

Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): adaptation of reproduction modes to cold water

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ABSTRACT: Many benthic invertebrates in the boreo-Atlantic region reproduce via pelagic larvae. Past investigations in polar areas suggested a greater predominance of species lacking a pelagic phase. In this study, the reproduction strategies of the main 88 species of the Kara Sea were investigated. Field observations were supplemented by literature studies (reproduction period and strategy, biogeographical affiliation). Larvae of 44 meroplanktonic species were identified, but adult forms of only 23 of these species are known from the region. For the other 21 larval types, adults were not present in the Kara Sea but have previously been recorded in the adjacent Barents Sea. Larval transport processes are thus potentially important for the import of species into the region. High numbers of species of temperate origin were common, and had a strong influence on the overall reproduction patterns of the region. The southern Kara Sea was mainly dominated by 2 groups: highly mobile crustaceans, which are obligate non-pelagic developers, and non-motile organisms with primarily pelagic reproduction modes. We propose that reproduction patterns are strongly influenced by the highly variable environmental conditions of the Kara Sea which, via ice-scouring and the high input of freshwater from the 2 adjacent rivers, regularly lead to a local depletion of the benthic species. The input of warm freshwater from the rivers enhances the survival of species with a boreal biogeographical distribution, which additionally contributes to the high number of species with pelagic development that were found. Overall, the reproduction modes of benthic invertebrates in the Kara Sea are thus strongly governed by the local environmental conditions characteristic of the region.

KEY WORDS: Arctic · Kara Sea · Benthos · Biogeography · Reproduction types · Reproduction period

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INTRODUCTION

Marine invertebrates display a great variety of development modes. These modes may differ according to the ecological niche they occupy during development e.g. the spatial location of larvae (benthic vs. pelagic), trophic types (feeding vs. non-feeding), as well as the degree of parental care (free vs. protected) (Poulin et al. 2001). Each type is found in all marine realms but comparisons of the principal reproduction modes have shown that they are not equally distributed among geographic regions (Thorson 1936, Mileikovskiy 1971, 1974, Poulin & Féral 1998).

Thorson (1950) stated that more than 70 % of the benthic invertebrates in the boreo-Atlantic regions repro-

duce via pelagic larvae, which potentially enables dispersal over large distances. This is obviously advantageous, especially in the case of sessile and less mobile species (Scheltema 1989). It allows for the fast colonization of new territories (Thorson 1950), and avoids persistent inbreeding and intra-specific food competition between new recruits and adults (Grosberg & Quinn 1986, Grosberg 1987). On the other hand, benthic development without a pelagic stage guarantees higher offspring survival rates since they are not endangered by drifting into unfavorable regions but rather remain at sites where the adults have survived.

In the first meroplanktonic surveys in polar waters conducted by Thomson (1878) the small number of

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pelagic larvae at high latitudes led to the assumption that in polar species the relative importance is shifted towards benthic development. The investigations of Thorson (1936, 1946, 1950) supported this hypothesis, which later became known as 'Thorson's rule' (see Mileikovsky 1971). Thorson (1936) explained the predominance of benthic development in polar seas by the mismatch between the prolonged development times of pelagic developers due to metamorphosis and the shortage in food availability of plankton at high latitudes, apparently selecting against species with a pelagic life history (Pearse & Lockhart 2004). His concept was supported by observations that many species at higher latitudes tend to produce larger but fewer yolk-rich eggs than their counterparts at lower latitudes, pointing to a non-pelagic, abbreviated developmental mode (Pearse 1994, Thatje & Fuentes 2003). Additionally, in the southern polar hemisphere higher proportions of species with parental care and non-feeding larvae were found (Pearse 1994).

Recently, larger numbers of pelagic larval types have been detected primarily in the shallow Antarctic waters, with a number of planktotrophs found even among the dominant species (Stanwell-Smith et al. 1999, Poulin et al. 2002). Pelagic development also seems to be more common than previously thought among Arctic benthic animals (Dayton 1990). Nonetheless, the percentage of species with pelagic development in Antarctic waters appears small when compared with the large number of benthic species in these waters. Moreover, larval peak abundances are estimated to be 2 to 6 orders of magnitude lower than in comparable data from temperate zones (Stanwell-Smith et al. 1999, Arntz & Gili 2001). Stanwell-Smith et al. (1999) hypothesized that the low abundances found can be explained by dilution of the larvae over larger regional and temporal scales due to a reduced spawning synchrony of the adults and the long duration of the larvae in the water column. Today Thorson's concept, 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, Arntz & Gili 2001, Gallardo & Penchaszadeh 2001).

Most of the recent research on this topic has been done almost exclusively in Antarctic regions (Pearse & Lockhart 2004). Due to the isolated status of this region, the development patterns of benthic invertebrates are more conspicuous. Among the benthic animals, exceptionally high proportions are pelagic-lecithotroph or show parental care. Poulin et al. (2002) explained this by selective extinctions of mainly planktotroph species during the last glacial period and the current

ecological success of the pelagic planktotrophs. Alternatively, Thatje et al. (2005) hypothesize that the current rarity of broadcasters among Antarctic marine benthic invertebrates is a consequence of the total extinction of all species from the shelves. Antarctic species survival was only possible in the deep sea (promoting sheltered lecithotroph development modes) and for planktotrophs in discrete shelters on the continental shelf. Pearse & Bosch (1994) suggested that the unique conditions of isolation resulting from the opening of the Drake Passage 30 million yr ago promoted new species formation of specious clades of brooders.

