Polar Biol (2016) 39:1527–1538
DOI 10.1007/s00300-015-1878-6

ORIGINAL PAPER

The dominant copepods *Senecella siberica* and *Limnocalanus macrurus* in the Ob Estuary: ecology in a high-gradient environment

A. V. Drits[1] · A. F. Pasternak[1] · A. B. Nikishina[1] · T. N. Semenova[1] · V. M. Sergeeva[1] · A. A. Polukhin[1] · M. V. Flint[1]

Received: 12 March 2015 / Revised: 16 December 2015 / Accepted: 17 December 2015 / Published online: 2 January 2016

Abstract Intensive transformation and sedimentation of suspended matter from riverine runoff occur in estuarine frontal zones. The mesozooplankton community plays an important role in these processes. In the Ob Estuary, the dominant copepods *Limnocalanus macrurus* and *Senecella siberica* form dense local aggregations, but only scarce data on the ecology of these species in the estuarine environment are available. We aimed at analyzing the main aspects of the ecology of the two species including their grazing impact on phytoplankton. The distribution (net tows), ingestion rates (gut fluorescence analysis), respiration and excretion rates (incubation experiments), diet composition, gonad development and size of the lipid sacs of these copepods in a high-gradient area of the Ob Estuary were studied during a cruise of the R/V Professor Stockman in September 2013. *S. siberica* predominantly inhabited the freshwater zone; *L. macrurus* was more abundant in the estuarine frontal zone. In *L. macrurus*, adult females and males dominated the population, the herbivorous feeding hardly met the metabolic demands, the specific lipid content was high, and the gonads were developed. In *S. siberica*, the fifth copepodite stage (CV) dominated. The feeding rate considerably exceeded the metabolic requirements, and the lipid content was variable. The gonads were undeveloped. The two species grazed one-fifth of the phytoplankton biomass and more than 100 % of primary production, with *S. siberica* responsible for the main part of the total grazing impact (up to 90 %). These results are discussed in connection with the hydrophysical parameters and phase of the population's life cycle. The obtained results contribute to the knowledge about zooplankton ecology and the transformation of suspended matter in an estuarine high-gradient environment.

Keywords Copepod ecology · *Senecella siberica* · *Limnocalanus macrurus* · Ob Estuary · Grazing impact · Kara Sea

✉ A. V. Drits
adrits@mail.ru

[1] P.P. Shirshov Institute of Oceanology, Russian Academy of Science, 36 Nakhimovskii Prospect, Moscow, Russia 117997

Introduction

Fresh and marine waters interact in the estuaries of large Arctic rivers. Estuaries play the role of the main biogeochemical borders where the suspended matter and energy of continental and oceanic origin are exchanged. Frontal zones with high physical gradients are formed in such regions (Lisitzin 1995; Vinogradov et al. 1995; Futterer and Galimov 2003; Flint et al. 2010). Intensive transformation and sedimentation of the suspended matter from the riverine runoff occur in estuarine frontal zones (described as a marginal filter by Lisitzin 1995). An important role in these processes is played by the mesozooplankton community, composed of several estuarine species (Vinogradov et al. 1995). In the Ob Estuary, these species form dense local aggregations with an extremely high biomass for the Kara Sea of 40–150 g m^{-2} over the depth of 10–12 m and 6–20 g m^{-3} in the layers of maximum concentration (Vinogradov et al. 1995; Flint et al. 2010). Such plankton aggregations have been found in the area of the most pronounced latitudinal salinity gradients (Flint et al. 2010).

Dominant copepod species responsible for these accumulations in the Ob Estuary are *Jashnovia tolli*,

Drepanopus bungei, *Limnocalanus macrurus* and *Senecella siberica* (Fetzer et al. 2002; Hirche et al. 2006; Flint et al. 2010). Dense aggregations with an abundance of 4000–6000 ind m^{-3} of the two latter species have been found at the southern periphery of the estuarine frontal zone (Vinogradov et al. 1995; Flint et al. 2010). Together they made up more than 80 % of the total zooplankton biomass. Preliminary estimates, obtained at the end of the productive season, indicate that these species play an important role in the transformation of primary production and form a powerful natural pelagic "biofilter," which accumulates the organic matter carried by the riverine runoff. The populations of these two species build an extremely high for Arctic zooplankton biomass (Flint et al. 2010).

