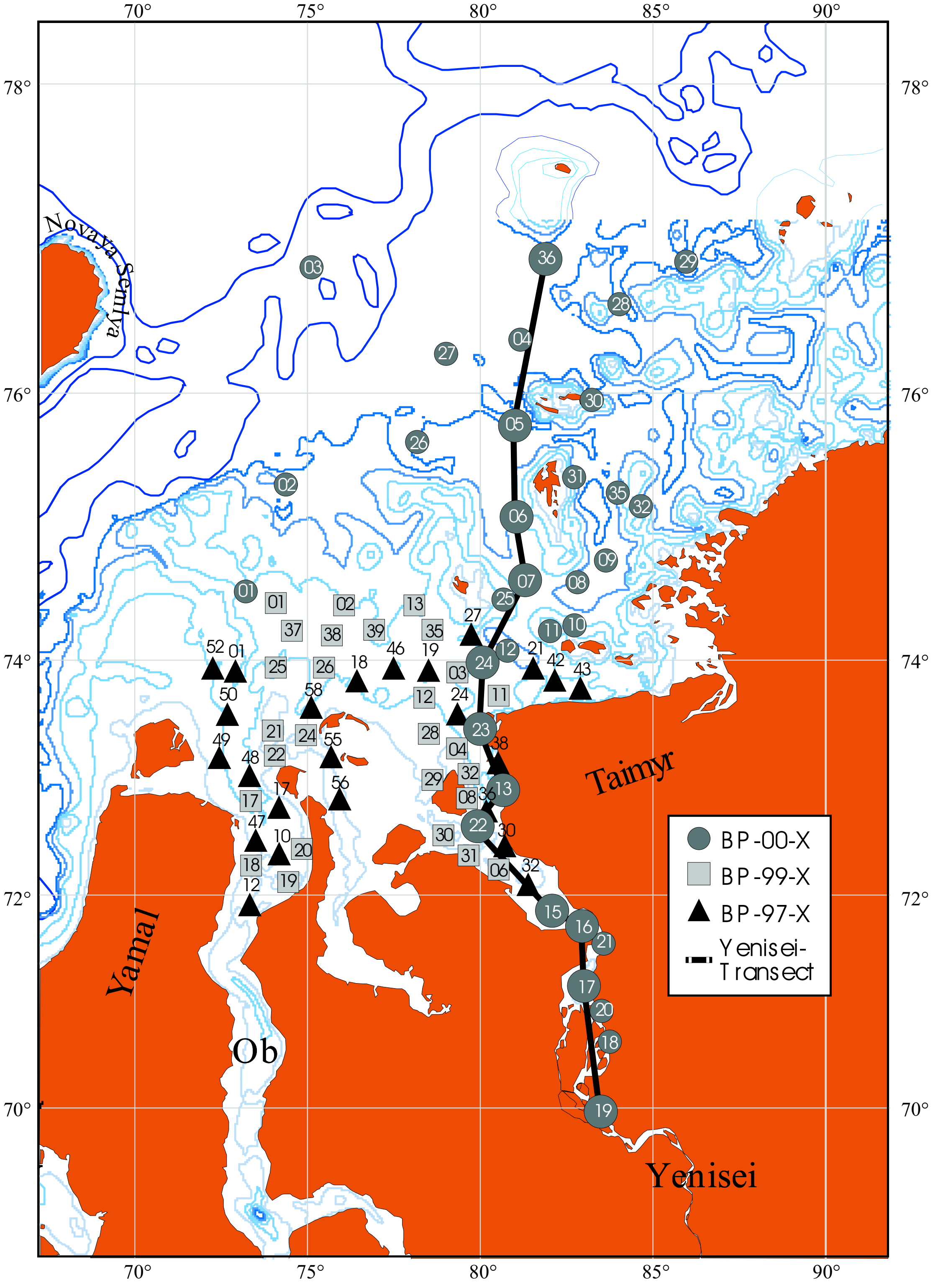


Figure 19: Biological stations during three cruises to the southern Kara Sea in 1997, 1999 and 2000.

their surface salinity with a minimum of about 2 in the inner parts of the Ob Bay, and 2.7 in the southernmost station in the Yenisei. Surface temperature ranged between 3.5° to 7°C in both rivers and their estuaries. At the northernmost stations the surface temperature decreased to 2.9°C. As in 1997, the bottom temperatures showed constant values between 0° and 1.9°C, but the bottom salinity was with 33 slightly higher than two years before. The pycnocline was deepest at the southernmost stations with 13m and flattened to 10m towards the north. As in 1997, high saline waters reached far into the rivers (Figs 20c and 20d) below the pycnocline.

In 2000 pure freshwater was met in the southern Yenisei, surface salinity increased from 0 to >24 in the north. Surface temperature decreased from 11°C to <1°C. The bottom layer of high saline water penetrated to 71°N into the river, in the north bottom salinity was around 33. Bottom temperature decreased from 5°C at the inner Yenisei to >-1°C on the northern shelf.

3.2 Phytoplankton

During all expeditions highest chlorophyll a values were found in the surface samples with almost no the exceptions; values below the pycnocline were generally less than 0.5 μg/L. In the rivers higher biomasses were found than in the estuary and the open Kara Sea. The only biomass values resembling a phytoplankton bloom were found in the Ob Estuary 1999.

During 1997 chlorophyll a (chl.a) concentrations ranged from 0.21 to 3.13 μg/L with maximum values in the surface layers; higher phytoplankton biomass was found in the more eastern part of the investigation area. In 1999 a phytoplankton bloom with maximum values of 13 μg chlorophyll a/L was observed in the Ob Estuary and in the open Kara Sea. Chlorophyll a concentrations in the Yenisei were much lower. The results were significantly different from 1997. The expedition in 1999 was carried out earlier in the year. The cruise in 2000 was again carried out somewhat later in the year and showed similar results like in 1997. During the expedition in 2000 phytoplankton biomass in the surface layer was lower than during 1997 and 1999. Chl.a values ranges from ca 0.4 μg/L to approximately 3,5 μg/L. One reason is the extension of the research area to the north where generally low chl.a values were measured. The distribution of pigments in the in estuaries of Ob and Yenisei were fairly similar in 1997 and 2000; higher chl.a concentrations were found in the Yenisei (see Nöthig et al., this volume).

A total number of 43 species with mentionable biomass (> 0.01 μg/L, Larionov and Makarevich 2001) were found at the longest transect of the three expeditions (Yenisei 2000, Fig. 21). At all other transects total species numbers were lower. Species numbers decreased from the Yenissei river towards the estuary and increased again in the more marine waters. In the rivers and in the open Kara Sea numbers were almost the same with slightly higher values in the Kara

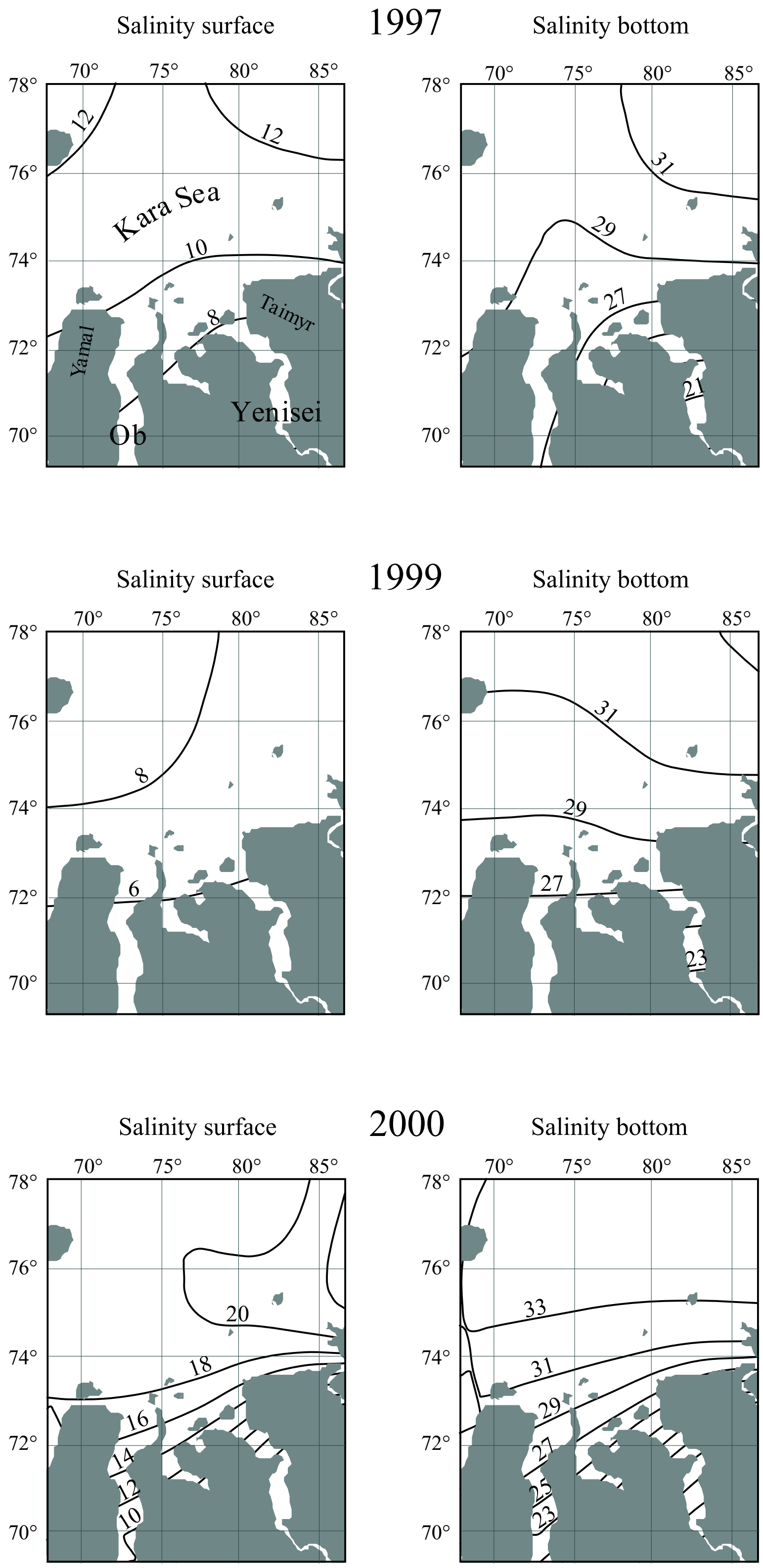
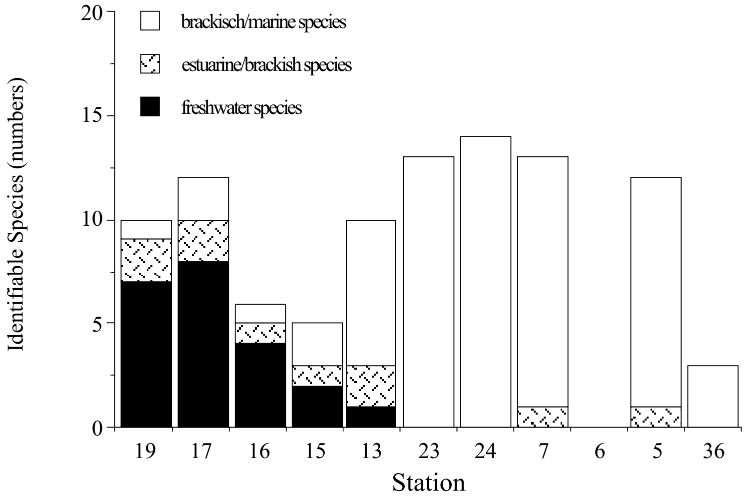


Figure 20: Salinity on the surface and near bottom for the expeditions 1997, 1999, 2000

a) Species Number



b) Species Composition

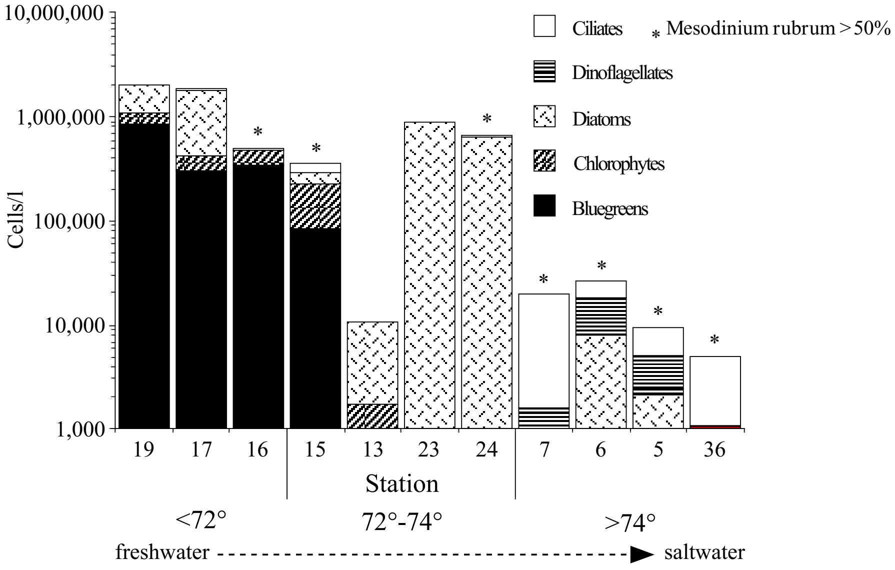


Figure 21: a) Numbers of identifiable species splitted into freshwater, estaurine/brackish and brackish/marine species along a transect from the Yenisei to the open Kara Sea during 2000. b) Composition of the main phytoplankton and protozooplankton groups along the transect from Yenisei to the open Kara Sea during 2000.

Sea. Whereas the numbers of recognizable species did not show much difference, the composition changed drastically from bluegreen algae dominating in the rivers to diatom/ dinoflagellates dominated populations in the open Kara Sea. The endosymbiontic algae carrying ciliate *Mesodinium rubrum* seemed to be an important component of the autotrophic population in the northern Kara Sea (Fig. 21).

Phyto- and protozooplankton species countings reflect almost the distribution of biomass. The general population patterns are fairly similar in all three years as shown here for 1999 (Fig. 22). However, some differences exist in species composition in both rivers and, the estuary and the open Kara Sea in the three years of investigation. In 1999 diatoms were the most dominant species with *Thalassiosira* cf *punctigera* and *Chaetoceros* spp in the more brackish/marine environment and Aulacosira spp in the freshwater influenced regions. During the other years, 1997 and 2000, bluegreens and chlorophytes were abundant in both rivers. Much higher abundances of those species were found in the Yenisei. Between 72°N and 74°N brackish water species were found. North of that region a more heterogeneous population was encountered consisting of marine diatoms, dinoflagellates, nanoflagellates, and *Mesodinium rubrum* (Nöthig et al., this volume).

3.3 Zooplankton

Zooplankton composition, abundance and distribution

The number of species identified during 3 cruises varied between 52 (1999) and 59 (1997). Crustacea made up the overwhelming part, and among them the copepoda were dominant (Tab.. 7). Meroplanktic larvae of Cirripedia, Polychaeta, Bivalvia, Gastropoda, Echinodermata, Bryozoa and nauplii of Copepoda, Euphausiacea and Ostracoda were counted but not determined to species level (see Fetzer, this volume). Species composition and distribution for 1997 and 1999 were described in detail in Fetzer et al. (2002). In 2000, taxa other than Copepoda were much more frequent, especially Appendicularia and Echinodermata.

Total abundance (mean of all stations) during the cruises in 1997 and 1999, which concentrated on the same working area, was very similar, while in 2000 in the eastern Kara Sea only half the concentration was found (Tab. 7). There was strong regional and interannual variability in species 8 number and abundance between the two river systems and along a latitudinal gradient (Fig. 23). In general, species number was lowest in the freshwater regions (15 to 18 species), and highest just at the entrance of the two rivers (28 to 32); in the northern regions it slightly decreased to 25 to 31 species (Fig. 23). Abundance maxima in the Ob were similar between

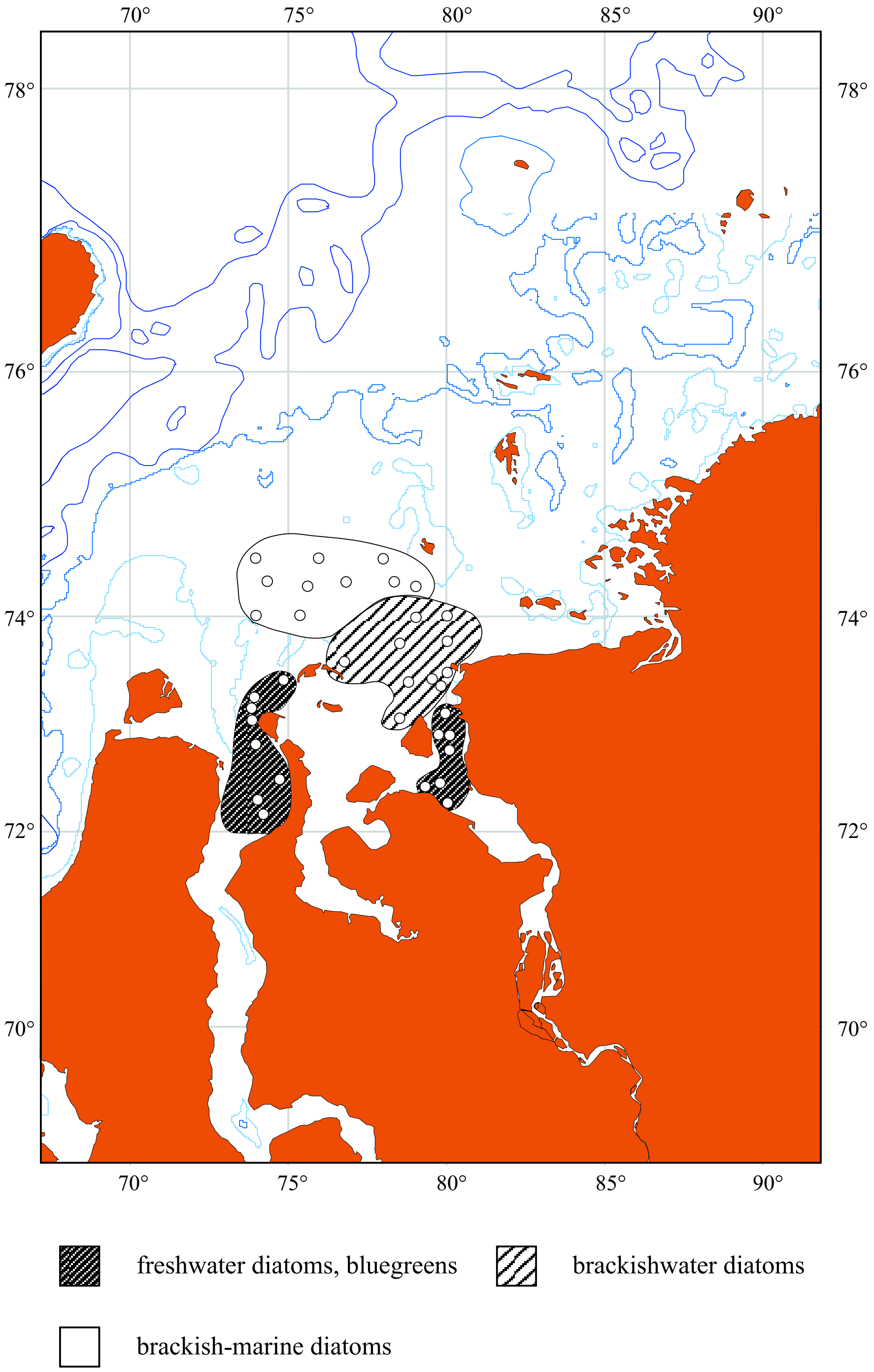


Figure 22: Dominating phytoplankton species groups in the rivers, in the estuary, and the marine realm during 1999.

Table 7: Mean abundance ± s.d., relative abundance (%) of zooplankton taxa / number of species per taxon, and most frequent (%) species in the Kara Sea during 3 cruises.

		1997	1999	2000
	Abundance m^{-3}	1960 ± 412	1955 ± 232	1007 ± 588
rel. abundance / no. species	Crustacea [total]	98.0 / 32	98.3 / 28	83.4 / 31
	Copepoda	97.9 / 25	97.6 / 21	82.3 / 22
	Hydrozoa	< 0.1 / 6	0.2 / 5	0.1 / 10
	Rotatoria	< 0.1 / 2	0.9 / 4	0.1 / 5
	Polychaeta	0.5 / n.d.	0.1 / n.d.	1.0 / n.d.
	Mollusca	0.4 / 2	0.1 / 2	0.4 / 2
	Chaetognatha	0.2 / 2	0.2 / 1	1.2 / 1
	Appendicularia	0.2 / 2	0.1 / 2	7.7 / 2
	Echinodermata	0.3 / n.d.	< 0.1 / n.d.	5.62 / n.d.
most frequent species [%]	*Drepanopus bungei*	58.7	44.7	6.9
	Limnocalanus macrurus	0.5	10.6	0.4
	Pseudocalanus major	3.5	12.6	5.8
	Pseudocalanus acuspes	3.5	3.5	9.9
	Cyclops strenuus	1.3	4.3	0.6
	Oithona similis	6.2	7.3	35.6
	Calanus glacialis	1.4	2.3	10.4
	Microcalanus pygmaeus	1.4	0.6	4.2

years both in magnitude and location (1997: sta 47/3734 ind.m^{-3}; 1999: sta 17/3714), just at the entrance of the river. In the Yenisei, a slightly higher maximum concentration was found slightly northward of the river mouth (sta. 8/4247 ind.m^{-3}), while in 1997 (sta. 24/1468 ind.m^{-3}) and 2000 (sta. 24/2334 ind.m^{-3}) the maxima were lower and further to the north, off the northeast corner of the Taymyr Peninsula. Lowest concentrations were observed at the southernmost stations in the rivers and at the northernmost stations in all years (Fig. 23). The much lower abundance in 2000 is partly explained by the strongly reduced occurrence of the copepods *Drepanopus bungei* and *Limnocalanus macrurus* (Tab. 7), which formed the bulk at the high-abundance stations in 1997 and 1999 with up to 37674 *D. bungei* m^{-2} (sta. 24, 1997) and 5990 *L. macrurus* m^{-2} (sta. 8, 1999). *Pseudocalanus major* also reached high densities, up to 7775 m^{-2} (sta. 29, 1999). The dominant species in 2000 were *Oithona similis* and *Calanus glacialis* (Tab. 7), which reached maximum densities of 60100 m^{-2} (sta. 24) and 20350 m^{-2} (sta. 28), respectively, at deep northern stations. It should be noted that Nauplii were not included in these numbers, as they were not determined to species level. Nauplii and young copepodite stages were present in high concentrations in all three years, with the portion of Nauplii ranging from 5.5% in 2000 to 13.6% in 1997.

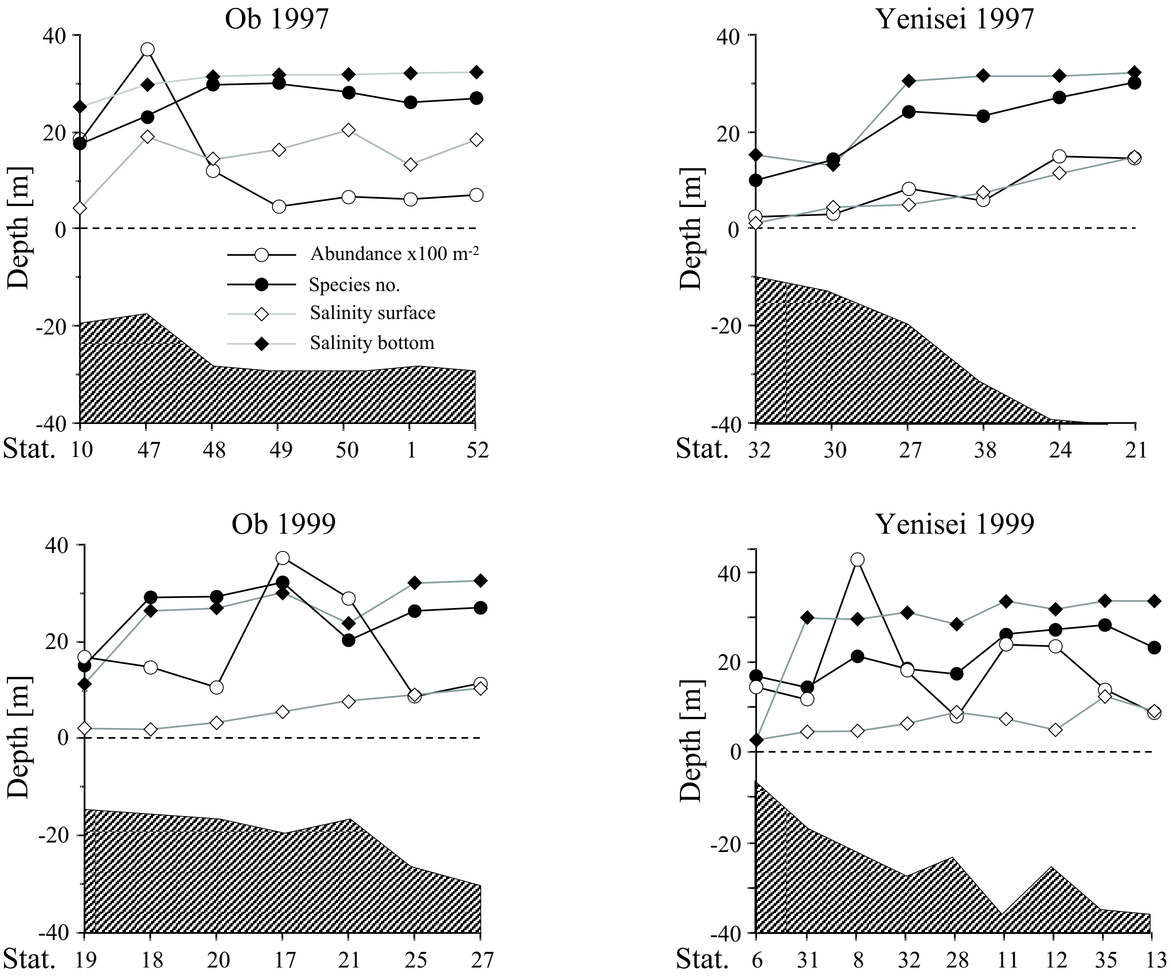


Figure 23: Comparison species number and abundance of zooplankton in relation to bottom and surface salinity along south-to-north transects starting in the Ob and Yenisei during 1997 and 1999.

Zooplankton biomass

Biomass also had great regional and interannual variability (Tab. 8). The biomass minima, however, were always at the innermost stations in the Yenisei; the maxima were west or northwest of the Taymyr Peninsula in 1997 (sta. 21) and 1999 (sta. 8), respectively, and at the four northernmost stations 28, 29, 30, 36 in 2000. There at sta. 30 the highest biomass of all cruises was observed with 6.8g, caused by large numbers of *Calanus glacialis*.

Table 8: Dry mass (mg m^{-2}) of copepoda in the Kara Sea during 3 cruises.

Dry mass (mg.m^{-2})	min	max	mean
1997	7.8	1235	280
1999	6.0	1207	523
2000	5.4	6688	1043

Vertical distribution

Due to the river discharge in summer, the water column in the southern Kara Sea was divided by a strong pycnocline over most of the study area during the cruises, with a lens of low salinity water on the surface extending faraway from the river mouths (Fig. 30), and below marine water masses penetrating deep into the rivers. Despite a drastic vertical gradient in salinity, most species did not show a clear preference for a certain depth layer. Thus *Calanus glacialis*, *Jaschovia tolli*, *Microcalanus pygmaeus*, *Pseudocalanus major* and *Oncaea borealis* were more frequent in the lower layers, but at some stations more specimens were found in the surface layer. A rare example for a clear vertical separation of different life stages is *Pseudocalanus acuspes*. While the young stages (CI to CIII) preferred the upper waters, the older copepodites and adults were more frequent in the lower layer.

