ORIGINAL PAPER

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

Accepted: 17 December 2001 / Published online: 14 March 2002 © Springer-Verlag 2002

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

Introduction

In the Arctic marginal seas, plankton communities are shaped by the strong seasonality of light intensity, ice cover and fresh water supply by large rivers. These re-

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E.G. Kolosova Faculty of Biology, Moscow State University, Vorobievy Gory, 119899 Moscow, Russia gions are of great importance for the formation of water masses and sea ice (Lisitsyn and Vinogradov 1995), and additionally are of great significance for zooplankton with respect to growth and reproduction (Kosobokova and Hirche 2000).

The Kara Sea covers an area of 883,000 km² and is one of the very shallow Siberian shelf seas, which in its central part hardly exceeds a depth of 40–50 m. It is separated from the influence of the Barents Sea by Novaya Semlya to the west and by the Vilkitsky Archipelago from the Laptev Sea to the east (Cherkis et al. 1991), while to the north it opens into the Arctic Ocean (Fig. 1).

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

In its southern part, the Kara Sea is strongly influenced by the immense freshwater discharge of the two river systems, Ob and Yenisej (Gordeev et al. 1996), which provide one-third of the total fresh water entering the Arctic Ocean and about 55% (1,290 km³ year⁻¹) of the total continental river run-off to the entire Siberian Arctic (e.g. Pavlov and Pfirman 1995). The two rivers contribute about 80% of the run-off to the Kara Sea. While the Ob has the largest length and drainage area, the Yenisej has, with 620 km³ year⁻¹, the greatest discharge volume of all the Siberian rivers (Telang et al. 1991; Gordeev et al. 1996). The river run-off shows a strong seasonal and interannual variability, with a maximum in June when the coastal zone is still icecovered (Gordeev et al. 1996).

Little is known of the influence of the large freshwater discharge on the pelagic fauna of the Kara Sea. The freshwater signal is assumed to be the main structuring factor for the marine fauna in the estuaries through rapid changes in salinity and temperature. Thus, during



Fig. 1. Sampling area

the Russian Mendeleev Expedition in August/October 1993 to the southern part of the Kara Sea up to 76°N, three types of zooplankton communities were identified (Vinogradov et al. 1995b): (1) one adapted to the eddy of the southwestern part of the sea, which was dominated by copepodite stage V (CV) Calanus finmarchicus s.l. (57% biomass); (2) a community of the coastal areas of the Yamal Peninsula and Baidara Bay consisting of Chaetognatha and small plankters such as Oithona similis, Pseudocalanus minutus and P. acuspes (20-77%) biomass); and (3) one associated with the detritus-rich brackish waters in the eastern regions. There the biomass was relatively high and consisted >50% of C. finmarchicus. The highest concentrations were found in the bottom layers and in the salinity mixing front. The communities within the estuaries of Ob and Yenisej showed strong differences, with Ob Bay much richer both in abundance and species number (Vinogradov et al. 1995a).

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

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

Materials and methods

The data were collected during two cruises of R/V "Akademik Boris Petrov" from 13 to 25 September 1997, and from 26 August to 9 September 1999, between 72 and 74°N and 72 and 83°E. During the expeditions, 20 (1997) and 24 (1999) stations were visited, respectively. Zooplankton samples were collected with a Nansen closing net (vertical net, 0.442 m² catching area, 150 µm mesh size; 0.5 m/s hauling speed). Four net samples were taken at each station: two below and two above the halocline, which was determined from a CTD profile before sampling. At shallow stations (<10 m depth), the Nansen net frame was mounted with a non-closing, short net of 1 m length. Since the short net could not be closed, only two samples of the whole water column were landed per station. The samples were preserved in 4% borax-buffered formaline. All specimens were counted and measured under a stereomicroscope and identified to species level if possible. Copepodite stages of calanoid copepods were also identified and counted. Prosome length was used to distinguish copepodites and adult females of the two closely related copepods C. finmarchicus and C. glacialis, according to Hirche et al. (1994). Prosome length was measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment.

