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The rotifer fauna of arctic sea ice from the Barents Sea, Laptev Sea and Greenland Sea

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Abstract

Samples from arctic sea ice were studied for their rotifer fauna. Ice core samples were collected in the northern Barents Sea and the Laptev Sea from August to October 1993 and in the Greenland Sea from July to August 1994. Eight rotifer taxa, *Encentrum graingeri*, *Proales reinhardti*, *Synchaeta bacillifera*, *S. cecilia*, *S. glacialis*, *S. hyperborea*, *S. tamara* and *S.* sp., were found. The geographical as well as the vertical distribution and abundance of the taxa in the ice is discussed, with regard to biotic and abiotic parameters of the sea ice environment. Species redescriptions are given for *Synchaeta glacialis*, *S. hyperborea* and *S. tamara*.

Introduction

Sea ice, as one of the most conspicuous characteristics of the polar Oceans, covers between 7×10^6 km^2 of the Arctic Ocean in summer and 14×10^6 km^2 in winter (Walsh & Johnson, 1979). Most of the Arctic sea ice is multi-year ice with a thickness of up to about 3 m (Eicken et al., 1995). Though the ice cover appears to be a harsh and uninhabited environment, it serves as a unique habitat for a variety of organisms. Due to its mode of formation (see Maykut, 1985; Weeks & Ackley, 1986), sea ice contains a branched system of brine filled channels and pockets from a few micrometers in diameter (Weissenberger, 1992) up to a few centimeters. The brine-salinity inside the ice as well as its volume shows strong variations in relation to the large seasonal temperature changes (Assur, 1958; Frankenstein & Garner, 1967). During winter, the ice temperatures may sink down to −10 °C and hence the brine salinity rises up to 144‰ because of the growth of freshwater ice and the resulting brine rejection (Morey et al., 1984), while during the arctic summer, melting processes can cause strong drops in salinity and brine drainage to the underlying water column.

This extreme habitat contains a specialized, so-called sympagic ice community, including bacteria, protozoans and metazoans, originating from benthic or pelagic environments or even being endemic (Carey 1985; Chengalath, 1985; Horner, 1985; Friedrich, 1997; Gradinger & Zhang, 1997). Among the metazoans, rotifers constitute an important group, which may occur in very high numbers in some ice floes (Friedrich, 1997). Rotifers have been reported as a gross taxonomic group from the lower layer of sea ice by Cross (1982), Kern & Carey (1983), Carey (1985) and Grainger & Hsiao (1990). The only study on rotifers from arctic sea ice to genus or species level was by Chengalath (1985), who found *Cephalodella* sp., *Encentrum graingeri*, *Proales reinhardti* and *Synchaeta* sp. in fast ice from Frobisher Bay, Northwest Territories, Canada. Up to now, no taxonomic investigations on rotifers from drifting multi-year ice in the Arctic exist.

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The present study attempts to investigate the rotifer fauna of multi-year ice of the 'Transpolar Drift' system, which transports sea ice formed in the Eurasian shelf regions over the central Arctic Basin to the Greenland Sea, where most of the ice finally melts (Gordienko, 1958; Maykut, 1985). Rotifer abundance inside the floes as well as their geographical distribution will be described with respect to the environmental conditions. Some *Synchaeta* species are redescribed, as their trophi could be studied with the modern technique of scanning electron microscopy, and seen that the original descriptions are in Russian and not easily accessible to the international community.

Table 1. List of Rotifera recorded

Proalidae
Proales reinhardti (Ehrenberg, 1834)
Dicranophoridae
Encentrum graingeri Chengalath, 1985
Synchaetidae
Synchaeta bacillifera Smirnov, 1933
S. cecilia Rousselet, 1902
S. glacialis Smirnov, 1932
S. hyperborea Smirnov, 1932
S. tamara Smirnov, 1932
S. sp.

Material and methods

Sea ice rotifers were collected during two 'Polarstern'-cruises ARK IX/4 to the Barents and Laptev Seas (August 6–October 5, 1993) and ARK X/1 (July 6–August 15, 1994) to the Greenland Sea. Sea ice stations are shown in Figure 1 (station number=day number of the year, 1–365). Ice cores were obtained with a 7.6 cm diameter ice corer and cut into 2–20 cm long sections directly after coring. To get a better resolution, the shortest sections were taken close to the bottom, where highest organism abundances occurred. Parallel cores were taken to determine temperature and salinity, and to establish cultures of ice organisms. Temperature was measured with a thermometer (Testo 770, THESTOTHERM) in the middle of each segment, and salinity was measured with a WTW conductometer in the melted segments. The brine salinity was calculated after Assur (1958). The segments for rotifer investigations were melted in an excess of 0.2 μm filtered seawater at 4 °C to avoid osmotic stress to the organisms (Garrison & Buck, 1986). After complete melting of the sample, organisms were concentrated over a 20 μm gauze. The rotifers were either sorted out alive under a dissecting microscope on board the ship prior to formalin fixation (1% end concentration), or due to the limited time the whole sample was fixed with formalin or Bouin's solution (Song & Wilbert, 1995), and sorted out in the home laboratory. No dead rotifers were observed after the melting process. Concentrated parallel samples were transferred into 250 or 500 ml culture bottles (CORNING) to establish cultures. All cultures were kept at salinities between 25 and 30‰ (ATAGO hand refractometer, 1‰ readability), a temperature of 0–1 °C, and a light:dark cycle of 12:12 hours.

Formalin fixed rotifers were stained with Bengal Rose (0.1 μg/l, SIGMA) prior to sorting in the home laboratory, while Bouin fixed specimens already had a striking yellow colour distinguishing them from the frequently occurring aggregates of algae and detritus. Live and formaldehyde (4%) fixed animals were examined and drawn using a Leitz Orthoplan microscope with camera lucida. Preparation of trophi for light and scanning electron microscopy (SEM) was done following De Smet (1998) using NaOCl solution. For SEM a Philips SEM 515 was used, operated at 20 kV.

Results

Survey and occurrence of species

A total of 1786 rotifer specimens was encountered in the ice samples (exclusive of the culture samples), 540 of which were identified to species or genus level: 247 from the Barents Sea (total 750), 244 from the Laptev Sea (total 959) and 49 from the Greenland Sea (total 77). Table 1 lists the eight identified rotifer taxa and Table 2 shows the species composition and rotifer abundance in the different sampling areas.

Rotifer eggs were present at most stations were rotifers occurred (Table 2). Only amictic eggs of *Proales reinhardti* and *Synchaeta* spp. were found.

***Proales reinhardti* (Ehrenberg, 1834) (Figures 2 and 3)**

Altogether, 14 females and two males were identified in sea ice from the Barents Sea, Laptev Sea and Greenland Sea. External and internal organization (Figure 2A) as well as trophi morphology (Figure 3A,B) of

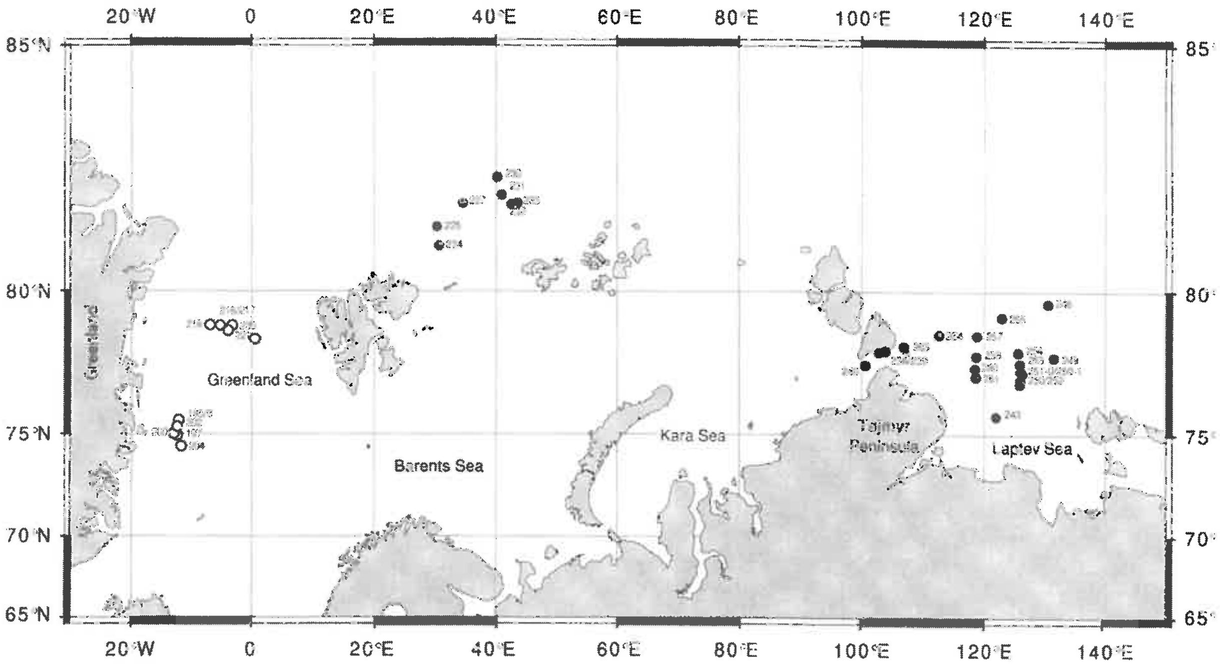

Figure 1. Sea ice stations during Polarstern cruises ARK IX/4 (black dots) and ARK X/1 (white dots).