Clusteranalysis

As separation of depth layers did not affect the clusters in 1997 and 1999 (Fetzer et al. 2002), abundance data integrated over the whole water column were used for all years. Cluster analysis produced similar regional zooplankton associations for all three cruises (Fig. 25). The clusters are always aligned along a latitudinal gradient from the innermost stations in the rivers to the marine environment in the north, indicating salinity as the main control of regional distribution. The innermost stations in Ob and Yenisei were clearly separated (Fig. 25) in 1997 and 1999. In addition, in 1999 cluster analysis (Fig. 25) and MDS (Fetzer et al. 2002) separated also the adjacent estuaries into different associations for each river. In 2000 in the Yenisei two stations were sampled which were located further south than in the previous years. These stations formed a separate association (Fig. 25). The more northern associations combined stations in the wake of the plumes of both rivers. In the northwestern Kara Sea, which was studied only in 2000, three associations were separated, a southern one leaning on the Taymyr coast, a northeastern one and a northwestern one.

3.4 Macrofauna

More than 290 species of marco-zoobenthos were identified on our grab samples from a total of at least 81000 individuals. Polychaeta (107 species), Crustacea (99), Mollusca (65) and Echinodermata (7) were the most important macrobenthic taxa. Other invertebrates like Cnidaria, Nemertini, Sipunculida and Priapulida occurred only in low numbers. Within the stations, the number of species varied from 2 to 71 and the abundance from 112 to 10270 ind.m^{-2}. Species number was lowest in the southern river estuaries, whereas maxima were found at the northern stations. The highest abundance was directly related to large amounts of the cumacean Diastylis sulcata (9800 ind.m^{-2}) at station 18 (1999). Interestingly, the stations of minimum (sta19, 1999) and maximum abundances were located close together in the Ob Estuary.

The salinity gradient plots (Fig. 26) show a remarkable increase in species number, biomass and diversity toward the higher salinity and hence in northern direction. The high abundance at station 13 (Fig. 26b) is based on the polychaetes *Prionospio cirrifera* and *Marenzelleria arctia*. However, in the salinity interval between 20 and 25, a local minimum is obvious. At the southern station 32 (1999, 72°N) the minimum of diversity (0.146) together with low evenness (0.0906) was found, whereas the highest diversity value (3.47; evenness 0.804) was observed in the southern Kara Sea at station 35 (1999, ~74°N).

For community analysis a modified species-station-list of approximately 63500 individuals and 199 macrobenthic taxa was used. Cluster analysis divided the 57 stations investigated during the three cruises into four assemblages, which follow a south-north gradient (Fig. 27). The seven southernmost stations of Ob and Yenisei were pooled into an assemblage SOUTH. The adjacent estuarien areas were combined into two different communities. 20 stations in the western and interestuarine part formed the cluster WEST, whereas community EAST comprised 22 stations, mainly located in the eastern area. Stations of the northern Kara Sea were combined in a welldefined group NORTH. The samples from stations 32 (1997) in the southern Yenisei and 18 (1999) in the southern Ob were isolated by the analysis and excluded.

Within the cluster SOUTH the bottom salinity ranged between 12 to 31; accordingly the macrobenthic community composed mainly of euryhaline organisms with a very low number of species (median 26) but relatively high abundances (median 860) (Tab. 9). The assemblage was dominated numerically by the deposit feeding spionids *Prionospio cirrifera* (55%) and *Marenzelleria arctia* (15%). The communities WEST and EAST were spatially not discrete, but showed some overlapping, with EAST stations in the mouth of the Ob and in the northwestern corner of the study area, and WEST stations north of the Taymyr Peninsula. Cluster analysis clearly separated the assemblages, although the number of taxa per station varied widely. WEST combined

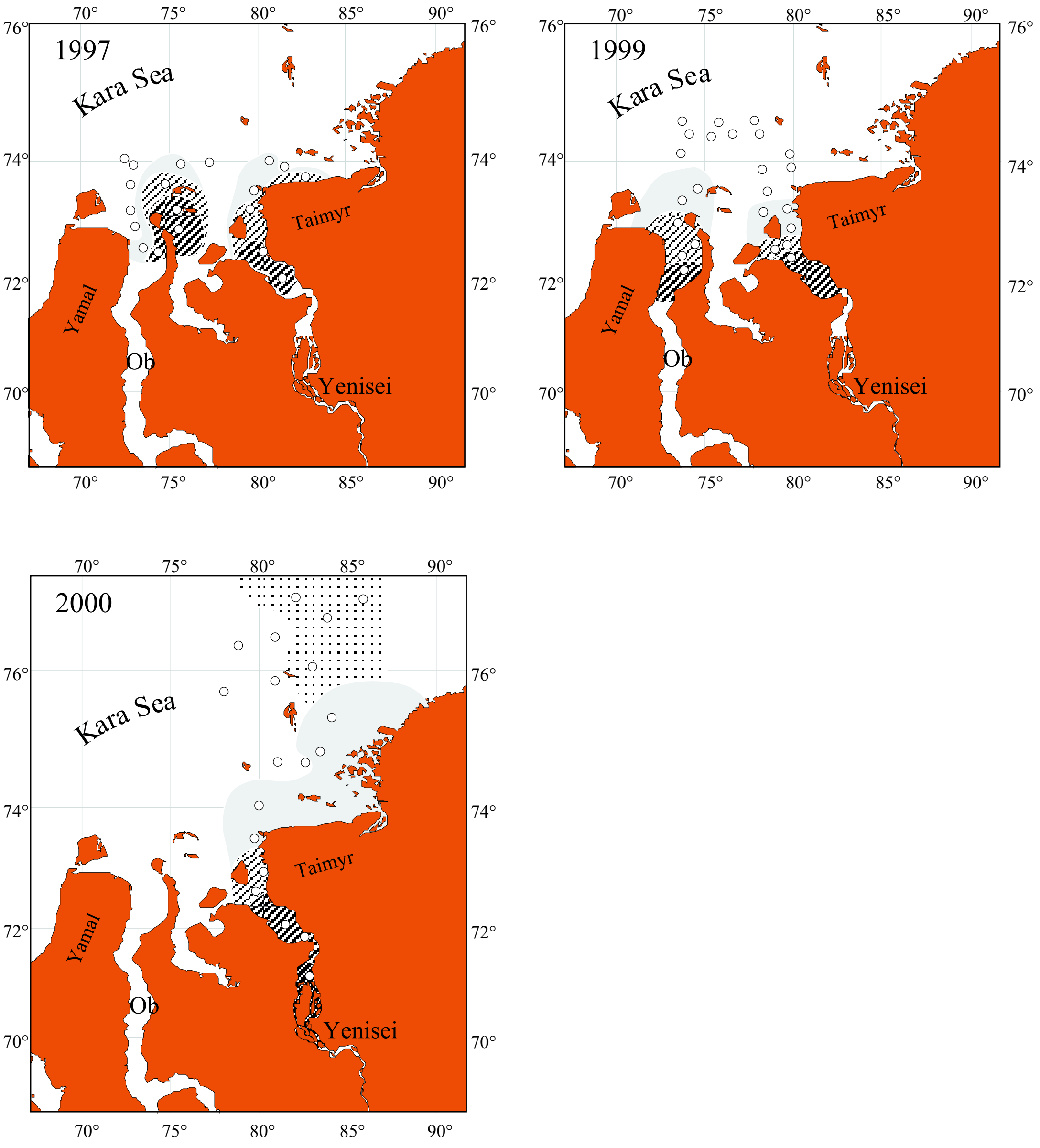
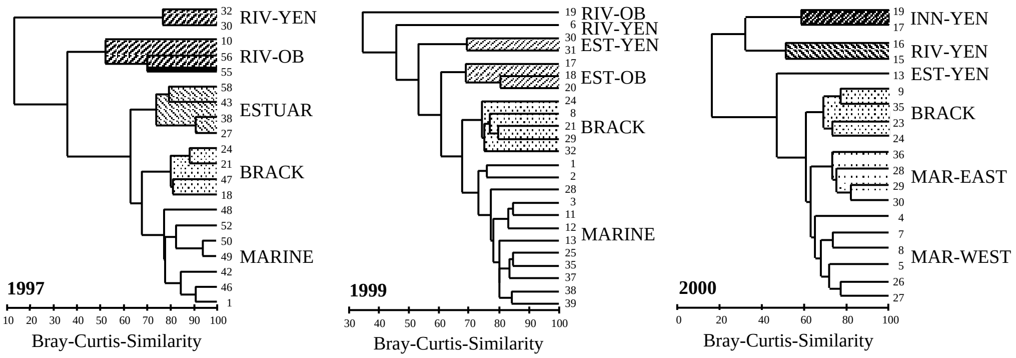


Figure 24: Regional distribution of zooplankton communities during 1997, 1999 and 2000

15 to 71 species (median 35), whereas in EAST from 5 to 46 species (median16) were found. In WEST the highest total species number (155) of all communities was found, the Cumacea *Diastylis sulcata* was the dominant species.

In EAST the low average abundance of 324 ind.m^{-2} is remarkable, the characteristic species was the Polychaeta *Micronephtys minuta*. The remaining 7 stations belong to NORTH, which had the highest values of abundance (median 1140 ind.m^{-2}) and number of taxa (median 36).



CHARACTERISTIC SPECIES	1997	1999	2000
YENISEI	RIV-YEN Diaptomus spp. *Cyclops strenuus* Sars, 1898	RIV-YEN Diaptomus spp. *Cyclops strenuus* Sars, 1898	INN-YEN *Cyclops strenuus* Sars, 1898 *Bosmina longirostris* (Mueller, 1786) *Daphnia sp.* RIV-YEN *Drepanopus bungei* Sars, 1898 *Eurytemora gracilis* (Sars, 1898)
OB	RIV-OB *Cyclops strenuus* Sars, 1898	RIV-OB *Cyclops strenuus* Sars, 1898 *Jaschnovia brevis* (Farran, 1936) *Keratella quadrata* (Mueller, 1786)	
ESTUARINE	ESTUAR *Eurytemora sp.* *Oithona similis* Claus, 1866	EST-OB *Pseudocalanus acuspes* (Giesbrecht, 1881) *Pseudocalanus major* (Sars, 1900) *Cyclops strenuus* Sars, 1898 *Oithona similis* Claus, 1866 *Keratella quadrata* (Mueller, 1786) EST-YEN *Diaptomus sp.* *Cyclops strenuus* Sars, 1898	EST-YEN *Pseudocalanus acuspes* (Giesbrecht, 1881) *Oithona similis* Claus, 1866 Copepoda nauplii
BRACKISH	BRACK *Pseudocalanus acuspes* (Giesbrecht, 1881) Pseudocalanus spp. *Oithona similis* Claus, 1866 *Calanus glacialis* Jaschnov, 1955 *Asteroidea juv.*	BRACK *Pseudocalanus major* (Sars, 1900) *Jaschnovia tolli* (Linko, 1913)	BRACK *Drepanopus bungei* Sars, 1898 *Oithona similis* Claus, 1866 Copepoda nauplii
MARINE	MARIN *Microcalanus pygmaeus* (Sars, 1900) *Pseudocalanus major* (Sars, 1900) *Pseudocalanus acuspes* (Giesbrecht, 1881) *Oithona similis* Claus, 1866 *Oncaea borealis* Sars, 1918 *Calanus glacialis* Jaschnov, 1955	MARIN *Oithona similis* Claus, 1866 *Calanus glacialis* Jaschnov, 1955 *Pseudocalanus acuspes* (Giesbrecht, 1881) *Pseudocalanus major* (Sars, 1900) *Microcalanus pygmaeus* (Sars, 1900)	MAR-EAST *Oithona similis* Claus, 1866 *Calanus glacialis* Jaschnov, 1955 *Pseudocalanus acuspes* (Giesbrecht, 1881) Pluteus larvae MAR-WEST *Oithona similis* Claus, 1866 *Calanus glacialis* Jaschnov, 1955 *Pseudocalanus acuspes* (Giesbrecht, 1881)

Figure 25: Cluster analysis of zooplankton stations during 1997, 1999, and 2000 and character species of the resulting communities

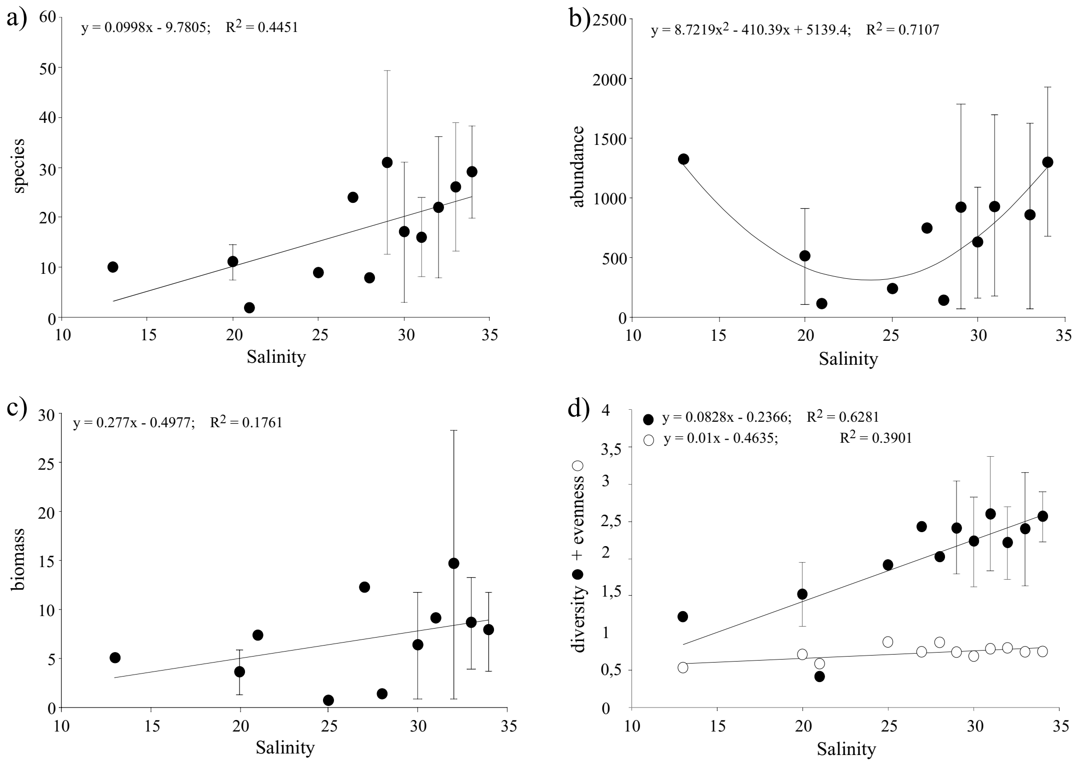


Figure 26: Relationship between salinity and a) species number, b) abundance, c) biomass, and d) diversity and eveness, for the macrofauna in the estuaries of Ob and Yenisei and adjacent southern Kara Sea

Characteristic species were the carnivore Polychaeta *Lumbrineris minuta* and the deposit feeding cirratulid *Chaetozone setosa*.

In contrast to SOUTH and WEST where most of the species belonged to the crustaceans, the polychaetes were slightly more numerous in EAST and NORTH (Fig. 28a). Molluscs were found in all benthic communities, but were secondary in species numbers (13%). Only in the northern area, their portion increased up to 17%. Echinoderms occurred in all communities but represented only 3% of the total species number. They showed a tendency of increase to the North, too.

In the study area Crustacea were the most abundant taxon with 51% specimens, followed by Polychaeta with 40% specimens and Mollusca with 6% of the individuals (Fig. 28b). Within the clusters, the proportions differed considerably. While in SOUTH, EAST and NORTH Polychaeta dominated the fauna (>70% individuals), crustaceans inhabited mainly the western shelf in considerable numbers. Here, the amphipod *Byblis gaimardi* and the cumaceans *Diastylis glabra* and *Brachydiastylis resima* accounted for more than 31% of the abundance. Stenohaline

Figure 27: Cluster analysis of macro-zoobenthos and spatial distribution of assemblages (sum of all years) in the Kara Sea

Echinodermata were found in appreciable quantity only in the northwestern and northern Kara Sea. The ophiuroid *Ophiocten sericeum* and the holothuroid *Myriotrochus rinkii* were subdominant in cluster WEST, whereas *O. sericeum* represented 4% of the individuals in the association NORTH.

All communities were absolutely dominated by molluscs, which in the different clusters made up between 38 to 60% (Fig. 28c). The share of the Polychaeta varied between 15 and 37% decreasing from north to south. In spite of high species number (47%) and abundance (59%) of crustaceans in WEST, they contributed only (16%) to total biomass there. Echinoderms had their highest biomass in NORTH (10%), where the salinity never dropped below 33. With respect to total biomass, the share of the major macro-zoobenthos groups is very constant within different years (Fig. 29).

3.5 Biomass of phytoplankton, zooplankton and macrozoobenthos along a south-north transect

Biomass of phytoplankton (chlorophyll a), zooplankton (dry weight) and macrozoobenthos (AFDW) is shown for a transect from the inner Yenisei along the Taymyr Peninsula to the north during 2000 (Fig. 30). Chl a integrated from surface to bottom decreased from the inner Yenisei to the open Kara Sea. Highest chl. a values were about 60 mg m^{-2} at sts 19 and 17 and about 20 mg m^{-2} at sts 15 and 13. Lowest values (<10 mg m^{-2}) were found in the Yenisei Estuary, where the population structure changed from bluegreen algae to diatom-dominated. Towards the open Kara Sea values slightly increased again, but stayed low between 5 and 17 mg m^{-2}. From station 7 to 36 *Mesodinium rubrum* and diatoms prevailed in the phytoplankton. Integrated biomass from bottom to surface (Fig. 30) showed a significant decrease of phytoplankton biomass towards the open Kara Sea. Three different populations could be distinguished in surface waters: (1) freshwater diatoms together with blue greens in both rivers, (2) *Chaetoceros* species and small pennate diatoms in the estuary and, (3) north of 74°N brackish/marine species dominated by *Thalassiosira* cf *punctigera* and *Chaetoceros* spp.

The lowest biomass of zooplankton with 0.005 and 0.023 mg m^{-2} was found in the southern stations 17 and 15, followed by slightly higher biomass to the north. The maximum was observed at the northernmost station 36 with 6.668 mg m^{-2}. There the large calanoid copepod *Calanus glacialis* was very abundant. Along the Yenisei transect, two areas of increased macrobenthic biomass values could be distinguished (Fig. 30), one in the estuary south of 74°N and the other in the adjacent Kara Sea north of 74°N. South of 74°N macrobenthic biomass ex-

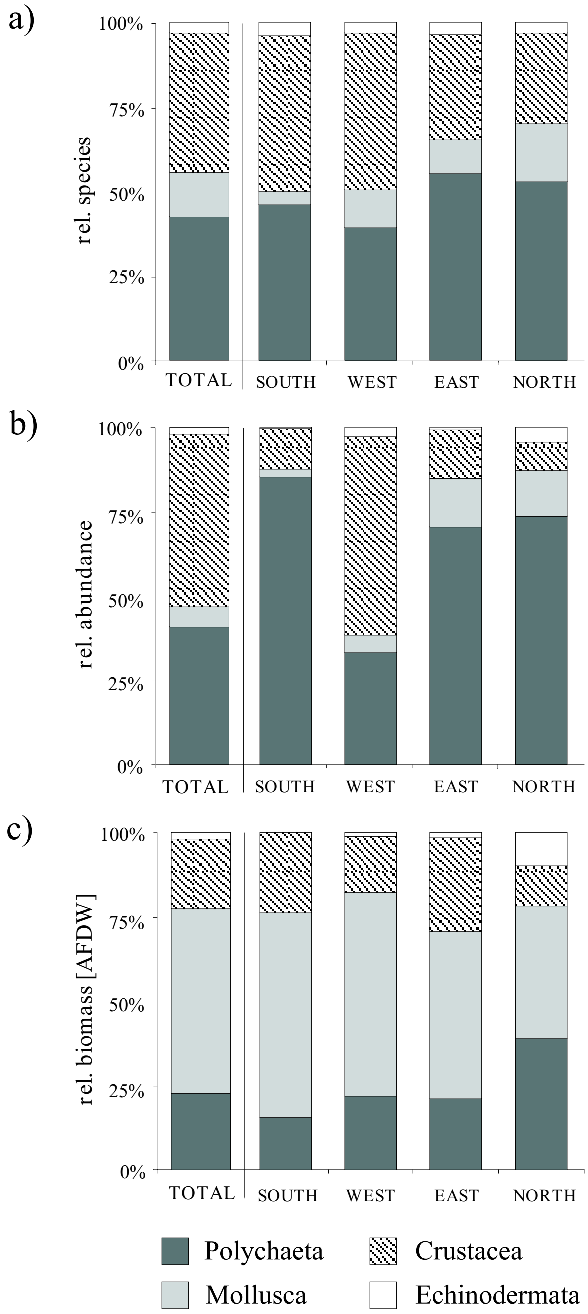


Figure 28: Dominant higher taxa (%) per total investigation area and cluster in terms of a) species number, b) abundance, c) biomass [AFDW]

ceeded 8.5 gAFDW.m^{-2} on station 23 (2000) and dropped towards the southern Yenisei. North of 74°N, macrobenthic biomass values varied from 2.9 gAFDW.m^{-2} on station 06 (2000) and 8.3 gAFDW.m^{-2} on station 36 (2000).

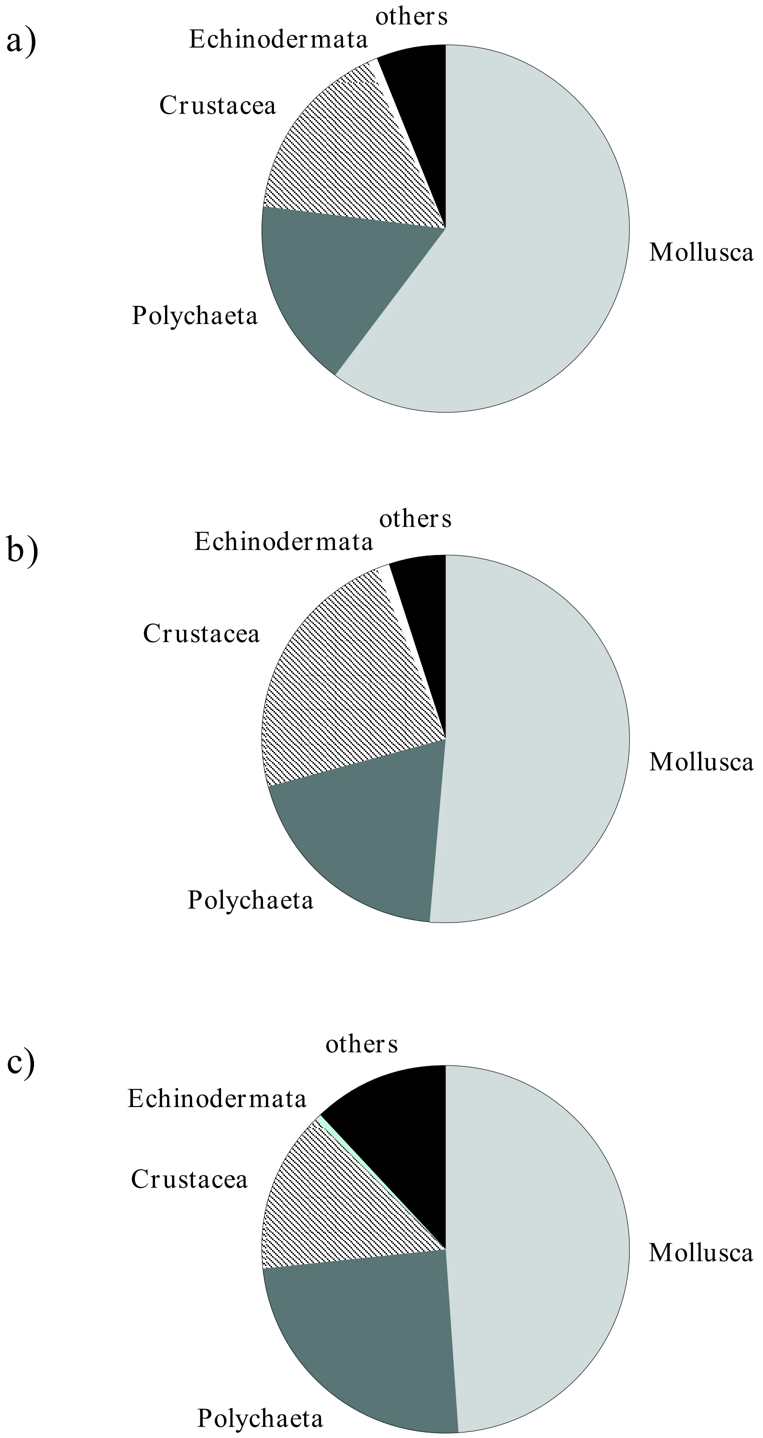


Figure 29: Overall biomass of major macro-zoobenthic groups for three different years; a) 1997, b) 1999, c) 1994 (after Jørgensen et al 1999)

4 Discussion

In the Kara Sea, biological production starts early in spring under land fastice and single year ice (Gradinger 1996, Werner & Arbizu 1999) which occupy large parts of the sea. During our cruises the maximum of discharge had already passed and the freshwater structured the southern Kara Sea. The distribution of the communities studied here mirrors the spreading of freshwater from the rivers in a north-eastern direction, along the eastern shorelines according to the general circulation patterns of the Yamal Current in the southern Kara Sea (Budgen et al. 1982, Pavlov & Pfirman 1995, Burenkov & Vasilkov 1995). This causes the hydrographic and biological gradients at least in the southern Kara Sea to run in a southeast-northwest direction rather than south to north. The structure of all three systems studied reflects the salinity gradient (Figs 22, 24, 27).

Table 9: Kara Sea, macrobenthic station groups. For each cluster, number of station investigated, total number of species, number of species per station, abundance per station, number of species who formed 90% of the cluster individuals [S(90%], names of character species. (Median values in parentheses)

Cluster	Number of stations	Species Cluster	Species stations	Abundance (ind.m^{-2})	S(90%)	Character species
SOUTH	7	26	2 - 12 (10)	112 - 1326 (860)	4	*Prionospio cirrifera* *Marenzelleria arctia*
WEST	20	155	15 -71 (35)	186 - 6882 (805)	30	*Diastylis sulcata*
EAST	22	109	5 - 46 (16)	140 - 874 (324)	14	*Micronephtys minuta*
NORTH	7	100	27 - 53 (36)	720 - 2015 (1140)	17	*Lumbrineris minuta* *Chaetozone setosa*

Phytoplankton biomass and species distribution showed a decrease from the rivers towards the Kara Sea with one exception: the bloom situation 1999 in the Ob estuary and the adjacent waters to the north. Although the numbers of species found were more or less the same in the rivers in the estuary and the Kara Sea, their total numbers and biomasses were much lower in the marine realm than in the rivers. Like Usachev (1947) cited in Zenkevitch (1963) we found diatoms and dinoflagellates as dominant groups of phytoplankton in the open Kara Sea.