Overall distribution and community analysis [hierarchical, agglomerative cluster analysis and non-metrical Multi-Dimensional Scaling (MDS)] in relation to abiotic data was performed using the PRIMER package (Clarke 1993; Clarke and Warwick 1994). To reduce the emphasis of abundant species, data were double squareroot transformed. Preliminary clustering analysis showed that samples of the two depth layers were more similar to each other than to all other samples, e.g. resulted in paired clusters, so the data of the net hauls were pooled in further analyses. In order to identify the characteristic species assemblages responsible for each cluster, the number of species was first reduced, retaining only those that accounted for >4% of the total abundance at any one site, and then the single stations were grouped according to the results of the cluster analysis. Afterwards the species were sorted according to occurrence and abundance (also referred to as Shade matrix). The species principally responsible for the sample grouping in the cluster analysis (e.g. the one with the highest abundances) were then highlighted. This simple but informative approach was chosen to concentrate on the species similarities (Clarke and Warwick 1994).

Results

Sea ice and river discharge

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

1997

Hydrography

In 1997, the depth range of the 20 stations varied between 40 m off the Taymyr Peninsula (st. 21) and 10 m within the Yenisej Estuary (st. 32; Table 1). The hydrography was described in detail by Churun and Ivanov (1998). Salinity and temperature distribution at 2 m depth, together with north to south transects in the two rivers, are presented in Fig. 2 (Fig. 3 gives the salinity and temperature distribution in 1999). Both salinity and temperature showed a sharp gradient from the innermost parts of the estuaries to the outer parts, with a strong gradient in an east to west direction in the Ob and in a south to north direction in the Yenisej. Salinity in the upper layer increased from 1 in the Yenisej and 4 in the Ob to 21 psu at the outermost stations, while temperature decreased from 8°C in the Yenisej and from

Table 1. Station data on the expeditions "Boris Petrov" 1997 and 1999. Stations marked with * were excluded in transects (see text for further explanations) (# indicates no lower layer available or too shallow)