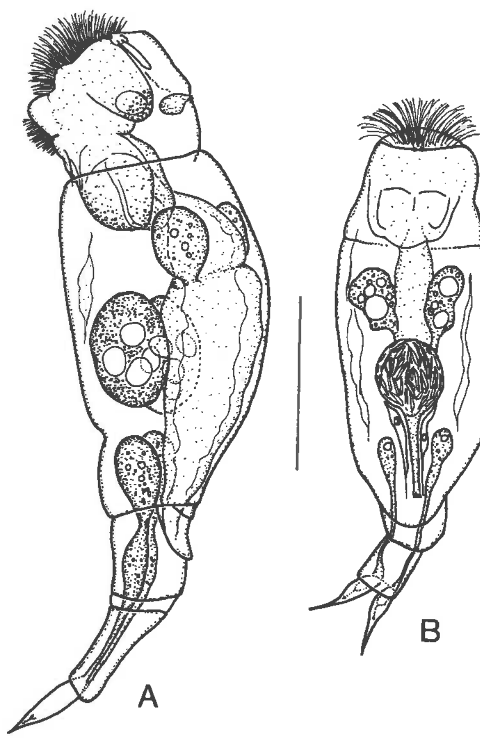

Figure 2. Proales reinhardti. (A) Female, lateral view. (B) Male, dorsal view. Scale bar 50 μm.

typical females (see e.g. De Smet, 1996), a single specimen excepted. This specimen (contracted) from the Greenland Sea showed an aberrant trophi structure (Figure 3C,D), characterized by the presence of a single, stout tooth on the inner margin of the right ramus, instead of a pair of more or less bifid teeth. Whether this feature should be included in the range of variability of *P. reinhardti*, or whether we are dealing with a new, closely related species, cannot be settled yet. So far, trophi examination of typical specimens of *P. reinhardti* from different localities has shown that the configuration of right rami teeth is very stable (De Smet, unpublished). The males (Figure 2B) of *P. reinhardti* are smaller (150–155 μm) than the females (up to 215 μm), with distinctly shorter foot apparently composed of a single pseudosegment. The lanceolate toes are more slender with slightly drawn-out and ventrally decurved tips. The corona is well developed with long cilia. A mastax and gut rudiment are present, as well as faint structures that remind of trophi but dissolve in hypochlorite solution. Testis fairly large, rounded. Penis long, opening dorsally to foot.

Proales reinhardti was found in small numbers in the Barents, Laptev and Greenland Sea between July 15, 1994 and September 3, 1993 (Figures 12 and 13, Table 2), in various regions from nearshore to deep water stations with more than 3000 m water depth. It

Table 2. Abundance and distribution of rotifers in ice core samples and cultures. Number of included males in brackets. *Core length in brackets. ** Temperature and Salinity shown only for the segments where rotifers were identified. Core-Number = day of the year; 224 = ARK IX/4, August 12 1993; 196 = ARK X/I, July 15 1994.

Core	Segment (cm)	Rotifers per m^{2}*	Number of rotifers in sample	Number of rotifers identified	*Synchaeta hyperborea*	*Synchaeta tamara*	*Synchaeta cecilia*	*Synchaeta bacillifera*	*Synchaeta glacialis*	*Synchaeta* sp.	*Encentrum graingeri*	*Proales reinhardti*	Rotifer eggs	Temperature (°C, lowest value)**	Salinity (‰, after Assur, 1985)
224-03	100–120	**6211**	1												
224-03	240–260	(0–282)	1												
224-03	260–270		7												
224-03	270–280		11	2	1			1					24	−1.6	28
224-03	280–282		5												
224-04	280–282	**4523**	21	12	1	10			1				27	−1.5	26
227-03	240–250	**42268**	102	18	10				2		1	5		−1.7	30
227-03	250–252	(0–252)	24												
227-05	250–252	**2154**	10												
230-03	140–160	**44437**	2												
230-03	180–190	(0–192)	75	31	25	6(5)							39	−1.4	24
230-03	190–192		106	40	8	22(6)	2		7			1		−1.3	23
230-04	lower 2 cm	**12210**	63	63		63(3)							181	−1.3	23
231-02	0–19	**220**													
231-02	19–21	(0–21)	1	1			1							−0.2	4
231-03	50–58	**5973**	1												
231-03	58–60	(0–60)	26	7	4				3					−0.3	5
231	53–55	culture			x							x			
232-03	198–218	**36504**	16												
232-03	218–238	(198–248)	92	52	50						1	1(1)	43	−1.7	30
232-03	238–246		42												
232-03	246–248		2												
232-04	lower 2 cm	**3179**	17												
233-03	100–120	**21888**	1												
233-03	170–178	(0–194)	3												
233-03	180–190		17												
233-03	190–192		18												
233-03	192–194		65	21	17				4				28	−0.7	12
233-04	182–192	**4952**	6												
233-04	192–194	(182–194)	15												
238-03	80–90	**9021**	6												
238-03	90–100	(0–110)	12												
238-03	100–110		18												
238-04	90–100	**500**	2												
240-03	140–160	**6794**	6	5	4						1			−1.3	24
240-03	160-170	(140–183)	13	5	5									−1.3	24
240-03	170–180		4	3							1	2		−1.3	24
240-03	180–183		6	3	2							1		−1.1	20
240-04	173–181	**716**	3												
240-04	181–183	(143–183)	0												
243-03	40–60	**14727**	1												
243-03	100–120	(0-168)	1												
243-04	138-148		4												
243-04	148–158		119	86	84				2					no data	
246-03	60–70	**3146**	1												
246-03	70–80	(0–83)	5												
246-03	80–83		3	3	1				2				7	−1.1	20
246-16	40–50	**8164**	22												
246-16	50–52	(0–52)	5												
246-27	0–9	**308**	1												
246-27	9–11	(0–11)	0												
246-28	0–8	**752**	1												
246-28	8–10	(0–10)	2												
246-17	52–54	**288**	1												
246	bottom	culture			x				x		x	x			
249-03	0–20	**8299**	6												
249-03	20–40	(0–124)	4												
249-03	40–60		1												
249-03	60–80		25												
249-03	80–100		4												
249-03	100–120		3												
250-04	0–20	**69087**	3												
250-04	20–40	(0–154)	1												
250-04	40–60		1												
250-04	60–80		38	19	17				2					no data	
250-04	80–100		72	48	46				2					no data	
250-04	100–120		118	46	46								21	no data	
250-04	120–140		71												
250-04	140–152		44	22	21(2)						1		13	no data	
250-04	152–154		4	2	1						1			no data	

Continued on p. 77

Table 2. contd.

Core	Segment (cm)	Rotifers per m^{2}*	Number of rotifers in sample	Number of rotifers identified	*Synchaeta hyperborea*	*Synchaeta tamara*	*Synchaeta cecilia*	*Synchaeta bacillifera*	*Synchaeta glacialis*	*Synchaeta* sp.	*Encentrum graingeri*	*Proales reinhardti*	Rotifer eggs	Temperature (°C, lowest value)**	Salinity (‰, after Assur, 1985)
251-13	77–87	**8894**	32												
251-13	87–90	(77–90)	2												
254-03	196–216	**38028**	31												
254-03	216–226	(196–228)	64												
254-03	226–228		37												
255-03	132–138	**5664**	4												
255-03	138–141	(0–141)	40												
257-03	117–119	**444**	2												
257-03		(0–119)													
258-23	202–222	**1509**	6	2	**2**								1	−0.8	15
258-23		(202–234)													
260-03	80–100	**20940**	11												
260-03	100–120	(0–201)	28												
260-03	120–140		19												
260-03	140–160		7												
260-03	160–180		7												
260-03	180–190		4												
260-03	199–201		7												
263-22	136–156	**550**	2												
263-22	156–166	(136–169)	1												
264-03	120–140	**7001**	1												
264-03	220–240	(0-258)	1												
264-03	150–255		3												
264-03	155–157		6												
264-03	257–258		13												
196-02	260–270	**4003**	2	2	2									−0.8	15
196-02	270–272	(0–272)	15	9		**8**						1	8	−1.6	29
197-03	239.5–259.5	**2658**	1	1	1									−0.5	9
197-03	259.5–279.5	(0–288.5)	6	4	2					2			9	−0.8	15
197-03	286.5–288.5		2												
200-04	210–220	**176**	1												
200-04		(0–222)													
202-02	220–240	**4400**	1	1		1							2	−1.1	20
202-02	240–250	(0–253)	17	10	7					3			27	−0.7	13
202-02	250–253		9	2	1					1			12	−0.9	16
204-08	238–248	**179**	1	1	1									−0.9	16
204-08		(218–250)													
216-02	180–200	**1726**	4	1	1									−0.7	13
216-02	200–204,5	(0–206.5)	6	6	1	1						4(1)	8	−0.7	13
218-02	244–254	**372**	2	3	2					1			1	−1.2	22
220-07	326–346	**1758**	10	9		8						1	26	−1.8	32

was found in older ice floes of a thickness between 183 and 346 cm, and cultures taken from thinner ice of about 55 cm. It mostly occurred within the lowermost centimeters but also up to 30 cm from the bottom of the ice. Temperatures ranged from −0.7 to −1.8 °C and the calculated brine salinities ranged from 13 to 32‰.