However, he did not recognize small solitary living nanoflagellates and the autotrophic ciliate *Mesodinium rubrum*. The latter occurred frequently in our samples in the open Kara Sea. Single-cell nanoflagellates were encountered as well. The drastic change of species composition in the estuary from freshwater diatoms, bluegreens and chlorophytes to the marine phytoplankton on our longest transect in 2000 is mainly due to changing salinity respective waters masses. The results of integrated biomass showed with the exception of the southernmost riverine stations 2000 and the bloom in 1999 chlorophyll a values in summer were moderate (Nöthig et al., this volume). The model of the pelagic ecosystem of the Kara Sea (Lebedeva et al. 1995) based on published data and data of the Dimitry Mendeleev cruise (SPASIBA 1993) show very high phytoplankton biomasses at the end of June/ early July; a lower and later peak in the northern part of the Kara Sea from mid July to mid August. The decline of nutrients after the stratification is the main argument for the decline of phytoplankton productivity, zooplankton is responsible for the decline of the bloom as well. Since we had no data from earlier in the season - having a summer situation during the three years of investigation - it might be difficult to connect these findings with the zooplankton and benthic communities which grow on longer timescales.

With the exception in 1999, the phytoplankton biomass values during the three Boris Petrov cruises show a late summer situation. Similar chlorophyll a values had been obtained by Vedernikov et al.. (1995). In 1999, we assume an earlier developmental stage of the pelagic system. Nutrient data and surface salinity values support these. More freshwater with higher nutrients were found in 1999 than in 1997 and 2000 (Nöthig and Kattner 1998, in Stein and Stepanets 2000 & 2001).

Zooplankton assemblages showed a distinct change from a low number of freshwater species at the innermost stations of the estuaries to a maximum number in the mixing region where brackish water overlay marine water masses and hence inhabitants of both systems were present (Fig. 23). Finally the northern regions with the strongest marine characteristics were inhabited by slightly less 13 species. Surprisingly, despite large salinity differences, there was no effect of the two different depth layers on cluster analysis. This points to a wide range of salinity tolerance in many species. Our species inventory of the southern Kara Sea agrees well with earlier observations in the Kara Sea (Timofeev 1989, Vinogradov et al. 1995, Fetzer et al. in press) and in the Laptev Sea (Kosobokova et al. 1998, Lischka et al. 2001, Peters 2001). The great importance of crustaceans and especially the calanoid copepods seems to be typical for Arctic Seas (Timofeev 1989, Kosobokova et al. 1998, Kosobokova & Hirche 2000). As observed also in the Laptev Sea, the 2 copepod species *Drepanopus bungei* and *Limnocalanus macrurus* had mass occurrences in some regions and in different years. *D. bungei* was observed earlier only in the Eastsiberian Sea and as relict population in Lake Tuborg and fjords around Ellesmere Island (Bowman & Long 1968). *L. macrurus* is reported from many cold and deep freshwater lakes of the northern hemisphere, but is also quite common in the coastal waters of Canada, Siberia and Alaska (Bowman & Long 1973, Roff & Carter 1972, Løvik 1979, Vanderploeg et al. 1998).

The reproductive season for the shelf zooplankton living under land fastice or single year ice probably commences with the onset of ice algae blooms in spring (Werner & Arbizu 1999). During our cruises for many species all life stages were found, suggesting successful breeding within the estuaries. This was also observed by Vinogradov et al. (1995).

Similarly to phyto- and zooplankton, structure and composition of the macrobenthic assemblages change northwards from the estuaries of Ob and Yenisei to the central Kara Sea and are distinguished by the distribution of water masses (Filatova & Zenkevitch 1957, Cochrane et al. 1997, Jørgensen et al. 1999, Poltermann 1999, Denisenko et al., this volume). The long-term changes of benthic populations in the Kara Sea a described by Kiyko & Progrebov (1997). The benthic communities in the southern part of the estuaries are substantially different form the others, since the strong continental outflow restricted the penetration of stenohaline marine organisms into riverine environments, whereas brackish water species were kept off the central parts of the sea by the marine conditions. In the present investigation, 18% of the 1580 known Kara Sea invertebrates (Sirenko & Piepenburg 1994) were identified, with Polychaeta and Crustacea being by far the most dominant groups. The macro-zoobenthos communities are not specific for the Kara Sea, since the majority of the species are widely distributed on Arctic shelf areas (Dahle et al. 1998, Gukov et al. 1999). According to Jørgensen et al. (1999) the southern estuaries were dominated by single species, like the euryhaline polychaetes *Prionospio cirrifera* and *Marenzelleria arctia*. Areas with fluctuating environmental conditions are inhabited by benthic assemblages with high species dominance and low diversity, with opportunistic species dominating. Feder et al. (1994) indicated that differences in faunal diversity were mainly related to environmental stress. In spite of comparatively high diversity values, some stations of the brackish water assemblages were strongly dominated by euryhaline deposit feeders like the cumacean *Diastylis* cf *glabra* and the bivalve *Portlandia* cf *arctica*. Vassilenko (1989) recorded that the genus *Diastylis* are typical for Arctic estuaries with low salinity and relatively high summer temperatures. *Portlandia* species can be found in high abundances in the White Sea and all Eurasian shelf areas except the Chukchi Sea (Deubel 2000, Lubinsky 1980). These species are characteristic for areas of high sedimentation rates (Syvitski et al. 1989). The fauna of the central shelf was strongly dominated by polychaetes, especially by the character species *Lumbrineris minuta* and the deposit feeding *Chaetozone setosa*. Kendall (1996) recorded numerical dominance of *Lumbrineris* ssp. and *Chaetozone* ssp. also in the open waters around Svalbard. On the central Kara Sea shelf Echinodermata were area-wide distributed, but found only in low species number and in low abundances. As described in related investigations, Echinodermata are usually the dominant macrobenthic taxa in open Arctic shelf areas (Piepenburg & Schmid 1996 1997, Anisimova et al. 1996, Denisenko et al., this volume) and were found in high species number in the Kara Sea between 150 to 200 m water depths (Anisimova 1989).

4.1 Transect

Well-mixed tidal estuaries are generally characterized by the presence of a high turbidity tone in the region of low salinity. Suspended particulate matter mostly derived from riverine sources has a longer residence time than in the river upstream, changes in light climate, lower primary production than upstream or downstream. Different nutrient regimes and mixing dynamics may lead to a different spring bloom dynamics. Thus in 1997 highest chlorophyll concentrations were measured in the Yenisei Estuary (Nöthig & Kattner 1999). In 1999 a strong phytoplankton bloom was observed in the Ob Estuary, but not in the Yenisei Estuary (Larionov & Kodina 2000).

Due to lack of kowledge on the timing and biomasses attained for the spring bloom in the study area, it is impossible to describe the coupling of primary producers to other trophic levels and to the benthos. Information from sediment traps deployed from 1999 to 2000 (in Stein & Stepanets 2000, 2001) may eventually fill the gab. Higher values in the summertime in the rivers might be a result of permanent input of nutrients immediately taken up by the phytoplankton and thus not reaching the outer shelf. Another reason for the low phytoplankton biomass could be a close coupling of primary producers and grazers, although copepod biomass in the estuaries was relatively low (Fig. 30)

Horizontal gradients of abundance and biomass of planktonic and benthic organisms in estuaries depend strongly on physiological potential and/or food environment.

Longer residence time enhances breakdown of the land and freshwater derived organic matter load because of the large amount of mineral particles and associated bacteria. Along the transect studied zooplankton biomass was apparently decoupled from phytoplankton abundance, suggesting other factors than food controlling it. Indeed biomass distribution followed closely the hydrographic regime, with lowest values in the freshwater region and highest biomass, when marine oceanic forms such as the large *Calanus* species dominated the community. Similar distributions were also reported from the Laptev Sea (Kosobokova et al. 1998, Lischka et al. 2001), where a similar range of biomass was found. Large zooplankton biomass does not necessarily

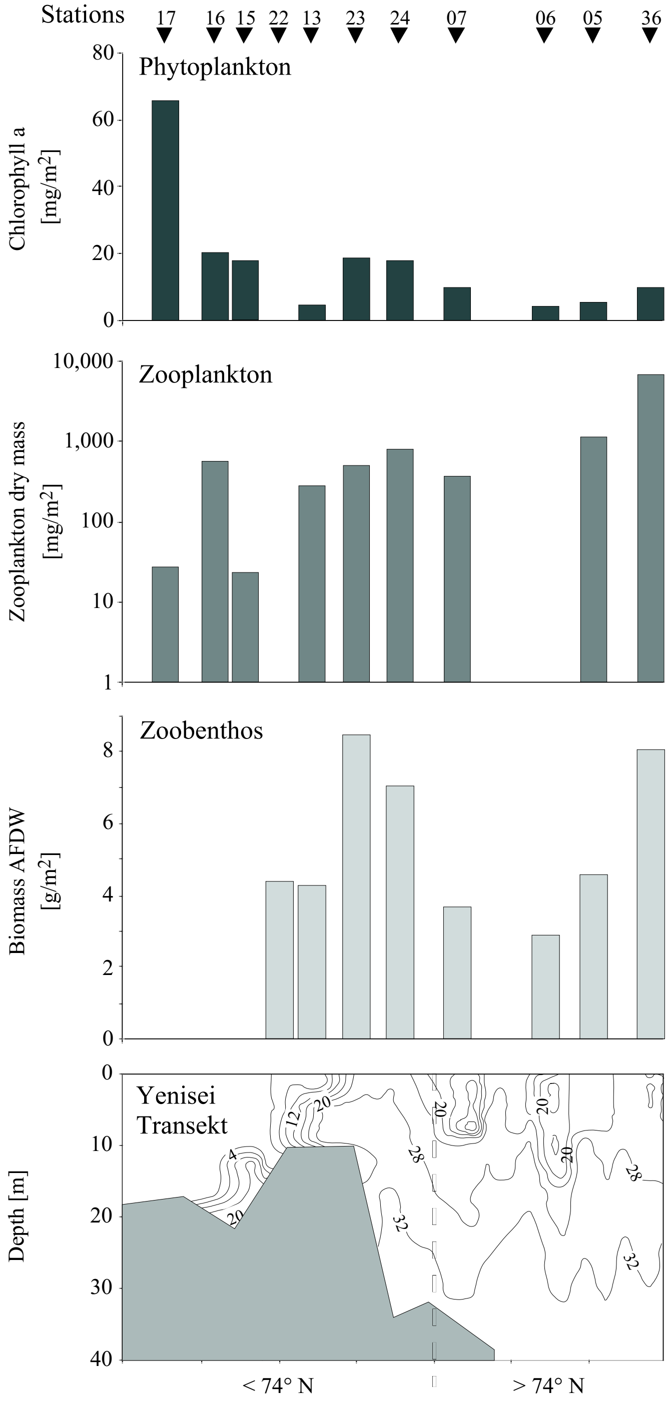


Figure 30: Biomass of phytoplankton (chlorophyll a), zooplankton (dry weight) and macrozoobenthos (AFDW) along a south-north transect during 2000 and salinity along the transect.

reflect high secondary productivity, which was hardly ever studied in Arctic estuaries. The large calanoids are able to survive long periods of food deprivation by using lipid deposits and maintain large standing stocks in the Arctic (Kosobokova & Hirche 2000). We rather assume that the smaller copepods in the brackish water regions take advantage of the food situation provided by the riverine input, although there is no direct support for this. For them it may be very difficult to build up large biomass, as their habitat undergoes strong seasonal changes in size. During winter at low freshwater discharge most of the brackissh water zone has disappeared. The estuarine copepods have to colonize the brackish water region *de novo* every year. Large outbursts of almost monospecific zooplankton populations close to the river mouths in the Kara Sea (this study) and the Laptev Sea (Peters 1991) show that they are able to respond rapidly to favorable conditions.

According to Cochrane et al. (1997) and Jørgensen et al. (1999) species number, abundance and diversity of macrobenthos increased from the estuarine bays in the south towards the open Kara Sea, which is consistent with studies from other estuaries and also fjords (Dahle et al. 1998, Holte & Gulliksen 1998, Petryashov et al. 1999). The distribution in macrobenthic biomass in the study area is similar to observations by Denisenko et al. (this volume). Grebmeier (1993) and Grebmeier & McRoy (1989) recorded that macrobenthic biomass was well correlated with production processes in the overlying water column. In the Yenisei Estuary highest macrobenthic biomass values occurred in the mixing zone of marine and riverine waters just south of 74°N, where large amounts of dissolved and particulate matter are transformed and sink to the sea floor. Lisitsin (1995) already described the attendant circumstances within the so-called “marginal filters”, where a combination of processes are responsible for the deposition of up to 90-95% of the suspended matter. Such significant import of organic matter supports allows a rich bottom fauna and high benthic biomasses. In regions of high sedimentation rates sea floor living organisms are important links within the bentho-pelagic coupling (see Klages et al., this volume). The rise of the biomass north of 74°N was mainly attributed to Echinodermata. Particularly the brittle star *Ophiocten sericeum* was observed quite regularly (see "*O. sericeum* community" in Denisenko et al., this volume), but found only in still contestable low abundances, since these taxon is not very tolerant to estuary environments. Extremely high densities of *O. sericeum* were reported from adjacent shelf areas, where abundances can exceed 2800 ind.m^{-2} in the Barents Sea and 500 ind.m^{-2} in the Laptev Sea (Piepenburg & Schmid 1996, 1997). The similarity in the occurrence of *O. sericeum* and the holothurian *Myriothrochus rinkii* in the narrow and deeper outer Yenisei Estuary may be a result of the prevailing hydrographical conditions with near-bottom advection of marine water moves southwards up to 72.30°N (Harms & Karcher 1999), which is supported by the fact that Ophiopluteus larvae were dominant within the meroplankton there (see Fetzer, this volume).

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5.3 Publication III

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

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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 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.

Table 10: Station number, position, depth, depth of halocline, meroplankton abundances (ind m^{-3}) 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.

Station label	Date day/ month	Lat N	Lon E	Depth [m]	Depth of Halocline [m]	Abundances ind. m^{-3}	Number of Species [S]
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

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 31).

Larval plankton was collected with a Nansen Closing Net (NCN) at 11 stations using 55μm mesh size and an opening of 70cm diameter (Table 10). 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).

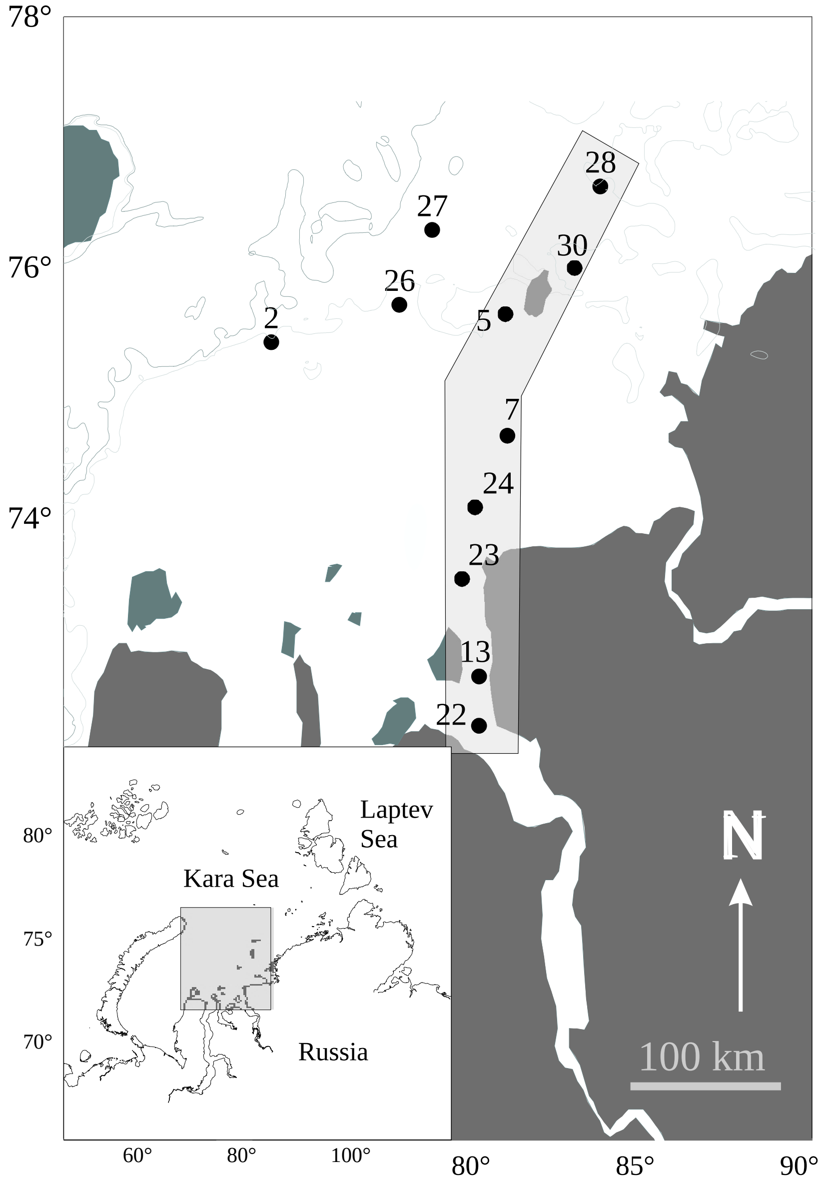

Figure 31: Map of the study area with all meroplankton stations in the central Kara Sea. The investigated transect out of the innerYenisei Estuary to the central Kara Sea is highlighted. The isolines on the map represent 50m and 100m depth lines, respectively

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^{-3} (ind. m^{-3}) for meroplankton (Table 11) and individuals m^{-2} (ind. m^{-2}) for benthos (Figure 35). For better comparison of meroplankton densities with earlier investigations the meroplankton data are also given in cumulative abundances (m^{-2}; Table 10).

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 11). The identified specimens were taxonomically grouped according to Westheide & Rieger (1996).

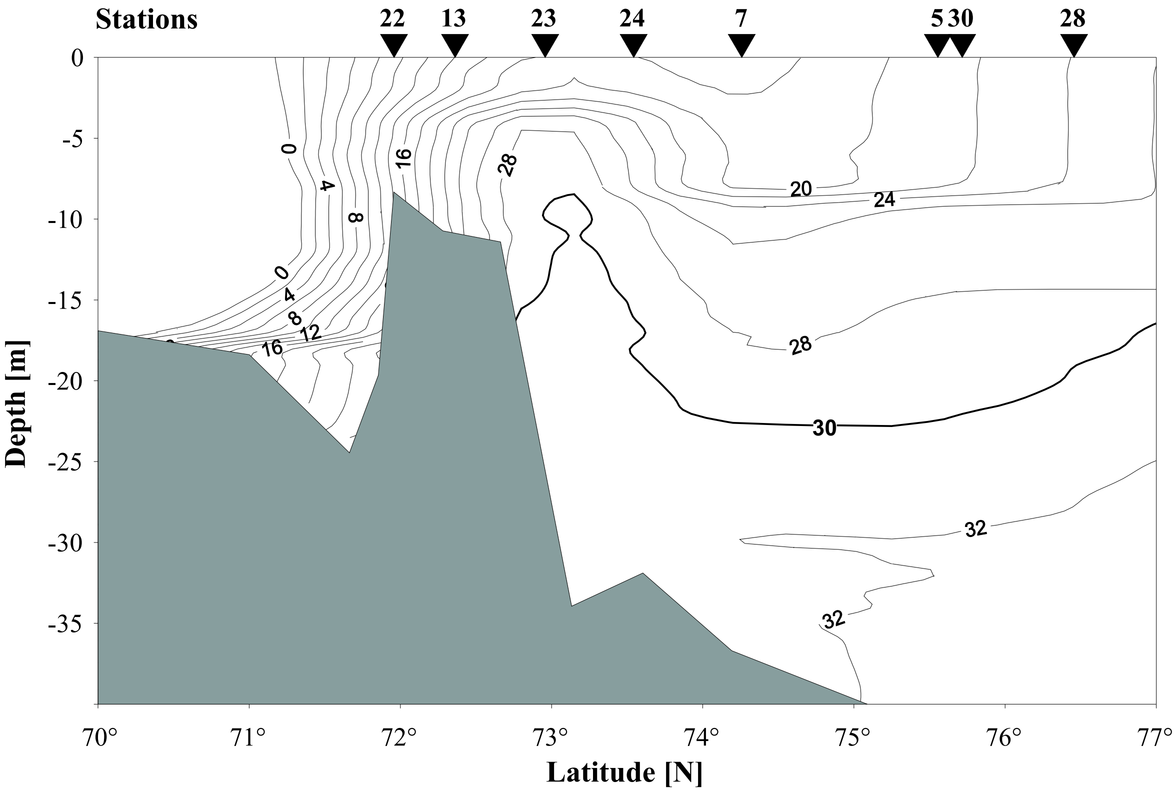

Figure 32: Latitudinal salinity profile of the transect from the inner Yenisei Estuary to the central Kara Sea showing the depth and the positions of stations.

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 31). 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 lavae 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 32). 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 11). 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 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.

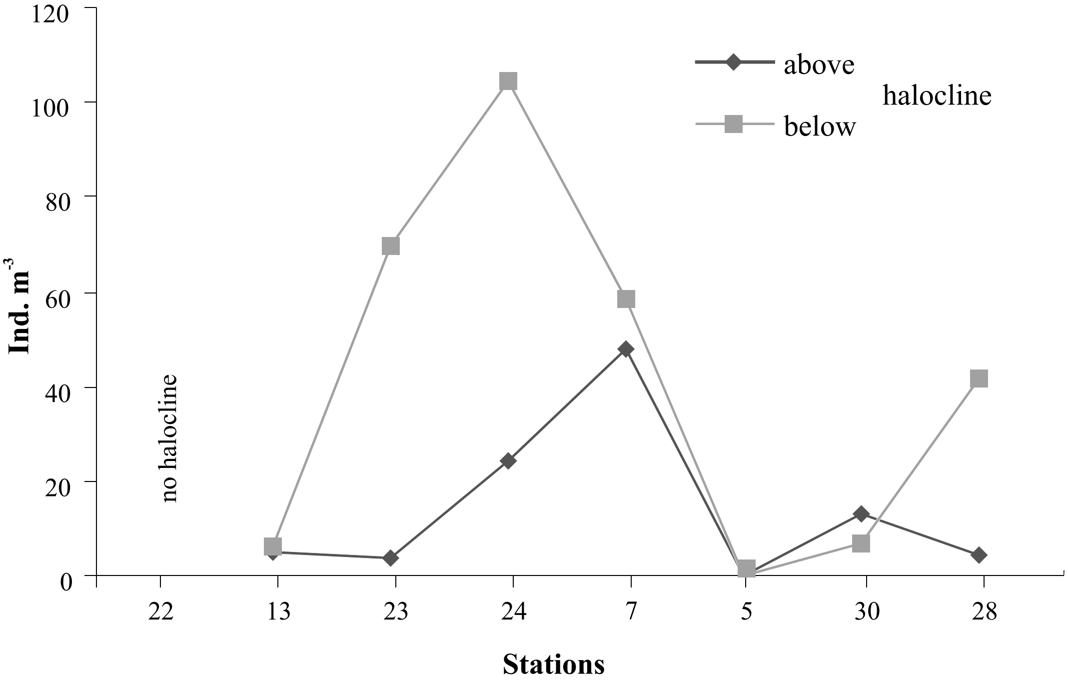

Figure 33: Total meroplankton abundances (ind m^{-3}) on the stations above and below the halocline of the transect from the inner Yenisei Estuary to the central Kara Sea.

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^{-3} (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

Table 11: 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).

Taxa				**Rel Abundance**	**Min**	**Max**	**occuring layer**
				%	**ind. m^{-3}**	**ind. m^{-3}**	
Cnidaria	**Hydrozoa**		**Actinula larvae**	0.3	0.1	0.6	b
	Anthozoa		***Cerianthus* cf *loydii***	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	***Eteone longa***	<0.1	*	0.1	b
			***Gattyana* sp.**	1.4	0.4	3.8	a/b
			***Glycera* sp.**	<0.1	*	0.2	b
			***Harmothoe* sp.**	<0.1	*	0.2	b
			***Nephtys* sp.**	2.1	0.1	3.4	a/b
			***Nereis* sp.**	0.3	0.1	0.7	a/b
			Pholoe* cf. *minuta	1.4	0.1	5.2	a/b
			Phyllodoce* cf. *groenlandica	5.3	0.1	9.9	a/b
			spherical Trochophora	4.6	0.3	7.1	a/b
			***Scoloplos* 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	0.1	0.6	a/b
Nemathelmintes	**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

the case for the ’Trochophora 1’ (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 33). Somehow Station 5 seems exceptional since the nearby Stations 26 and 27 showed high densities (Table 10). Towards Stations 28 the abundance increased again to 40 ind. m^{-3} (above) and 5 ind. m^{-3} (below), respectively. The species numbers followed about this same pattern (Table 10).

Total abundances along the transect showed generally higher concentrations of larvae in the lower more saline water layer (Figure 33). 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 34a). 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 34b). 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 35).

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^{-3}. The highest abundances of larvae were found at Stations 23, 24 and 28, but only with very few (<1 ind. m^{-3}) 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 36c). The larvae had their main distribution in the northern area, but a larval ’plume’ extends to the area further south into the estuary (Figure 36a). Below the halocline, the highest densities were found close to Stations 24 and 7 (Figure 36b).

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.

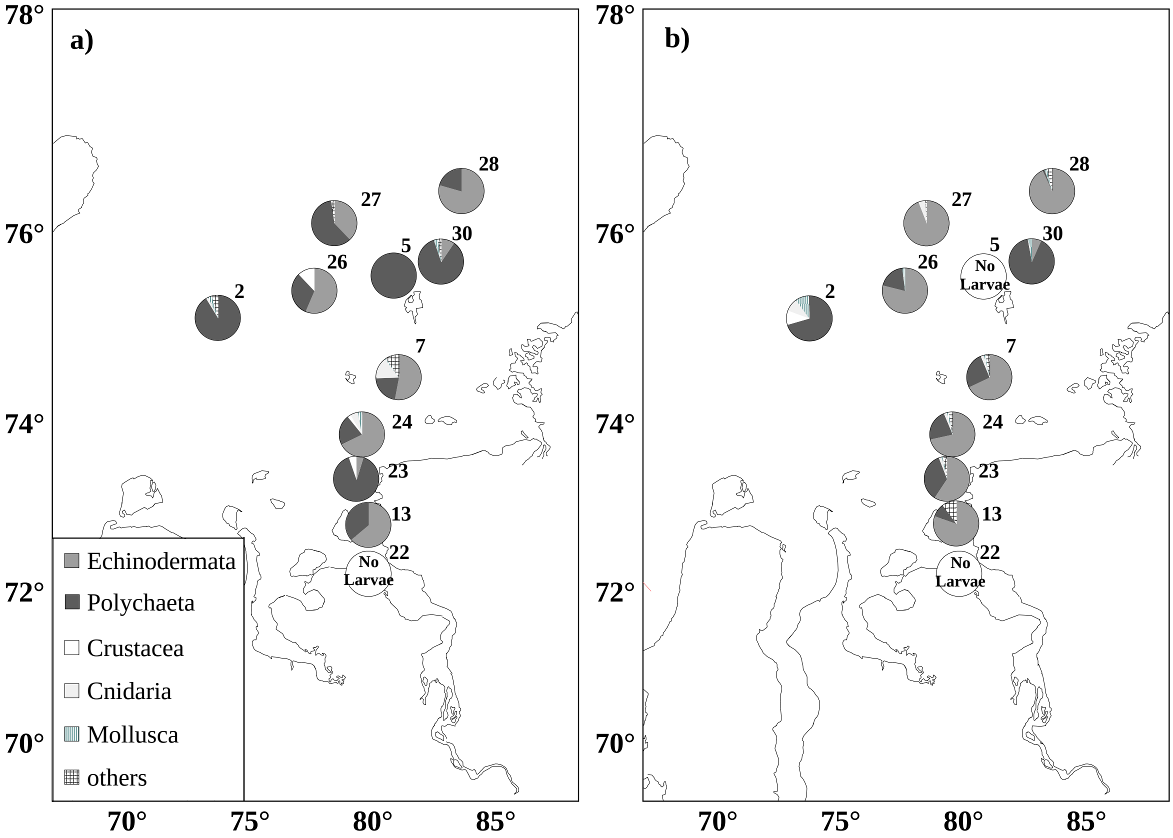

Figure 34: Relative group abundances a) above and b) below the halocline of all meroplankton stations.