	Station	Date	Latitude (N)	Longitude (E)	Depth (m)	Salinity surface/ bottom	Temp. (°C) surface/ bottom	No. of species (N)	Abundance upper layer (ind. m ⁻²)	Abundance lower layer (ind. m ⁻²)
1997										
Ob transect	10	14 Sep	72°30′	74°04′	19	4.5/25.2	6.3/-0.2	18	795	5029
	47	22 Sep	72°35′	73°44′	18	19.3/29.5	4.1/0.5	23	2943	4639
	48	22 Sep	72°57′	73°00′	28	13.9/31.1	4.5/-1.3	30	342	1773
	49	23 Sep	73°12′	72°53′	29	16.6/31.5	4.3/-1.5	30	302	599
	50	23 Sep	73°36′	72°57′	29	21.0/31.8	4.2/-0.7	28	729	556
	1	13 Sep	73°54′	73°10′	28	13.0/32.0	5.3/-1.9	26	73	1080
	52	24 Sep	74°00′	72°39′	29	18.1/32.0	4.2/-0.3	27	651	717
Yensisej transect	32	19 Sep	72°05′	81°28′	10	1.0/15.0	8.3/5.8	10	241	#
.	30	18 Sep	72°30′	80°20′	13	4.3/13.1	7.2/5.0	14	285	#
	27	18 Sep	72°53′	80°05′	19	4.8/30.3	6.5/-0.1	24	749	985
	38	20 Sep	73°12′	80°00′	31	7.2/31.3	6.4/-0.9	23	552	558
	24	17 Sep	73°32′	79°55′	39	11.3/31.4	6.0/-1.7	27	588	2128
	21	17 Sep	74°00'	81°00′	40	14.8/32.0	5.9/-1.8	30	930	1717
Middle transect	56	25 Sep	72°53'	75°28′	14	9.1/16.3	4.5/-0.1	12	694	
inidale transcer	55	23 Sep 24 Sep	73°13'	75°37′	14	9.8/17.9	4.4/-0.2	16	538	# #
	58	25 Sep	73°39'	74°50′	21	9.0/30.7	6.3/-0.1	27	499	1131
	18	16 Sep	73°57′	76°08′	31	_/_	_/_	27	841	2438
	46	21 Sep	73°59′	77°12′	27	12.4/32.0	6.4 / -1.4	25	274	820
	42*	20 Sep	73°53′	81°40′	30	15.1/32.0	5.9/-1.8	29	221	1983
	43*	20 Sep	73°42′	82°48′	31	11.2/21.4	6.0/0.5	27	523	279
1999										
Ob transect	19	1 Sep	72°11′	74°11′	14	1.9/11.0	2.5/0.6	15	1649	#
	18	1 Sep	72°19′	74°00′	15	1.7/26.0	4.0/-0.4	29	760	690
	20	2 Sep	72°30′	74°43′	16	2.8/27.0	3.9/0.1	29	1017	#
	17	31 Aug	72°51′	73°56′	19	5.3/29.9	3.6/-1.2	32	1444	2270
	21	3 Sep	73°14′	74°02′	16	7.0/23.5	3.5/-1.4	20	550	2314
	25	4 Sep	74°00′	73°59′	26	8.9/32.0	3.4/0.1	26	277	575
	37	8 Sep	74°18′	74°20′	30	9.8/32.3	2.9/-1	27	416	665
Yenisej transect	6	28 Aug	72°17′	80°01′	7	2.6/3.0	6.6/6.6	16	1386	#
j	31	6 Sep	72°29'	79°45′	17	4.4/29.6	5.8/-1.1	14	1139	# #
	8	28 Aug	72°55′	79°59′	22	4.7/29.0	5.9/-1.3	21	1630	2617
	32	7 Sep	73°08'	79°57′	27	5.9/31.1	5.3/-1.5	18	480	1353
	28	5 Sep	73°25'	78°48′	23	8.8/28.0	3.3/-1.4	17	191	554
	11	29 Aug	73°46′	79°59′	36	7.0/33.2	3.1/-1.5	26	2005	357
	12	29 Aug	73°45′	78°28′	25	4.6/31.5	4.5/-1.3	27	1876	451
	35	7 Sep	74°18′	78°20′	34	12.1/33.3	2.9/-1.3	28	911	421
	13	30 Aug	74°29'	78°00′	36	8.8/33.1	4.4/-0.6	23	732	131
Middle transect	24	3 Sep	73°26′	74°52′	20	6.4/29.5	3.6/-1.4	15	927	1856
	38	8 Sep	74°15′	75°36′	30	11.1/32.2	3.1/-0.3	24	560	509
	39	9 Sep	74°17'	76°49′	38	10.6/33.0	2.9/-0.8	24	74	523
	2	26 Aug	74°30'	75°55′	30	5.5/29.3	4.1/-1.9	25	2151	525 545
	1*	26 Aug 26 Aug	74°50′ 73°59′	73°33′ 74°30′	30 27	6.0/31.0	3.9/-1.8	31	2747	479
	3*	20 Aug 27 Aug	73°48′	79°59′	32	5.9/30.6	3.7/-1.7	23	1703	604
	29*	5 Sep	73°05′	79°39′ 78°30′	32 17	8.7/26.9	3.7/-1.7 3.4/-1.0	23 18	454	4000
	29* 30*	6 Sep	73°03 72°27'	78'50 79°17'	17	5.3/13.0	5.5/3.9	18	434 937	4000 #

Fig. 2. 1997: salinity and temperature at 2 m and along the 2 transects based on 59 CTD stations. Station *numbers* indicate biological stations. *Boxes* show stations included in hydrographic transects

1997 Salinity (2m)















Salinity Ob Transect



72°N 74°N 7 Temperature Yenisej transect



74"N

76°N

Depth [m]

72"N

Fig. 3. 1999: salinity and temperature at 2 m and along the 2 transects based on 37 CTD stations. Station *numbers* indicate biological stations. *Boxes* show stations included in hydrographic transects 6° C in the Ob to 4° C further north (Table 1). In the south, a pronounced halocline was established at around 10 m depth, which on the Ob transect flattened out through progressive mixing towards the northern parts. The halocline was deeper on the Yenisej transect than on the Ob transect, suggesting a higher discharge of fresh water in the former. Below the halocline, a tongue of high-saline water reached far into the estuaries. In the Ob at the southernmost sta. 10, salinities >25 were registered near the bottom; in the Yenisej, salinities were around 15. The deeper layer had temperatures between 0° and -1° C except at the shallow stations (30, 32) in the Yenisej, where temperatures up to 5.8° C were measured. In depressions, cold winter water of -1.5° C and a salinity of 32 were found (Churun and Ivanov 1998).