P. reinhardti is a cosmopolitan species, found among algae of the marine littoral and in marine and brackish tide puddles. So far, the species was only reported from arctic sea ice of the Canadian Arctic (Frobisher Bay, N.W.T.) by Chengalath (1985), who found it in February, March and May up to 150 cm from the bottom of the ice, at temperatures and brine salinities varying from −1.6 to −2.2 °C and 29–80‰, respectively. It constituted one of the dominant species in this area.

Encentrum graingeri Chengalath, 1985 (Figure 4)

Six females of this rare species were found in sea ice from the Barents and Laptev Sea. The animals agree well with the original description by Chengalath (1985), and can be reliably distinguished from other species of the genus by the characteristic trophi bearing a strong, more or less acute tooth on the inner margins of the rami posteriorly (Figure 4B).

Encentrum graingeri was found in the Barents and Laptev Seas between August 15 and September 9, 1993, in different regions from nearshore to deep water stations with more than 3000 m water depth. It occurred up to more than 40 cm from the bottom of the ice, in floes of a thickness between 154 and 252 cm, and cultures taken from thinner ice of about 55 cm. Temperatures ranged from −1.3 to −1.7 °C and the calculated brine salinities ranged from 24 to 30‰ (Figure 12, Table 2).

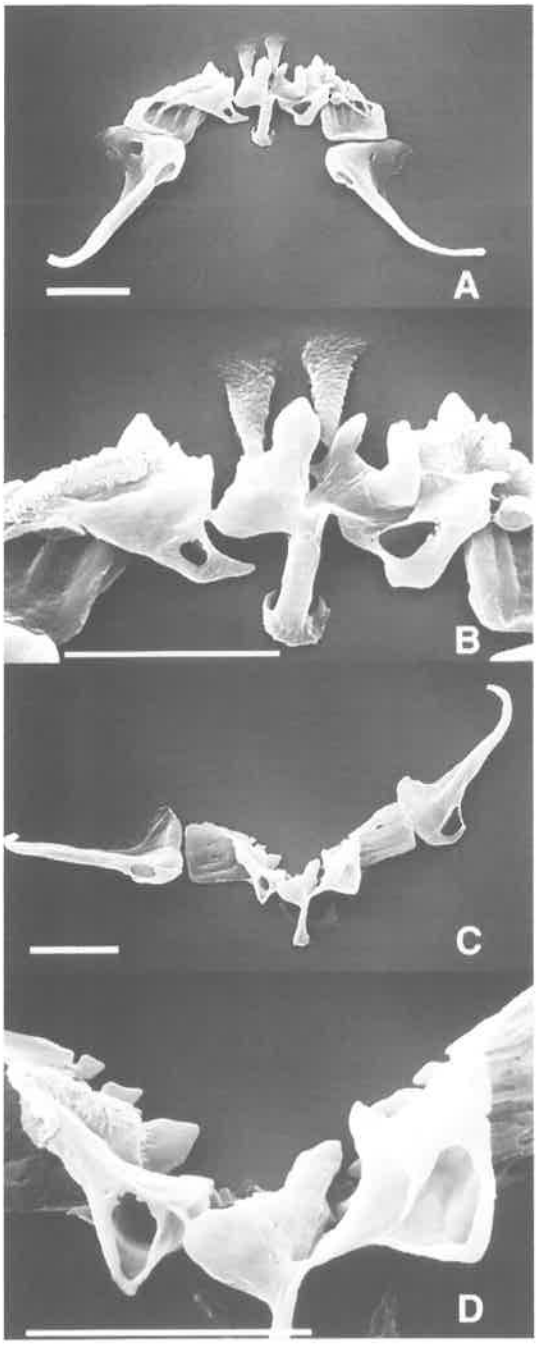

Figure 3. Proales reinhardti, SEM pictures of trophi in dorsal view. (A)(B) typical trophi, (C)(D) aberrant type. Scale bars 10 μm.

The species was described from Canadian Arctic Sea ice (Frobisher Bay, N.W.T.), where it was found in February and May up to 20 cm from the bottom of the ice, at temperatures varying from −1.6 to −2.4 °C and a brine salinity of 29‰ (Chengalath, 1985). The only other records are from a Spitsbergen fjord

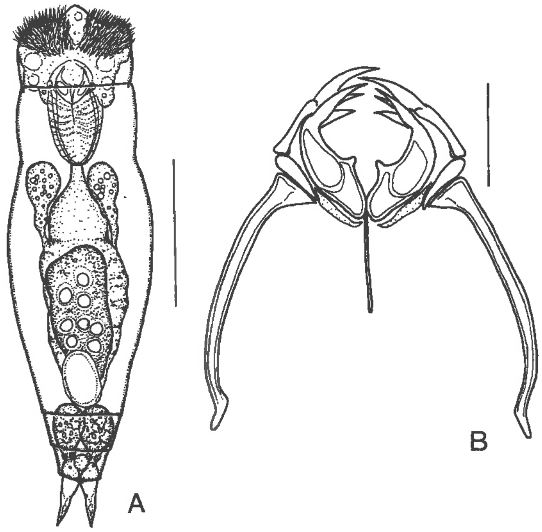

Figure 4. Encentrum graingeri. (A) Female, ventral view. (B) Trophi, dorsal view. Scale bars: (A) 50 μm, (B) 10 μm.

(Svalbard) (De Smet, 1995), the North Sea (Belgium) and the river Eastern Scheldt (the Netherlands) (De Smet in De Smet & Pourriot, 1997), and a beach at Disko Island, West Greenland (Sørensen, 1998). It was collected among littoral algae and in sandy psammon. Considering the distribution records, it is clear that *E. graingeri* is probably a wide-spread species. It also appears to be a cold-stenotherm species, being reported from the Arctic and the cold season at the localities with temperate climate.

Synchaeta bacillifera Smirnov, 1933

A single specimen (female) of this rare species was observed in sea ice from the Barents Sea on August 12, 1993, northeast of Spitsbergen, over a water depth of about 200 m. It occurred in the lowermost 12 cm of an ice floe of 282 cm thickness, at a temperature of about −1.6 °C and a salinity of about 28‰ (Figure 12, Table 2).

The species is only known from its type locality, i.e. the northern Kara Sea, where it was found in small numbers in the plankton during August and September (Smirnov, 1933).

Synchaeta cecilia Rousselet, 1902

Three specimens (females) of this species were found in sea ice from the Barents Sea between 18 and 20

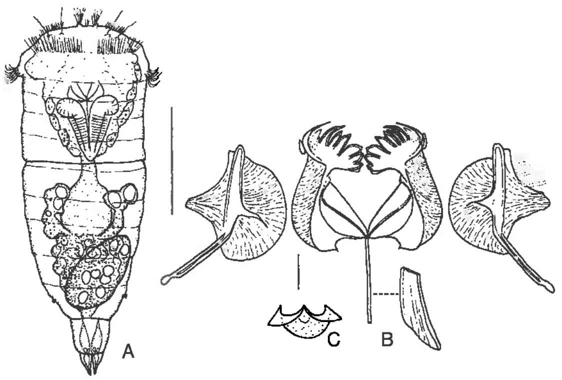

Figure 5. Synchaeta glacialis. (A) Female, ventral view. (B) Trophi. (C) Epipharynx. Scale bars: (A) 50 μm.

August 1993 northwest of Franz-Joseph Land over water depths of about 2000–3000 m. The specimens occurred in the lowermost 2 cm of floes of 21 and 192 cm thickness, at temperatures of −0.21 and −1.25 °C, respectively, and corresponding salinities of 4 and 23‰ (Figure 12, Table 2).

S. cecilia is a widely distributed planktonic species recorded from thalassic and athalassic saline waters (marine and brackish tide pools, coastal waters, shore of lakes) of Europe and North America. It is eurytherm and exists at a wide range of salinities.

Synchaeta glacialis Smirnov, 1932 (Figures 5 and 6)

Twenty-five specimens of this species were observed in ice samples from the Barents and Laptev Sea. We originally doubted on the identity of this taxon and listed it sub *Synchaeta* sp. in Friedrich (1997). After further study, we are now convinced that part of this *Synchaeta* sp. is the species Smirnov (1932) had before him when describing *S. glacialis*.

Differential diagnosis

S. glacialis resembles the probably closely related *S. hyperborea*, from which it can be differentiated by its shorter foot, the fusiform pedal glands without large reservoir (with large, rounded reservoir in *S. hyperborea*), and small differences in trophi morphology e.g. the kinked manubria with narrow cauda and relatively shorter fulcrum with strongly oblique posterior margin (manubria more or less straight with expanded cauda and fulcrum less oblique in *S. hyperborea*).