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^{-3} which reveals to 13,000 ind. m^{-2}) of investigations done by Thorson (1946), who reported densities of 17,500 ind. m^{-2} for the Danish Sea. Although in some Arctic fjords peaks of >500,000 ind. m^{-2} 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

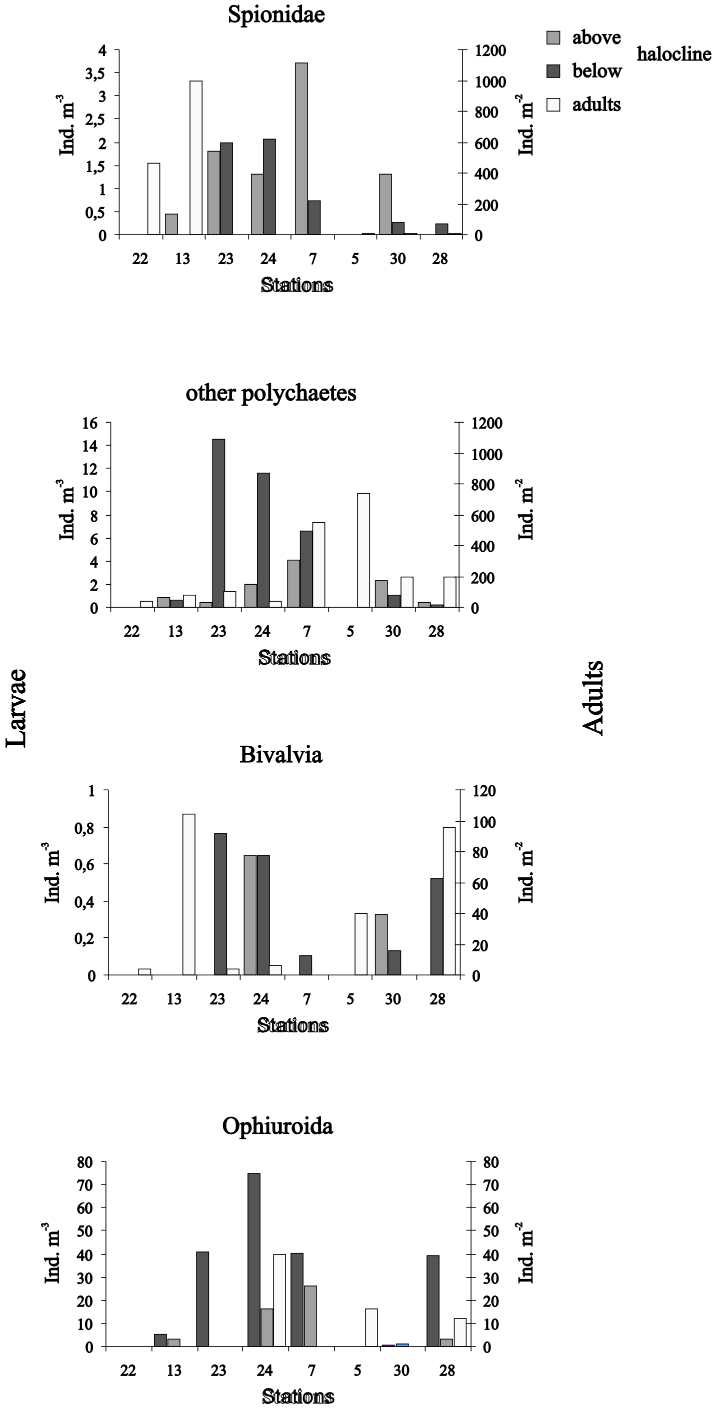

Figure 35: Distribution of absolute abundances of larvae (ind m^{-3}) above/below the halocline and adults (ind m^{-2}) of Spionida, ’other polychaetes’, Bivalvia and Ophiuorida along the transect from the inner Yenisei Estuary to the central Kara Sea.

1994 within the Yenisei Estuary did not report any occurrence of echinoderm larvae. The maximum densities of echinoderm larvae (~75 ind. m^{-3} at Station 27) we found were similar to observations done by Schlüter & Rachor (2001), who found maximum densities of 50 ind. m^{-3}.

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 dis-

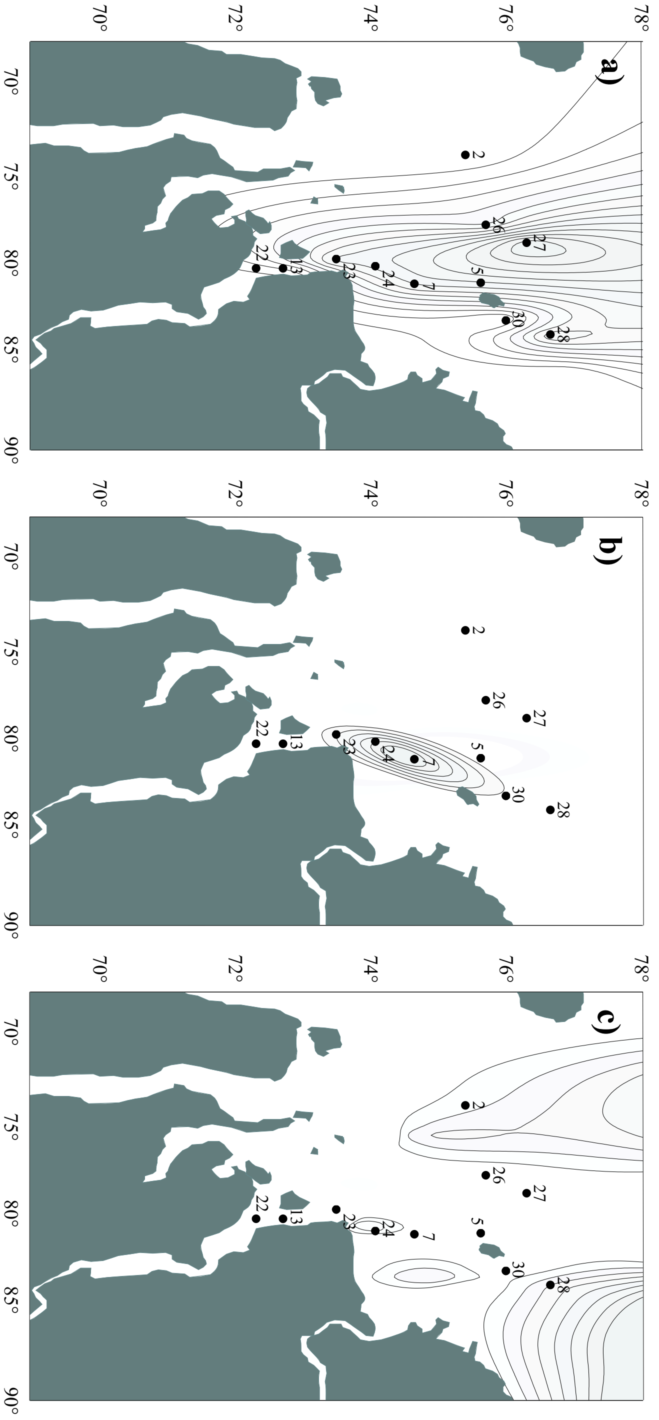

Figure 36: Spatial distribution of Ophiuroida larvae a) above and b) below the halocline and c) adults in the study area. Iso-lines show areas of equal densities. No values are given since the plot is only intended to reveal trends.

tance 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 10cm 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 1500 km 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 hypothise 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 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° 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.

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5.4 Publication IV

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Effect of river run-off on the distribution of marine invertebrate larvae in Arctic shelf seas

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Abstract

River outlets are favoured by many planktonic and benthic organisms due to their high discharge organic carbon fostering food availability. Especially in oligotroph arctic areas estuaries enhance the establishment of benthic communities. Retention of larvae of benthic invertebrates within nursery grounds and/or the ability to return to their parental grounds prior to settlement is an important factor in communities' persistence. The aim of this study is to determine the capability of invertebrates in the Kara Sea and the influence of the spatial distribution of their larvae and settled juveniles on the shape of these communities. The physical environment is strongly influenced by high freshwater input of the Rivers Ob and Yenisei and this riverine freshwater discharge creates strong physical or physiological barriers for larvae. The distribution of adults releasing larvae and juveniles of the brittle star *Ophiocten sericeum*, and the polychaetes *Micronephtys* c.f. *minuta*, *Nereimyra* c.f. *aphroditoides*, *Phyllodoce groenlandica* and *Prionospio* c.f. *cirrifera* were estimated in the water column and on the bottom. Spatial interpolating was performed by krigging. The hydrographical regime during the sampling period revealed a pronounced bi-layered structure with fresh/brackish water layer on top and a high saline marine layer below. Adults *O. sericeum* were restricted to the northern, not river influenced parts while larvae were found exclusively in the upper brackish water layers. Freshwater discharge retains larvae of *N. aphroditoides* and *P. groenlandica* to the areas where juveniles and adults of these species were found. Larvae and juveniles of *M. minuta* were evenly distributed across the observed area showing no influence by the run-off. While adults of the *P. cirrifera* were exclusively found in the estuary of Yenisei River, larvae of *P. cirrifera* were only found in the upper water layers most probably taking advantage of the prevailing near bottom counter current returning to their hattching areas.

Keywords: Kara Sea, juvenile distribution, larvae, meroplankton, benthos, hydrography, estuary, *Ophiocten sericeum*, *Micronephtys minuta*, *Nereimyra aphroditoides*, *Phyllodoce groenlandica*, *Prionospio cirrifera*, interpolation, kriging

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1 Introduction

Retention of larvae of benthic invertebrates within nursery areas and/or the ability to return to their parental grounds prior to settlement is an important factor in communities' persistence. This especially applies for many estuarine species in freshwater influenced areas, where the net seaward flow presents a great challenge to larvae not to get flushed out of their habitat (Laprise & Dotson 1994, Bilton et al. 2002). Larval behaviour, such as daily vertical migration (e.g. Banse 1964, Sulkin 1984), adapted to the estuarine flow field adjudicate whether the larvae will be retained or even enter an estuarine realm (Anger et al. 1994). It was shown that many larvae of estuarine crab species undertake endogenously controlled tidal vertical migrations, upward on floods downward on ebbs to counteract net seaward transport (Cronin & Forward 1986, Tankersley & Forward 1994). In estuaries showing a bi-layered flow, ontogenetic changes in larval behaviour facilitates upstream transport by compensatory currents (Thiébaut et al. 1992, Moore 1977). Currents may generally enhance larval dispersal but also create physical barriers (e.g. density gradients, mixing zones) restricting the spreading of larvae (Scheltema 1988).

Hydrodynamic processes alone can passively accumulate small planktonic larvae that may not be able to overcome local flow or density regimes. The asymmetry of the tidal flow field during ebb and flood within the estuary may cause retention or even net up stream transport of inactive particles (Chen et al. 1997). Hence, even passive larvae might be retained if they sink towards the bottom on ebb tides and are re-suspended on more energetic flood tides (DeWolf 1974, Chen et al. 1997). The above-mentioned mechanism may also account for the occurrence of larvae of marine origin as they are accidentally transported into estuaries where they have to face unfavourable conditions. This has been shown crucial for plankton organisms in melt water-influenced fjords (Weslawski & Legezynska 1998, Weslawski et al. 2000).

Physical structuring of the water column can cause redistribution of the planktonic organisms through mixing, or it can isolate biological communities from neighbouring water masses. Entrainment of plankton organisms within meso-scale eddies has been demonstrated in a number of studies (e.g. Trinast 1970, McGowan 1967, Wiebe et al. 1976). Thus, larvae can be dislocated from their spawning area into unsuitable habitats. This, however, is still more obvious in freshwater influenced areas producing strong hydrographical gradients between fresh- and marine waters acting as barriers for the larvae.

In arctic areas, gradients may be even more pronounced. Here not only saline differences account for establishing boundaries but also temperature show great differences, which enhance barriers. Arctic marine waters are found all year round at temperatures below zero while the freshwater encountered in estuaries, usually originated from much warmer areas. Thus, stronger hydrographical clines are established.

Another characteristic of Arctic estuaries is strong annual fluctuation in freshwater input from the rivers. River discharge increases in late spring to early summer and rapidly decreases to autumn with very little input during winter (Pavlov & Pfirman 1995). Thus, a pronounced bi-layered water column is established in summer, additionally enhanced by melting sea ice (Pivovarov et al. 2003).

River outlets are favoured by many planktonic and benthic organisms due to their high discharge of nutrients and organic carbon fostering food availability (Klages et al. 2003). Additionally estuaries serve for many euryhaline species as refuge to scavengers and reduce inter-specific food competitors. Enhanced food availability especially in such oligotroph regions as the Arctic Seas also promote food availability of planktotrophic larvae and such enhance reproduction success of benthic species.

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 and can last from several hours in some Spionida (Blake & Arnofsky 1999) to six months after hatching in some Ophiuroids (Pearse 1969). The length of larval life even within a species varies widely - many species can delay settlement for several additional months if no suitable habitat is found (e.g. Chia 1974, Pearse 1969, Pearse et al. 1991). The duration in the plankton is determining the distance the larvae can be transported (Mileikovsky 1960, 1966).

The aim of this study is to determine the capability of invertebrates in the Kara Sea and the influence of the spatial distribution of their larvae and settled juveniles on the shape of these communities. The environment is strongly influenced by high freshwater input of the Rivers Ob and Yenisei and this riverine freshwater discharge creates strong physical or physiological barriers for larvae. The peculiar hydrographical situation created by the 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 of adult populations.

2 Materials and Methods

2.1 Study area

The Kara Sea is a marginal shelf area located in the Eurasian part of the Arctic Ocean (Fig. 37). It is influenced by oceanic water masses from the Arctic Ocean, the North Atlantic and the Barents

Sea. Additionally the Kara Sea receives large amounts of freshwater through the Siberian rivers Ob and Yenisei (Harms et al. 2003).

Except for the summer months (Jun-Aug) the Kara Sea is ice covered about 9 months of the year (Blanchet et al. 1995). Ice formation usually starts at the end of October. Break up coincides with main river discharge of the two adjacent rivers Ob and Yenisei in early to late June (Mironov et al. 1994). The large freshwater run-off and strong ice melting causes intense vertical haline stratification (Harms et al. 2000). 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 & Pfirman 1995, Gordeev et al. 1996). Seasonal changing wind fields are reported to have a strong effect on general hydrography and variability of currents (Harms et al. 2000). The dominating wind direction in summer is from north to northeast shaping an anti-cyclonic circulation pattern. Towards the end of the year in winter and autumn the prevailing wind direction more or less reverses. It changes to southwest creating a cyclonic surface circulation pattern flushing the Kara Sea water from southwest to northeast (Harms & Karcher 1999, Harms et al. 2000).

2.2 Sampling of meroplankton

Samples were collected at 15 stations during the cruise with R/V 'Akademik Boris Petrov' in the south-eastern Kara Sea from 4 to 19 September 2000 (Stein & Stephanets 2001). A Nansen closing net was used (0.442 m2 catching area, 55 μm mesh size; 0.5 m s^{-1} hauling speed) for meroplankton sampling. At each station, one haul below and above the pycnocline was carried out. 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 the sediment of 3-6 tubes was taken and subsequently separated into fractions of 500/250/125μm by wet sieving.

Adult organisms were sampled with a Large Box Corer (0.25 m^2) and animals were extracted by sieving the sediments over 500μm screen. For the determination of distribution and abundance, all samples were preserved in 4% borax-buffered formaline. All adult and juvenile benthic organisms were identified to the lowest feasible taxon, counted and measured separately under a stereomicroscope. Meroplanktonic larvae were picked out the plankton samples, identified and also measured. In Ophioplutei the length of the lateral arms were measured. For present juvenile Ophiuorids disc diameter was recorded. Juveniles Ophiuorida were found both floating in the water column and settled on the substratum. For polychaete larvae and juveniles additionally the number of segments was reported. Juveniles were defined as all specimens not larger than $^1/_3$ of the species adult size given in literature. Specimens from parallel Multicorer tubes were pooled and their numbers averaged. Counted abundances were calculated to ind. m^{-3} for meroplanktonic larvae and ind. m^{-2} for adults and juveniles, respectively.

In order to get as adequate distribution as possible accumulated data of adult fauna from expeditions 1997, 1999, 2000 were taken (Deubel & Poltermann 1999, Deubel 2000, Lubin & Eckert 2001, but see also Deubel et al. 2003, Klages et al. 2003). This seems admissible since most benthic organisms of Arctic realms are relatively long living and communities do not show great inter-annual fluctuations (Deubel et al. 2003).

To determine range and size at settlement for larvae minimum mean and maximum size for each species was calculated. For polychaetes additionally the minimum mean and maximum number of segments were estimated.

To gain a better understanding of the distribution of adults, juveniles and larvae, abundances between withing the sample area was interpolated by statistical gridding method. The interpolation methods termed ’Kriging’ was chosen since it seems best to reflect the biological situation in the investigation area. The method interpolates data on weighted means basis, but additionally tries to detect trends between data points. In relation to other gridding methods this method best to depict spatially irregularly distributed data as our sampling station net (Abramowitz & Stegun 1972, Isaaks & Srivastava 1989).

In this study, results of the five most abundant larval species are presented. Those were (in order of abundances) the brittle star *Ophiocten sericeum*, and the polychaetes *Micronephtys* c.f. *minuta*, *Nereimyra* c.f. *aphroditoides*, *Phyllodoce groenlandica* and *Prionospio* c.f. *cirrifera*.

Descriptions of meroplankters in Arctic areas are generally rare. Good morphological descriptions are found for the larvae of the highly abundant brittle star *Ophiocten sericeum* (Thorson 1934, Semenova et al. 1964). While for the larvae of *N. aphroditoides* (formerly described by Thorson (1934) and Banse (1955) as *Castalia punctata* (see Andersen 1984)), *P. groenlandica* and *P. cirrifera* good descriptions exist in literature (e.g. Thorson 1934, Andersen 1984) nothing is known about the larvae of *M. minuta*. Adults of *M. minuta* were very common on the Kara Sea shelf and the only species occurring within the taxon Nephtidae (Poltermann et al 1999, Deubel 2000, Lubin & Eckert 2001, but see also Deubel et al. 2003). Except a remark in Hartmann-Schröder (1996) about an indirect reproduction in this species nothing is found in literature. The very abundant nephtid larvae must therefore resemble the larvae of *M.minuta*.

3 Results

3.1 Topography and hydrography

Depth of the investigated areas in the south-eastern Kara Sea varied from 6m in the estuary of the Yenisei River (Station 16) to 78m at the north-western rim of the area (Station 2). At most stations average depth did not exceed 30-50m (Tab. 12). During the sampling period, weather conditions were bad with high waves and prevailing strong easterly winds. In the north-eastern part between 75°N and 85°E, some sea/pack ice occurred and prevented further sampling.

The hydrographical regime during the sampling period revealed a pronounced bi-layered structure with a fresh/brackish water layer on top and a high saline (>30psu) marine layer below (Fig. 38). The average depth of pycnocline was at about 10m getting slightly shallower as mixing processes proceeds towards the northern shelf. The top layer increased in salinity from 0 to >25psu from south to north while temperature decreased from 11° to <2°C (Fig. 38). In the northern part, water masses got less saline again due to melting sea/pack ice we encountered there. Saline bottom waters penetrated to 71° N into the river (for more details see Stephansev & Shmelkov 2001).

3.2 Size ranges

Size in *Ophiocten sericeum* larvae ranged from 550μm to 1950μm lateral rod length (Tab. 13). For this species also the highest number of individuals was measured (N=1114 individuals). For the floating juveniles a disk diameter between 280 - 680μm was recorded. But here only 13 specimens were found in all samples. Larval ranges from 808 metatrochopores of *Micronephtys minuta* varied between 120 - 990μm in size and owned segment numbers between 0 - 11 chaetigers. Present larvae of *Nereimyra aphrodioides* had almost the same size range (180 - 810) as *M. minuta*. In *Phyllodoce groenlandica* and *Prionospio cirrifera* the biggest larvae showing maxima of 1420μm and 2700μm respectively and the highest number of chaetigers were found for all investigated species.

For juvenile *O. sericeum* disk diameter varied between 310 - 950μm (Tab. 14). As with larvae juveniles of *M. minuta* and *N. aphroditoides* showed the same size range and number of segments. The size of the juveniles of *M. minuta* fluctuated between 420 - 4000μm and 7 - 26 segments. For *N. aphroditoides* juvenile sizes ranged between 300 - 4700μm (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 350μm and 8800μm were recorded. For spionid *P. cirrifera* no juveniles were found.

3.3 Species distribution

The most abundant species concerning larvae and adults was the brittle star *Ophiocten sericeum*. Larvae of this species were found mainly in the upper water masses in almost all net samples except for the inner estuary (Fig. 39). Maximum densities of up to 200 ind. m^{-3} (Station 35) were found. Generally, there was a trend to higher abundances from the southern estuarine part to the northern region. With exception of a few specimens at station 7 no animals below the pycnocline were present.

Adults were distributed generally in the north-eastern part reaching maximum values of 150 ind. m^{-2}. Few animals were also found in the north-western part, between the wake of the two rivers. Floating juveniles of *O. sericeum* occurred exclusively in the upper waters in the north-eastern part of the investigated area (Fig. 40). At two north-eastern stations abundances of 1 ind. m^{-3} were found in the plankton hauls. In the lower waters only very few specimens have been detected.

Distribution of juveniles revealed a different picture. Newly settled animals were also exclusively found in the northern area showing up to 600 Ind. m^{-2}. In contrary to the adults were populations establish more in the western part Larvae of *Micronephtys* c.f. *minuta* concentrated mainly in the northern and western part (Fig. 41). Highest concentrations have been 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, 4 ind. m^{-3} were found. Juveniles of this species were found in very high abundances (4000 ind. m^{-2}) equally distributed on all stations of the investigated area. This was the highest density with respect to settled juveniles found within 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 *Nereimyra aphroditoides* had their main distribution at stations 23 and 35 with 8 ind. m^{-3} (Fig. 42). Below the pycnocline single specimen were found occasionally in the nets. However, juvenile settlers were present in high abundances of up to 350 ind. m^{-2} in the northern region of the area, with decreasing abundances from the south.

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

A similar distribution pattern was found among larvae of *Phyllodoce groenlandica* (Fig. 43). Up to 0.6 ind. m^{-3} were found in the north-eastern 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 interestuary area. 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*.

The only species occurring with higher abundances below the pycnocline were larvae of the spionid *Prionospio cirrifera* (Fig. 44). 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 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 800 ind. m^{-2}.

4 Discussion

Interpolation of the data may not display distribution in reality (especially on small scales). A better spatial resolution could only be achieved through massive sampling of a dense station grid covering the explored area. Nevertheless, on large scales and with scarcely distributed data interpolation gives feasible results. Event though the kriging method used is known to be an exact interpolator (exact interpolators honour data points exactly when the point coincides with the grid node being interpolated) but due to its feature to interpret trends it may create results much higher as the one found in the fields. However, this was not the case for the data in this study. Since the data points were classified into defined groups the interpolation sometimes even resulted in slightly lower estimates than found.

Additionally distribution of meroplankton is only of short temporary character and reflects only the local distribution at the moment of sampling. Conclusions have thus to be taken with care.

4.1 Physical conditions

Meroplanktonic organisms are subject to passive transport processes since they are mainly very weak swimmers (Pedotti & Fenaux 1992). Therefore, good knowledge of hydrography and especially prevailing currents are necessary to understand larvae distribution patterns in comparison with the community arrangement of the adults, origin and further fate of the organisms.

Salinity distribution in the observed area showed a typical late summer situation with a pronounced brackish water layer on the surface and a high saline bottom layer as described by Harms et al. (1999). In addition, prevailing strong easterly winds (Stein & Stephanets 2001) indicate the summer situation since autumn and winter is characterised by strong south-westerly winds (Harms et al. 2001). The outflow of the Yenisei River is already deflected to the east indicating that the river run-off has already passed its maximum discharge (Pavlov & 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 due the Coriolis effect, the Yenisei shows a rather straight run-off discharging into the Central Kara Sea during spring and summer. Harms & Karcher (1999) explained this feature by prevailing north-easterly wind fields causing an Ekman deflection of the currents to the west together with the topography of the Yenisei River. Generally, the Ob River behaves in the same way, although being much weaker. In contrast to the Yenisei, which has a narrow and deep opening, the shape of the Ob Estuary is shallow and rather broad. The estuary's shape together with a much smaller run-off volume (Pavlov & Pfirman 1995, Harms et al. 2000) results in a lesser deflection of the Ob discharge to the east.

General surface flow of the Kara Sea in spring and summer is anti-clockwise with very strong currents close to the river estuaries. Anti-cyclonic wind fields and strong river run-off mainly create these patterns. In autumn and winter, a contrary situation is present leading to a north-western flow of surface currents. Freshwater from the rivers follows the Siberian coast to the Vilkitzky Strait and is imported into the Laptev Sea.

The horizontal transition zone between freshwater and brackish water in the Yenisei, as observed in summer 2000, was located between 71° 30'-72° N which has been reported earlier at periods with high outflow (Stanovoy & Nøst 2002).

Penetration of high saline water deep into the Yenisei Estuary is the result of a near bottom counter flow as predicted by the models of Harms & Karcher (1999). The inflow of high saline marine waters into the Ob and Yenisei Rivers has already been noted in earlier descriptions of the hydrological regimes of these areas by Antonov (1962) and Antonov & Maslaeva (1965). It has also been subject to more recent investigations (e.g. Ivanova 1984, Stanovoy 1984, Ivanov & Sviyatsky 1987). Harms et al. (2003) reported this phenomenon as a result of strong river run-off creating a strong onshore counter flow close to the bottom reaching velocities of 5-10 cm s^{-1}. It follows the Siberian shores into the Yenisei estuary and reaches its strongest characteristics in late summer and early autumn (Harms & Karcher 1999). This feature has formerly been reported for areas with strong baroclynic pressure gradients as enclosed areas, such as shallow estuaries and fjords (Moore 1977, Weslawski & Legezynska 1998, Weslawski et al. 2000). Since tidal forces in the realm are very weak, this counter flow is mainly responsible for the transport of re-suspended particles into the estuary (Harms & Karcher 2003).

For a more detailed description of seasonal variability of Kara Sea currents, see Harms & Karcher (1999) and Harms et al. (2000, 2003).

4.2 Distribution of larvae, juveniles and adults

Ophiocten sericeum

All larvae, except those of *P. cirrifera* were found with highest abundances in the upper water column where salinity did not exceed 25psu (Fig. 38 and Fig. 39).