Zooplankton composition

A total of 58 species were identified, with 25 species of Copepoda (20 Calanoida, 1 Harpacticoida and 4 Cyclopoida), 6 gelatinous species, 3 Amphipoda, 2 Cladocera, 2 Rotatoria, 2 Pteropoda, 2 Chaetognatha, 2 Appendicularia and 1 Mysidacea and Euphausiacea. Meroplanktic larvae of Cirripedia, Polychaeta, Bivalvia, Gastropoda, Echinodermata, Bryozoa and nauplii of copepods, Euphausiacea and Ostracoda were counted but not determined to species level (Table 2). Of all animals collected, 84.9% belonged to the Copepoda, with 74.3% Calanoida, and 10.6% Harpacticoida and Cyclopoida. Within the Calanoida, Drepanopus bungei (58.7%) was by far the most abundant species and dominated the zooplankton communities at all stations (Table 3). Other species showed much lower abundances, such as C. glacialis (1.4%), Microcalanus pygmaeus (1.4%), P. acuspes (3.5%), P. major (3.5%) and within the Cyclopoida, Cyclops strenuus (3%) and O. similis (6.2%). The next largest group was that of the copepod nauplii (13.6%). All other groups contributed with < 1% to the total (Table 2). Dominant copepodite stages within the Calanoida were CIII to CV, which made up 72%. This stage composition was characteristic of most families. Early copepodites were mostly found in D. bungei and Pseudocalanus spp., while Limnocalanus macrurus was dominated by adults.

Regional distribution

An overall mean of $1,960 \pm 412$ individuals m⁻³ was calculated for all stations. However, there was a strong regional variability both in abundance and species number between the two river systems and along a south to north gradient (Tables 1, 3). In the Ob estuary, the highest abundances (sts. 10, 47, 48) and the highest number of species (sts. 30, 48, 49) were found. Along a transect from the inner Ob estuary to the north (Table 1), species numbers first increased from 18 species at st. 10 to 30 species at sts. 48 and 49, and then slowly

decreased to 26 species at the northernmost st. 52. In the Yenisej river, both abundance and species number were much lower than in Ob Bay, but increased towards the north to high abundances at sts. 21, 24 and 42 to the northeast of the Taymyr Peninsula (Table 1). The distribution of dominant species is presented in Table 3. It shows clearly that high zooplankton abundances were mostly due to mass occurrences of the copepod *D. bungei*, which was found at all stations.

Vertical distribution showed strong differences between the two depth layers sampled (Table 1). Generally, the lower layers showed 2–4 times higher abundances and slightly higher species numbers than the upper layers. Several species were more frequent in the lower layers, such as *Calanus glacialis*, *Jaschnovia tolli*, *M. pygmaeus*, *P. major* and *Oncaea borealis*. Only at the innermost st. 10 in the Ob were more specimens present in the surface layer. There, *D. bungei* dominated the bulk. This species was generally less abundant in the marine waters below the halocline

Cluster analysis resulted in five distinctive groups identified as "Yenisej River", "Ob River", "Estuarine", "Brackish" and "Marine" (Fig. 4a). The species that mainly characterised the clusters were *Diaptomus* spp. and *Cyclops strenuus* in the "Yenisej River", *Cyclops strenuus* in the "Ob River", the combination of *Eurytemora* sp. and *Oithona similis* in the "Estuarine", and *P. major, Oithona similis, Pseudocalanus* spp., *Calanus glacialis* and juvenile Asterioida in the "Brackish". The "Marine" stations were mainly characterised by *M. Xpygmaeus, P. major, Oithona similis, P. acuspes, Calanus glacialis* and *Oncaea borealis.* Copepod nauplii occurred in all groups except "Brackish". The regional distribution of the clusters (Fig. 5a) closely reflects the surface pattern of salinity and temperature (Fig. 2).

Community analysis using MDS based on species assemblage and abundance showed a strong gradient from the inner estuaries to the outer more marine areas, but the distinction between brackish and marine stations was less clear (Fig. 4b). Differences between the zooplankton assemblage of the "Yenisej estuary" and the "Ob estuary" showed up in both the cluster analysis and MDS. On the latter, the stations are aligned in a south to north direction, which probably reflects the salinity gradient. The large statistical distance between the neighbouring sts. 30/27 and 10/47 indicates pronounced hydrographic fronts between these stations, but only minor differences further to the north along the transect. Differences between the two rivers probably reflect their different salinity regimes (Fig. 2).