In prior studies covering the period from August to September (the logistics are very difficult in other seasons), researchers' attention has mainly focused on the distribution patterns of *L. macrurus* and *S. siberica* and their dependence on the environmental conditions (Vinogradov et al. 1995; Deubel et al. 2003; Flint et al. 2010). For quantitative assessment of the role of these copepods in the bioenergetics of the plankton community and transformation of organic matter, knowledge on the main ecological parameters in conjunction with high-gradient environments is needed. Only scarce data on the ecological physiology of these species are available. The majority of the data on *L. macrurus* were obtained from freshwater Arctic lakes (Roff and Carter 1972; Roff 1973; Warren 1985; Vanderploeg et al. 1998). In the Kara Sea (the Ob Estuary), only fragmentary data exist on the feeding activity, lipid composition and halotolerance of *L. macrurus* (Hirche et al. 2003; Arashkevich et al. 2010). Feeding rates of another dominant species, *S. siberica*, have been assessed in a single study (Arashkevich et al. 2010). Data on the feeding behavior, diet and lipid composition have been obtained for a congeneric of *S. siberica*, *S. calanoides,* collected from Arctic lakes (Wong 1984; Nero and Sprules 1986; Wong and Sprules 1986; Cavaletto et al. 1989).

In September 2013, observations were carried out in the Ob Estuary where dense zooplankton aggregations dominated by the two species, *L. macrurus* and *S. siberica,* were found. The main objectives of the current study were to analyze the distribution and assess the ingestion rates, diet composition, diel feeding rhythms, respiration and excretion rates, gonad development and size of the lipid sacs of these copepods in a high-gradient area. We attempted to assess the physiological state and phase of seasonal development of the *L. macrurus* and *S. siberica populations.* Finally, we tried to estimate their role in shaping the "biological filter" in the frontal zone of the Ob Estuary.

Materials and methods

Sampling

The material was collected during a multidisciplinary cruise of the RV "Professor Stockman" to the Kara Sea at the seven stations along a transect in the Ob Estuary carried out on 4–6 September 2013 (Fig. 1). Station 125-17 sampling was performed at the same location as for st. 125-14, and at st. 125-18 as for st. 125-12 (Table 1). The information on the sampling details and type of analyses performed at each station is given in Table 1. Data on the temperature, salinity and turbidity were obtained with a CTD probe (Seabird Electronics SBE-32).

For assessing the chlorophyll *a* concentration, water samples were collected with 5-l Niskin bottles from three depth layers: subsurface, maximum fluorescence and near bottom. One liter was filtered through GF/F filters. Filters were then placed into 5-ml tubes, and chlorophyll *a* was extracted with 90 % acetone for 24 h at 5 °C in the dark. The concentration of chlorophyll *a* was measured according to the technique of Holm-Hansen et al. (1965) using a Turner Design Trilogy fluorometer that was calibrated with Sigma Chl *a* as a standard. Mesozooplankton was sampled using a Juday closing net (0.1 m^2 mouth area, 180 µm mesh size) towed from 2 m from the bottom to the surface. At the two neighboring stations (st. 125-13 and 125-14),

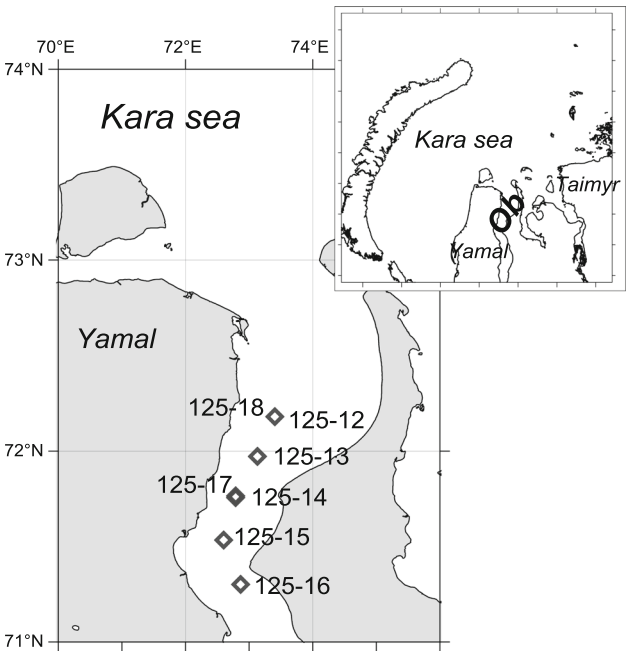

Fig. 1 Map of the study area with station location

Table 1 Position of stations, sampling details and type of analyses performed at each station