Larvae of *O. sericeum* revealed the highest abundances of all found larvae. In studies by Thorson (1946) in Greenlandic fjords, larvae of *O. sericeum* played only a subordinate role. Further plankton investigations done by Formin (1989) reported ophioplutei in the Kara Sea to be present throughout the year. Also Thorson (1946) found larvae of *O. sericeum* throughout the year in Greenlandic fjords, except in February where no larvae were present. In the northernmost areas larval densities of 200 ind. m^{-3} were found, which is much higher than reported from any earlier studies. Schlüter & Rachor (2001) found a maximum of 50 ind. m^{-3} in the upper water masses near the ice edge. Also in our study the highest abundances were found near an 'ice edge': During the cruise we encountered drifting ice at the northernmost station indicated by less saline and cooler surface waters due to melting (Fig. 38). It is unclear whether the larvae are physically trapped in the melt water zone or if they somehow actively move into these areas to utilise higher food availability at edge zones (Weslawski et al. 1997). Phytoplankton investigations did not reveal significantly higher primary production (Makarevich & Larionov 2001, Deubel et al. 2003) in the northern areas, indicating that the latter is probably less realistic. Also Clough et al. (1997) and Schlüter & Rachor (2001) did not find any significant correlation between abundance of meroplankters and food availability at an ice edges during investigations in the Barents Sea. Gallagher et al. (1996) reported that passive drifter as ophiopluteus larvae, which are usually randomly distributed in uniform water bodies, tend to accumulate at interfaces between water masses and are not able to pass them. Banse (1964) hypothesised that larvae are retained in the water masses into which they are spawned.

These significant higher abundances in the northern areas might be due to the fact that the origin of larvae is most probably located in the shallow shelf areas north and east towards the Taymyr peninsula and the Vilkitsky Strait. Adult densities up to 566 ind. m^{-2} were reported from the adjacent Laptev Sea (Piepenburg & Schmidt, 1997). Lubin & Eckert (2001) found occurrences of 200 ind. m^{-2} in the Kara Sea. Ophiuroid eggs and developing larvae are strongly positive buoyant (Hendler 1991,Westheide & Rieger 1996), explaining why few larvae are found in the lower water masses (Fetzer 2003). After spawning and hatching on the northern shelf areas larvae are most probably driven into the Kara Sea by the prevailing north-eastern wind causing also the found thinning of the densities to the south and west.

Although Ophiuroids have a developmental time of about 2-3 weeks in temperate waters Pearse (1969) reported developmental times up to six month after hatching in *O. sericeum*. Harms & Karcher (1999) calculated an average current speed for the Kara Sea of 10cm s^{-1}. According to this a larvae may drift more than 1500km until metamorphosis. Currents may even be enhanced in ice-free wind-driven areas. Keeping this in mind the larvae found most probably do not belong to single isolated population but rather to a metapopulation (see Bortsford et al. 1994) spreading over the whole Siberian Arctic shelf area (Piepenburg & Schmidt 1996, 1997). As larvae come into a competent stage and metamorphose (the juvenile is growing as bud on the larval body and later assimilates the larval tissue), they still keep floating for a certain period (Fig. 40). Later, as they grow they sink to the bottom (Gallager et al. 1996). The fact that all found juveniles were rather small (mean size disk diameter = 456μm), having only rudimentary podia and that they were found exclusively in the upper water layers indicates their recent metamorphosis.

Gallager et al. (1996), using an Optical Plankton Recorder (OPR), found drifting juveniles exclusively in water masses where larvae were virtually absent. This could not be confirmed in our study.

Adult Ophiuroida are known to be very stenohaline avoiding areas with instable salinities (as e.g. the mouth of the rivers were freshwater of the rivers may reach the bottom during flushing events, Piepenburg & Schmidt 1997). Deubel et al. (2003) and Denisenko et al. (2003) reported high abundances of *O. sericeum* only north of 74° N. The same holds true for settling juveniles since we found them only in the northern area. However, this seems not the case for larvae. Larvae seem to tolerate even salinities <15psu although highest abundances were found in surface waters of ~25psu. Drifting juveniles were also present in waters with <25psu. This stays in contrast to the predication made by Thorson (1946) that echinoderm larvae are more sensitive to changes in temperature and salinity than other meroplanktonic larvae.

Micronephtys minuta

Larvae of *Micronephtys minuta* were the second abundant species concerning larvae in the Kara Sea reaching densities of 7 ind. mm^{-3} (Fig. 41). 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 deeper layers. Intrusion from fresh Ob river waters from the west overlaid brackish waters and pushed larvae to greater depths (Stephansev & Shmelkov 2001). As with the Ophioplutei, larvae of *M. minuta* have a local maximum at Station 36 but they are more or less equally distributed over the whole area, which corresponds to the homogenous distribution pattern of the adults in the area.

Juveniles, as well, do not seem to have preferable colonising regions since they showed the same equal distribution as adults and larvae. Local maximum abundances of 4000 ind. m^{-2} were the highest densities found among the settled juveniles within the five described species 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 many of the species descendants have already passed the larval stage and settled.

According to the large size range of larvae found in the water column reaching from newly hatched trochophores to old individuals of 980μm body size and 11 segments (Tab. 13) *M. minuta* rather continuously release larvae into the water instead of having a single spawning event as known from many other benthic invertebrates (e.g. Günther et al. 1998). Interestingly already small settled juveniles of minimum body size of 430μm and seven segments have been found (Tab. 14). This may lead to the assumption that this species gets larval competent for settling at a size of 430μm but may be able to prolong their planktonic life period to grow up to a size of 990μm reaching 11 segments. Since large larvae were exclusively found in the upper water layers resuspension of larvae could be excluded. A second explanation would be an additional direct developing mode of this species, as known from many Spionids switching 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 literature (see Jirkov 2001).

Adults were more predominant in the wake of the Yenisei estuary than the Ob River. 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 (Lisitsin, 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 (Lisitsin et al. 1995, Jørgensen et al. 1999, see also Klages et al. 2003). Most likely, rather food availability than hydrography shape the adults presence since both the adults and larvae seem to tolerate high salinity and temperature changes. Jirkov (2001) describes this species as typical for the shallow artic shelf area 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)

Nereimyra aphroditoides

Densities and distribution of larvae of *Nerimyra aphroditoides* are almost equivalent to those of *M. minuta*, although their larvae occur more southerly and are restricted to two localities west and east of the Yenisei outflow (Fig. 42). Hydrographic pattern may play an important role restraining the larvae in the two areas. Both areas are off 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 moving water and calm shore-zone, may stabilise the location of the larvae. Although, 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 & Karcher 1999). Adults were roughly restricted to the same areas as larvae suggesting the area as the species settling site. This seems not to be the case since juvenile stages were found in the northern plume of the Yenisei River. How juveniles may migrate later to adult sites remains unclear. Such behaviour is known from juvenile settlers of the lugworm *Arenicola maritima*, where juveniles settle closer onshore and later migrate into deeper waters to the settling grounds of the adults (Flach & Beukema 1994). It is assumed that juveniles this way avoid intraspecific food competition with adults and, in case of carnivore species as all members of the genus *Nereimyra* sp. (Hartmann-Schröder 1996, Jirkov 2001), circumvent cannibalism.

As with *M. minuta* in *N. aphroditoides* a wide range in body size of both larvae and juveniles was found suggesting a prolonged reproduction window and, hence, a continuous settlement of larvae (Tab. 13). Although juveniles of *N. aphroditoides* have the almost the same size range as juveniles found of *M. minuta* the mean body size of the juveniles showing only half of that of *M. minuta* indicating a much earlier successional settlement state of *N. aphroditoides*.

Phyllodoce groenlandica

Larvae of *Phyllodoce groenlandica* are restricted to two areas in the investigation area with very low frequencies of 0.55 ind. m^{-3} (Fig. 43). Although most of the larvae are found in the upper water column, a comparatively high amount is found below the pycnocline. These larvae were mainly advanced nectochaeta stages with many segments. The first settled animals were actually smaller and showed less numbers of segments than the smallest specimen near the surface. In contrary to the larvae of *M. minuta* larvae of *P. groenlandica* may settle but are also capable to return to plankton again. Thorson (1946) described 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 3000μm (26 segments). This agrees with our findings.

In this survey large numbers of undeveloped phyllodocid larvae were present, reaching maxima of 7 ind. m^{-3} (pers. observation, see also Fetzer 2003). All were still trochophores with no segments visible. Since *P. groenlandica* was the only adult phyllodocid polychaete in mentionable 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 to them, in highest amounts below the pycnocline. Nevertheless, it remains obscure whether these trochophores belong to a second spawning event.

Adults are distributed very patchy all over the sampling area with a tendency towards the river mouths. *P. groenlandica* is known to inhabit a wide range of habitats and tolerating 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).

Prionospio cirrifera

In contrary to all other observed larvae, larvae of *Prionospio cirrifera* were distributed mainly below the pycnocline (Fig. 44). Most larvae were big (mean body size= 1513μm) and well developed. According to their size and horizontal distribution, these larvae were about to settle shortly. This agrees with finding of Schlüter & Rachor (2001), which found also trochophores of *Prionospio* spp. in the lower water masses on the Barents Seas Shelf in June. Small larvae of <1000μm were exclusively found in the upper water column. Hannerz (1956) and Plate & Husemann (1994) mentioned size at metamorphosis to 1200μm, which accounts to 15-19 chaetigers. The mean body size of the larvae we found were 1513μm in size, although the biggest planktonic larvae we encountered had a size of 2700μm 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. 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 get back into the estuary (Hannan 1961). Release and development time needs to be synchronised to a high degree to 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 & Arnofsky (1999 and citations therein) found that the release of many spionids is triggered by temperature and salinity. In spionidiforms peaks of reproduction appear during periods when water temperature is highest. Additional stimuli such as low salinity may enhance the precision of the release. In June, at time of maxima water discharge both temperature and salinity changed drastically in the estuary most probably serving as the motivation to spawn.

4.3 Biotic factors shaping meroplanktonic patterns

One general pattern, which was observed in all species, is lowest abundances in the area of direct influence of the river. This observation may be explained by the fact that this area of 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 seem be fast temporal changes intolerable. This may concern the above-mentioned tolerance of *Ophiocten sericeum* larvae to low salinities.

Except abiotic factors restricting the allocation of meroplanktonic organisms, also predators may cause strong reduction in abundances and, hence, in the found distribution pattern. Drifting carnivores as cnidarians may heavily prey on planktonic animals (Schneider & Behrends 1998). Additional mesozooplankton investigation done in the same period (see I. Suck 2001, Deubel et al. 2003) revealed the presence of Hydromedusa reaching 4 ind. m^{-3} in the mixing zone. Schneider & Behrends (1998) found that already concentrations of 0.004 ind. m^{-3} (40 ind. 1000 m^{-3}) have a significant effect on pelagic systems in the Baltic Sea. Another possible scavengers as e.g. 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.

4.4 Conclusions

Our results show that despite the fact of the occurring high river output, it is remarkable that many larvae are retained in the distribution areas of their adults. Still the question arises whether the larvae are there because presence of the adults and certain traits in larval behaviour and/or spawning strategy of the adults restrain larvae locally or if local concentrations of larvae due to hydrographical pattern determine the ensuing settlement area of species. The latter would imply that benthic communities are exclusively shaped by the hydrology.

Nevertheless, it has been shown that hydrography changes immensely during the season and nothing is known about how future hydrographical pattern may influence the distribution of larvae. Interannual variations of currents may have crucial effect on the reproduction success of species (Cushing 1990). Our findings represent only a ’snapshot’ of the ongoing processes in the water column. 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. Small-scale processes may also have an effect on distribution.

Improved insight in the life strategies of benthic species and larval ecology, as growth, duration in the water column etc. would help to understand the interaction of how species can either actively influence the distribution of their larvae in the water column by adult reproduction strategy and larval behaviour, versus passive forces.

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Captions

Table 12: Station number, sampling date, position and station depth of meroplankton stations in the Kara Sea.

Table 13: Number of measured specimens (N), mean, minimum and maximum body size and (in polychaetes) number of body segments of larvae and drifting juveniles of *Ophiocten sericeum* and larvae of *Micronephtys minuta*, *Nereimyra aphroditoides*, *Phyllodoce groenlandica* and *Prionospio cirrifera*

Table 14: Number of measured specimens (N), mean, minimum and maximum body size and (in polychaetes) number of body segments of juveniles of *Ophiocten sericeum, Micronephtys minuta, Nereimyra aphroditoides, Phyllodoce groenlandica* and *Prionospio cirrifera*

Figure 37: Overview of the investigation area (indicated by grey box)

Figure 38: Salinity and Temperature distribution in the investigation area in 2000

Figure 39: 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 in 2000. Larvae are calculated to ind. m^{-3} and juveniles and adults to ind. m^{-2}. Dots indicate the sampling stations

Figure 40: Distribution of floating juveniles above and below the pycnocline of the brittle star *Ophiocten sericeum* in the investigation area during the expedition in 2000. Larvae are calculated to ind. m^{-3}. Dots indicate the sampling stations

Figure 41: Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Micronephtys minuta* in the investigation area during the expedition in 2000. Larvae are calculated to ind. m^{-3} and juveniles and adults to ind. m^{-2}. Dots indicate the sampling stations

Figure 42: Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete *Nereimyra aphroditoides* in the investigation area during the expedition in 2000. Larvae are calculated to ind. m^{-3} and juveniles and adults to ind. m^{-2}. Dots indicate the sampling stations

Figure 43: Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaete P*hyllodoce groenlandica* in the investigation area during the expedition in 2000. Larvae are calculated to ind. m^{-3} and juveniles and adults to ind. m^{-2}. Dots indicate the sampling stations

Figure 44: Distribution of larvae above and below the pycnocline and juveniles and adults of the polychaets *Prionospio cirrifera* in the investigation area during the expedition in 2000. Larvae are calculated to ind. m^{-3} and juveniles and adults to ind. m^{-2}. Dots indicate the sampling stations

Table 12:

Station	Date	Lat [°N]	Lon [°E]	Depth [m]
2	04. Sep	75°24'	74° 11'	50
5	06. Sep	75°50'	81°00'	50
7	07. Sep	74°39'	81°08'	38
8	08. Sep	74°39'	82°38'	41
13	09. Sep	72°56'	80°33'	13
16	10. Sep	71°49'	82°36'	26
23	14. Sep	73°28'	79°51'	33
24	14. Sep	74°00'	79°59'	31
26	15. Sep	75°42'	77°57'	68
27	15. Sep	76°18'	78°55'	78
28	16. Sep	76°39'	83°52'	50
29	16. Sep	76°56'	85°45'	68
30	17. Sep	75°59'	83°02'	52
35	18. Sep	75°20'	83°48'	46
36	19. Sep	76°57'	81°57'	66

Table 13:

Larvae

Species	N	Mean size [µm]	Min size [µm]	# seg	Max size [µm]	# seg
Ophiocten sericeum [*1]	1114	1229	550		1950	
***Ophiocten sericeum* juveniles**[*2]	13	456	280		680	
Micronephty minuta	808	459	120	0	990	11
Nereimyra aphroditoides	473	541	180	3	810	10
Phylodoce groenlandica	117	1121	780	5	1420	15
Prionospio cirrifera	59	1513	450	9	2700	26

[*1]: Lenght of postero-lateral rod

[*2]: disk diameter

Table 14:

Juveniles

Species	N	Mean size [µm]	Min size [µm]	# seg	Max size [µm]	# seg
***Ophiocten sericeum* juveniles**[*1]	110	585	310		950	
Micronephtys minuta	348	2235	430	7	4000	26
Nereimyra aphroditoides	113	1054	300	6	4700	26
Phyllodoce groenlandica	100	2002	350	4	8800	44
Prionospio cirrifera [*2]	--	--	--	--	--	--

[*1]: disk diameter

[*2]: no juveniles found

Figure 37:

Figure 38:

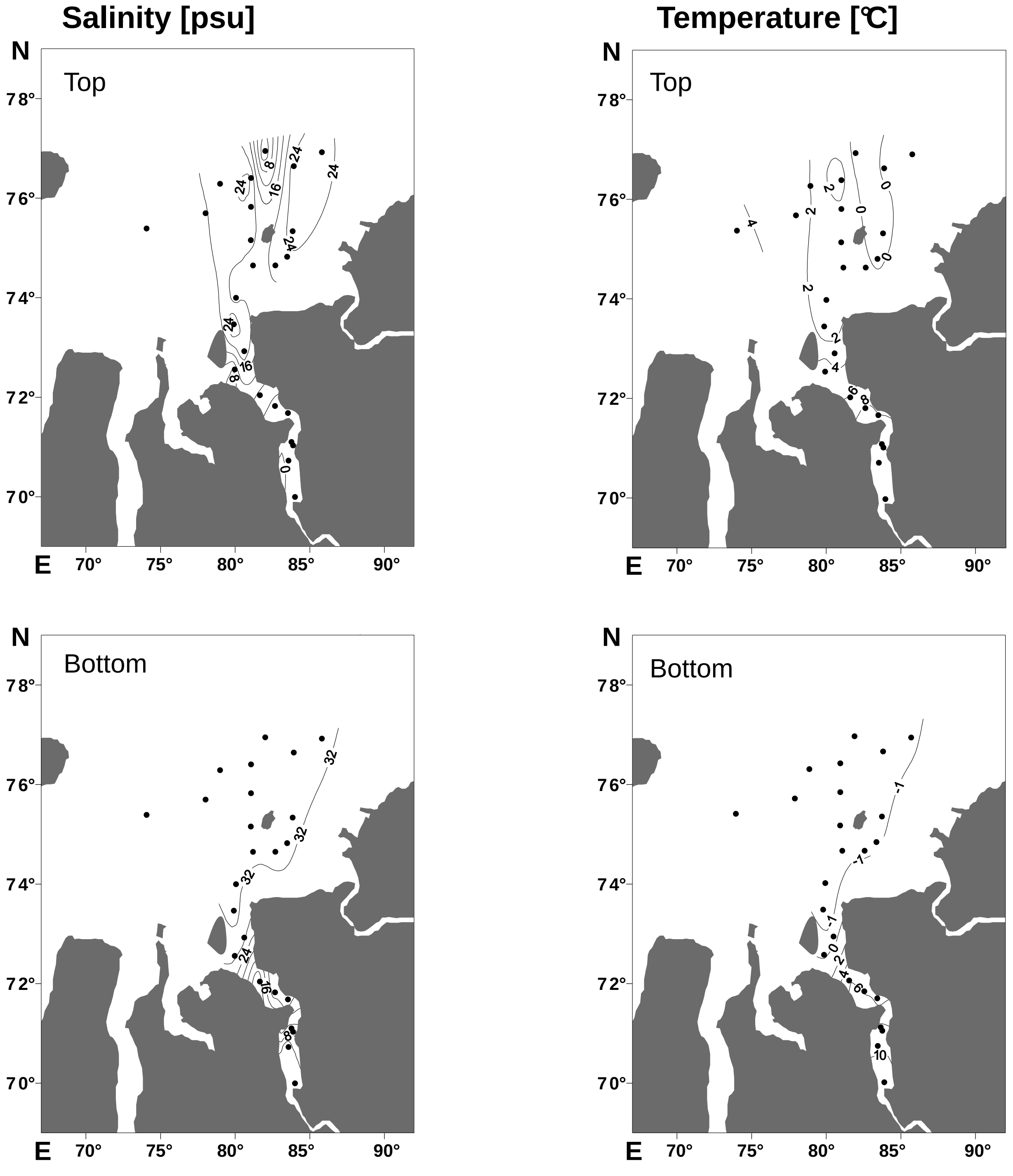

Salinity [psu]
Temperature [℃]
Top
Bottom
N
E
78°
76°
74°
72°
70°
70°
75°
80°
85°
90°
0
8
16
24
32
-1
2
4
6
8
10

Figure 39:

Ophiocten sericeum

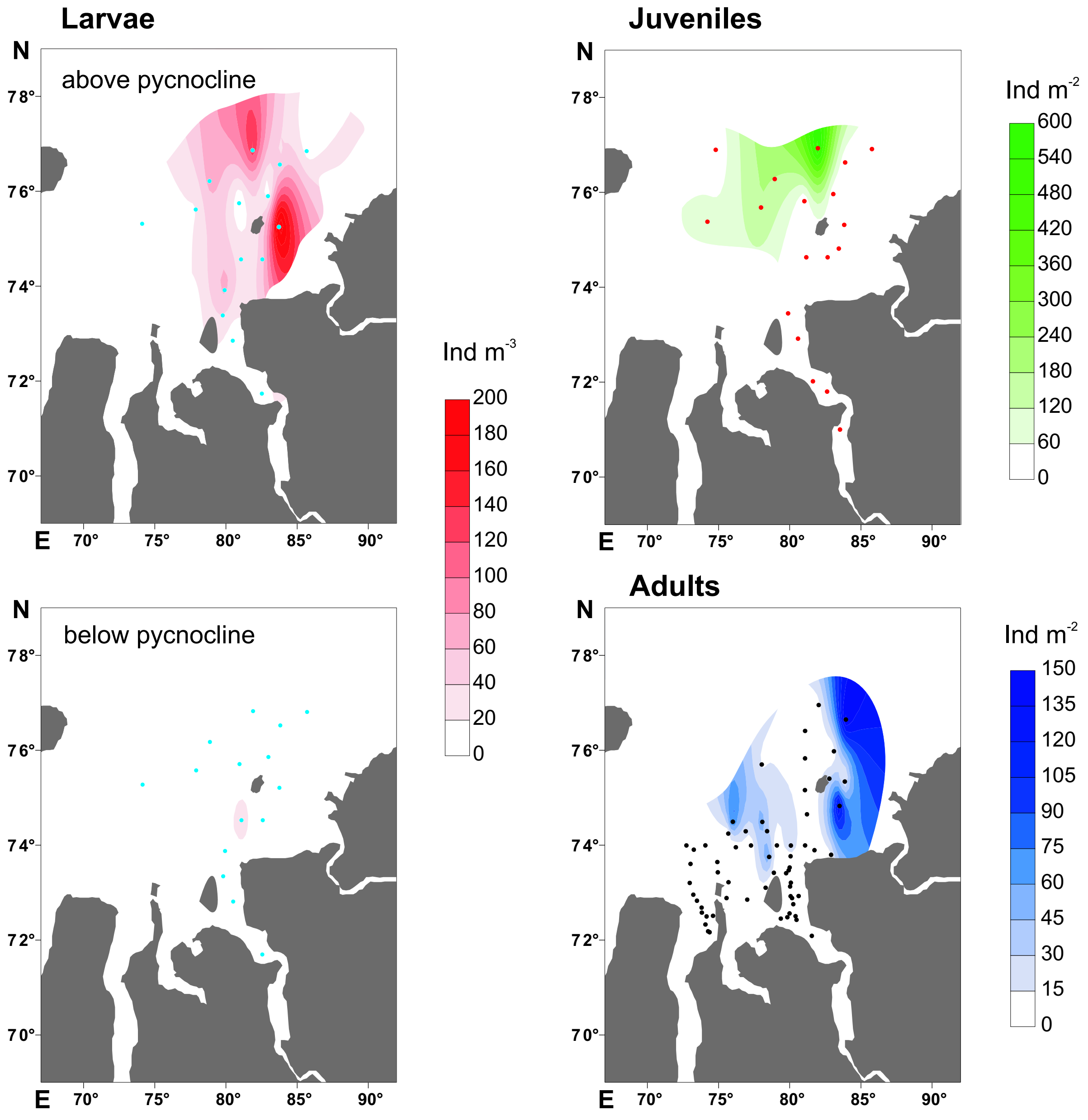


Figure 40:

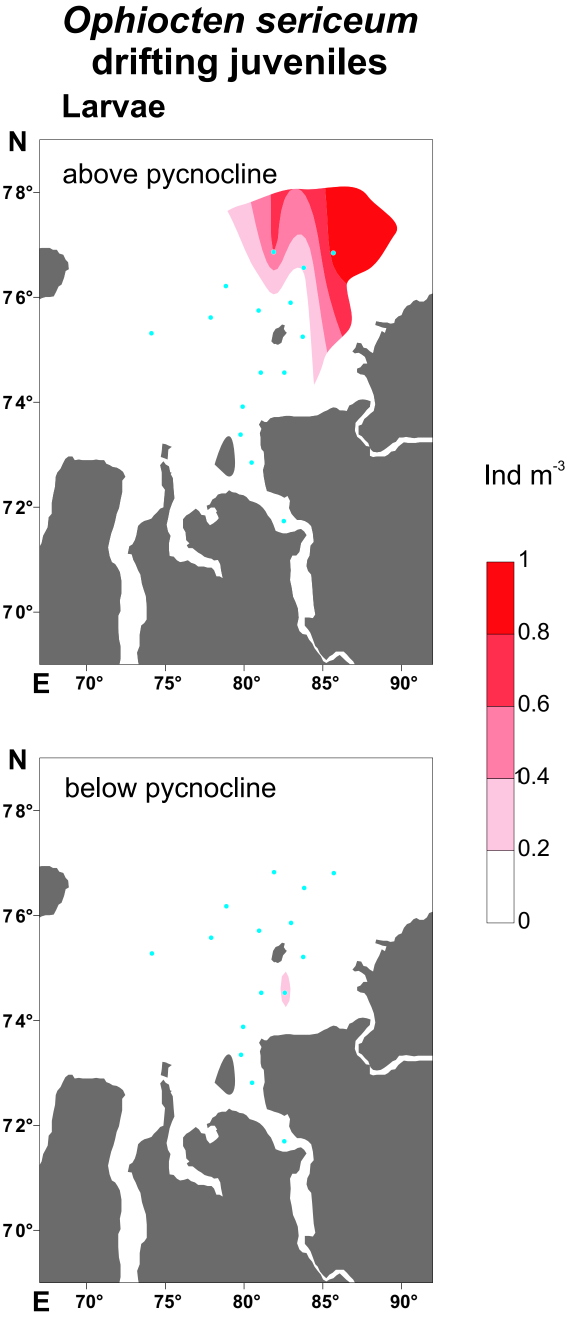

Ophiocten sericeum
drifting juveniles
Larvae
N
above pycnocline
78°
76°
74°
72°
70°
E
70°
75°
80°
85°
90°
N
below pycnocline
78°
76°
74°
72°
70°
E
70°
75°
80°
85°
90°
Ind m-3
1
0.8
0.6
0.4
0.2
0

Figure 41:

Micronephtys minuta

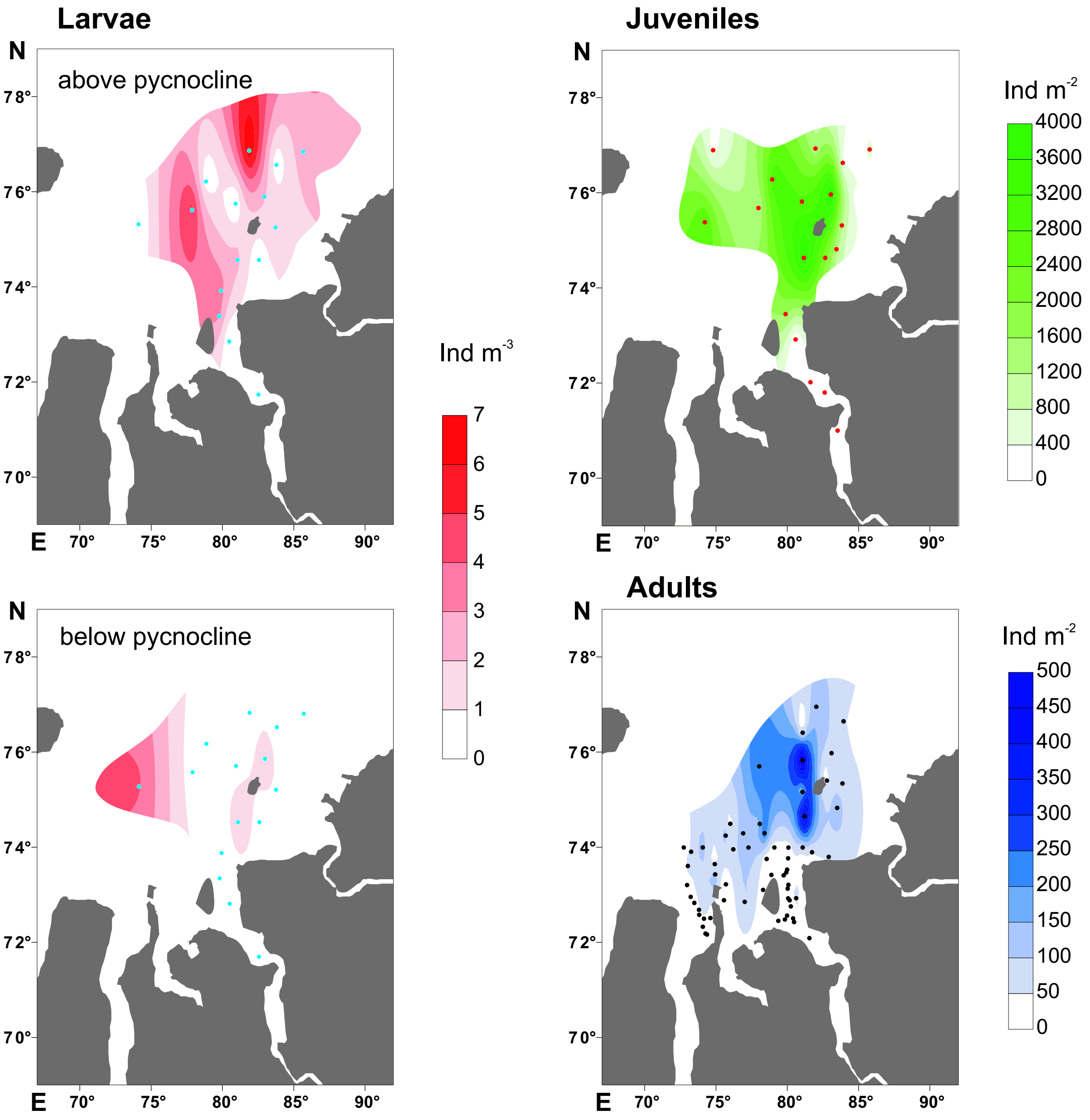


Figure 42:

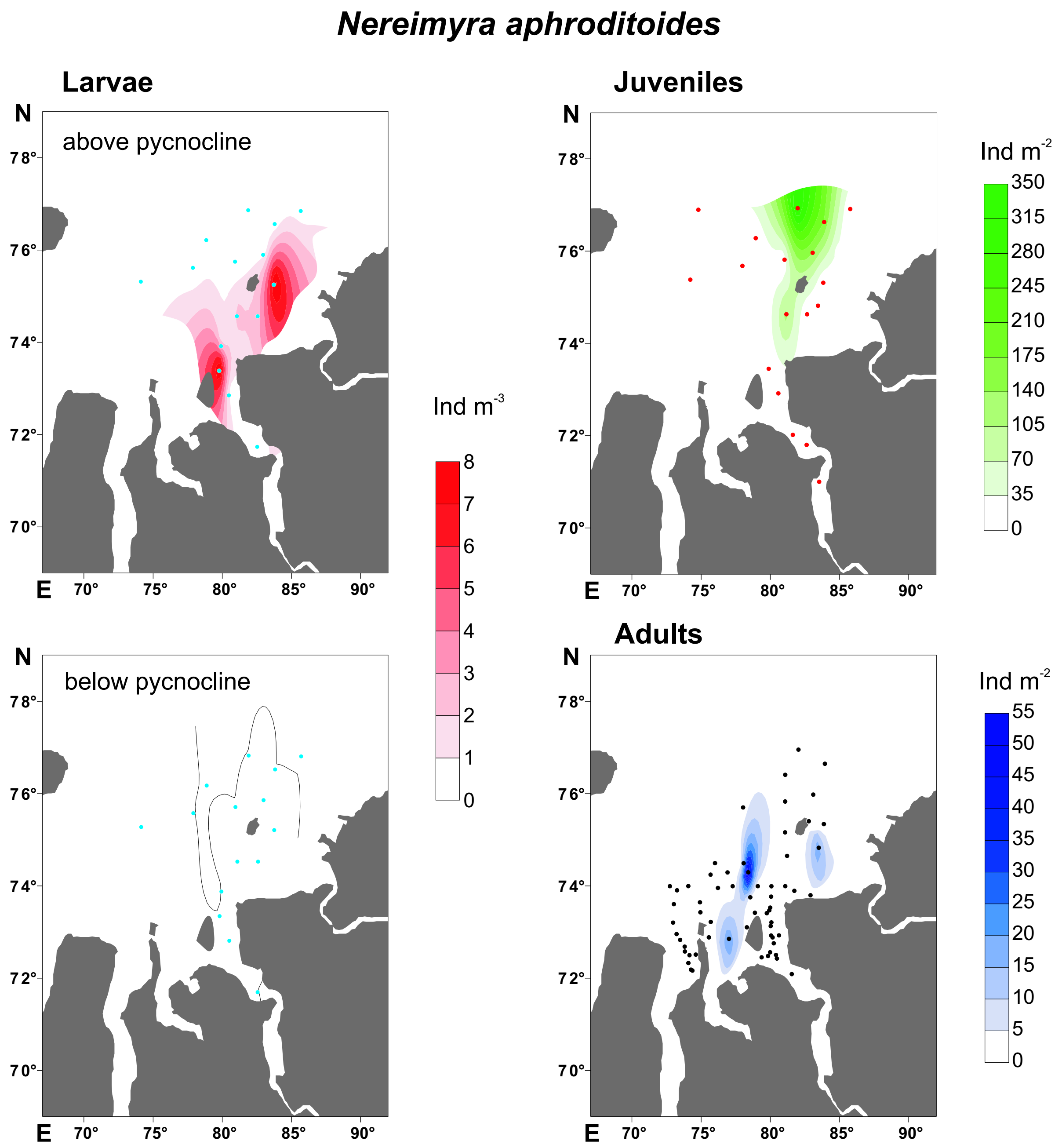

Nereimyra aphroditoides
Larvae
above pycnocline
below pycnocline
Juveniles
Adults
N
78°
76°
74°
72°
70°
E
70°
75°
80°
85°
90°
Ind m-3
8
7
6
5
4
3
2
1
0
Ind m-2
350
315
280
245
210
175
140
105
70
35
0
Ind m-2
55
50
45
40
35
30
25
20
15
10
5
0

Figure 43:

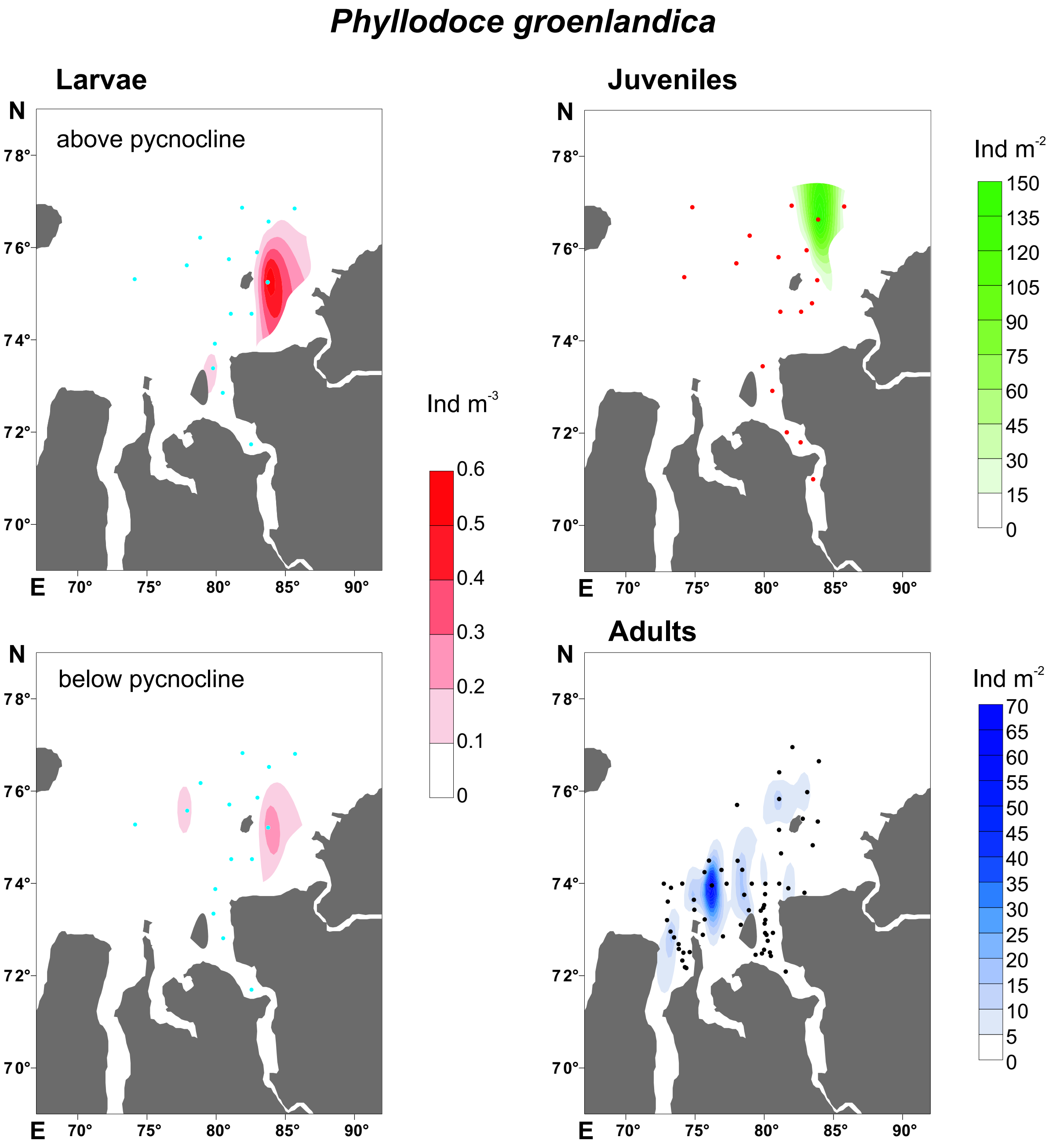
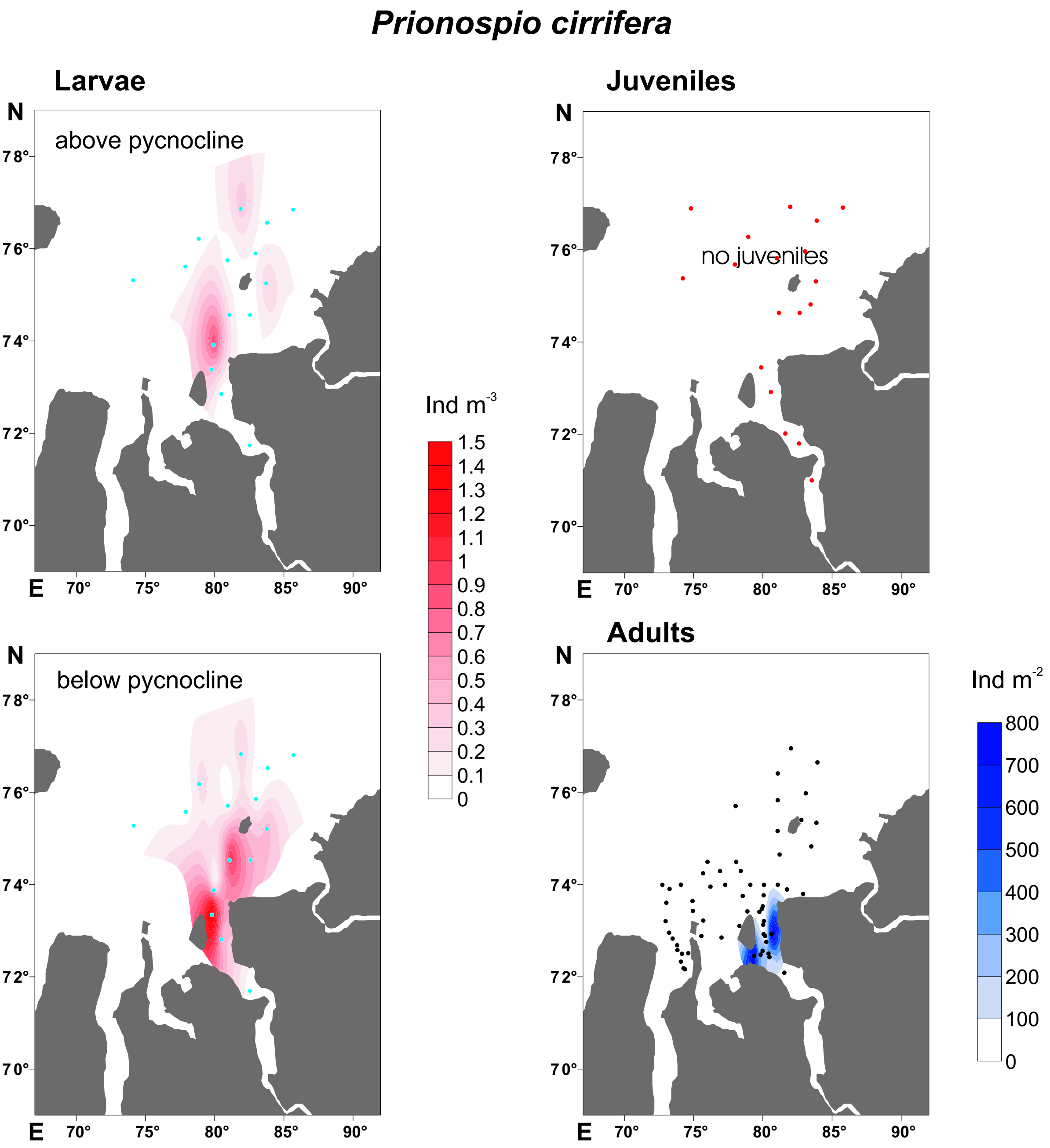

Phyllodoce groenlandica
Larvae
above pycnocline
below pycnocline
Juveniles
Adults
N
78°
76°
74°
72°
70°
E
70°
75°
80°
85°
90°
Ind m^{-3}
0.6
0.5
0.4
0.3
0.2
0.1
0
Ind m^{-2}
150
135
120
105
90
75
60
45
30
15
0
Ind m^{-2}
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0

Figure 44:


Prionospio cirrifera
Larvae
above pycnocline
below pycnocline
Juveniles
no juveniles
Adults
N
E
78°
76°
74°
72°
70°
70°
75°
80°
85°
90°
Ind m^{-3}
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Ind m^{-2}
800
700
600
500
400
300
200
100
0

5.5 Publication V

submitted to: Marine Ecology Progress Series

Life-history traits of benthic invertebrates in the Central and Southern Kara Sea (Russian Arctic) - adaptation of reproduction modes to cold waters?

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Abstract

The majority of benthic invertebrates in the boreo-Atlantic region reproduce via pelagic larvae, which ensures a wide distribution of the species and a good ability for fast exploitation of new territories. From early investigations in polar regions a greater relevance of species with direct development is proposed. In this study, the presence of larvae and juvenile stages in relation to adult organisms was investigated. Plankton and sediment samples were taken to study the occurrence of meroplankton, juveniles and adults in the central and southern Kara Sea. 88 adult species contributing >4% to the total abundance were recovered from sediment samples. For 52 benthic species juvenile stages were present. In the water column 44 larval types could be identified but only for 23 meroplanktonic species also the adults were present. For the other 21 larval types adults were recorded from the adjacent Barents Sea. Transport processes with prevailing currents may account for the presence of larvae. Most adults found belonged to Arctic species. When these crustaceans that are direct developers are excluded from the species list, organisms with pelagic development dominated in the Kara Sea.

Keywords: Arctic, Kara Sea, benthos, meroplankton, juveniles, reproduction types, direct/ indirect development, zoogeography, dispersal, life-history traits, reproduction periods

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1. Introduction

Marine invertebrates display a great variety of life-history traits and reproductive strategies. Reproductive strategies may differ in spatial location of larvae (benthic vs. pelagic), trophic types (feeding vs. nonfeeding), as well as with the degree of parental care (free vs. protected) (Mileikovsky 1974, Poulin et al. 2001). Each type is found in all oceans but comparisons of the principal reproductive modes from different marine habitats have shown that they are not equally distributed among geographic regions (Mileikovsky 1971, 1974, Thorson 1936, Poulin & Feral 1998).

More than 70% of benthic invertebrates in the boreo-Atlantic region reproduce via a pelagic and planktotrophic larval type, which ensures dispersal over greater distances, especially in case of sessile and less mobile species (Thorson 1950, Scheltema 1989). This should allow for a better exploitation of new territories (Thorson 1950) and avoids persistent inbreeding (Grosberg & Quinn 1986, Grosberg 1987).

Already in the first meroplanktonic surveys of Thomson (1876 *fide* Pearse & Bosch 1994) the small number of pelagic larvae so far known from polar waters led to the assumption that many polar species reproduce directly, avoiding pelagic stages. Thorson (1936, 1946, 1950) supported this hypothesis, which later became known as ‘Thorson’s rule’ (see Mileikovsky 1971). Thorson explained the predominance of direct development in polar seas by the mismatch between the prolonged development times and short periods of food availability at polar temperatures, apparently selecting against species with a pelagic life history. His hypothesis was supported by observations indicating that many species at higher latitudes tend to produce larger and fewer yolk-rich eggs than their counterparts of lower latitudes, indicating a nonpelagic, direct developmental mode (Pearse & Bosch 1986, Thatje & Fuentes 2003). Comparative studies of life history patterns of benthic invertebrates throughout the world’s oceans revealed a latitudinal cline in the proportion of indirect development in many taxa (such as bivalves, prosobranchs, and decapods) from high numbers in the tropics to almost none in polar regions (Thorson 1950, 1966, Ockelmann 1965, Mileikovsky 1971, Curtis 1975, Hain & Arnaud 1992, Poulin & Féral 1996).

Observations of increasing records of pelagic larvae in Arctic and Antarctic waters, however, imposed doubts on the general validity of this rule (e.g. Clarke 1992, Pearse 1969, 1994, Pearse & Bosch 1986, Stanwell-Smith et al. 1997, 1999, Buzhinskaja & Jørgensen 1997).

Recently, larger amounts of pelagic larval types have been found in shallow Antarctic waters, with a number of planktotrophs even among the dominant species (Stanwell-Smith et al. 1999, Poulin et al. 2002). Pelagic reproduction also seems to be more common than anticipated among Arctic benthic animals (Dayton 1990). Nonetheless, the percentage of species with indirect developments in Antarctic waters appears low compared with the large number of benthic species in these waters, and their abundance is much lower than at lower latitudes. Larval peak abundances are estimated to be 2-6 orders of magnitude lower than in comparable data from temperate zones (Stanwell-Smith et al. 1999, Arntz & Gili 2001). The low abundances are explained by spreading of the larvae over larger temporal scales due to reduced spawning synchrony and slow development rate of the larvae (Stanwell-Smith et al. 1999).

Today Thorson's paradigm, which has been partly replaced by one in which latitudinal shifts are observed in the proportions of planktotrophy and lecithotrophy among planktonic larvae (Clarke 1992, Pearse 1994, Poulin & Féral 1998), is still one of the most debated topics in meroplankton research (e.g., Clarke 1992, Pearse 1994, Gallardo & Penchaszadeh 2001, Arntz & Gili 2001).

Except for the studies of Thorson (1934, 1936, 1950, 1966), Chia (1970), Mileikovsky (1959a,1960, 1966, 1967, 1968, 1971), Smidt (1979), Lacalli (1980), Andersen (1984), Coyle & Paul (1990), Buzhinskaja & Jørgensen (1997), Clough et al. (1997), Schlüter & Rachor (2001) little is known on the ecology of meroplankton in the Arctic.

Extensive studies on the ecology of invertebrate larvae of the Norwegian and Barents Sea have been conducted by Mileikovsky (1959a, 1960, 1966, 1971). Some mainly descriptive work on the reproduction ecology of invertebrates was done by Mileikovsky (1959b), Chivilev et al. (1991), Shilina (1994), Beer (2000), and Günther & Fedyakov (2000) in the White Sea. However, there is still a lack of studies for the polar realm. Especially for the Siberian parts of the polar region almost nothing on life cycle strategies of benthic invertebrates is known.

The aim of this study is, (1) to determine reproductive strategies for benthic invertebrates in the Kara Sea, (2) to relate the presence of larvae and juveniles to reproduction periods known from the literature, (3) to correlate life history traits with zoogeographic affiliations of occurring adult invertebrate species in the Kara Sea.

2. Material & Methods

2.1 Study area

The Kara Sea is located on the shallow Siberian shelf, which in its central part hardly exceeds a depth of 40-50 m (Figure 45). The area has an open boundary with the Arctic Basin to the north while it is framed in its western part by the St. Anna trough (maximum depth 600 m), which is stretching along the east coast of Novaya Semlya. To the east, Severnaya Semlya and Taymyr Peninsula separate the Kara Sea plateau from the Laptev Sea (Cherkis et al. 1991). Seasonal water exchange with the Barents Sea proceeds through the Kara Strait between the Siberian main land and Novaya Semlya as well as around the northern tip of the island. Waters from the Arctic Ocean and the Laptev Sea periodically swash into the area from the north and along Severnaya Semlya/Vilkitski Strait.

The Kara Sea is ice covered about 9 month of the year (Blanchet et al. 1995). Ice formation usually starts at the end of October and break up coincides with the main river discharge of the two largest rivers Ob and Yenisei in early to late June (Mironov et al. 1994). Discharge immensely influences hydrography in the southern part of the study area, but also has a strong influence in the central part of the Kara Sea, causing a pronounced bi-layered stratigraphy of the water column (Pivovarov et al. 2003). River run-off shows a pronounced variability with a maximum discharge from June to September and a minimum during the winter period (Pavlov & Pfirman 1995). Cumulative freshwater input of the rivers was estimated at 1350 km^3 a^{-1} (Gordeev et al. 1996). Details on the hydrography are published in Harms & Karcher (1999), Harms et al. (2000, 2003), Stephantsev & Shmelkov (2001), Shmelkov et al. (2002), and Pivovarov et al. (2003).

2.2 Sampling

Adult fauna was analysed during four expeditions to the Kara Sea onboard R/V ‘Akademic Boris Petrov’ in 1997 and 1999-2001 (Figure 45). Expeditions took place in August/September each year. Samples were collected at 26 stations in 1997, 24 stations in 1999, 16 stations in 2000, and 55 in 2001. Benthos samples were taken with a large box corer (0.25m^2 coverage area) and a dredge (‘Kieler Kinderwagen’, frame size 150x50cm). Samples were then gently washed over a 500μm sieve and animals preserved in 6% borax-buffered formalin until further treatment.

For meroplankton and juvenile investigations, samples were taken at 30 stations in 2000 and 2001 (Figure 45). Meroplanktonic larvae were caught with a vertically drawn Nansen closing net (0.442 m^2 catching area, 55μm mesh size, 0.5 m s^{-1} hauling speed). Meroplankton was then sorted under a stereomicroscope and preserved in 70% ethanol or Carriker solution (a $NaCO_3$ buffered sugar-formalin suspension).

To study the distribution of juveniles, multicorer samples (28 cm^2 tube coverage area) were taken (Figure 45). 3-6 tubes were deployed at each station to account for mesoscale patchiness of juveniles. The upper 10-15cm of each core were removed and screened over a sieve column into fractions of 500/250/125μm. All animals found in each fraction were picked out and preserved in 70% ethanol. In animals having brood pouches (as e.g. Amphipoda) adult specimen were carefully inspected for juveniles or eggs.

All animals were identified to the lowest possible taxon and counted. For juveniles the body length of each specimen was defined with a microscale to $\pm 10\mu$m. Measurements were only conducted on complete animals. Juveniles were defined as specimens less than $^1/_3$ of adult size according to the literature (e.g. Hartmann-Schröder (1996) for polychaetes). In order to reduce the number of species for the study of reproduction types, only those contributing >4% to total adult abundance were considered. Many larvae and juveniles could not be directly determined to species level. Comparison of larvae, juveniles and the local adult fauna facilitated matching larvae and juveniles to adult species. However, larvae and juveniles that could not be clearly determined to species level are marked with brackets around their presence mark '(x)' in Table 15. If more than one adult species within one taxonomic group (e.g., genus) existed, the presence mark in brackets for larvae and juveniles, respectively, was set for all adult members of the taxonomic group.

2.3 Life history and zoogeographical distribution of species

Life-history traits and zoogeographical distribution of the adult benthos were determined from the literature (e.g., Mortensen 1927, Thorson 1936, 1946, Ockelmann 1958, Smidt 1979, Price & Warwick 1980, Lacalli 1980, Andersen 1984, Hartmann-Schröder 1996, etc., see 'remarks' in Table 15). Known reproduction types, time of spawning, reported presence of eggs and/or ripe females, and duration of the pelagic stage in the water column of each species were compared with field data (Table 15 + 16). Since for many species real duration of the larval time is uncertain, question marks have been put in the tables to indicate proposed presence for the species.

2.4 Reproduction types

Reproduction strategies of benthic invertebrates have been the topic of many investigations in temperate latitudes and thus, life cycles of most marine invertebrates of boreal areas are nowadays fairly well described. Since the accessibility of polar seas is mainly confined to the summer, information on reproduction strategies and -periods in high latitudes is very limited. For the Arctic realm, knowledge of most life cycles of species has been mainly determined by plankton surveys (e.g. Rasmussen 1973, Smidt 1979, Lacalli 1980, Andersen 1984). Contrary to the more comprehensively investigated Antarctic regions (e.g. Bosch & Pearse 1990, Hain & Arnaud 1992, Clarke 1992, Chiantore et al. 2002) hardly any information on parental care (brooding - free) or adult's nutrient supply to their larvae (planktotrophic - lecithotrophic) is existent. Due to this limited knowledge of Arctic meroplankton ecology and based on the given literature, reproduction types have been classified into the following groups according to the spatial occurrence of larvae (Poulin et al. 2001). This, however, allows to make predictions on the amount of direct and indirect reproduction traits of benthic animals for the investigation area and the adjacent Arctic seas, and helps to estimate the species' potential ability to disperse (see also Table 15 + 16):

• pelagic	species with a defined pelagic larval stage (≙ indirect development)
• pelagic? short	species with a presumed pelagic larval stage
• pelagic or demersal	species with a short pelagic phase or demersal larvae
• direct	species lacking a pelagic phase (≙ direct development)
• direct?	species presumed non-pelagic
• unknown	species with undetermined reproduction mode

For the classes 'pelagic?' and 'direct?' either larvae or juveniles have been found but could not be clearly assigned to a species, or the reproduction mode was only presumed from the amount of yolk in eggs found, indicating a direct or indirect development (Thorson 1936, Hines 1986).

3. Results

3.1 Zoogeographical distribution of benthos

Adults of 88 species were found during the expeditions in the Kara Sea of all benthic species contributing >4% to the total abundance (Table 15). Most of them belonged to polychaetes (45 species; 51%) (Figure 46). The next largest group was crustaceans with 25 species (28%). Crustaceans were exclusively composed of Cumacea ((*Brachy-*)*Diastylis* spp. and *Leucon* spp.), Isopoda (*Saduria sibirica*) and Amphipoda. Molluscs contributed with 13 species (15%) to the share. Except for *Cylichna* cf. *occulta* (Gastropoda) they belonged to Bivalvia. Only 5 species (6%) belonged to echinoderms, which were composed of the three groups Holothuroidea (*Eupurgus scaber*, *Myriotrochus* spp.), Ophiuroidea (*Ophiocten sericeum*) and Asteroidea (*Ctenodiscus crispatus*).