During the last glacial maximum in Arctic realms, however, extinction processes were similar to those in the Antarctic (Piepenburg 2005). But since the Arctic region never became isolated from the adjacent Pacific and Atlantic, a potential immigration of non-polar species of boreal regions tolerant to the polar conditions was still possible (Zenkevitch 1963, Dayton et al. 1994). As a consequence, regions with favorable environmental conditions can be preferably populated by species other than those with an Arctic biogeographical distribution, thus altering the overall ratio of development modes towards those more characteristic of boreal regions. Moreover, in regions with unstable environments where the immobile adult benthic organisms are periodically erased (e.g. due to ice-scouring) re-occupation by species with pelagic development should be favored (Palma et al. 2007). It is still unknown how far the interrelationship between local environmental characteristics and species composition affects the presence of certain reproductive traits in order to ensure the survival of species within a region. Therefore, we investigated development modes of benthic invertebrates of the Arctic Kara Sea. Generally, the waters of this polar region are characterized by low water temperatures, high salinity and oligotroph conditions (Volkov 2002). The Kara Sea is an 'intermediate' sea, the western part being influenced by the boreal Barents Sea while the eastern region borders on the high Arctic Laptev Sea. The Ob and Yenisei Rivers discharge large amounts of freshwater into the adjacent shallow marine realm, significantly altering the thermal, saline and nutrition regime of the Kara Sea on a regional scale through the constant input of warm, low salinity and highly nutrient-loaded waters (Pavlov & Pfirman 1995, Volkov 2002).

The aims of this study are (1) to give a first indication of the main development modes prevailing for the benthic invertebrates of the Kara Sea, (2) to investigate the adaptation in life history traits of the benthic species and (3) to investigate how far local environmental characteristics have an influence on the prevailing species and thus also on the overall reproductive traits of the Kara Sea species. In addition to field data

on adults, juveniles and planktonic larvae gathered during several expeditions, a general overview of the development modes of the main benthic invertebrates is compared with findings from the literature together with the biogeographical affiliations of the adult species occurring.

MATERIALS AND METHODS

Study area. The Kara Sea is located on the shallow Siberian shelf, which in its central part hardly exceeds a depth of 40 to 50 m (Fig. 1). The area has an open boundary with the Arctic Basin to the north while it is framed in the west by the St. Anna trough (maximum depth 600 m), which stretches along the east coast of Novaya Zemlya. To the east, Severnaya Zemlya and the 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 mainland and Novaya Zemlya as well as around the northern tip of the island. Waters from the Arctic Ocean and the Laptev Sea periodically wash into the area from the north and along Severnaya Zemlya through the Vilkitski Strait.

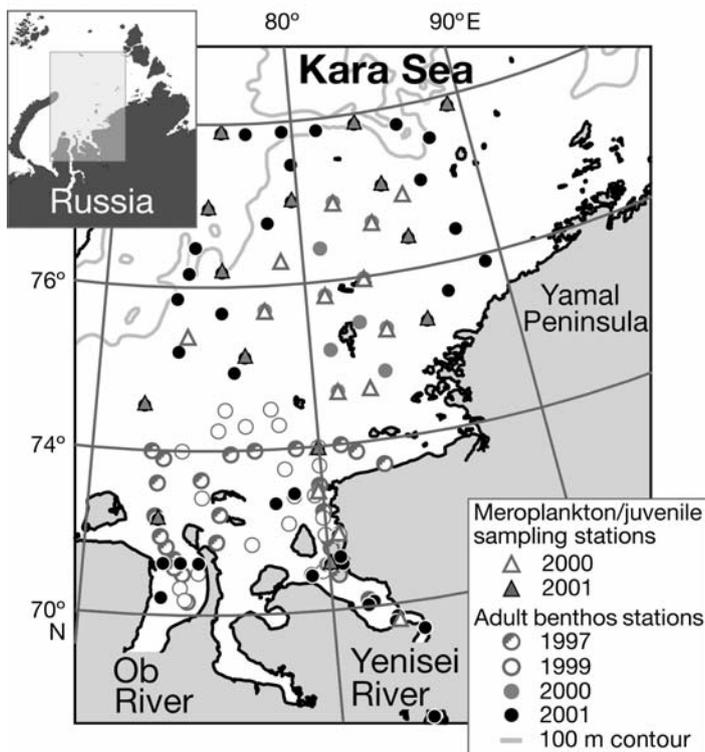


Fig. 1. Sampling area in the Kara Sea, with location of adult benthos stations in 1997, 1999, 2000 and 2001, and meroplankton/juvenile sampling stations in 2000 and 2001

The Kara Sea is covered by ice for about 9 mo 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 2 largest rivers Ob and Yenisei in early to late June (Mironov et al. 1994).