Station no.	Position	Date	Depth (m)	Layer (m)	Time (h)	Analysis
125-12	72.17°N, 73.40°E	04.09	12	10–0	21:00	HD, ZA, GF
125-13	71.94°N, 73.13°E	04.09	16	10–0	23:30	ZA, FP, LV, DC, GS
				14–10		ZA, FP, LV, DC, GS
				14–0		HD, ZA, GF, PT
125-14	71.73°N, 72.79°E	05.09	18	9–0	14:30	ZA, FP, LV, DC, GS
				16–9		ZA, FP, LV, DC, GS
				16–0		HD, ZA, GF, PT
125-15	71.49°N, 72.59°E	05.09	16	14–0	4:25	HD, ZA, GF
125-16	71.25°N, 72.88°E	05.09	25	24–0	7:00	HD, ZA, GF, FR, RE, BC
125-17	71.73°N, 72.79°E	06.09	18	16–0	2:15	HD, ZA, GF
125-18	72.17°N, 73.40°E	06.09	12	10–0	20:00	HD, GF

HD, hydrophysical parameters (temperature, salinity, turbidity, Chl *a* concentration); ZA, zooplankton abundance; GF, gut fluorescence; PT, gut passage time; FP, fecal pellet measurement; LV, lipid volume; DC, diet composition; GS, gonad stage; FR food removal experiment; RE, respiration and excretion experiment; BC, body carbon content

samples were collected below and above the pycnocline (Table 1), which was determined according to the CTD profiles. For determination of the abundance and biomass, zooplankton samples were immediately preserved in 4 % borax-buffered formalin. Zooplankton were identified, staged and counted in the laboratory. The wet weight of each species was calculated using nomograms (three-dimensional forms vs. biomass) by Chislenko (1968).

Feeding

To study diet composition, ten *S. siberica* (5 females and 5 CVs) and ten *L. macrurus* (5 females and 5 males) from selected stations (Table 1) were dissected. Identifiable items were measured and counted.

To assess the feeding activity in the sea, the presence of food in the gut of adult *L. macrurus* and CV and female *S. siberica* from selected stations (Table 1) was visually recorded under a dissecting microscope at 32× magnification. The proportion of copepods containing food in the guts was determined and the length of the food pellet in the gut measured.

Ingestion rates of adult *L. macrurus* and CV *S. siberica* were assessed with both the gut fluorescence method (Mackas and Bohrer 1976) and food removal experiments.

Copepods for gut fluorescence analysis were collected in the same manner as described above. The content of the cod-end was diluted in a 1-l plastic bucket and immediately anesthetized with carbonated sea water. Copepod CV *S. siberica* and adult female and male *L. macrurus* were sorted under a dissecting microscope for subsequent fluorescence analysis. To measure the gut pigment content, 3–5 animals per replicate were picked up with forceps and placed in test tubes with 3 ml of 90 % acetone. Three to five replicates for each species/stage were done. Pigments were extracted for 24 h at 5 °C in the dark. The chlorophyll and phaeopigment were measured by a standard fluorometric procedure (Holm-Hansen et al. 1965). The gut content of copepods (G) in units of chlorophyll *a* equiv. ind^{-1} was calculated as $G = \text{Chl } a + 1.51 \times$ phaeopigment (ICES Zooplankton Methodology Manual 2000).

The gut passage time (T) in CV *S. siberica* and adult female *L. macrurus* was measured in the incubation experiments. Immediately after collection, copepods were picked up with a wide-mouth pipette and placed individually in 10 ml unfiltered seawater in multiwell chambers where they were incubated at 7 °C. The time interval (t) between successive defecations was estimated by counting the egested fecal pellets on the bottom of the cells every 5 min. It usually took less than 1 min to check all of the cells for the egested pellets. It is essential to do this quickly to prevent a considerable increase of water temperature. Ten to 15 fecal pellets were collected on GF/F filters for subsequent fluorescence analysis. Gut passage time T (h) was calculated as:

$$T = G/(G_{\mathrm{f}} x t)$$

where G_{f} is the chlorophyll-related pigment content of the fecal pellets (ng Chl *a* pellet^{-1}) and t (h) as defined above (ICES Zooplankton Methodology Manual 2000).