Concerning zoogeographic distribution, 41 species were of Arctic origin while 32 species had an Arctic-boreal distribution (Figure 47). Another 4 species were assigned to boreal regions while 11 species were cosmopolitans. Cosmopolitans were exclusively polychaetes whereas in Arctic-boreal and Arctic species no taxon dominated.

Larvae of 26% of the benthic species were found in plankton samples, accounting for 23 different larval types (Table 17). Most of them belonged to polychaetes (19 larval species), 4 to echinoderms, whereas no larvae of present adult crustacean and mollusc species were detected (Table 15). Of the larval types found 16 could be definitely identified to species level.

Juveniles of 52 species (59%) of the bottom fauna present were localised. 39 juvenile types could be determined to species level. The biggest share of juveniles found again belonged to Polychaeta (30 species), 9 species to Mollusca, 8 species to Crustacea and 5 species to Echinodermata. No ripe female Crustaceans were detected during the study period.

Additionally, 21 larval types were identified of species whose adults were not found in the Kara Sea (Table 16). Eight of them are, according to literature, of Arctic-boreal origin. Another 4 species were cosmopolitans. Those two zoogeographical groups were exclusively shared by polychaetes and echinoderms. However, the mollusc larvae found were exclusively of Arctic zoogeographic distribution.

3.2 Presence of larvae and juveniles: field data vs. literature

Comparing the time of occurrence of meroplanktonic larvae in the water column of sampled data with data of earlier investigations from the literature (e.g., Thorson 1936, Gajevskaja 1948, Ockelmann 1958, Hannerz 1961, Andersen 1984, etc.; see `remarks` in Table 15), reveals that for the period August/September (time of expeditions) occurrence of 12 of the 23 larval types found corresponds to the known time span (Table 15). Besides that 6 polychaete species (*Cistenides hyperborea*, *Laonice cirrata*, *Micronephtys minuta*, *Ophelina cylindricaudata*, *Scolelepis metsugae*, *Spio limicola* (*arctica*)) were present in August/September where there is lack of information on the occurrence of larvae in polar waters. For the larvae found of the polychaetes *Capitella capitata*, *Eteone barbata*, *Owenia fusiformis*, *Polydora quadrilobata* and *Scoloplos armiger* field data do not correspond with data given in literature. For these species the reproduction period is reported to be earlier in the year (e.g., Sveshnikov 1959, Thorson 1946, Lacalli 1980, Hartmann-Schröder 1996, etc.; see Table 15). Polychaeta and Echinodermata are the best investigated groups. Nothing is reported on the larval period of most Mollusca. All crustaceans found do not have pelagic larvae. This group consisted only of peracarid taxa (Amphipoda, Isopoda, Cumacea), in which a pelagic reproduction trait is completely missing.

Checking the coincidence of juveniles with the respective larvae is somehow more difficult because it is unknown when they have settled (for indirectly developing species) or hatched from their eggs (directly developing species). However, assuming an age of no more than 3 months after settlement or release from their parents, the presence of juveniles fitted for 24 of the 52 juvenile species (Table 15). Nothing is known about the occurrence of the juveniles of another 25 species in the benthos. Only in 3 species (*Scalibregma inflatum*, *Sphaerodorum flavum*, *Astarte borealis*) the theoretical settlement times do not correspond to our observations.

Literature data (Table 15) reveal that apparently most species reproduce directly (33% = 28 species) without a pelagic phase. Only 25% (22 species) have planktonic larvae (Figure 48a). In 11% (9 species) direct development is presumed but has not been proven yet. Another 11% (9 species) seem to have a short pelagic stage. In 1% (1 species = *Portlandia arctica*) pelagic larvae are assumed.

3.3 Reproduction strategies

Both Arctic Mollusca and Polychaeta show a broad spectrum of reproduction strategies (Figure 50). Most Polychaeta species reproduce via pelagic larvae, however, in >30% of polychaete species reproduction modes are still unknown. Direct development plays only a subordinate role within this group. Short pelagic development dominates the life cycle strategy of Mollusca. Here again, the reproduction mode is unknown in about 20% of the species. With echinoderms, on the other hand, pelagic reproduction clearly predominates. In all crustaceans found during the expeditions in the Kara Sea direct development is obligatory.

Comparison of known reproduction types of all adult species found with respect to their zoogeographical distribution reveals that the proportion of direct development is obviously greatest in animals of Arctic distribution (49%) and decreases continuously from Arctic-boreal species (38%) and boreal (33%) to only 11% in cosmopolitans (Figure 49a). Pelagic development dominates among Arctic-boreal (42%), boreal (33%) and cosmopolitan (44%) species. Short pelagic larval life is of importance in Arctic (11%), Arctic-boreal (13%) and in cosmopolitan (33%) species, but seemingly absent in species with boreal affiliation. Here direct development is assumed in 33% of all adult species.
The total number of species found in the Kara Sea has a large share of crustaceans (Figure 46) that develop directly, irrespectively of their zoogeographic status (Table 15, Figure 50). To remove this bias, relations were re-determined for all species excluding crustaceans. The result reveals a different picture about the importance of direct development of Arctic species.

Excluding crustaceans, pelagic development is the prevailing life strategy in 37% of all species opposed to 5% with direct development (Figure 48b). Assumed direct development is found in 32% of the Arctic species (Figure 49b). In 21 % of the species a short pelagic pattern dominates. In Arctic-boreal species pelagic development is the main reproduction type (67%). About 20% of the species have short-pelagic or demersal larvae. Species with known direct development are virtually absent in this zoogeographical unit. Direct development is assumed in 13% of the species. Since the Cumacea, Amphipoda and Isopoda found consisted only of Arctic and Arctic-boreal species, the reproduction types in boreal and cosmopolitan species remain unchanged.

4. Discussion

4.1 Identification and species affiliation of Bivalvia

Identification of meroplankters from Arctic areas is difficult since literature is very limited. Only few studies by Thorson (1934, 1936, 1950), Mortensen (1942), Ockelmann (1958), Mileikovsky (1966, 1967, 1968), Chia (1970), Smidt (1979), Lacalli (1980), Andersen (1984), Coyle & Paul (1990) deal with identification of larvae from high latitudes. Even less is known about newly settled juveniles (e.g. Burkovsky et al. 1997, Fetzer et al. 2002). Knowledge of the benthic adult inventory and comparison of newly settled post larvae with meroplanktonic stages is advantageous in identifying larvae. Especially individuals of post larvae (recently settled juveniles) and young juveniles are helpful since they often combine larval traits with adult appearance.

In the Kara Sea samples two types of bivalve larvae could be identified. According to Lutz et al. (1982) one type most probably belongs to *Arctica islandica*. For the second type the shape of the larger specimens very much resembles that of juvenile *Portlandia arctica*. Both Thorson (1936) and Ockelmann (1958) were uncertain about the reproduction strategy of *P. arctica*, but suggest a short pelagic development.

4.2 Composition of the adult fauna and zoogeography

High numbers of polychaete species, followed by crustaceans and bivalves are typical of the shallow Kara Sea plateau (Figure 46). Other studies performed in the Kara Sea confirm the dominance of polychaete species on the Kara Sea shelf (e.g. Cochrane et al. 1997, Deubel 2000, Denisenko et al. 2003, Deubel et al. 2003). Contrary to these studies, however, Curtis (1975) described the Kara Sea community to be dominated by crustaceans with >300 species.

Most of the polychaete species in the Kara Sea are detritivorous. Their presence may thus be enhanced by the high organic carbon input from the two large rivers Ob and Yenisei (Klages et al. 2003). Molluscs, which mainly consist of bivalves, also thrive well on the supply by the rivers. Amphipods, cumaceans and isopods are omnivorous and feed on the enriched sediments (Deubel et al. 2003).

Echinoderms are underrepresented in the area of study, although they are usually the most abundant group in Arctic shelf areas (Piepenburg & Schmid 1996, 1997). According to Piepenburg & Schmid (1997), 9 of the 13 most common benthic species in the adjacent Laptev Sea belong to echinoderms. The poor number of echinoderm species on the Kara Sea shelf may be explained by the strong seasonal freshwater discharge from the rivers, which creates physiological barriers for the stenohaline echinoderms. Piepenburg & Schmid (1997) found highest abundances of *O. sericeum* in the deeper parts of the shallow Laptev Sea Shelf. Organisms accumulate in slopes and depressions of old riverbeds, most probably to avoid strong salinity fluctuations of the upper water masses due to ice melting and river discharge (Deubel et al. 2003, Fetzer 2003).

As expected, most of the adult species found in the Kara Sea show an Arctic zoogeographical distribution (Figure 47). Arctic-boreal and boreal species continuously decrease in numbers with increasing distance from their zoogeographical origin. Curtis (1975) mentioned that faunistic differences in Arctic and sub-Arctic regions are generally not extreme, since many warm water as well as cold water species are found in more than one zoogeographic zone. Ekman (1953) found that 75% of the fish genera observed in the Arctic are also present in temperate waters. 8% are even common in temperate and subtropical regions.

Faunal composition of the Kara Sea is strongly influenced by Arctic waters. However, water exchange with the Barents Sea also causes immigration of Arctic-boreal and boreal species (Figure 47). Additionally, the adjacent rivers import warm water masses into the area endorsing the survival of eurytherm species of warmer regions.

4.3 Meroplankton composition

Comparison of the presence of larvae with other investigations is difficult, since meroplankton assemblages strongly fluctuate in their composition during the year (Raymont 1983). Occurrences of larvae depend on the composition of benthic communities, and, moreover, their distribution patterns are strongly shaped by local hydrography resulting in different compositions even if the benthic communities are identical (Mileikovsky 1968, Clough et al. 1997, Schlüter & Rachor 2001).

The meroplankton species in the Kara Sea roughly resemble the meroplankton assemblage found by Schlüter & Rachor (2001) in the Barents Sea although the latter survey was conducted much earlier in the year (May/June). As with the Kara Sea, the Barents Sea meroplankton was dominated by polychaete species. Contrary to our study Schlüter & Rachor (2001) found 8 different echinoderm larvae. Clough et al. (1997) carried out a meroplanktonic inventory off the northeast coast of Greenland in the same period as we did (July-August). Unfortunately they grouped their findings only into orders, so comparison on presence of species is not possible. The most comprehensive studies on meroplankters in polar waters, except those by Thorson (1936), have so far been made by Andersen (1984) and Smidt (1979). These authors present meroplankton data from two fjords in North (Andersen 1984) and Southwest Greenland (Smidt 1979), which contain all larval species found in the Kara Sea. Although these fjords mainly have an Arctic fauna, larvae of boreal species are transported into the fjords by warm bottom water, especially during the winter months (Smidt 1979).

Exchange of water and introduction of larvae from the adjacent Barents Sea may explain the presence of larvae whose adult stages are lacking in the Kara Sea (Table 16). These larvae most probably have been spawned in the Barents Sea and transported into the Kara Sea through the Kara Strait or around the northern tip of Novaya Semlya. Planktotrophic larvae of boreal species typically require 2-6 weeks to develop into a competent state (Day & McEdward 1984). Mileikovsky (1968) described that within this period the northeastward current along the Norwegian coast may transport larvae and juveniles from the shallow shelf bottoms over distances of more than 600 miles.

Since sampling has mostly been conducted in the eastern part of the Kara Sea, adults of the larvae found might be present in the western part, which is more influenced by the warmer waters of the Barents Sea. Faunistic investigations done by Zenkevitch (1963) and Sirenko (2001) reported the presence of the missing adult polychaete and echinoderm species from the Barents-, Petchora- and White Sea. The gastropod larvae present in our samples (*Cratena* sp., *Dendronotus* sp., *Trichotopis conica*, *Coryphella* sp.), the Ectoprocta *Electra* sp. and the cirripede *Balanus* sp. are typical of rocky bottoms and their associated fauna, which was not sampled for adult benthos in this survey.

4.4 Reproduction modes and zoogeographic affiliation

The zoogeographic affiliation of the benthic species in combination with their reproduction modes seems to determine the colonisation pattern of the shelf area (Figure 49). Short or no dispersal abilities are mainly found within species of Arctic zoogeographic status whereas species with larvae that can be transported over long distances are mainly among taxa originating from boreal regions.

Interestingly, species with short pelagic or demersal development are most common among cosmopolitan species. However, this reproduction mode seems also important among the other zoogeographic types. Distribution via short pelagic or demersal larvae may be advantageous in many regions since it balances between a good dispersal of species and the avoidance of unfavourable areas. Clarke (1992) assumed that demersal reproduction is of great importance among Arctic species. Given that demersal larvae are rarely detected by common net sampling and considering that the reproduction mode of many species is still unknown, it might be assumed that their share within this zoogeographic group in the Kara Sea is even greater. Another explanation for the low numbers of demersal larvae would be that sampling has so far not coincided with larval release; however, this is true for all larval types.

4.5 Pelagic vs. non-pelagic development

At first sight, reproduction modes in the Kara Sea show an obviously higher proportion of directly to indirectly developing species, which is in agreement with the rule proposed by Thorson (1936, 1950) and Mileikovsky (1960, 1971) for Arctic areas (Figure 48a). This tendency becomes even more distinct when splitting reproduction types according to their zoogeographical range. Here, highest numbers of directly developing species are found within Arctic specimens, decreasing gradually when moving from Arctic species towards those with boreal distribution (Figure 49a).

However, careful analyses of the species composition (Figure 50) reveal that the high share of directly developing species can be attributed to the high numbers of peracarid species found in the study area. The large proportion of directly developing peracarids might have been a reason for Thorson's fewer findings of species reproducing via pelagic larvae (Thorson 1936). In his studies, which formed the basis for his view of reproduction patterns, 119 of the 215 species found in Franz-Josef Fjord and Scoresbysound in North-East Greenland belonged to crustaceans. All of them but 14 forms were Peracarida. 13 of the species with planktonic development belonged to natant decapods (which were totally absent in this study) and 1 cirripede.

82% of the crustaceans Thorson found in his study were of exclusively Arctic origin. In our study, a high amount (64% = 16 species) of the peracarids is confined to Arctic regions (Table 15). On evolutionary timescales directly developing species have been suggested to exhibit a much higher speciation rate than species dispersing via larvae (Jablonski & Lutz 1983, Duda & Palumbi 1999, Jablonski & Roy 2003). Species with direct development therefore may easier evolve into species better adapted to the Arctic environment. This may explain a higher endemism in polar waters for many peracarid crustaceans with direct development.

When removing the peracarid species from the dataset, pelagic development becomes the main reproductive strategy in Arctic-boreal species (Figure 48). This, however, is somewhat contrary to the traditional view on reproduction modes in the Arctic. Thorson (1950) reported that only 5% of Arctic marine invertebrates reproduce by larvae in the waters off East Greenland, a value that was clearly too low in the light of the studies cited above. However, in contrast to the Greenland shelf, the Kara Sea shelf is a comparatively unstable environment. Especially the shallow parts of the Kara Sea are characterised by pronounced interannual seasonality of ice-coverage, river discharge, and sedimentation rates complemented by strong intraannual fluctuations (e.g., Pavlov & Pfirman 1995, Makkaveev & Stunzhas 1994, Volkov 2002). Benthos communities are periodically reduced by freshwater discharge and ice scouring. Accumulations of large amounts of bivalve shells found in sediment cores of bottom surface layers indicate occasional mass mortalities among benthic organisms (Stein 2001, Stein & Levitan 2002). Instability of the regime may therefore promote fast recolonising species with planktonic larvae and highly mobile species such as amphipods and isopods (Mileikovsky 1971, Santos & Simon 1980, Burkovsky et al. 1997). Johst & Brandl (1997) found that low dispersal (direct development) is favoured in spatially heterogenous and temporally constant environments whereas high dispersal (indirect development) is favoured either in a spatially homogenous or temporally varying environment. The fact that species with planktonic larvae have a much higher potential to occupy new territories, might explain the relatively high amount of species with pelagic larvae (even among the Arctic species) in comparison to the findings of Thorson (1936).

4.6 Temporal occurrence of larvae

According to Table 15 most benthic organisms release their larvae during spring and summer irrespectively of their zoogeographic distribution or reproduction types. This seems reasonable since from temperate regions it is known that benthic productivity is tightly coupled to primary production in the upper water masses. Larval release should therefore occur predominantly into the plankton bloom. Additionally, the higher water temperatures in summer may also shorten the time to metamorphosis. Only the species *Ophiocten sericeum*, *Eteone longa*, and *Balanus* sp. seem to have continuous reproduction. Formin (1989) reported ophioplutei of *O. sericeum* as typical of the open Kara Sea throughout the year. Continuous reproduction seems to be a common pattern also for many bivalve species (Thorson 1936, Ockelmann 1958). Conversely Hain and Arnaud (1992) reported from Antarctic bivalves that many do not reveal distinct seasonal pattern.

Uncoupling from primary production has been explained by either utilisation of different food sources (e.g., bacteriotrophy, detritivory as reported for some ophiuroids (Rivkin et al. 1991, Chiantore et al. 2002), the uptake of dissolved nutrients (Chia 1970)). Lecithotrophy has been found in many invertebrate larvae. Lecithotrophy may be achieved by the production of large yolky eggs with an adequate amount of ooplasmic nutrient to support development until the specimen is able to feed. Nutrients may even be sufficient until settlement (Chia 1970, Day & McEdward 1984). Investigations done by Pearse (1994) and Clarke (1992) indicated a tendency towards lecithotrophic larvae in polar regions.

Of 36 species off west Greenland found by Curtis (1973), for which reproductive information was obtained, 30 were found to produce lecithotrophic eggs and the majority of those appeared to spawn during autumn or winter. Pearse (1994) reported that 70% of the echinoderms in Greenlandic waters reproduce via lecithotrophic larvae. The same seems to hold true for Antarctic echinoderms (Pearse & Bosch 1986, Pearse et al. 1991). Klages (1993) reported the presence of eggs and hatched juveniles in the marsupium of Antarctic Amphipoda in autumn. Antarctic cnidarians seem to spawn predominantly in autumn (Gili et al. in Arntz & Brey 2001, Orejas et al. 2002).

Uncoupling from primary production and the release of lecithotrophic larvae may be an advantageous adaptation to polar regions. Thorson (1936, 1950) based his argumentation against pelagic larvae in Arctic regions on the short period of primary production (=food availability) and much longer time required for larvae to finish metamorphosis. Lecithotrophic larvae are uncoupled from food availability. Since they are provided with sufficient food resources, release and survival of larvae do not any longer depend on the right timing with primary production.

Independence of food does not limit the larvae to certain reproduction periods either, and as drifting larvae the ability of dispersal remains.

Subdivision into feeding types is often questionable since many larvae exhibit mixed development (Barnes et al. 1993). Larvae are often lecithotrophic when hatching but subsequently have to feed for further development. This may ensure, that larval release and the beginning of primary production have not to match properly but guarantees the larvae a certain period to survive until food is available.

In summary, feeding types of larvae should be further separated in future studies on Arctic meroplankton. The high number of pelagic larval types found in this study indicates that planktonic development is important in the Kara Sea ecosystem, but we do not know which of them are planktotrophic. More studies are needed on life history strategies of benthic species in polar realms. This investigation shows the importance of direct and indirect development for the ecology of the benthos in the Kara Sea. Regarding those larvae that are advected with water masses from adjacent seas, changes of water temperature and currents due to global warming may influence larval transport and, thus, have a strong effect on the future composition of benthic communities in the Arctic.

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Captions

Table 15: List of adult benthic species from the Kara Sea contributing >4% of the total abundance. Presence of larvae and/or juveniles of these species in samples are marked with 'x' (see text for explanation). Larvae/juveniles of unsure adult species affiliation marked with '(x)'. Additionally the zoogeographical affiliation (A=arctic, AB=arctic-boreal, B=boreal, C=cosmopolite) and reproduction type (P=pelagic, P?=presumed pelagic, SP=short pelagic (demersal), D=direct, D?=presumed direct, ?=unknown) are indicated. Occurrence of ripe females (dark grey), larvae (light grey) and maximal occurrence of larvae (black) according to literature (see comments). '?' designate proposed presence of species. Grey bars indicate time of sample-taking in the Kara Sea August/September 2000 and 2001.

Table 16: List of larvae and juveniles were no adult species have been present in the Kara Sea. Presence of larvae and/or juveniles of these species in samples are marked with 'x' (see text for explanation). Larvae/juveniles of unsure adult species affiliation marked with '(x)'. Occurrence of ripe females (dark grey), larvae (light grey) and maximal occurrence of larvae (black) according to literature (see comments). '?' designate proposed presence of species.Grey bars indicate time of sample-taking in the Kara Sea August/September 2000 and 2001.

Table 17: Number of identified larval, juvenile and adult species, number of larvae and juveniles relative adult species, number of definitely identified larvae and juveniles, relative to number of adult species.

Figure 45: Overview sampling area, with location of adult benthos stations (!) 1997, 1999, 2000 and meroplankton/juvenile sampling stations (°) 2000 and 2001. The grey line indicates the 100m isobath.

Figure 46: Relative taxa composition of the adult benthos fauna in the Kara Sea

Figure 47: Species number and zoogeographical affilation of the adult benthos species of the Kara Sea

Figure 48: Reproduction modes of the adult benthos a) all species b) without Crustacea (for explanation see text); species with unknown reproduction strategy were excluded

Figure 49: Reproduction modes and zoogeographical affilation of the adult benthos a) all species b) without Crustacea (for explanation see text); species with unknown reproduction strategy were excluded

Figure 50: Reproduction modes of Crustacea, Echinodermata, Mollusca and Polychaeta for benthic species found in the Kara Sea

Table 15:

		Presence of		Zoogeo-graphy	Reproduction type	Presence of larvae/spawning females												Comments
		Lar	Juv			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Polychaeta	*Aglaophamus malmgreni*			C	P						🟨							Lacalli 1980
	Ampharete acutifrons			AB	D?		🟧	🟧	🟧									Price & Warwick 1980, Thorson 1946
	Ampharete arctica			A	D?													Thorson 1946: non-pelagic ?
	Aphaelochaeta aff. *multibranchis*		x	B	D?				🟧					🟧	🟧			Hartmann-Schröder 1996
	Aricidea nolani		(x)	AB	?													
	Aricidea cf. *suecia*		(x)	AB	?													
	Artacama proboscidea		x	AB	P				🟨	🟨	🟨			🟧	🟧	🟧	🟧	Thorson 1946
	Capitella capitata	x	x	C	SP			?	■	🟨	?							Lacalli 1980, Sveshnikov 1959
	Chaetozone setosa		x	C	D?					🟧	🟧	🟧						Hartmann-Schröder 1996
	Chone duneri	(x)	(x)	AB	P					?	🟨	🟨	🟧	🟨	🟨	?		Hartmann-Schröder 1996, Andersen 1984
	Cistenides hyperborea	(x)		AB	P													own observations
	Cossura longicirrata		x	A	D?													Thorson 1946
	Diplocirrus longisetosus			A	?													
	Eteone barbata	x	x	AB	P	?	?	🟨	🟨					🟧	🟧	🟧	🟨	Thorson 1946, Hartmann-Schröder 1996
	Eteone longa	x		C	P	🟨	🟨	🟨	🟨	🟨	■	■	🟨					Thorson 1946, Hartmann-Schröder 1996, Smidt 1979, Rasmussen 1973, Andersen 1984
	Exogone naida		x	AB	?													
	Gattyana cf cirrosa	x	x	A	P					🟨	🟨	🟨	🟨	?				Andersen 1984, own observation
	Laonice cirrata	x		A	P	🟧							🟧	🟧	?	?	🟧	Hartmann-Schröder 1996, Hannerz 1956, 1961, Plate & Husemann 1994
	Levinsenia gracilis		x	B	?								🟧					Hartmann-Schröder 1996
	Lumbrineris minuta		(x)	A	?						🟧	🟧	🟧					Hartmann-Schröder 1996
	Lysippe labiata		x	AB	?													
	Maldane sarsi			C	?													Thorson 1946
	Marenzelleria artica		x	A	?													
	Micronephtys minuta	(x)	(x)	A	P													Hartmann-Schröder 1995
	Nephtys ciliata	(x)	(x)	C	P					🟨	🟨	🟨	🟨					Thorson 1946, Smidt 1979, Mileikovsky 1959b
	Nereimyra aphroditoides	x	x	B	P		🟧	🟧			🟨	🟨	🟨	?eggs ?				Thorson 1946, Banse 1955, Andersen 1984, Sveshnikov 1959

Table 15 (continued)

		Presence of		Zoogeo-graphy	Reproduction type	Presence of larvae/spawning females												Comments
		Lar	Juv			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Polychaeta	*Nereis zonata*		x	A	D?				?	🟧	🟧	🟧	🟧 ?					Thorson 1936: cannot have pelagic larvae
	Nicomache lumbricalis			A	D?													Thorson 1946: big eggs direct development
	Ophelina acuminata		x	C	?													
	Ophelina cylindricaudata	x	x	AB	?													
	Owenia fusiformis	(x)	x	C	P			🟨	🟨	🟨	🟨							Thorson 1946
	Pholoe minuta	x	x	AB	P					🟧	■	🟨	🟨					Thorson 1946, Rasmussen 1973, Blake 1975, Andersen 1984, Sveshnikov 1959
	Phyllodoce groenlandica	x	x	A	P					🟧	🟨	🟨	🟨	?	🟨			Thorson 1946, Smidt 1979, Andersen 1984, Thorson 1936
	Polydora quadrilobata	x		AB	P			🟨	🟨	🟨								Lacalli 1980, Blake 1975: booding in tube + short pelagic phase
	Praxillella praetermissa			AB	?													
	Prionospio cirrifera	x		AB	P					?	?	🟨	🟨					Hannerz 1961, Mileikovsky 1968
	Sabellides borealis		(x)	AB	?													
	Scalibregma inflatum		x	C	SP										🟧 epitoke stadia	🟧	🟧	Thorson 1946: Short pelagic or floating
	Scolelepsis metsugae	x		A	P													Hannerz 1956
	Scoloplos armiger	x	x	C	SP		🟨	🟨	■	🟨								Andersen 1984, Smidt 1979, Rasmussen 1973, Banse 1955, Thorson 1946, Sveshnikov 1959, Burkovsky et al 1997
	Sphaerodorum flavum		x	AB	D?									🟧	🟧	🟧		Thorson 1946, own observation
	Spio limicola (arctica)	x	x	A	?													
	Terebellides stroemi		x	C	D					🟧								Thorson 1936: troch develop in egg mass and/or probably demersal
	Tharyx cf killariensis			B	D				🟧	🟧	🟧							Thorson 1946
	Trochochaeta carica			A	D								🟧	■				Buzhinskaja & Jørgensen 1997:larvae brooded in tubes with short pelagic phase