1999

Hydrography

In 1999, the station positions were slightly different. In the west, the working area was limited to $74^{\circ}E$, and in the north to $74.5^{\circ}N$. The depth range of the 24 stations **Table 2.** Species list and relative abundance (% of total abundance per station) during the expeditions "Boris Petrov" 1997 and 1999. Species with $\geq 1\%$ rel. abundance in **bold** type

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		Calanus glacialis	1.4	2.3
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	Bruozoo			_
Number of species $\Sigma = 58$ $\Sigma = 51$		Diyozoa larvae		- 5 - 51

Table 3. Abundance (individuals m^{-3}) of dominant zooplankton species during the expeditions "Boris Petrov" 1997 and 1999. Stations are sorted according to clusters (Fig. 4a, c)

1997 Sta 30 Sta 32 Sta 10 Sta 55 Sta 56 Sta 27 Sta 38 Sta 43 Sta 28 Sta 10 Sta 27 Sta 27 Sta 28 Sta 43 Sta 27 Sta 18 Sta 21 Sta 21 Sta 21 Sta 1 Sta 47 Sta 1 Sta 42 Sta 43 Sta 43 Sta 43 Sta 44 Sta 45 Sta 45 Sta 46 Sta 48 Sta 49 Sta 50	Example 2003 Example 2003 Examp	and the second state of th	siliuuis euooptio 0.2 18.9 27.5 13.2 54.3 22.6 272.0 90.8 59.1 85.3 231.6 21.3 68.0 51.0 21.3 68.0 51.0	snnueuts sdojo/O 89.4 94.3 256.6 1.0 62.2 14.2 11.2 45.8 0.6 1.5 	bsendocajauna major bsendocajauna major bsendocajauna major 10.2 10.2 10.2 10.2 10.2 10.2 11.4 10.2 10.2 10.2 10.2 10.2 10.2 10.2 10.2		Calanus glacialis 	Limmocalanus macrurus 2.2 31.3 5.3 2.9 5.1 2.2 0.3 1.3 2.9 0.5 50.3 29.1 2.2 0.3 2.9 0.5 50.3 29.1 2.2 0.3 2.9 0.5 5.0 3 2.9 1.3 2.9 2.0 5.1 2.2 0.3 2.9 2.9 2.0 5.1 2.2 0.3 2.9 2.0 5.1 2.2 5.3 2.9 2.0 5.1 5.3 5.3 5.3 2.9 2.9 5.1 5.3 5.3 5.3 5.3 5.3 5.3 5.3 5.3 5.3 5.3		UUCaeea porealis 2.3 0.2 2.0 0.4 0.5 0.8 8.7 12.4 4.2 2.7 89.7 1.3 14.5 10.8 12.5	22.1 39.6 7.0 7.0 2.3 0.8 	b. b. b. b. c. c. c. c. c. c. c. c. c. c	
Sta 50 Sta 52	69.6 26.8	158.6 156.1	42.8 142.7		28.0 51.5	152.8 131.0	31.1 23.8	0.2	13.2 13.9	12.3 7.7			0.2 1.4
1999	Copepod nauplii	Drepanopus bungei	Oithona similis	Cyclops strenuus	Pseudocalanus major	Pseudocalanus acuspes	Calanus glacialis	Limnocalanus macrurus	Microcalanus pygmaeus	Jaschnovia tolli	Jaschnovia brevis	Diaptomus sp.	Keratella quadrata
Sta 6	124.9	52.5	45.2	558.4	4.5	<u> </u>	1.8	10.4	2	0.5	<u>~</u> 	343.9	<u> </u>
Sta 30	5.6	719.1		4.2	13.6		0.2	172.6		5.9	8.7	1.7	
<u>Sta 31</u> Sta 19	102.6 807.2	<u>514.0</u> 30.3	1.8	<u>171.9</u> 201.4	13.3	<u>2.4</u> 0.5		249.8		28.7	0.5	45.9	
Sta 19 Sta 17	371.4	1120.9	 624.6	478.2	331.5	371.2	55.3	108.1 142.8	44.1	22.3	359.7 20.7	0.2	76.9 6.9
Sta 18	288.5	544.1	18.9	279.4	14.4	29.1	19.5	53.3	1.1	6.4	3.7	0.6	88.2
Sta 20	232.9	264.3	30.2	190.0	6.3	73.6	3.0	21.6	0.3	6.5	1.7	0.8	113.4
Sta 8	89.1	2022.7	115.4	85.0	927.8	32.8	31.0	745.3	5.4	150.8		6.4	
Sta 21 Sta 24	50.0 425.6	1214.4 1742.1	41.4 32.3	28.3 20.9	793.2 157.7	79.6 1.7	18.3 10.4	614.0 380.7		14.3 2.9	0.8		
Sta 29	78.7	1964.3	15.3	20.5	1546.8	28.3	18.8	520.4	0.2	268.1		0.2	
Sta 32	36.9	1324.2	25.9		176.9	37.2	6.9	170.2	0.5	37.2	0.1	6.7	
Sta 1	139.8	1892.8	589.2		124.0	97.6	98.4	34.9	17.8	61.6			
Sta 2	98.0	762.4	525.6		121.0	305.8	379.1	384.8	21.9	16.8			
Sta 3	66.0	1055.1	204.0	0.6	359.4	211.2	135.1	163.8	43.4	30.9			
Sta 11 Sta 12	170.9 61.2	1322.9 1542.1	182.2 119.2	1.1 1.8	241.6 328.7	45.6 34.4	37.2 24.4	300.3 89.3	30.0 13.0	5.3 88.2	 0.2	0.8 0.6	
Sta 13	21.9	297.5	29.0		61.5	51.1	111.1	266.3	4.8	6.6	0.2	0.0	
Sta 25	18.0	358.7	259.7		60.8	28.1	16.1	76.3	11.1	2.1			
Sta 28	80.8	374.4	46.6	0.6	157.9	8.8	10.1	36.9	5.6	13.7			
Sta 35	12.8	813.0	105.7		255.2	32.6	22.9	36.6	16.5	4.9			
Sta 37	207.7	395.2	160.2		106.8	89.5	20.1	54.4	15.4	2.0			
Sta 38	83.3	447.3	101.3		43.5	30.5	22.1	316.7	6.9	0.4			