The amount of pigment ingested by copepods (I, ng Chl *a* ind^{-1} day^{-1}) was estimated as:

$$I = (G_{\mathrm{d}} t_{\mathrm{d}} + G_{\mathrm{n}} t_{\mathrm{n}})/T$$

where G_{d} and G_{n} are the average day and night gut pigment contents (ng Chl *a* ind^{-1}); t_{d} and t_{n} are the durations of the day and night periods (h). The data on day and night duration were provided by A.B. Demidov (personal communication).

To convert pigment ingestion into carbon units, the average C:Chl *a* ratio was estimated for each station. The data on phytoplankton biomass in carbon units were calculated according to Menden-Deuer and Lessard (2000). The mean C:Chl *a* ratio was 46 ± 25, $n = 10$.

For the food removal experiments, adult female and male *L.macrurus* and CV of *S. siberica* were collected at st. 125-16 and preconditioned for 10 h in GF/F filtered water. Ten specimens were transferred to 1-l plastic bottles filled with unfiltered subsurface water and incubated in the dark at 6 °C on a bottle rotating wheel at 2 rpm. Three replicates for *S. siberica* and four replicates for *L. macrurus* were made. Similarly prepared bottles without animals (3 replicates) served as control. Duplicate subsamples of 100 ml were drawn from control bottles to determine the initial pigment concentration. At the end of incubations, the contents of the bottles were vigorously mixed and subsamples taken in triplicate to assess the final pigment concentration. The subsamples from the bottles with copepods were checked under a dissecting microscope, and copepods and fecal pellets were removed. Pigment samples were concentrated on GF/F filters and extracted in 90 % acetone. The ingestion rate for chlorophyll *a* was calculated using the equations of Frost (1972).

Grazing impact

The grazing impact was estimated using the ingestion rates determined with the fluorescence method and the abundance of *L. macrurus* and *S. siberica* for the integrated (0-bottom) chlorophyll *a* content and primary production. Primary production was measured using on-deck ^{14}C incubations (unpublished data of A.B. Demidov using the method of Steemann Nielsen 1952).

Metabolism

For respiration and excretion experiments, copepods collected at st. 125-16 were used. Eight to ten copepods, *S. siberica* CV and *L. macrurus* females, were suspended in 60-ml glass-stoppered bottles filled with GF/F filtered water and incubated 24 h in the dark at 8 °C. Similarly prepared bottles without animals served as controls. Oxygen was measured by a standard Winkler method, ammonia by the Solorzano method (Solorzano 1969) at the beginning (controls) and end of incubation (controls and experiment bottles).

Body state

For determination of the body carbon content, ten adult specimens of *L. macrurus* and ten CVs of *S. siberica* from st. 125-16 were sorted onto GF/F filters, frozen in liquid nitrogen and stored until analysis. Measurements of organic carbon were carried out in the laboratory with a Shimadzu NOC-VCPH carbon analyzer.

For measurement of the length and width of the oil sacs, 37 females and 30 males of *L. macrurus* and 33 females and 43 CVs of *S. siberica* were picked out at random from preserved zooplankton samples. Measurements were conducted under a dissecting microscope at 32× magnification. The volume of the lipid sacs was calculated assuming an ellipsoid shape of sacs and equability of their width and height. Several studies have demonstrated a high degree of correlation between the total content of lipids, as measured by biochemical assays, and the estimated oil sac volume in copepods (Arashkevich et al. 1996; Miller et al. 1998; Davies et al. 2012). As it has been shown that preservation with formalin can alter the oil sac shape and cause bursting of the oil sacs (Davies et al. 2012), only individuals with intact oil sacs were selected.

In order to assess the reproductive state, 20 females of *L. macrurus* and 10 females and 10 CVs of *S. siberica* were stained in 2 % borax carmine solution, dehydrated and stored in glycerine according to Tande and Hopkins (1981) and Niehoff and Hirche (1996). Gonads were examined under a dissecting microscope, and the gonad maturity stage (GS) was assessed according to the classification scheme for *Calanus* spp. (Niehoff and Hirche 1996).