Sampling. Adult fauna were analyzed during 4 expeditions to the Kara Sea on board RV 'Akademic Boris Petrov' in 1997, 1999, 2000 and 2001 (Fig. 1). All expeditions took place in the period August–September of each year. Samples were collected at 26 stations in 1997, 24 stations in 1999 and 16 stations in 2000. Since the bottom in the study area consists mainly of medium to very soft sediments with occasional pebbles and shells, benthos samples were taken with a large box corer (0.25 m² coverage area) and a dredge ('Kieler Kinderwagen', frame size 150 × 50 cm). Animals were extracted by rinsing sediments on 500 µm screens, and preserved in 6% borax-buffered formalin.

For meroplankton and juvenile investigations, specimens were sampled at 30 stations during each expedition in 2000 and 2001 (Fig. 1). Meroplanktonic larvae were caught with a vertically hauled Nansen net (0.442 m² catching area, 55 µm mesh size, 0.5 m s⁻¹ hauling speed). The sampling depths varied between 6 m in the southeastern part of the sampling area to about 200 m in the northwest (for details see Deubel et al. 2003). Samples were then directly sorted for meroplankton under a stereo-microscope and the specimens preserved in Carrier solution (a Na₂CO₃-buffered sugar-formalin solution).

To study the distribution of already settled juveniles or released offspring of species with benthic development modes, multicorer samples (280 cm² coverage area per tube) were taken (Fig. 1). At each station, 6 tubes were deployed. The upper 10 to 15 cm of each core was taken and screened over a sieve column into fractions of 500, 250, and 125 µm. All animals found in each fraction were extracted and preserved in 70% ethanol. Additionally, adult animals possessing brood pouches (e.g. amphipods or bivalves) were carefully inspected in the laboratory for juveniles or eggs.

Taxonomic identification. All animals were identified to the lowest possible taxon. For juveniles the body length of each specimen was measured with a microscale to ±10 µm. Measurements were only conducted on complete animals. Juveniles were defined as immature specimens less than 1/3 of mean adult size according to the literature (e.g. Hartmann-Schröder 1996 for polychaetes). Many larvae and juveniles could not be directly determined to the species level. Therefore, the comparison of larvae, juveniles and the local adult fauna was often necessary to match larvae and juveniles to adult species.

Reproduction types. For the classification of development patterns in benthic marine invertebrates Poulin et al. (2001) propose a comprehensive scheme of different niche occupation by the offspring during their development. They distinguish development patterns by habitat (pelagic vs. benthic development), physically free vs. protected (brooded) development of the larvae and by the mode of nutrition uptake (feeding vs. non-feeding). Since reproduction strategies often cannot be confined exclusively to one of these groupings, and larval types thus often possess transitive characteristics between the extremes, they proposed a multispaced model to place all larval types.

However, in contrast to the more comprehensively investigated Antarctic regions (e.g. Bosch & Pearse 1990, Clarke 1992, Hain & Arnaud 1992, Chiantore et al. 2002) little information exists on the development modes of Arctic animals. Due to the limited knowledge of Arctic meroplankton ecology of species present in the Kara Sea, the development types were classified by the habitat occurrence of the larvae (i.e. the most apparent characteristic), with reference to existing literature. This approach represents only one aspect of the multidimensional approach given by Poulin et al. (2001) and should be seen as a first approximation for investigating planktonic development modes in the Kara Sea. However, this approach allows one to make predictions on the relationship between pelagic and benthic development traits of benthic animals as an adaptation to the environment in the investigated area and the adjacent Arctic seas. It also helps to estimate the species' potential ability to disperse (see also Tables 1 & 2). All species have therefore been placed in one of the following categories:

- Pelagic: species with a defined pelagic larval stage
- Pelagic?: species with a presumed pelagic larval stage
- Short pelagic or demersal: species with a short pelagic phase or demersal larvae
- Benthic: species lacking a pelagic phase
- Benthic?: species with presumed non-pelagic development
- Unknown: species with undetermined development mode

For the classes 'pelagic?' and 'benthic?' the reproduction mode was assumed to be pelagic or benthic but either the literature was inconclusive on this point or it was not confirmed by our own observations.

Life history and biogeographical distribution of species. Life-history traits and the biogeographical distribution of the adult benthic species were determined from the literature (see 'Comments' in Tables 1 & 2). 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 summarized and compared with field data. Since for many species the real duration of the larval time is uncertain, question marks have been used in the tables to indicate the proposed presence for the species.

RESULTS

Biogeographical distribution of benthos

For the benthic species, the adults of 88 species were found during the expeditions in the Kara Sea (Table 1). Most of these belonged to the Polychaeta (45 species; 51%). The next largest group was the Crustacea containing 25 species (28%). Crustacea were exclusively composed of the groups Cumacea ([*Brachy-*] *Diastylis* spp. and *Leucon* spp.), Isopoda (*Saduria sibirica*) and Amphipoda. Mollusca contributed 13 species (15%) to the total. Except for *Cylichna* cf. *occulta* (Gastropoda) all species within this group were Bivalvia. Only 5 species (6%) belonged to the echinoderms, which were composed of the 3 groups Asterozoa (*Ctenodiscus crispatus*), Holothurozoa (*Eupurgus scaber*, *Myriotrochus eurycyclus*, *Myriotrochus rinkii*), and Ophiurozoa (*Ophiocten sericeum*).