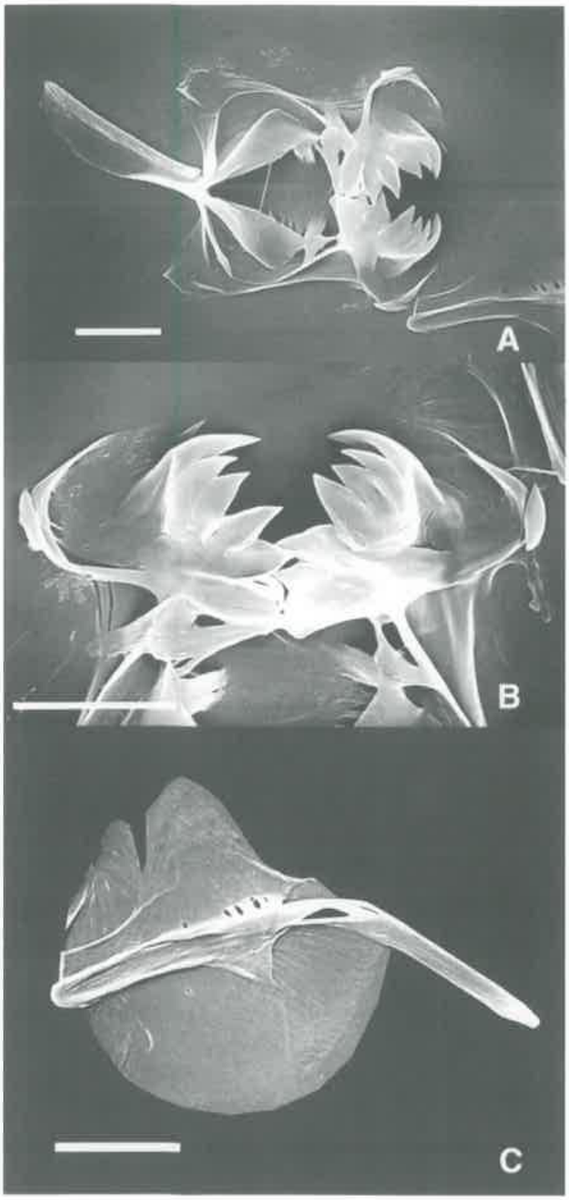

Figure 6. Synchaeta glacialis, SEM pictures of trophi. (A) Incus, ventral view. (B) Unci, ventral view. (C) Manubrium, lateral view. Scale bars 10 μm.

Description

Female (Figure 5A): Body fairly cylindrical, head long, c. 1/3 total length. Foot relatively short, c. 1/10 or less total length. Two equal, short conical toes. Corona fairly convex; two fairly shallow ciliated prominences; four weak coronal styles. Auricles small. Two small, close set or single cervical eyespot(s). Lateral antennae near base of foot. Gastric glands elongate-pyriform to irregular elongate. Pedal glands fusiform, foot-length; two small accessory glands open in the reservoir of each toe. Vitellarium with eight nuclei.

Trophi (Figures 5B,C and 6A–C): Unci composed of frontal hook and toothplate with six (right) or seven (left) teeth; three posterior teeth shorter and broader; posterior tooth with small triangular lamella; frontal hook with short basal spine; gap between frontal hook and toothplate narrow with web and apparently single membranaceous tooth. Rami lamellar, each composed of inner, elongate-triangular lamella, a semi-lunate median lamella and a rounded outer lamella connected to posterior margin of uncus; anterior half of inner margin of inner lamella with row of furcate scleropili. Epipharynx has two delicate thorn-shaped elements forming a wide V. Fulcrum short with strongly oblique posterior margin in lateral view. Manubria distinctly kinked, anterior half of shaft broader, cauda offset, narrow; dorsal lamella broad triangular, anterior to it a small and delicate lamella with 15–20 sclerites, ventral lamella semi-lunate, c. $\frac{1}{2}$ manubrium length, bearing triangular thickening.

Dimensions: Length up to 240 μm, toe 10 μm; trophi 62–65 μm: ramus c. 26 μm, fulcrum 22–25 μm, uncus 17–20 μm × 12–14 μm, manubrium 43–48 μm.

Distribution and ecology

S. glacialis was found in different regions of the Barents and Laptev Seas between August 12 and September 7, 1993 (Figure 12, Table 2), over water depths between about 200 and more than 3000 m. It occurred in ice floes of a thickness between 60 and 282 cm, mostly within the lowermost centimeters, but also in a segment 94 cm from the bottom of the ice. Temperatures ranged from −0.3 to −1.7 °C and the calculated brine salinities ranged from 5 to 30‰.

S. glacialis was described by Smirnov (1932) on five preserved specimens from plankton collected in the northern Barents Sea near Franz-Joseph Land. The only subsequent reports are from the northern Kara Sea and Arctic Ocean (Smirnov, 1933). It was collected in August and September, and always found in very low numbers.

Synchaeta hyperborea Smirnov, 1932 (Figures 7 and 8)

A total of 363 specimens (among which 2 males) of this species was identified from all three sampling areas.

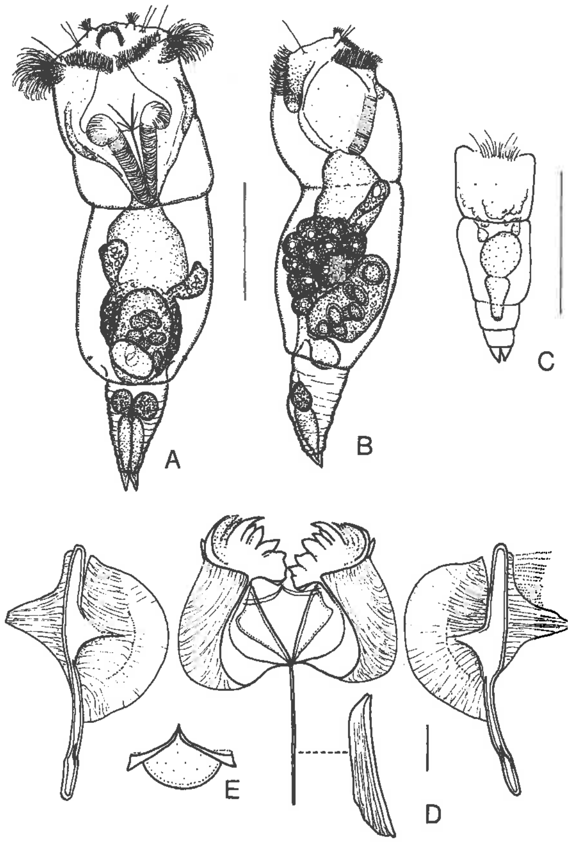

Figure 7. Synchaeta hyperborea. (A) Female, ventral view. (B) Female, lateral view. (C) Male, dorsal view. (D) Trophi. (E) Epipharynx. Scale bars: (A)–(C) 50 μm, (D)(E) 10 μm.

Differential diagnosis

S. hyperborea resembles *S. glacialis* but is easily distinguished from it and the other congeners by the long conical and wrinkled foot, and the characteristic pedal glands composed of a long fusiform part and a rounded reservoir connected with each other by a short and narrow canal.

Description

Female (Figure 7A,B): Body almost cylindrical, head distinctly offset from trunk, c. $\frac{1}{3}$ of total length, in lateral view slightly tilted ventrally. Foot wrinkled, fairly long c. $\frac{1}{3}$–$\frac{1}{6}$ total length, conical in dorsal view, base usually smaller than posterior margin of trunk, in lateral view with more or less straight dorsal margin and recurved ventral margin. Toes short, conical. Corona fairly convex; two widely separated, shallow ciliated

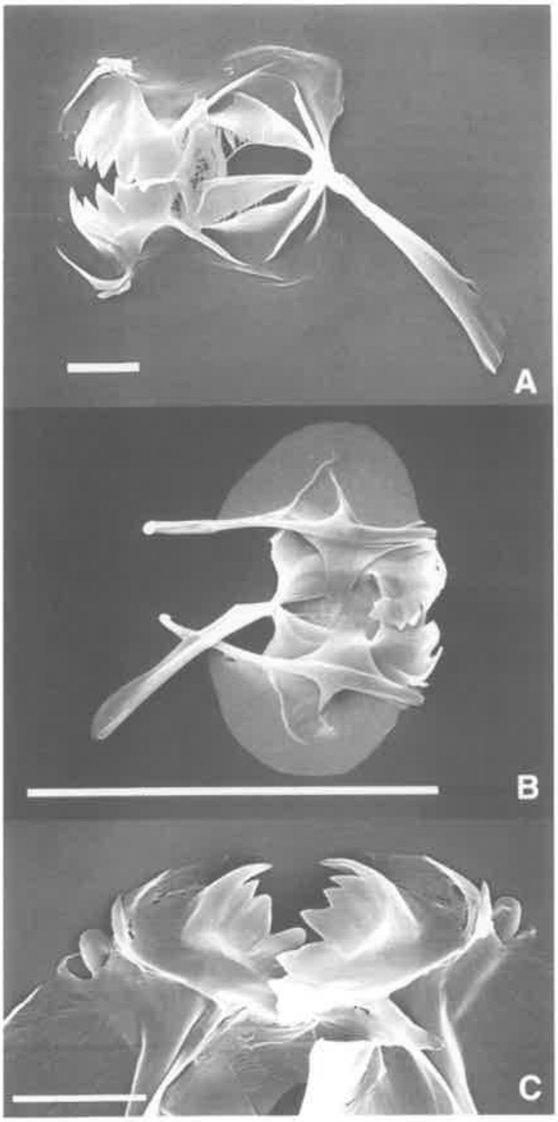

Figure 8. *Synchaeta hyperborea*, SEM pictures of trophi. (A) Incus, ventral view. (B) Incus, dorsal view; manubria, lateral view. (C) Unci, ventral view. Scale bars: (A)(C) 10 μm, (B) 100 μm.