Results

Study area

The latitudinal transect of five stations was located in the inner part of the Ob River Estuary (Fig. 1). The depth along the transect varied from 10 m in the south to 25 m in the north. Following Flint et al. (2010), two zones were defined in the study area on the basis of the salinity and temperature distribution in the surface and bottom layers (Fig. 2). The freshwater zone located in the southern part of the transect (stations 125-15 and 125-16) was characterized by the lack of vertical gradients, salinity of 0.1–0.3 and temperature of 8.2 °C throughout the water column. This zone was well marked by the highest chlorophyll concentrations (95.2 mg m^{-2}). The rest of the stations (125-14 to 125-12) were located in the estuarine frontal zone, which was about 190 km in the latitudinal direction. In the frontal zone, vertical stratification of the water column was well pronounced. The surface and bottom salinity varied within 1.8–2.3 and 13–20, respectively, and the bottom temperature declined to 3.8 °C. Chlorophyll concentrations decreased from 40 mg m^{-2} at the southernmost to 27 mg m^{-2} at the northernmost stations (Fig. 3).

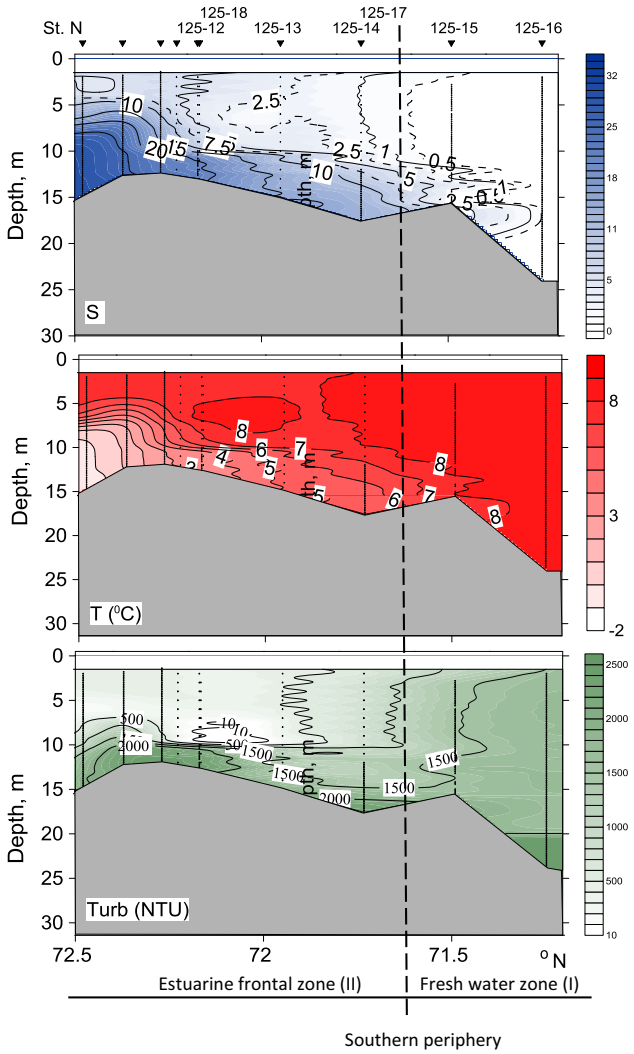

Fig. 2 Latitudinal salinity (*upper left*), temperature (*upper right*) and turbidity (*lower panel*) section in the studied area

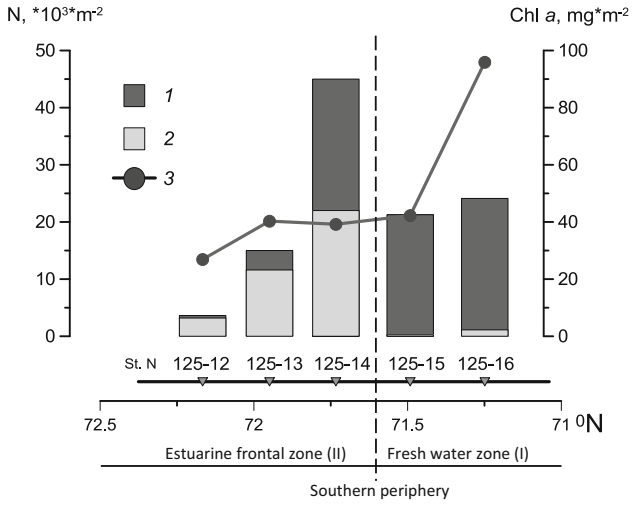

Fig. 3 Abundance of *S. siberica* (*1*) and *L. macrurus* (*2*), N, and chlorophyll *a* concentration (*3*) along the south-to-north transect