With regards to the biogeographical distribution, 41 species (47%) were of Arctic origin, while 32 species (36%) had an Arctic-boreal distribution. Another 4 species (4.5%) were assigned to boreal regions, while 11 species (12.5%) were cosmopolitans. Cosmopolitans were exclusively polychaetes, whereas no taxon dominated among the Arctic-boreal and Arctic species. Larvae of 26% of the benthic species were found in plankton samples, accounting for 23 different larval types (Table 1). Most (19 larval species) belonged to the polychaetes, and 4 species to the echinoderms, whereas no larvae of the adult crustacean and mollusc species were detected. Of the larvae found, 16 types could be definitely identified at the species level.

Juveniles of 52 benthic species (59% of adult species) were found. Of these, 39 juvenile types could be determined at the species level. The biggest share of juveniles found belonged to the Polychaeta (30 species), with 9 species belonging to the Mollusca, 8 species to the Crustacea and 5 species to the Echinodermata. No ripe female crustaceans were detected during the study period. Additionally, 21 larval types were identified belonging to species whose adults were not found in the Kara Sea (Table 2). According to the literature, 8 of these are of Arctic-boreal origin. Another 4 species were cosmopolitans. Mollusc larvae found were exclusively of an Arctic biogeographical distribution.

Table 1. Benthic invertebrates in the Kara Sea. Presence of larvae and/or juveniles of these species in samples are marked 'x' (see 'Materials and methods: Sampling' for explanation). Larvae/juveniles with an uncertain adult species affiliation are marked '(x)'. Biogeographical affiliation (Zoogeog.): A = arctic, AB = arctic-boreal, B = boreal, C = cosmopolitan. Reproduction type (Reprod.): P = pelagic, P? = presumed pelagic, SP = short pelagic (demersal), Bt = benthic, Bt? = presumed benthic, ? = unknown. Occurrence of ripe females (dark grey), larvae (light grey) and maximal occurrence of larvae (black) according to the literature (see 'Comments'). '?' = proposed presence of species, M = metamorphosis, S = settling phase, E? = eggs?, epitoke st. = epitoke stadia. Vertical grey lines show the sampling period in this study: August–September 2000 and 2001

	Presence of Larvae/Juvenile		Zoo-geog.	Reprod. type	Presence of larvae/spawning females												Comments
	Larvae	Juvenile			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Polychaeta																	
<i>Aglaophamus malmgreni</i>			AB														Lacalli (1980)
<i>Ampharete acutifrons</i>			AB														Thorson (1946), Price & Warwick (1980)
<i>Ampharete arctica</i>		x	A														Thorson (1946): non-pelagic?
<i>Aphaelochaeta aff. multibranchis</i>		(x)	B														Hartmann-Schröder (1996)
<i>Aricidea nolani</i>		(x)	AB														Thorson (1946)
<i>Aricidea cf. suecia</i>		x	AB														Sveshnikov (1959), Lacalli (1980)
<i>Aritacama proboscidea</i>		x	C														Hartmann-Schröder (1996)
<i>Capitella capitata</i>		x	C														Andersen (1984)
<i>Chaetozone setosa</i>		(x)	AB														Hartmann-Schröder (1996)
<i>Chone duneri</i>		(x)	AB														Authors' pers. obs.
<i>Cistenides hyperborea</i>		(x)	AB														Thorson (1946)
<i>Cossura longicirrata</i>		x	A														Thorson (1946), Hartmann-Schröder (1996)
<i>Diplocirrus longisetosus</i>		x	A														Thorson (1946), Rasmussen (1956), Smidt (1979), Andersen (1984), Hartmann-Schröder (1996)
<i>Eteone barbata</i>		x	AB														Andersen (1984), authors' pers. obs.
<i>Eteone longa</i>		x	C														Hannerz (1956, 1961), Plate & Husemann (1994), Hartmann-Schröder (1996)
<i>Exogone naida</i>		x	AB														Hartmann-Schröder (1996)
<i>Gaityana cf. cirrosa</i>		x	A														Andersen (1984), authors' pers. obs.
<i>Laonice cirrata</i>		x	A														Hannerz (1956, 1961), Plate & Husemann (1994), Hartmann-Schröder (1996)
<i>Levinsenia gracilis</i>		x	B														Hartmann-Schröder (1996)
<i>Lumbrineris minuta</i>		(x)	A														Hartmann-Schröder (1996)
<i>Lysippe labiata</i>		x	AB														Hartmann-Schröder (1996)
<i>Maldane sarsi</i>		x	C														Hartmann-Schröder (1996)
<i>Marenzelleria artica</i>		x	A														Thorson (1946)
<i>Micronephthys minuta</i>		(x)	A														Hartmann-Schröder (1996)
<i>Nephtys ciliata</i>		(x)	C														Hartmann-Schröder (1996)
<i>Nereimyra aphroditoides</i>		x	B														Thorson (1946)
<i>Nereis zonata</i>		x	A														Hartmann-Schröder (1996)
<i>Nicomache lumbricalis</i>		x	A														Thorson (1946), Mileikovsky (1959), Smidt (1979)
<i>Ophelina acuminata</i>		x	C														Thorson (1946), Banse (1955), Sveshnikov (1959), Andersen (1984)
<i>Ophelina cylindricaudata</i>		x	AB														Thorson (1936): cannot have pelagic larvae Thorson (1946): big eggs, direct development