prominences; four weak coronal styles, the midst pair divided into individual setae. Auricles small. Dorsal antenna near posterior of brain. Lateral antennae at base of foot. Two small cervical eyespots. Mastax c. $\frac{1}{4}$ total length. Gastric glands elongate-pyriform. Pedal glands large, foot-length, with large fusiform distal part and rounded reservoir, connected with each other by a short and narrow canal. Vitellarium with eight nuclei.

Trophi (Figures 7D,E and 8A–C): Unci well developed, slightly asymmetrical, with very strong frontal hook separated by a wide gap from the row of 6–8 plate-shaped teeth (6 according Smirnov, 1932); first tooth the longest, followed by a first set of 4–3 (left) or 2–3 (right) relatively narrow teeth separated by shallow sulci, and a second set of 2–3 broader teeth separated from the first by a broader and deeper sulcus; sulci between teeth of second set broader; posterior tooth with small triangular lamella; gap between frontal hook and toothplate with 2 membranaceous, weakly sclerotized, tooth-like structures; a short basal spine ventro-laterally from frontal hook. Rami lamellar, each composed of an elongate-triangular inner lamella, a more or less semilunate median lamella, and a large and thin outer lamella connected to the outer margin of the inner lamella and the posterior margin of the uncus; inner margin of inner lamellae with row of scleropili. Epipharynx two thorn-shaped elements forming a wide V, posteriorly connected by rounded lamella. Fulcrum long, plate-shaped, in lateral view slightly expanding posteriorly, posterior margin oblique. Manubria long, almost straight, posterior half of shaft slightly narrower with slightly offset and thicker cauda, anterior half of dorsal margin with fairly small, more of less triangular lamella, anterior 2/3 of ventral margin with semi-lunate lamella bearing triangular thickening; anterior to dorsal lamella a delicate lamella composed of 20–25 scleropili.

Male (Figure 7C): Body elongate-conical. Foot with single pseudosegment. Two short conical toes. Corona with four styli. Two small, red cervical eyespots. Gut rudiment present. Testis small, rounded; penis dorsal to foot, opening with cilia.

Dimensions (measurements by Smirnov (1932) bracketed):

Female: length up to 315 μm (300 μm on average), head length up to 93 μm (120 μm), foot up to 82 μm (37 μm), toe 9–12 μm (16 μm); trophi 56–96 μm: ramus c. 23–39 μm, fulcrum 26–54 μm, uncus 19–21 μm × 12–14 μm, manubrium 38–72 μm.

Male: length 77–80 μm, toe 6 μm.

Distribution and ecology

S. hyperborea was the most common species in the sea ice of the Transpolar Drift system. It was found in the Barents, Laptev and Greenland Seas (Figures 12 and 13, Table 2) between July 12, 1994 and September 16, 1993 at all stations where rotifers were identified except one in the Fram Strait, nearshore over shallow water depths as well as over deep water of more than 3000 m. It occurred in ice floes of a thickness between

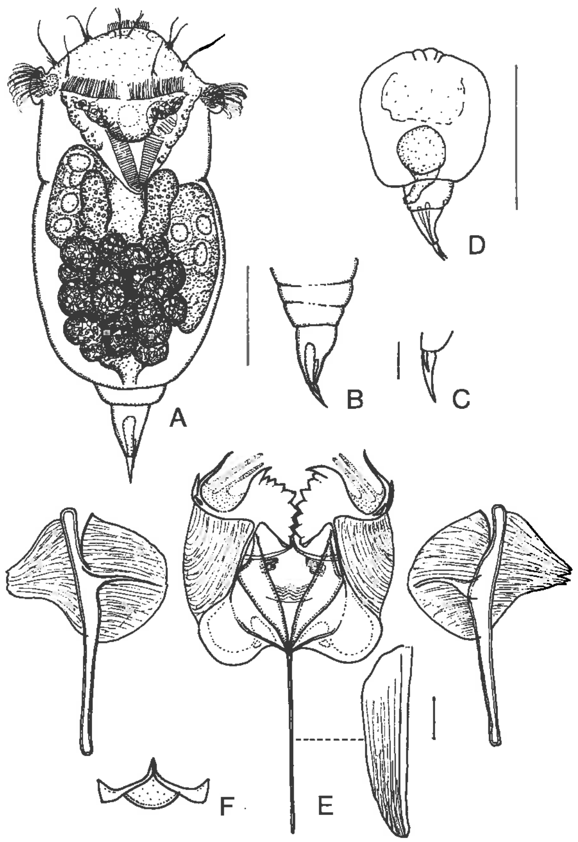

Figure 9. Synchaeta tamara. (A) Female, dorsal view. (B) Female, foot, lateral view. (C) Female, detail toes. (D) Male (slightly contracted), lateral view. (E) Trophi. (F) Epipharynx. Scale bars: (A)(B)(D) 50 μm, (C)(E)(F) 10 μm.

60 and 282 cm, and was found frequently within the lowermost 50 cm, and even in a segment 94 cm from the bottom of the ice. Temperatures ranged from −0.3 to −1.7 °C and the calculated brine salinities ranged from 5 to 30‰.

S. hyperborea was described from plankton collected in the northern Barents Sea near Franz-Joseph Land (Smirnov, 1932), and has only been reported afterwards from the northern Kara Sea and the Arctic Ocean near Severnaya Zemlya (Smirnov, 1933). Smirnov (l.c.) always found it at very low numbers, in August and September.

Synchaeta tamara Smirnov, 1932 (Figures 9 and 10)

Altogether 119 specimens, inclusive 14 males, of this species were identified in sea ice from the Barents Sea and the Greenland Sea.

Differential diagnosis

S. tamara is one of the *Synchaeta* species without two equal toes. These species are *S. cecilia* Rousselet, 1902, *S. monopus* Plate, 1889, *S. neapolitana* Rousselet, 1902, *S. hutchingsi* Brownell, 1988, *S. triophthalma* Lauterborn, 1894 and the insufficiently described *S. neapolitanoides* Sudzuki, 1964. *S. tamara* is easily distinguished from *S. neapolitana* and *S. hutchingsi* by the absence of a ventral spur on the dorsal side of the foot. It differs from *S. monopus* by its well developed foot. The most remarkable feature that distinguishes *S. tamara* from *S. cecilia* and *S. triophthalma* are the unci with the frontal hook separated by a very wide gap from the row of shallow teeth (gap narrower and sulci between teeth deeper in the latter species).

Description

Female (Figure 9A–C): Body bell-shaped; head distinctly offset from trunk by neckfold, c. 1/3 total length. Foot distinctly offset from trunk, relatively long, c. 1/5 total length, conical in dorsal view, 2–3 pseudosegments, last pseudosegment in lateral view with slightly arched dorsal margin and oblique, slightly indented ventral margin. Toes strongly asymmetrical, tips acute; left toe largest, claw-shaped, elongate-conical in dorsal view, slightly decurved ventrally in lateral view; right toe strongly reduced, half or less length left toe, apressed to left toe (this reduced toe was not observed by Smirnov (1932, 1933)). Corona convex; coronal styles moderately developed, the midst pair two individual setae. Auricles small. A single lateral antenna (not seen by us) posterolaterally, slightly displaced to the right of body axis. Eyespot cervical. Gastric glands large, cylindrical (may be rounded also according Smirnov (1932)). Pedal glands asymmetrical, left large, more or less tubular, right reduced. Vitellarium with eight nuclei.