Stations 125-14 and 125-17 were located in the southern periphery of the frontal zone where the surface and bottom salinity values were 0.7 and 15.3, correspondingly, and the bottom salinity gradients were most pronounced, reaching 0.6 km^{-1} (Fig. 2). Well-pronounced stratification with the pycnocline at 8–11 m was recorded there.

Abundance and distribution of *Limnocalanus macrurus* and *Senecella siberica*

Limnocalanus macrurus and *S. siberica* dominated the copepod community of the study area. Together they comprised 60–90 % of the total zooplankton biomass. The population of *S. siberica* was represented mostly by CVs and was much more numerous than that of *L. macrurus* at st. 125-15 and 125-16; it almost disappeared at st. 125-12 (Fig. 3). *L. macrurus*, with a predominance of the adults, was the dominant species at st. 125-12 and 125-13. At st. 125-14, the abundance of the two species was almost equal. Among *S. siberica*, CV females were more abundant (>60 % total abundance) than males at st. 125-12 to 125-13, while CV males contributed more than 60 % at st. 125-15 and 125-16. Within the *L. macrurus* population, the abundance of females and males was similar at st. 125-12 and 125-13, while males were more abundant (55-70 % of total abundance of the population) at st. 125-14 to 125-16. Among the hydrophysical parameters studied (surface and bottom salinity, surface and bottom temperature, turbidity, thickness of the mixed layer), only the surface salinity influenced the distribution of *S. siberica* (correlation analysis: $r = -0.76$, $p = 0.030$), while the distribution of *L. macrurus* was not significantly affected by any these parameters.

The day and night distribution patterns of *L. macrurus* and day distribution of CV *S. siberica* above and below the pycnocline are presented in Fig. 4. During midday (14:30), most of the *L. macrurus*, both males and females, were concentrated in the deep (16–9 m) layer, while the abundance of *S. siberica*, CV males and females, was similar in both layers. By midnight (23:30), *L. macrurus* was equally abundant above and below the pycnocline.

Feeding

Gut content analysis of *L. macrurus* adults and *S. siberica* CVs from st. 125-17 and 125-13 showed that a considerable portion of their food pellet was comprised of an unidentified mass. Copepods of both species contained freshwater diatoms *Aulocoseira* sp. However, while *Aulocoseira* sp. dominated the identified portion of the gut content in *S. siberica*, in *L. macrurus* the dominant items

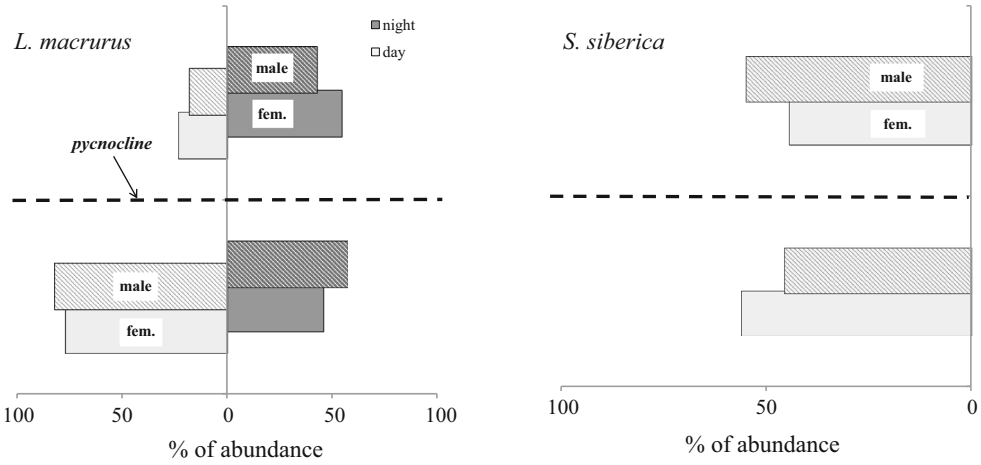

Fig. 4 Day (st. 125-14) and night (st. 125-13) vertical distribution of adult *L. macrurus* and day (st. 125-14) vertical distribution of CV *S. siberica* (% of abundance of respective stages)