(Table continued on next page)

Table 1 (continued)

	Presence of		Presence of larvae/spawning females												Comments
	Larvae	Juvenile	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Paroeciderus lynceus</i>															Sars (1895)
<i>Photis tenuicornis</i>															Sars (1895)
<i>Pontoporeia affinis</i>															Sars (1895): artic freshwater relict form
<i>Pontoporeia femorata</i>															Sars (1895)
<i>Protomedeia fasciata</i>															Sars (1895)
<i>Saduria sibirica</i>	x														Sars (1895)
Mollusca															
<i>Astarte borealis</i>	x														Thorson (1936): non-pelagic, Ockelmann (1958): short pelagic or direct development
<i>Axinulus ferruginosus</i>	x														Gajevskaja (1948), Golikov (1994)
<i>Cylichna cf. acculla</i>	x														Thorson (1936, 1946): non-pelagic, Ockelmann (1958): pelagic development, Muus (1973), Smidt (1979): found larvae, Andersen (1984)
<i>Macoma calcareo</i>	x								M						
<i>Musculus corrugatus</i>		x													Ockelmann (1958): short pelagic or direct development
<i>Nucula bellotii</i>															Thorson (1936), Ockelmann (1958, 1965)
<i>Nuculana pennula</i>															Ockelmann (1958): short pelagic or direct development
<i>Pandora glacialis</i>	x														Thorson (1936), Ockelmann (1958): demersal, authors' pers. obs.: Bivalvia type B
<i>Portlandia arctica</i>	x														Thorson (1936), Ockelmann (1958): demersal, authors' pers. obs.: Bivalvia type B
<i>Thyasira gouldii</i>															Thorson (1936): non-pelagic, Ockelmann (1958): short pelagic or direct development; first stages develop inside adult
<i>Yoldiella lenticula</i>															Thorson (1936), Ockelmann (1958): demersal
<i>Yoldiella nana</i>	x														Thorson (1936)
<i>Yoldiella solidula</i>	x														Thorson (1936)
Echinodermata															
<i>Ctenodiscus crispatus</i>		x													Mortensen (1927), Thorson (1936), Falk-Petersen (1982): winter breeder
<i>Eupyrigus scaber</i>	x														Andersen (1984), authors' pers. obs.
<i>Myriotrochus eurycylus</i>	(x)														Andersen (1984), authors' pers. obs.
<i>Myriotrochus rinki</i>	(x)														Andersen (1984), authors' pers. obs.
<i>Ophiotecten sericeum</i>	x														Thorson (1934, 1936), Geiger (1964), Semenova et al (1964), Pearse (1965): one spawning season?, Smidt (1979), Andersen (1984)
Total species		88													

(Table continued on next page)

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; see 'Comments' in Table 1), reveals that for the period August/September (time of expeditions) the occurrence of 12 of the 23 larval types found corresponds to the spawning period estimated in earlier studies (Table 1). In addition, 6 polychaete species (*Cistenides hyperborea*, *Laonice cirrata*, *Micronephthys minuta*, *Ophelina cylindricaudata*, *Scolelepis metsugae*, *Spio limicola* [arctica]) were present in August/September. For the polychaete larvae (*Capitella capitata*, *Eteone barbata*, *Owenia fusiformis*, *Polydora quadrilobata* and *Scoloplos armiger*) the field findings do not correspond with the occurrence times given in the literature. For these species the reproduction period is reported to be earlier in the year (e.g. Thorson 1946, Sveshnikov 1959, Lacalli 1980, Hartmann-Schröder 1996; see Table 1). Polychaeta and Echinodermata are the best investigated groups. Nothing is reported on the larval period of most Mollusca. None of the crustaceans found have pelagic larvae; this group consisted only of peracarid taxa (Amphipoda, Isopoda, Cumacea), in which a pelagic reproduction trait is completely absent.

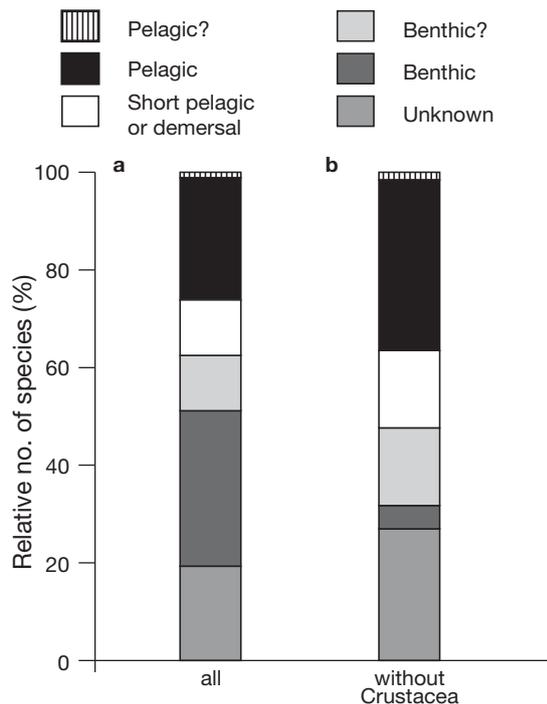


Fig. 2. Reproduction modes of the adult benthos either for all species, or all excluding Crustacea (for explanation see 'Results: Reproduction strategies')