Trophi (Figures 9E,F and 10A–D): Unci well developed, with very strong frontal hook separated by a wide gap from the toothplate bearing (5)6–8 blunt teeth, the first of which is somewhat longer and more acute; posterior tooth with small platelet; sulci between teeth shallow; gap between frontal hook and toothplate with membranaceous web and 2 weakly sclerotized tooth-like structures; frontal hook with short, anteriorly projecting spine on outer margin prior to base; basal spine relatively long, kinked near midlength. Rami lamellar, each composed of an elongate-triangular inner lamella, a strongly rounded median lamella, and a delicate, short outer lamella connecting

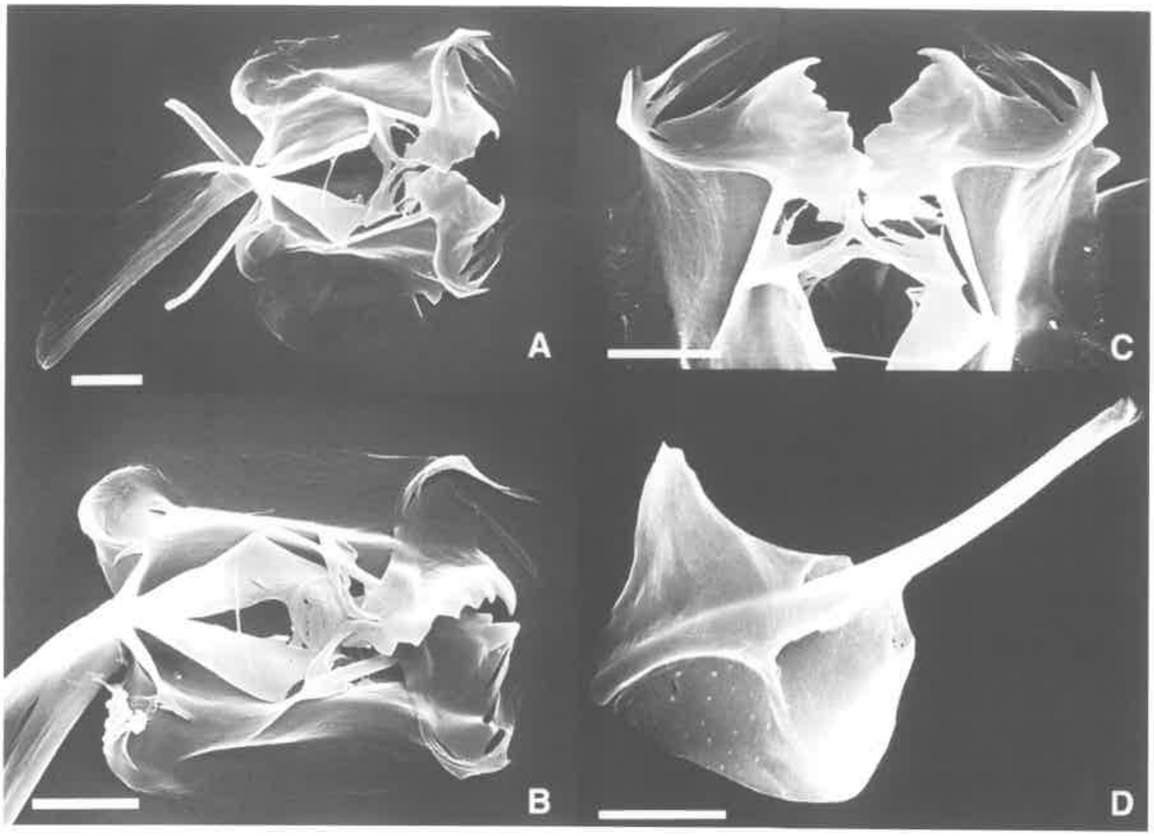

Figure 10. *Synchaeta tamara,* SEM pictures of trophi. (A) Trophi, ventral view. (B) Rami and unci, ventral view. (C) Unci, ventral view. (D) Manubrium, lateral view. Scale bars 10 μm.

posterior margin of uncus with antero-lateral margin of median lamella; inner margin of rami anteriorly with row of scleropili of unequal length, posteriorly broadly W-shaped ligaments. Epipharynx two strong, thorn-shaped elements posteriorly connected by rounded lamella. Fulcrum long, plate-shaped, in lateral view dorsal margin straight, ventral margin slightly decurving posteriorly. Manubria long, almost straight, shaft broadest at c. $\frac{1}{3}$ from anterior end; anterior half of dorsal margin with large blunt triangular lamella, anterior half of ventral margin with semi-lunate lamella and narrow, elongate-triangular thickening.

Male (Figure 9D): Males attributed to the species were present in both sampling areas. All specimens seen from preserved material and slightly contracted. They show a relatively long, characteristically bent foot with two, equally shaped claw-like toes.

Dimensions (measurements by Smirnov (1932) bracketed):
Female: length 225–235 μm (200–270 μm), foot 45–51 μm (70 μm), toe: left 11–14 μm (14–17 μm), right 5–6 μm; trophi 94 μm: ramus c. 32 μm, fulcrum 44–48 μm, uncus 23–26 μm $\times$ 14–18 μm, manubrium 55–58 μm.

Male: length 85 μm, toe 6–7 μm.

Distribution and ecology

S. tamara was found in the Barents Sea during August 12–19, 1993 and in the Greenland Sea between July 15 and August 8,1994 (Figures 12 and 13, Table 2), over water depths between about 200 and 3000 m, it could not be demonstrated in samples from the Laptev Sea. The species was only observed within the lowermost 30 cm of older ice of a thickness between 192 and 346 cm. Temperatures ranged from −0.7 to −1.8°C and the calculated brine salinities ranged from 13 to 32‰.

S. tamara was described from plankton collected in the northern Barents Sea near Franz-Joseph Land (Smirnov, 1932). The only other reports of the species are from the Barents Sea, northern Kara Sea and Arctic Ocean (Smirnov, 1933). It was the most common and wide-spread *Synchaeta* found in August and September, up to a depth of 25 m (Smirnov l.c.).

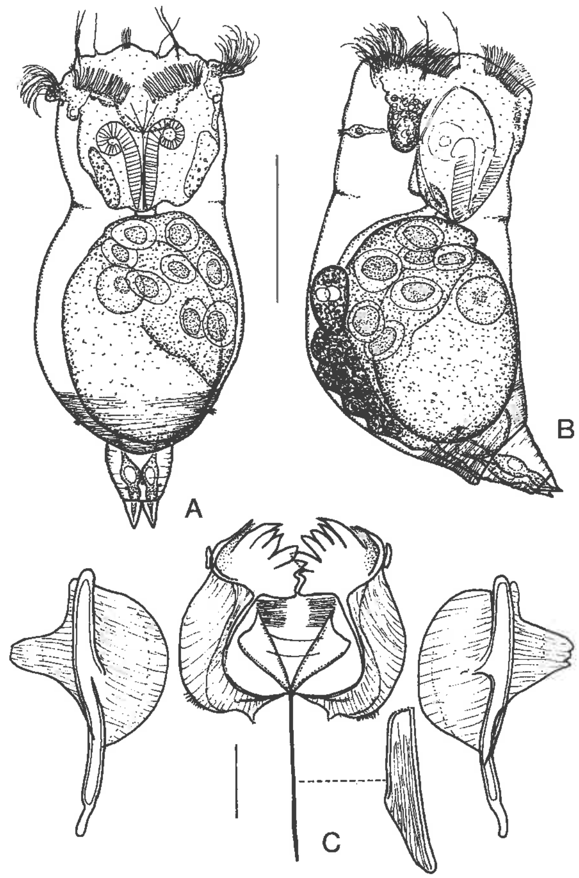

Figure 11. Synchaeta sp. (A) Female, ventral view. (B) Female, lateral view. (C) Trophi. Scale bars: (A)(B) 50 μm, (C) 10 μm.

Synchaeta sp. (Figure 11)

Seven specimens of a peculiar *Synchaeta* sp. were found in samples from Greenland Sea ice. The female has a bell-shaped body in dorsal view, with large head, c. 1/3 total length, and a fairly short, weakly wrinkled foot; the trunk has a characteristic arched dorsum and a flattened ventrum; trunk wrinkled posteriorly. Toes equal and conical. Auricles small. Coronal styles weak. Pedal glands fusiform, slightly constricted basally, foot-length. Unci composed of frontal hook and toothplate with one more or less long tooth, and a set of 2–3 smaller teeth separated by a more or less deep sulcus from a posterior set of 1–2 large teeth and 1–2 small teeth; gap between frontal hook and toothplate narrow, with web and apparently single membranaceous tooth-like structure. Fulcrum long, posterior margin strongly oblique in lateral view. Manubria almost straight, anterior half of shaft slightly wider, a triangular lamella dorsally, ventral lamella semi-lunate about 2/3 manubrium length; cauda offset, narrow. Length 150–180 μm, foot 18–27 μm, toe 8–11 μm; trophi 58 μm: ramus c. 23 μm, fulcrum 28 μm, uncus 16–17 μm $\times$ 12–13 μm, manubrium 45 μm.

The small auricles, weak coronal styles and trophi remind *S. glacialis* and *S. hyperborea. Synchaeta* sp. is distinguished from these species by e.g. the arched dorsum and differences in the morphology of the pedal glands and trophi, and might represent an undescribed species. However, considering that only a few and preserved specimens were available, more studies are needed to warrant the description of a new species.

Synchaeta sp. was found only in the Greenland Sea during July 16–August 7, 1994 (Figure 13, Table 2) over water depths between about 900 and 1500 m. It was observed only in older ice of a thickness between 253 and 288 cm, within the lowermost 30 cm. *Synchaeta* sp. was found at rather high temperatures from -0.7 to -1.2 °C and calculated brine salinities of 13–22‰.