visited in 1999 varied from a maximum of 38 m (st. 39) in the central part of the Kara Sea to 5 m (st. 6) in the inner estuary of the Yenisej river. Details of the hydrographic situation are described by Stephansev and Shmelkov (2000) and Amon and Köhler (2000). Both surface salinity and temperature in the study area were generally lower in 1999. The distribution pattern of surface salinity was similar to 1997 (Fig. 3); differences in the distribution pattern of surface salinity in the southwestern part were at least partly due to the shift of several stations on the Ob transect to the east in 1999. The 1999 data showed a strong east to west gradient Fig. 4. 1997: Cluster dendrogram (a), MDS plot (b). 1999: Cluster dendrogram (c), MDS plot (d)



there. Both rivers showed differences in their surface salinity (Fig. 3). While the inner parts of Ob Bay showed a minimum salinity value of about 2, which slowly increased to about 10 towards the outer parts, in the southernmost station in the Yenisej river, surface salinity was at 2.7 slightly higher. Surface temperature ranged between 3.5 and 7°C in both rivers and their estuaries. At the northernmost stations, where the influence of the cooler marine water masses became more prominent, the surface temperature decreased to 2.9°C. As in 1997, the bottom temperatures showed constant values between 0 and -1.9° C, but the bottom salinity was at 33 slightly higher than 2 years before. The halocline was deepest at the southernmost stations with 13 m and flattened to 10 m towards the north, where the marine water masses became more important. As in 1997, high-saline waters reached far into the rivers (Fig. 2c, d) below the halocline.