Checking the coincidence of juveniles with the respective larvae is more difficult because it is unknown when they have settled (for species with pelagic development) or hatched from their eggs (benthic developing species). However, assuming an age of no more than 3 mo after settlement or release from their parents, the presence of 24 of the 32 juvenile species fitted with occurrence times given in the literature (Table 1). Nothing is known about the occurrence of the juveniles of 25 species found in the benthos. There were only 3 species (*Scalibregma inflatum*, *Sphaerodorum flavum*, *Astarte borealis*) for which the theoretical settlement times did not correspond to our observations.

Literature data (Table 1) reveal that apparently most species show benthic development (33% = 28 species) without a pelagic phase. Only 25% (22 species) have planktonic larvae (Fig. 2). In 11% (9 species) benthic development is presumed, but has not as yet been proven. Another 11% (9 species) seem to have a short pelagic stage. In 1% (1 species = *Portlandia arctica*) pelagic larvae are assumed.

Reproduction strategies

Both Arctic Mollusca and Polychaeta show a broad spectrum of reproduction strategies (Fig. 3). Most Polychaeta species reproduce via pelagic larvae. However, in >30% of polychaete species reproduction modes are still unknown. Benthic development plays only a subordinate role within this group. Short pelagic develop-

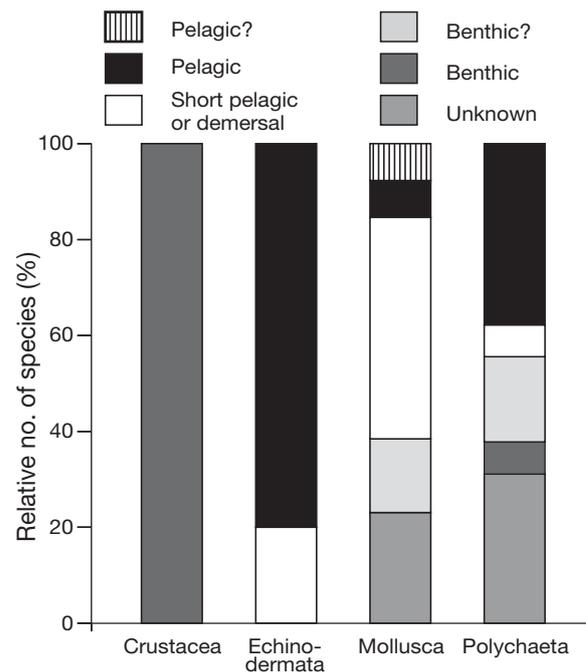


Fig. 3. Reproduction modes of benthic species found in the Kara Sea

ment dominates the life cycle strategy of Mollusca. Here again, the development mode is unknown in about 20% of the species. With echinoderms, on the other hand, pelagic development strategies clearly dominate. In all crustaceans found during the expeditions in the Kara Sea benthic development occurs.

A comparison of known reproduction types for all adult species found with their biogeographical distribution reveals that the proportion of benthic development is obviously greatest in animals of Arctic distribution (49%) and decreases continuously from Arctic-boreal (38%) and boreal (33%) species to only 11% in cosmopolitans (Fig. 4a). Pelagic development