Abundance

Rotifers frequently occurred in sea ice of different regions of the Transpolar Drift. The total abundance calculated per square metre of ice for the different stations is shown in Figure 14. One of the striking observations are the highly variable rotifer densities. The highest rotifer concentrations were reached in the Laptev Sea with about 69.100 animals/m^2, while in most other stations of this region the abundances were below 20.000 animals/m^2, and in 6 cores no rotifers were found (239-03, 246-11, 251-03, 252-03, 261-03, 263-02). In the Barents Sea, high abundances up to 44.400 animals/m^2 occurred in stations 227 and 230. In the remaining stations of this region, the densities were lower, and in cores 225-03/-12/-22, 231-01 no rotifers were found. Lowest rotifer numbers were counted in the Greenland Sea, where maximum abundances of 4.400 animals/m^2 occurred. No rotifers were found in cores 204-02–07.

Rotifer abundances are summarized for the Laptev, Barents and Greenland Sea in Figure 15. In the Laptev Sea, the abundances show a median value of 7.600 animals/m^2 with one high outlier of 69.100 animals/m^2. In the Barents Sea, a higher median abundance of 14.000 animals/m^2 occurred with a wide range of rotifer densities. Lowest densities with least variability occurred in the Greenland Sea, where a median value of 2.200 animals/m^2 was calculated.

Vertical distribution

The vertical distribution of rotifers frequently showed a typical pattern with highest concentrations in the lowermost centimeters, as shown for core 231-03 from the Barents Sea and core 196-02 from the Greenland Sea (Figure 16). However, rotifers were also observed further away from the bottom and in the top of some floes, as shown for core 249-03 from the Laptev Sea, where the maximum density was between 44 and 64 cm from the bottom. The median value of all maximum distances from the bottom of the floes in which rotifers were found amounted 23 cm, while the absolute maximum distance (unidentified species) was 172 cm away from the bottom. Maximum distances for identified species was as follows: *Synchaeta cecilia* 2 cm, *S. bacillifera* 12 cm, *Proales reinhardti* and *S. tamara* 30 cm, *Encentrum graingeri* 40 cm, *S. glacialis* and *S. hyperborea* 94 cm.

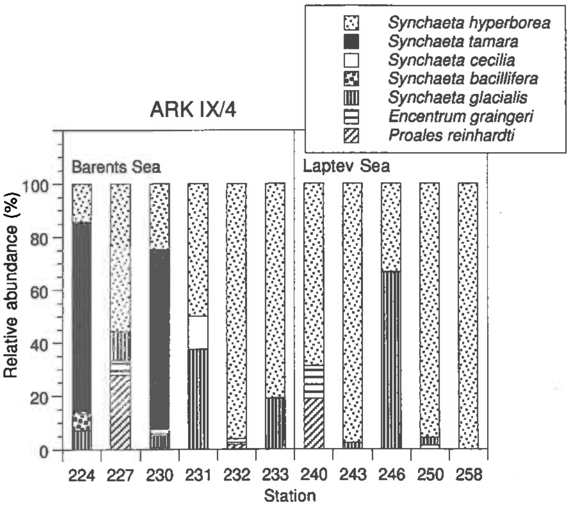

Figure 12. Relative abundance of rotifer taxa in the Transpolar Drift; Barents and Laptev Seas. 100% = total investigated number of rotifers.

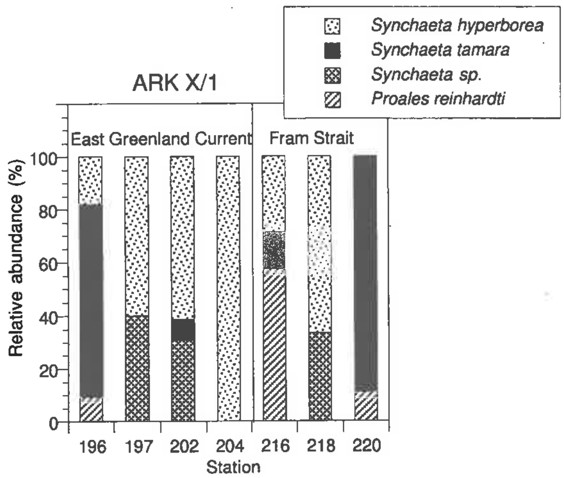

Figure 13. Relative abundance of rotifer taxa in the Transpolar Drift: Greenland Sea. 100% = total investigated number of rotifers.

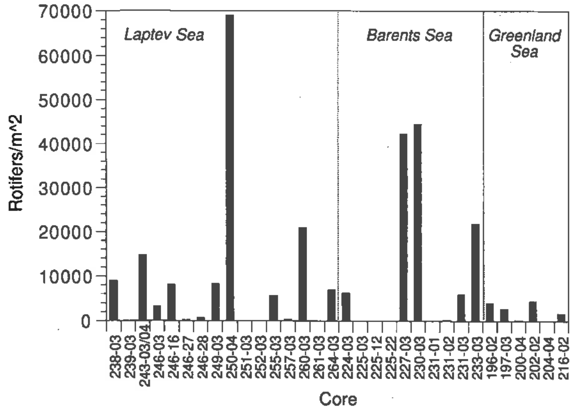

Figure 14. Rotifers per m^2 in the sea ice of the Transpolar Drift. Numbers only shown from stations where whole cores were investigated.

Discussion

Comparing our results with those of Chengalath (1985), we found significant differences between the rotifer fauna of the sea ice of the Transpolar Drift, and the Canadian Arctic. In the Transpolar Drift, rotifers of the genus *Synchaeta* dominated the community, constituting 96% of the abundance.The remaining 4% was shared by *Proales reinhardti* and *Encentrum graingeri.* In contrast, the latter species were dominant in the fast ice of Frobisher Bay, Canadian Arctic, while the genus *Synchaeta* made up only 2.4% of the abundance (Chengalath, 1985). Furthermore, the genus *Cephalodella* was found in the Canadian Arctic sea ice (Chengalath, 1985), but was missing in ice from the Transpolar Drift. Representatives of these taxa are known from marine and freshwater habitats. The genus *Synchaeta* shows a mainly pelagic way of life, and some of its members are the only true mid-oceanic rotifers. *Proales*, *Encentrum* and *Cephalodella* are typically benthic and/or periphytic inhabitants of the intertidal and sublittoral habitats. This indicates that the rotifer fauna of the Transpolar Drift sea ice, which was sampled mostly over deep water up to 3000 m, might be drawn mainly from the underlying water column. Rotifers were indeed frequently observed in the water column directly under the ice in the Greenland and Laptev Seas (Werner, 1997).

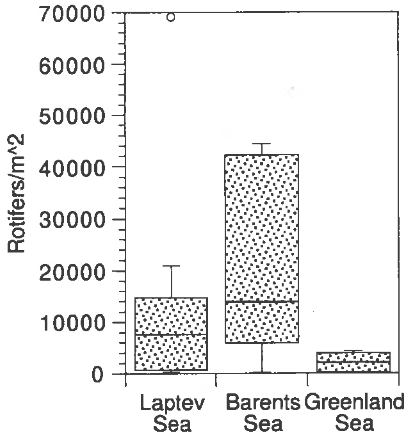

Figure 15. Rotifer abundances in the Laptev, Barents and Greenland Seas shown as box plot (middle line = median, two boxes = upper and lower quartils, dot = outlier).

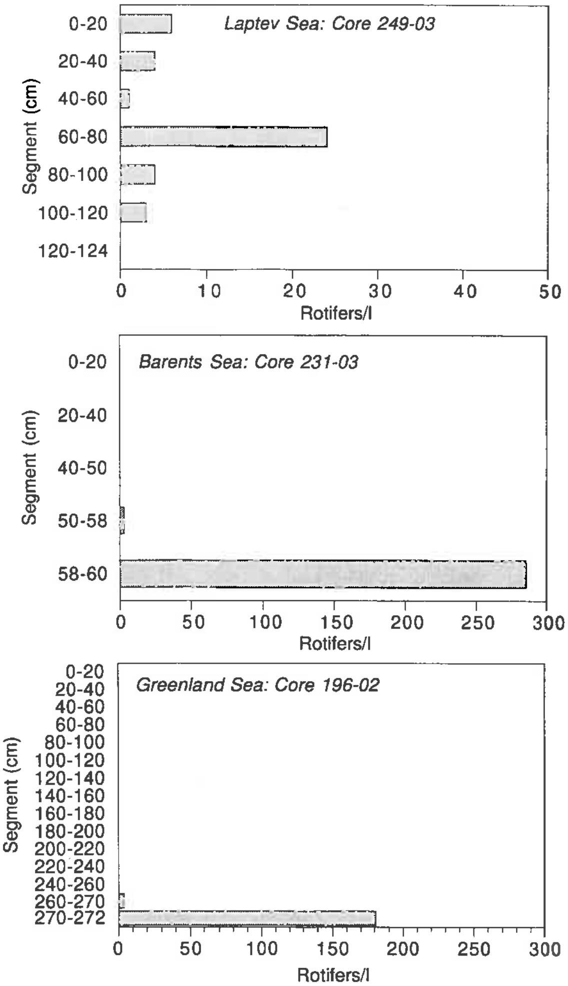

Figure 16. Vertical distribution and concentration of rotifers in sea ice cores of the Laptev, Barents and Greenland Seas. Note the different scale of the x-axis in core 249.