Zooplankton composition

In 1999, only 51 species were identified (Table 2). Again, the largest share belonged to the Copepoda with 21 species (16 Calanoida, 1 Harpacticoida, 4 Cyclopoida). In addition, three Cladocera species, three Amphipoda,

one Mysidacea, four Hydromedusa, one Ctenophora, two Tintinnida, four Rotatoria, two Pteropoda, one Chaetognatha and two Appendicularia species were found. Furthermore, Ostracoda, as well as larvae and juveniles of Polychaeta, Echinodermata and Nematoda, were observed, which were not determined to species level. Some of the meroplanktic groups such as Bivalvia, Gastropoda, Cirripedia and Bryozoa larvae were missing this year. Although copepod nauplii were present, no nauplii of euphausiids were found in the samples. In addition, several species common in 1997, such as the calanoids Acartia longiremis, Centropages hamatus, Diaptomus gracilis, P. minutus, Temora longicornis, the amphipod Acanthostepheia malmgreni, the hydromedusa Aglantha digitale, Obelia sp. and Ctenophora spp., were absent. In contrast, other species such as the calanoids Heterocopte appendicularia and Neoscolethrix farrani, the amphipod Themisto libellula, the ctenophore Beroe curcuma, pelagic Foraminifera and Tintinnida, the Rotatoria Brachionus quadridentata and Keratella quadrata, the Nematoda and juvenile Polychaeta pelagobia, were new in the samples (Table 2).

Copepods again dominated abundance with 89.9% (Table 2). Twelve percent of the total was represented by Cyclopoida, 0.2% by Harpacticoida and 77.7% by Calanoida. The most common calanoid copepods were





Drepanopus bungei (44.7%), followed by Pseudocalanus major (12.6%) and L. macrurus (10.6%). Other quite common species of this group were Calanus glacialis (2.3%), J. tolli (1.7%) and Pseudocalanus acuspes (3.5%). Copepoda nauplii (7.7%) were also fairly common. Within the Cyclopoida, Oithona similis (7.3%) and Cyclops strenuus (4.3%) were again the most important. In contrast to 1997, many copepod species were represented by all copepodite stages. Only L. macrurus was dominated by adults; earlier copepodites were only found at the two southernmost stations in Ob Bay.

Regional distribution

An overall mean of $1,955\pm232$ individuals m⁻³ was calculated for all stations, which is very similar to 1997. One of the biggest differences was the much higher density of animals in the upper water layers in 1999

 $(1,084 \pm 142 \text{ individuals } \text{m}^{-3})$ than in 1997 (638 ± 132) individuals m^{-3}). In contrast, the lower layers showed fewer individuals in 1999 $(1,101 \pm 210 \text{ individuals m}^{-3})$ than in 1997 (1,652 \pm 313 individuals m⁻³). In 1999, the highest densities occurred in the central parts (Table 1) while the numbers of specimens in the inner Ob and Yenisej estuaries were only moderate. The highest concentration was found at st. 29 (4,000 individuals m^{-3}) in the southeastern Kara Sea. The species richness showed a slight tendency to higher values further outside. Both along the Yenisej and at the inner stations of the middle transect, 15 species were caught. This number increased to 25 species at the outer marine parts. Along the Ob transect (Table 1), a sharp increase from 15 species (st. 19) to 29 (st. 18) was observed within a short distance. As on the other transect, the number of species finally decreased to 27 at the northernmost st. 37.

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

The characteristic changes in species number and abundance along the transect described above are clearly expressed in the community analysis. Cluster analysis produced six groups, named "Ob River", "Yenisej River", "Yenisej Estuary", "Ob Estuary", "Brackish" and "Marine" (Fig. 4c). The MDS plot (Fig. 4d) shows the gradual change from different community types in both rivers that converge to a homogenous marine community with increasing marine conditions. The most important species for the cluster "Ob River" were J. brevis, Cyclops strenuus and K. quadrata, for the "Yenisej River" Diaptomus spp. and Cyclops strenuus, for the "Ob Estuary" Pseudocalanus acuspes, Pseudocalanus major, Cyclops strenuus, Oithona similis and K. quadrata. The copepods Diaptomus spp. and Cyclops strenuus were the characteristic species combination of the "Yenisej Estuary". The presence of *Pseudocalanus major* and *J. tolli* mainly structured the group "Brackish", while Oithona similis, Calanus glacialis, Pseudocalanus acuspes, Pseudocalanus major and M. pygmaeus contributed to the "Marine" cluster. The regional distribution of the clusters (Fig. 5b) was very similar to 1997 (Fig. 5a), given the differing station locations between these years.