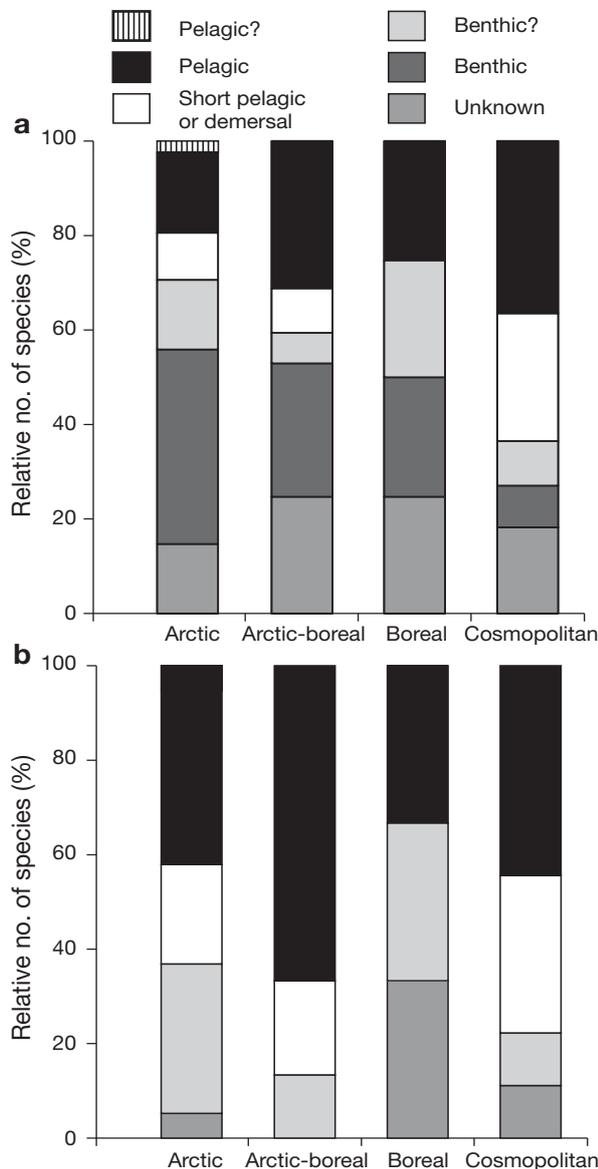


Fig. 4. Reproduction modes and biogeographical affiliation of the adult benthos for (a) all species, and (b) all species excluding Crustacea (for explanation see 'Results: Reproduction strategies')

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 a boreal affiliation. Here benthic development is attributed in 33% of all adult species.

The highest numbers of species found in the Kara Sea are crustaceans that exclusively have a benthic development mode, irrespective of their biogeographical status (Table 1, Fig. 3). To remove this bias, the relationships were re-examined for all species excluding crustaceans. The results reveal a different picture concerning the importance of benthic development among Arctic species.

When excluding crustaceans, pelagic development is the prevailing life strategy in 37% of all species as opposed to 5% displaying benthic development (Fig. 2). Benthic development is assumed in 32% of the Arctic species (Fig. 4b). 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 a known benthic development are virtually absent in this biogeographical unit. Benthic 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.

DISCUSSION

Species biogeography

Most of the adult species found in the Kara Sea have an Arctic biogeographical distribution. Arctic-boreal and boreal species continuously decrease in numbers with increasing distance from their biogeographical origin. Curtis (1975) noted that, when no distribution barriers exist, faunistic differences in Arctic and sub-Arctic regions are generally not extreme, since many warm- and cold-water species are found in more than one biogeographical zone. Ekman (1953) found that 75% of the fish genera observed in the Arctic are also present in temperate waters, and 8% are common in temperate and subtropical regions.

The faunal composition of the Kara Sea is generally strongly influenced by Arctic waters. However, water exchange with the Barents Sea also supports immigration of Arctic-boreal and boreal species. Moreover, the import of relatively warm river water from the Ob and Yenisei Rivers into the area may facilitate the survival of boreal, eurytherm species.

Meroplankton composition

Comparison of larval composition with other studies is often difficult, since meroplankton assemblages undergo considerable successional changes (Raymont 1983). The occurrence of larvae depends in principle on the composition of the benthic communities, but their distribution patterns are strongly shaped by the local hydrography, resulting in different compositions even if the benthic communities are identical (Mileikovsky 1968, Clough et al. 1997, Schlüter & Rachor 2001).

However, the meroplankton species composition in the Kara Sea roughly resembles the assemblage found by Schlüter & Rachor (2001) in the Barents Sea, although the latter survey was conducted some months earlier in the year (May/June). As with the Kara Sea, the Barents Sea meroplankton was dominated by polychaete species. By far the most comprehensive studies on meroplankters in polar waters have been made by Andersen (1984) and Smidt (1979). Although they investigated a fjord in north (Andersen 1984) and southwest Greenland (Smidt 1979), their inventory contained all larval species present in the Kara Sea. This provides evidence that the main pelagic reproducing species have a very broad distribution in the Arctic realm and/or indicates a high distribution potential of pelagic larvae.

Long-distance transport processes or a result of water exchange from the adjacent Barents Sea may be responsible for our finding larvae whose adult stages are lacking in the Kara Sea (Table 2). Periodical water exchange with the Barents Sea occurs through the Kara Strait or around the northern tip of Novaya Zemlya (Volkov 2002). These larvae most probably spawned in the Barents Sea and were transported into the Kara Sea. Planktotrophic larvae of boreal species typically require 2 to 6 wk before settling (Day & McEdward 1984), during which time currents can transport larvae and juveniles over distances of 100 to 1000 km (Mileikovsky 1966, 1968).

Faunistic investigations by Zenkevitch (1963) and Sirenko (2001) revealed the presence of the missing adult species from the adjacent Barents, Petchora and White Seas. Therefore, these seas obviously can serve as an important source for the import of new species into the Kara Sea.

The gastropods (*Cratena* sp., *Dendronotus* sp., *Trichotropis conica*, *Coryphella* sp.), Ectoprocta (*Electra* sp.) and the cirripede *Balanus* sp. larvae present in the samples are typical of rocky bottoms, and untypical for the soft-bottomed Kara Sea. They most probably originate from the nearby Novaya Zemlya Islands or the shore of the mainland. The few larval and adult species indicate that species associated with rocky bottom only play a minor role in the Kara Sea.