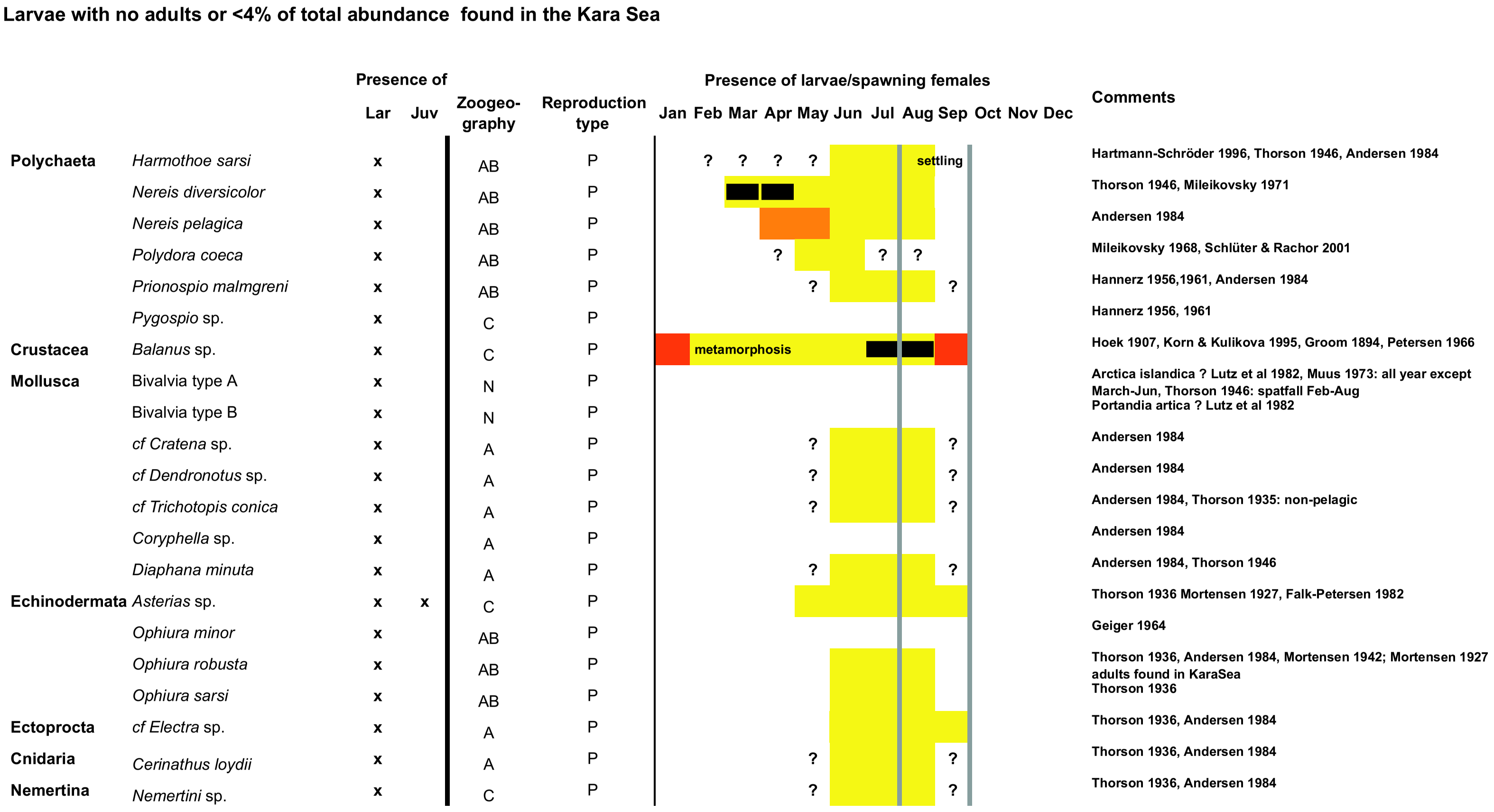
Table 15 (continued)

		Presence of		Zoogeo-graphy	Reproduction type	Presence of larvae/spawning females												Comments
		Lar	Juv			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Crustacea	*Aceroides latipes*		x	A	D													Sars 1895
	Atylus carinatus			A	D													Sars 1895
	Brachydiastylis resima			AB	D													Sars 1895
	Byblis gaimardi			AB	D													Sars 1900
	Diastylis edwardsi			A	D													Sars 1900
	Diastylis glabra			A	D													Sars 1900
	Diastylis goodsiri			A	D													Sars 1900
	Diastylis nucella			A	D													Sars 1900
	Diastylis rathkei sarsi			AB	D													Sars 1900
	Diastylis spinulosa			A	D													Sars 1900
	Diastylis sulcata			A	D													Sars 1900
	Eudorella emarginata		x	AB	D													Sars 1895
	Haploops laevis		x	A	D													Stephensen 1942, Sars 1895
	Leucon acutirostris		(x)	AB	D													Sars 1895
	Leucon fulvus		(x)	A	D													Sars 1900
	Leucon nasica typicus		(x)	AB	D													Sars 1900
	Leucon nathorsti		(x)	A	D													Sars 1900
	Onisimus affinis			A	D													Sars 1895
	Onisimus botkini			A	D													Sars 1895
	Paroeciderus lynceus			A	D													Sars 1895
	Photis tenuicornis			AB	D													Sars 1895
	Pontoporeia affinis			A	D													Sars 1895: artic freshwater relict form
	Pontoporeia femorata			AB	D													Sars 1895
	Protomedeia fasciata			AB	D													Sars 1895
	Saduria sibirica		x	A	D													Sars 1895

Table 15 (continued)

		Presence of		Zoogeo-graphy	Reproduction type	Presence of larvae/spawning females												Comments
		Lar	Juv			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Mollusca	*Astarte borealis*		x	AB	SP										🟧	🟧	?	Thorson 1936: non-pelagic, Ockelmann 1958: short pelagic or direct development
	Axinulus ferruginosus		x	AB	?													
	Cylichna cf *occulta*		x	A	?													Gajevskaja 1948, Golikov 1994
	Macoma calcarea		x	A	P					🟧	🟨	🟨 metamorphosis	🟨					Andersen 1984, Smidt 1979: found larvae, Ockelmann 1958: pelagic development, Thorson 1936, 1946: non-pelagic, Muus 1973
	Musculus corrugatus			A	?													
	Nucula bellotii		x	A	SP													Ockelmann 1958: short pelagic or direct
	Nuculana pernula			AB	SP								🟧	?	?	?		Thorson 1936, Ockelmann 1958
	Pandora glacialis		x	A	SP													Ockelmann 1958: short pelagic or direct
	Portlandia arctica		x	A	P?							🟧	🟧					Thorson 1936, Ockelmann 1958: demersal, own observations: Bivalvia type B
	Thyasira gouldii			AB	SP								🟧	🟧				Thorson 1936: non-pelagic, Ockelmann 1958: short pelagic or direct; first stages develop inside adult
	Yoldiella lenticula			A	SP													Thorson 1936, Ockelmann 1958: demersal
	Yoldiella nana		x	A	D?													Thorson 1936
	Yoldiella solidula		x	A	D?													Thorson 1936
Echinodermata	*Ctenodiscus crispatus*		x	A	SP			spawning whole year ?										Mortensen 1927, Thorson 1936, Falk-Petersen 1982: winter breeder
	Eupyrgus scaber	x	x	A	P					?	🟨	🟨 ?	🟨	?				Andersen 1984, own observation
	Myriotrochus eurycyclus	(x)	(x)	AB	P					?	🟨	🟨	🟨 ?	settling				Andersen 1984, own observation
	Myriotrochus rinki	(x)	(x)	AB	P					?	🟨	🟨	🟨 ?	settling				Andersen 1984, own observation
	Ophiocten sericeum	x	x	AB	P	⬛	?	🟨	🟨	🟨	🟨	⬛	⬛	⬛	🟨	🟨	⬛	Thorson 1936, Andersen 1984, Smidt 1979, Semenova et al 1964, Geiger 1964
	Species number		88															
	Adult species cut-off = 4%																	

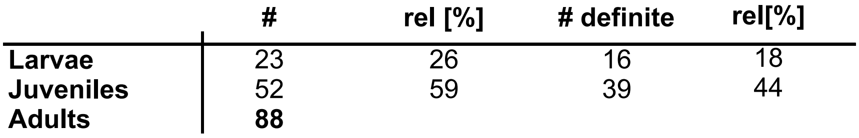
Table 16:



Larvae with no adults or <4% of total abundance found in the Kara Sea

		Presence of		Zoogeo-graphy	Reproduction type	Presence of larvae/spawning females												Comments
		Lar	Juv			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Polychaeta	*Harmothoe sarsi*	x		AB	P		?	?	?	?	🟨	🟨	🟨 settling					Hartmann-Schröder 1996, Thorson 1946, Andersen 1984
	Nereis diversicolor	x		AB	P			🟨■	🟨■	🟨	🟨	🟨	🟨					Thorson 1946, Mileikovsky 1971
	Nereis pelagica	x		AB	P				🟧	🟧	🟨	🟨	🟨					Andersen 1984
	Polydora coeca	x		AB	P				?	🟨	🟨	?	?					Mileikovsky 1968, Schlüter & Rachor 2001
	Prionospio malmgreni	x		AB	P					?	🟨	🟨	🟨	?				Hannerz 1956,1961, Andersen 1984
	Pygospio sp.	x		C	P													Hannerz 1956, 1961
Crustacea	*Balanus* sp.	x		C	P	🟥	🟨 metamorphosis	🟨	🟨	🟨	🟨	🟨■	🟨■	🟥				Hoek 1907, Korn & Kulikova 1995, Groom 1894, Petersen 1966
Mollusca	Bivalvia type A	x		N	P													Arctica islandica ? Lutz et al 1982, Muus 1973: all year except March-Jun, Thorson 1946: spatfall Feb-Aug
	Bivalvia type B	x		N	P													Portandia artica ? Lutz et al 1982
	cf Cratena sp.	x		A	P					?	🟨	🟨	🟨	?				Andersen 1984
	cf Dendronotus sp.	x		A	P					?	🟨	🟨	🟨	?				Andersen 1984
	cf Trichotopis conica	x		A	P					?	🟨	🟨	🟨	?				Andersen 1984, Thorson 1935: non-pelagic
	Coryphella sp.	x		A	P													Andersen 1984
	Diaphana minuta	x		A	P					?	🟨	🟨	🟨	?				Andersen 1984, Thorson 1946
Echinodermata	*Asterias* sp.	x	x	C	P					🟨	🟨	🟨	🟨	🟨				Thorson 1936 Mortensen 1927, Falk-Petersen 1982
	Ophiura minor	x		AB	P													Geiger 1964
	Ophiura robusta	x		AB	P						🟨	🟨	🟨					Thorson 1936, Andersen 1984, Mortensen 1942; Mortensen 1927 adults found in KaraSea
	Ophiura sarsi	x		AB	P						🟨	🟨	🟨					Thorson 1936
Ectoprocta	*cf Electra* sp.	x		A	P						🟨	🟨	🟨	🟨				Thorson 1936, Andersen 1984
Cnidaria	*Cerinathus loydii*	x		A	P					?	🟨	🟨	🟨	?				Thorson 1936, Andersen 1984
Nemertina	*Nemertini* sp.	x		C	P					?	🟨	🟨	🟨	?				Thorson 1936, Andersen 1984

Table 17:



	#	**rel [%]**	**# definite**	**rel[%]**
Larvae	23	26	16	18
Juveniles	52	59	39	44
Adults	**88**			

Figure 45:

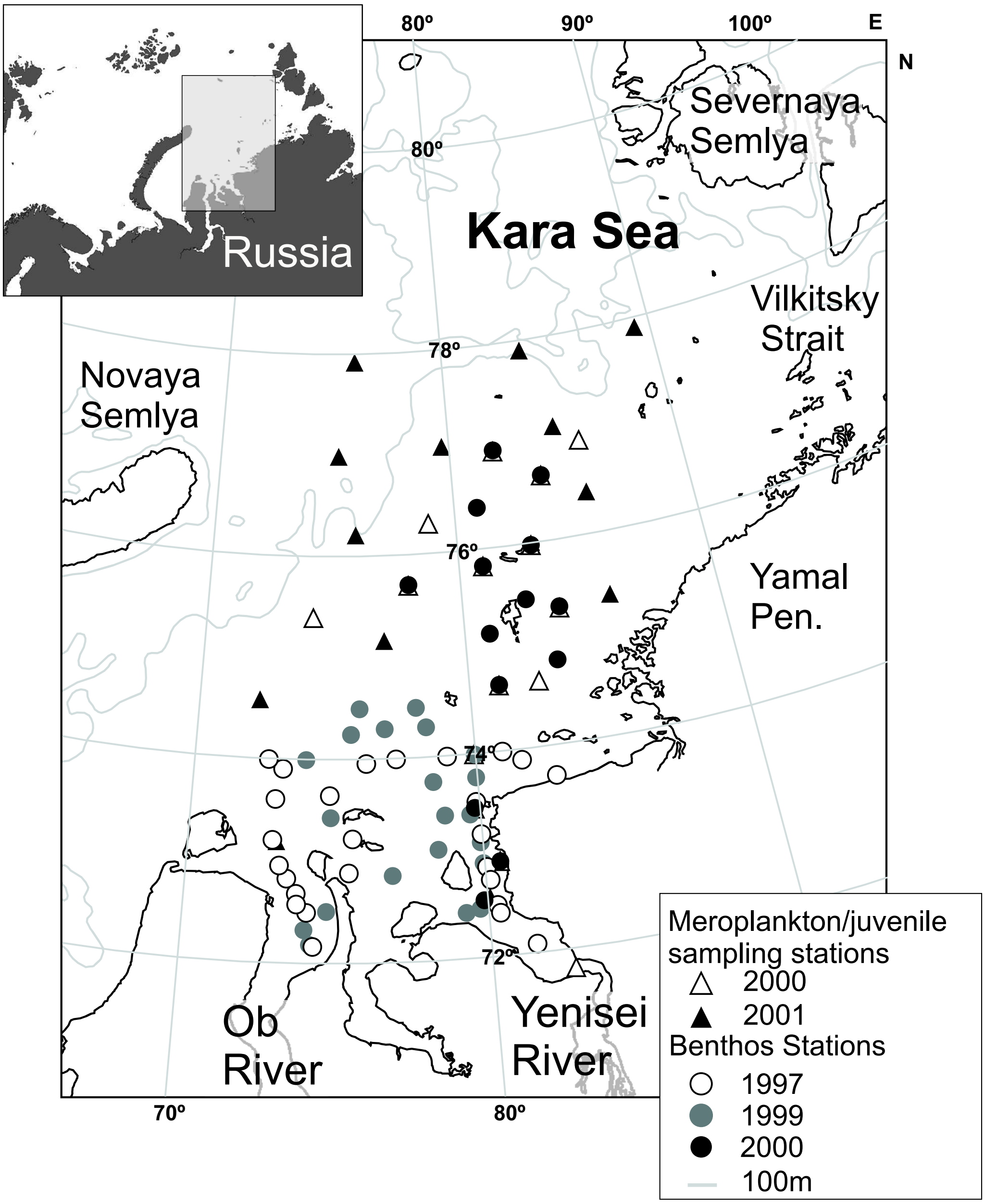

Russia
80°
90°
100°
E
N
80°
Severnaya
Semlya
Kara Sea
Vilkitsky
Strait
78°
Novaya
Semlya
76°
Yamal
Pen.
74°
72°
Ob
River
Yenisei
River
70°
80°
Meroplankton/juvenile
sampling stations
△ 2000
▲ 2001
Benthos Stations
○ 1997
● 1999
● 2000
100m

Figure 46:

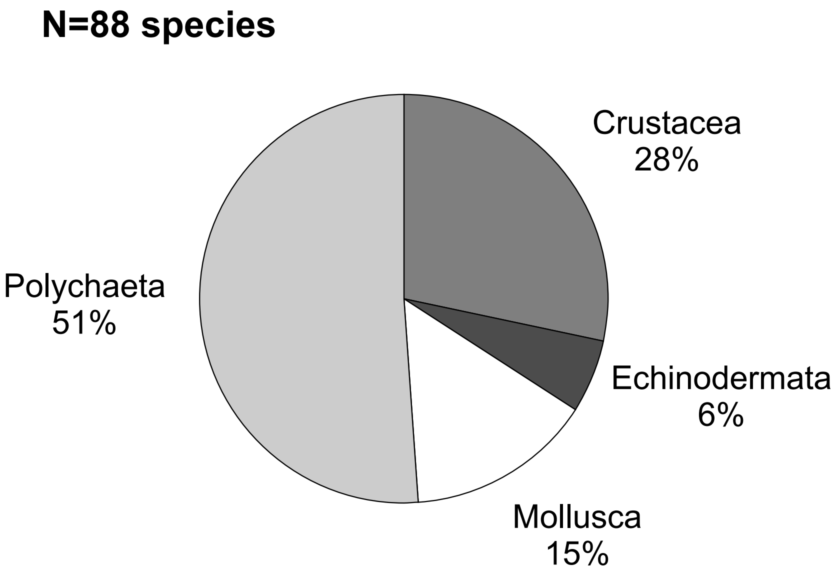


Figure 47:

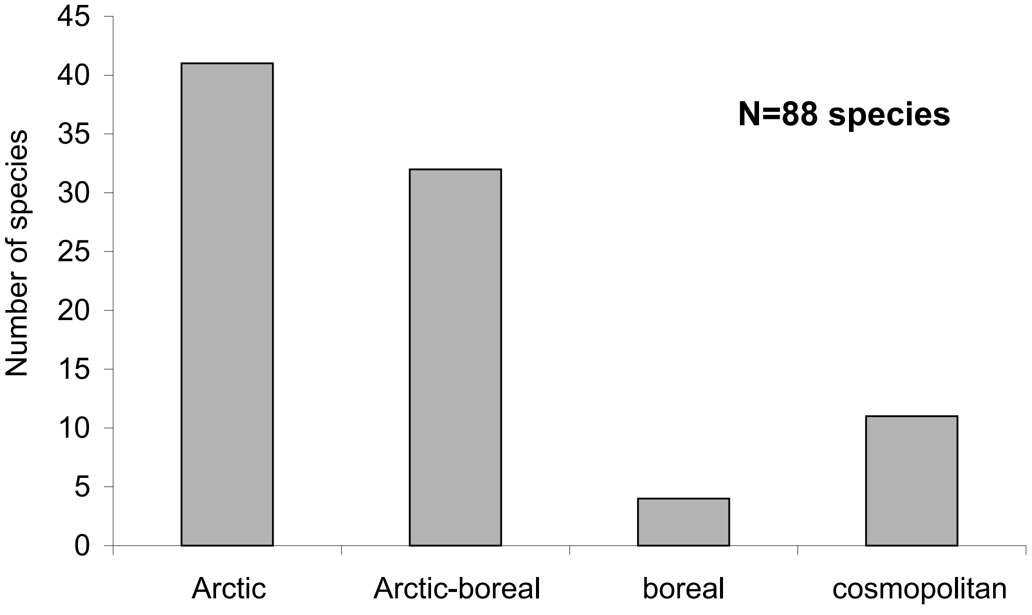


Figure 48:

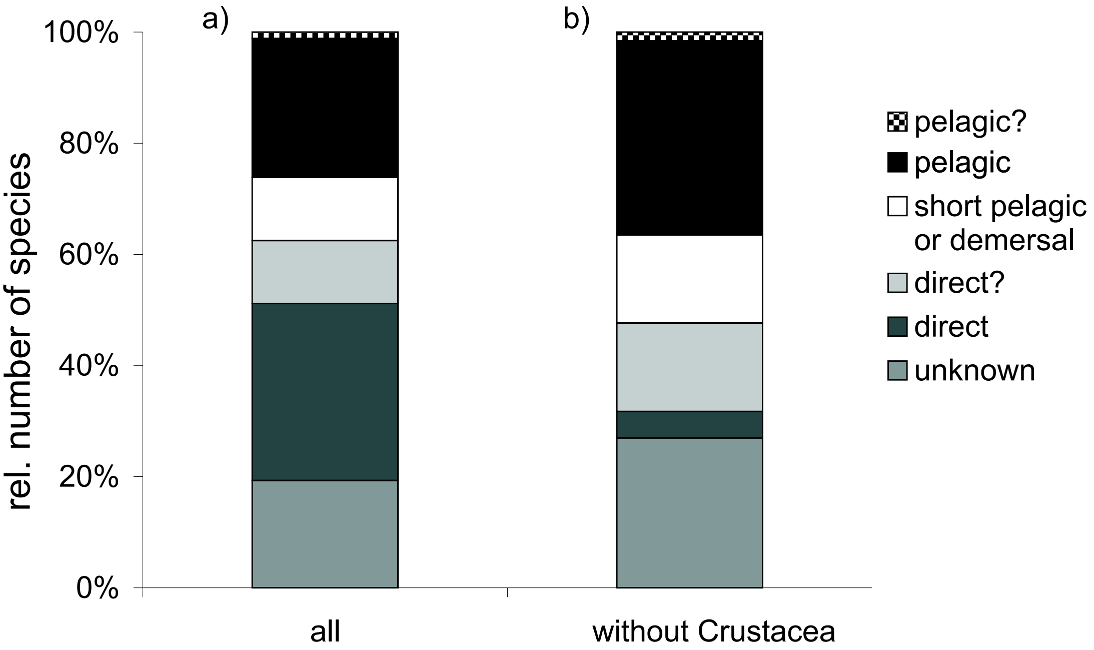

a)
b)
100%
80%
60%
40%
20%
0%
rel. number of species
pelagic?
pelagic
short pelagic or demersal
direct?
direct
unknown
all
without Crustacea

Figure 49:

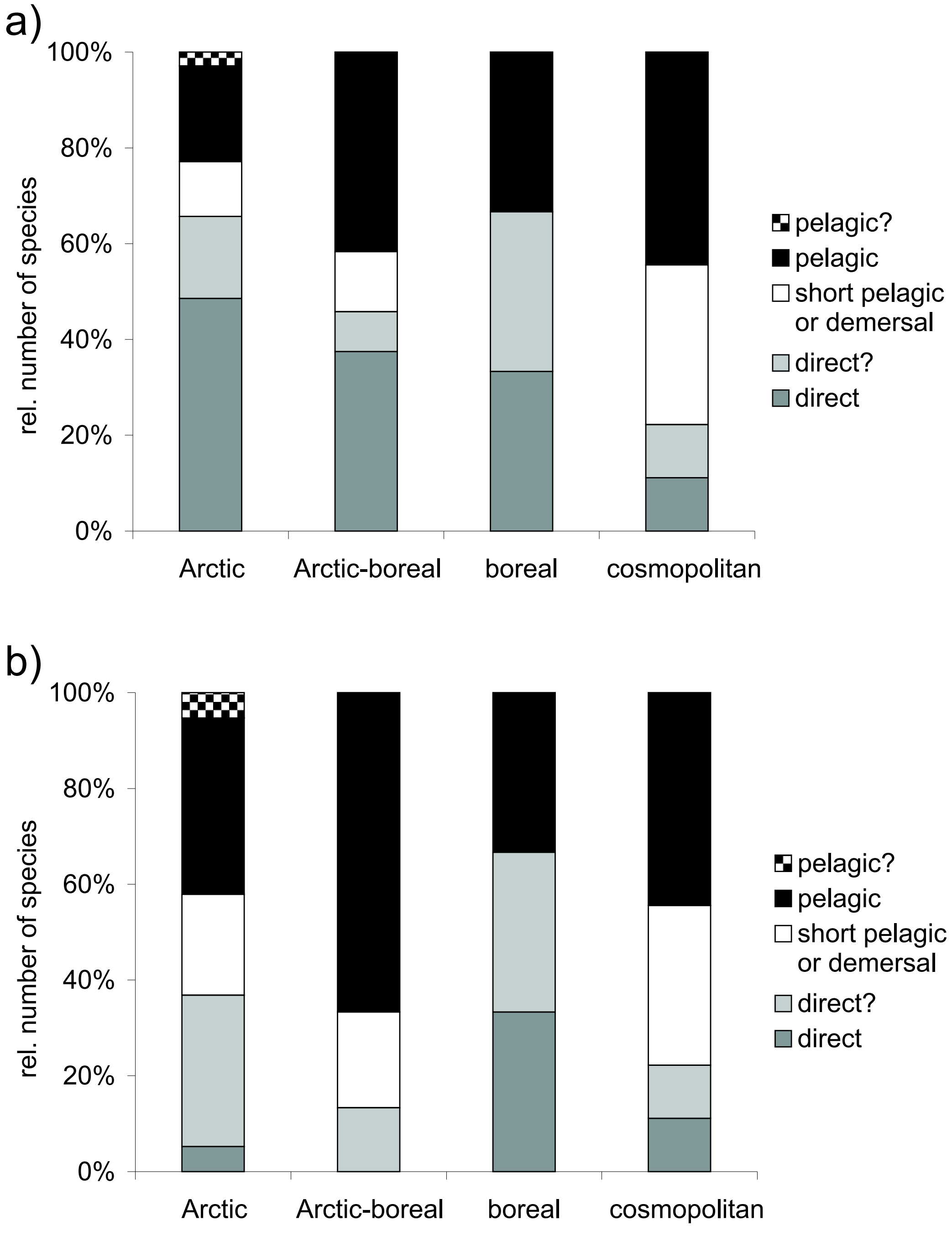
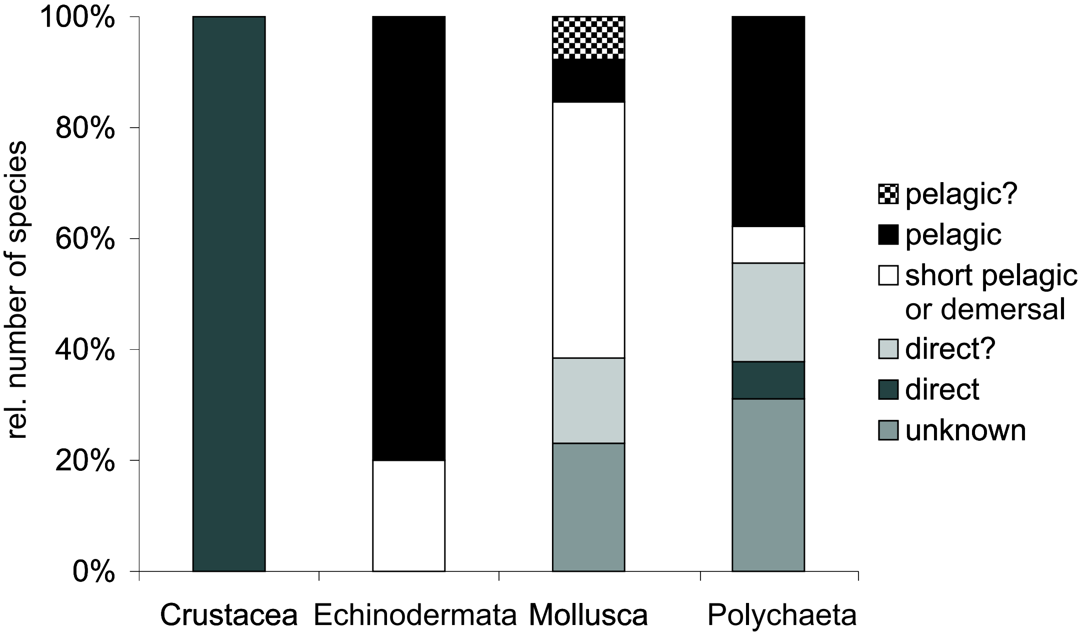

a)
100%
80%
60%
40%
20%
0%
rel. number of species
Arctic
Arctic-boreal
boreal
cosmopolitan
pelagic?
pelagic
short pelagic or demersal
direct?
direct
b)
100%
80%
60%
40%
20%
0%
rel. number of species
Arctic
Arctic-boreal
boreal
cosmopolitan
pelagic?
pelagic
short pelagic or demersal
direct?
direct

Figure 50:


100%
80%
60%
40%
20%
0%
rel. number of species
Crustacea
Echinodermata
Mollusca
Polychaeta
pelagic?
pelagic
short pelagic or demersal
direct?
direct
unknown

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