Discussion

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

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

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

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

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

- While the Ob is a typical river of the plains, flowing through the taiga forest and tundra zones, the Yenisej drains the upper and middle mountain areas of the Ural (Telang et al. 1991). It may, therefore, transport more mineral components and less organic material, thus creating a different food environment. Nöthig and Kattner (1999) reported the highest silicate concentrations during the 1997 cruise for the mouth of the Yenisej river, reflecting the river's rocky origin (Sukhoruk and Tokarev 2000). This is also supported by samples taken during the expedition where high contents of lithogenic clastics were observed (Unger et al. 2000).
- In contrast to the Ob, the Yenisej has a rather narrow but deep opening into the Kara Sea, which may result in different mixing processes. This in turn may affect, directly or via phytoplankton development, the structure of zooplankton communities.
- Different nutrient regimes and mixing dynamics may lead to different spring bloom dynamics. Thus, in 1997, highest chlorophyll concentrations were measured in

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

The regional distribution patterns of the clusters, especially in 1997 (Fig. 5a, b), mirror the spreading of fresh water from rivers in a northeastern direction, along the eastern shorelines according to the general circulation patterns of the Yamal current in the southern Kara Sea (Budgen et al. 1982; Burenkov and Vasilkov 1995; Pavlov and Pfirman 1995). This causes the hydrographic and biological gradients, at least in the southern Kara Sea, to run in a southeast-northwest direction rather than south to north. Recent modelling studies modified the current view of the circulation in the Kara Sea, and showed a strong seasonality of the circulation patterns in the southern region (Harms et al. 2000). They suggest that the circulation patterns and hence the zooplankton distribution described here are typical only for the autumn/winter period. A seasonal change of the currents, together with the interannual variability of the freshwater supply by the rivers, should strongly affect the zooplankton distribution and should be considered in future studies. Of special interest is the fate of the brackish-water fauna, which is spread over a large area in summer. The models also predict seasonal variability of the trajectories of particles exported by the two rivers.

Interannual comparison of the two cruises is difficult due to different timing and different station position, especially at the southernmost riverine stations, where the freshwater and the brackish-water communities are separated by steep fronts (e.g. in 1997, sts. 10 and 47 in Fig. 5a). The cruise in 1997, which started 3 weeks later than in 1999, met higher water temperatures, and higher salinities. Nevertheless, the general distribution patterns of the zooplankton communities were very similar, but there were marked differences in species composition and abundance. Fewer species were found in 1999, mainly due to the absence of most meroplanktic and several copepod species (Table 2). Evidently, the pelagic larvae were not yet released. However, Fomin (1989) reported that, for example, Polychaeta and Bivalvia are commonly found in the Kara Sea throughout the year.

A striking difference between the 2 years was the much higher abundance in the upper water layers in 1999 (Table 1). The difference in abundance is mainly due to the enormous increase of *L. macrurus* and *Pseudocalanus major* (Table 3) in 1999. The total number of *L. macrurus* increased by a factor of 21. Also, its distribution was more widespread. While it occupied (>1% of individuals present at each station) only 50% of all stations in 1997, it was present at 96% in 1999. Its spatial distribution patterns covaried with those of the copepod *D. bungei*. The abundance of *Pseudocalanus major* increased by a factor of 5, but in the opposite way to *L. macrurus*. While its main centre of distribution was at the northeastern edge in the study area in 1997, it had shifted south into the Yenisej estuary in 1999. In contrast, the number of calanoid nauplii was more prominent in 1997. Similarly to the meroplanktic species, the copepods may not have spawned before the 1999 cruise.

These differences in zooplankton composition and abundance between 2 years point to large variability of the pelagic system of the southern Kara Sea. The factors controlling mass occurrences of one or the other species are not understood, partly because there is little knowledge of the life cycles of these species.

Acknowledgements We thank the captain and crew of the RV "Akademik Boris Petrov". Victor Khorshev and Alexandr Latko helped onboard during sampling. Also, thanks go to Leonid Stephantsev, Boris Shmelkov and the Vernadsky Institute for providing the CTD data. This work was supported by BMBF 03G0539A1, Project Siberian River Run-Off (SIRRO).

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