On the contrary, the fast ice of the shallower Canadian Arctic (Chengalath l.c.) was mainly inhabited by benthic-periphytic species, which may originate from the marine sediments or sublittoral vegetation. In shallow waters, benthic-periphytic rotifers can be passively transported into the water column by water currents and become incorporated into the ice, as has been suggested for nematodes, harpacticoid copepods and meroplanktonic larval forms of benthic polychaetes and cirripedes (e.g. Carey & Montagna, 1982; Kern & Carey, 1983; Carey, 1985). On the other hand, rotifers usually display a positive phototaxis and they may actively migrate upwards from the bottom to the overlying ice ceiling, attracted by the greater light intensities, and become trophically related to the sub-ice and ice communities with their rich micro-algae flora.

In the Barents Sea, the rotifer density was very variable but the median abundance (14.000 ind./m^2) was highest compared to the other regions of the Transpolar Drift. With a share of about 25% of the whole meiofauna density estimate, they belonged to the numerical dominant taxa, together with nematodes, turbellarians, copepods and ciliates (Friedrich, 1997). In the Laptev Sea, the rotifers made up about 16% of the total meiofauna density. Their density was very variable also, with a maximum of 69.100 rotifers/m^2 but a on average smaller median value (7.600 ind./m^2) than in the Barents Sea. The variations in ice thickness (10–312 cm), salinity and brine volume which may cause variation in rotifer density, were greatest in the Laptev Sea, as one of the major regions of ice formation for the Transpolar Drift (Gordienko, 1959; Timokhov, 1994), and the northern Barents Sea. Rotifers already occurred in very young ice of 10 cm thickness, indicating that they are trapped in the ice or actively migrate into the ice in an very early stage of ice formation. In the old and thick ice of the Greenland Sea (192–346 cm), the rotifers occurred at smaller densities (median 2.200 ind./m^2), with less variation (maximum 4400 rotifers/m^2). They only made up about 1% of the total meiofauna abundance. The fact that rotifer abundance was lowest in the Greenland Sea ice might be due to the success of the more resistant taxonomic groups, during the several years (and cold winters) lasting ice drift with the Transpolar Drift system. Turbellarians, nematodes and ciliates, which show a very high tolerance for temperature and salinity changes (Lee & Fenchel, 1972;

Friedrich, 1997), dominated the ice community of this region.

Rotifers have been reported as taxonomic group from the ice of the shallow water regions of the Beaufort Sea (Carey & Montagna, 1982; Carey, 1992), Hudson Bay (Grainger, 1988) and Frobisher Bay (Grainger et al., 1985; Grainger and Hsiao, 1990). A comparison of our results on rotifer abundance with other studies is difficult, because of the different sampling methods used. Most investigations from the Canadian Arctic sampled only the lowermost centimeters or the ice-water interface, and moreover used mesh sizes of 63–76 μm, which probably resulted in an underestimation of abundance. Grainger et al. (1985) found 14 up to 2694 rotifers/m^2 in sea ice of the Frobisher Bay between February and June in the lowermost 3 cm, which is still below the rotifer abundance we found in the Greenland Sea. Besides being the result of different sampling techniques, abundances could have been lower because of seasonal effects like, e.g. changes in chlorophyll content. A study conducted in the Fram Strait by Gradinger et al. (1991) in May counted about 200 rotifers/m^2 sea ice (whole cores) and a chlorophyll content of 0.1–0.4 mg m^2, which is significantly lower compared to the rotifer densities and chlorophyll concentrations (0.1–2.9 mg m^2) we found during summer (Friedrich, 1997; Gradinger, 1999).

The vertical distribution of rotifers showed a similar pattern in most ice cores, with single or no specimens close to the top and maximum abundances near the bottom of the floes. This pattern of a 'bottom community' is also known for other sea ice organisms like algae, bacteria, protozoa and metazoa (Horner, 1985; Gradinger & Härtling, 1992; Friedrich, 1997; Gradinger & Zhang, 1997). We demonstrated that the chlorophyll concentrations within the lowermost centimeters were significantly higher (medians of three regions 0.7–5.5 μg/l) than in the upper segments of the ice (0.03–0.05 μg/l) (Friedrich, 1997). The fact that sea ice algae and bacteria may serve as food for the rotifers (Grainger et al., 1985; Grainger & Hsiao, 1990) might be one reason for their similar vertical distribution. The rotifers of the Canadian Arctic sea ice had their stomach filled with diatoms and other algae (Chengalath, 1985), indicating that they had a sufficient food supply. The species we found are known to feed on small diatoms, flagellates, bacteria etc. It must be mentioned also that *Encentrum graingeri, Proales reinhardti, Synchaeta glacialis* and *S. hyperborea* were easily cultured when fed with bacteria- and ciliate-rich rice water.

Vertical distribution of organisms not only depends on the food supply, but also on abiotic parameters inside the ice. During the sampling period the temperature was lowest close to the bottom (medians of three regions −1.3 to −1.1 °C), while near the top of the floes the temperature was slightly below 0 °C (Friedrich, 1997). Salinities (measured from melted cores) were highest in the bottom of the floes (medians of three regions 2.4–2.8‰), while the salinities in the upper layers might sink to about 0‰ (Friedrich, 1997). In general, conditions are more stable near the bottom due to the close contact to the underlying water column, while there are severe annual changes in temperature and hence salinity of the ice in the upper layers (Grainger & Mohammed, 1986). Moreover the higher porosity of the ice at the bottom favours the formation of a bottom community due to a higher pore space (Martin, 1979; Spindler, 1990). The influence of available space on abundance and distribution of organisms becomes evident by the fact that antarctic sea ice, which has a higher salinity and hence more pore space, contains significantly higher numbers of organisms compared to arctic sea ice (Spindler, 1990).

Occasionally, we also found internal maxima of rotifers. For example, core 249-03 from the Laptev Sea differed from most others, because no rotifers occurred in the lowermost segment of the ice, while copepods, ciliates and nematodes dominated there. This can be explained by the presence of a slight internal chlorophyll-maximum, pointing towards an algae food supply for the rotifers (Friedrich, 1997). Internal maxima were also found for the abundance of rotifers in the central Arctic Ocean (Gradinger & Härtling, 1992), and for bacteria (Gradinger & Zhang, 1997), and nematodes and ciliates (Friedrich, 1997) in the Laptev Sea and the northern Barents Sea. Due to their small diameter and great flexibility, rotifers are very well adapted to move inside the brine channel system, where they probably find shelter from larger predators and avoid competition for food with the larger consumers of the ice microfauna and flora. The pores and channels get smaller the further away they are from the bottom, and hence serve as a sieve for larger organisms (Melnikov, 1997). When the temperature sinks at the end of the summer, and consequently brine salinity rises and pore space becomes less in the upper segments, migration of rotifers to the lower segments of the floes may occur.

Specific information on the maximum distance from the bottom of the sea ice for rotifer occurrence is only reported by Chengalath (1985), who found 3 cm for *Cephalodella* sp., 20 cm for *Encentrum* *graingeri* and *Synchaeta* sp., and 150 cm for *Proales reinhardti*. These observations suggest that the highest distances may be reached by the species which are morphologically best adapted to the brine channels.

Distributional and ecological differences are apparent among the seven fully identified rotifers from sea ice. *Synchaeta bacillifera*, *S. glacialis*, *S. hyperborea* and *S. tamara* are restricted to the arctic seas. *Encentrum graingeri* and *Synchaeta cecilia* have a holarctic distribution, and are coldstenothermous and eurythermous, respectively. *Proales reinhardti* is a cosmopolitan and eurythermous element. All species can inhabit a wide range of salinities, although no experimental investigations on the temperature and salinity tolerances of sea ice rotifers are available. Rotifera are known to occur in a wide range of salinities and temperatures, and to flourish in other extreme habitats like meltwater pools (Thomas, 1965) and localized pockets of meltwater on glaciers, called cryoconite holes (De Smet & Van Rompu, 1994). The widespread occurrence of a number of rotifers in the vast ice cover of the Arctic Ocean and its shelf regions is another example of successful adaptation to extreme conditions. The presence of amictic eggs and males indicates that they are able to reproduce both parthenogenetically and sexually. We do not actually know whether the observed species are perennial or not in the region studied, and whether they produce resting eggs with planktonic behaviour. If not, it is conceivable that the arctic sea ice may play an important role in the colonization of the pelagial each spring, at least over the deep water of the arctic oceans. It is to be expected that resting egg production of rotifers in the ice will increase at the end of the summer, in anticipation of the winter that challenges them with the greatest ecological stress. These eggs may be trapped in the brine channel system when pore diameter decreases with decreasing temperature. When ice melts the following year, they enable the re-establishment of populations in the brine channels of the sea ice and the underlying water mass.

Acknowledgements

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