The surprisingly high numbers of planktotrophic larvae found during the survey provide evidence that the environment does not select against planktonic larvae in the way Thorson (1936, 1946, 1950) proposed. Thorson (1950) thought that the prolonged development of planktotrophic larvae, characteristic of polar species, would not permit them to get enough food during the short period of phytoplankton production. The present study provides strong argument against this notion. Indeed, the finding of so many larvae of species that are rare or absent in the Kara Sea suggests that there is no selection against the larvae preventing their establishment there. However, import of nutrients through the Ob and Yenisei Rivers may extend the feeding period for larvae and support their survival.

Reproduction modes and biogeographical affiliation

The onset of the last glacial and interglacial periods induced pronounced global sea-level variations over intervals of 100 m, which have repeatedly drained the shelf regions of the Arctic ocean and/or (partly) covered them by huge glaciers. The last such glacial event occurred only 13000 yr ago (Zenkevitch 1963). Thus, the Arctic Shelf is not only inhabited—in evolutionary terms—by 'young' benthic assemblages, but also had to be repeatedly recolonized by marine fauna (Piepenburg 2005).

The biogeographical affiliation pattern of the benthic species in combination with their reproduction modes seems to reflect the colonization pattern of the shelf area, given that the Arctic species were the first colonizers on the Kara Sea shelf and it was only as the Kara Sea became gradually warmer that they were followed by species with Arctic-boreal and boreal affiliations (Fig. 4). Limited or no dispersal abilities are mainly found among species with an Arctic biogeographical status. On the other hand, species with larvae that can be transported over long distances are found mainly among taxa originating from boreal regions. This may reflect the young evolutionary status of the region as stated above, since no boreal species with limited or no dispersal abilities have as yet invaded the region. The strong correlation between biogeographical affiliation and dispersal abilities is also an indication that so far no evolutionary adaptation has occurred, i.e. a high dispersal and recolonization potential is most evident in species with a boreal affiliation, while Arctic species obviously lack these characteristics.

Interestingly, species with short pelagic or demersal development are most common among cosmopolitan species. However, this reproduction mode seems to also be important among the other biogeographical

types. Distribution via short pelagic or demersal larvae is advantageous since it provides a good balance between the dispersal abilities of a species, thus maintaining the potential for the recolonization of new territories, but also avoids the drifting away from favorable parental settling grounds. Therefore, a short drifting period keeps the survival rate at a maximum and additionally allows the offspring to find new favorable sites close to the parental settling grounds. Retention of larvae, especially within the river-influenced southern parts of the Kara Sea has been found to be crucial for some species (Fetzer & Deubel 2006).

Pelagic vs. non-pelagic development

At first sight, the reproductive development modes in the Kara Sea show an obviously higher proportion of benthic to pelagic developing species, which is in agreement with the concept proposed by Thorson (1936, 1950) and Mileikovsky (1960, 1971) (Fig. 2a). This tendency becomes even more distinct when displaying the reproduction types according to their biogeographical range. Here, the highest numbers of non-pelagic developing species are found among Arctic specimens, decreasing gradually when moving from Arctic species towards those with a boreal distribution (Fig. 4a).

However, careful analysis of the species composition (Fig. 3) reveals that the high share of benthic developing species can be attributed to the high numbers of peracarid species found in the study area. As mentioned earlier, within the taxonomic group Peracarida only one reproduction strategy (no larvae, juveniles kept in brood pouches) is predominant, irrespective of the geographical region they inhabit. In our study, a high proportion (64% = 16 species) of the peracarids are exclusively confined to Arctic regions (Table 1). On an evolutionary timescale species lacking a dispersal phase have been suggested to exhibit a much higher speciation rate than species distributing via larvae (Jablonski & Lutz 1983, Duda & Palumbi 1999, Jablonski & Roy 2003). Species with a limited dispersal rate therefore evolve more readily into new species that are better adapted to the Arctic environment. This may explain a higher endemism in polar waters for many peracarid crustaceans with benthic development.

Omitting the peracarid species from the data set, pelagic development becomes the main reproductive strategy in the Kara Sea realm (Fig. 2). 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 polar realms, a value that is clearly too low in the light of the studies cited above. However, in con-

trast to many parts of the polar zone, the Kara Sea shelf is a comparatively unstable environment. The shallow parts of the Kara Sea in particular are characterized by a pronounced inter-annual seasonality in the ice-coverage, river discharge, and sedimentation rates complemented by strong intra-annual fluctuations (e.g. Makkaveev & Stunzhas 1994, Pavlov & Pfirmann 1995, Volkov 2002). Benthos communities are periodically reduced by freshwater discharge and ice scouring. Accumulations of large numbers of bivalve shells found in sediment cores of bottom surface layers indicate occasional mass mortality among benthic organisms (Stein 2001, Stein & Levitan 2002). The instability of the regime obviously promotes fast recolonizing 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 (benthic development) is favored in spatially heterogeneous and temporally constant environments whereas high dispersal (pelagic development) is dominant in a spatially homogeneous or temporally varying environment. The fact that species with planktonic larvae have a much higher potential to occupy new territories may additionally explain the relatively high number of species with pelagic larvae (even among the Arctic species) in contrast to the findings of Thorson (1936).

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