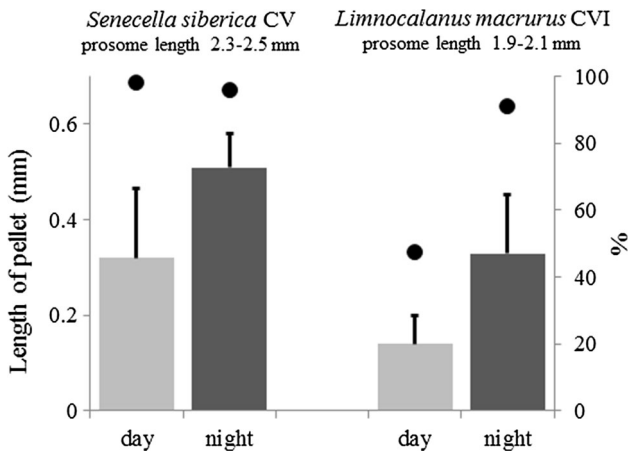

Fig. 5 Length of fecal pellets (*bars*, mean ± SD) and percentage of copepods with food in the gut (*black dots*) estimated at st. 125-14 (day) and st. 125-13 (*night*)

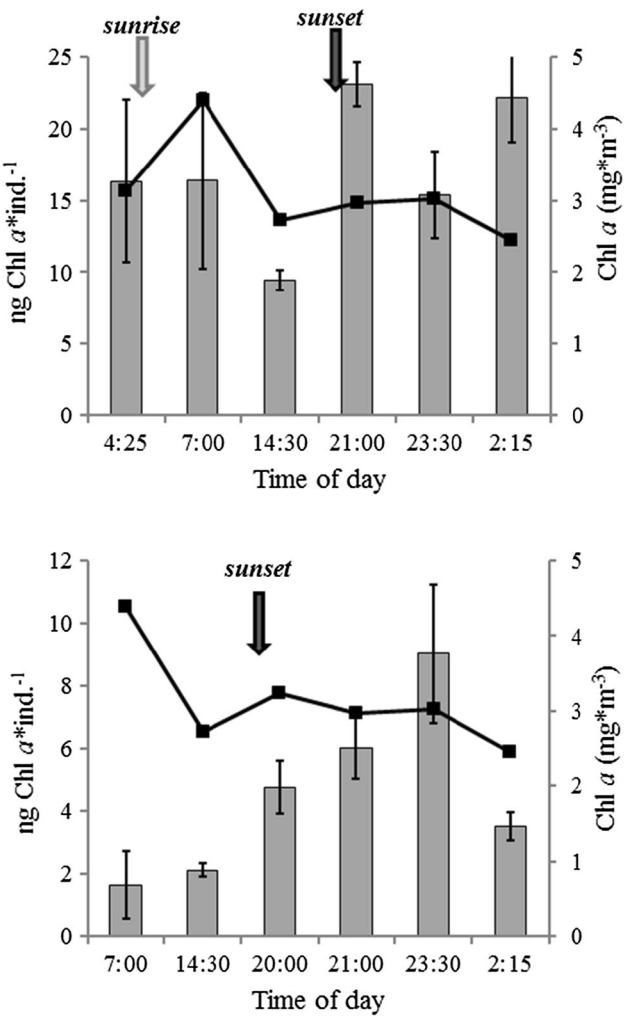

Fig. 6 Gut pigment content of copepods (*bars*, mean ± SD) and Chl *a* concentration (*line*) at stations taken at different times of day. *Upper*, *S. siberica* CV; *lower*, *L. macrurus* adults

were Peridinea of about 20 µm diameter. Zooplankton remnants have never been found in either of the species.

The lengths of the fecal pellets of *L. macrurus* collected at night and in the daytime were significantly different (Fig. 5, Mann-Whitney U test, $p = 0.001$, $n = 20$). No difference was found between the upper and deeper layers (Mann-Whitney U test, $p > 0.05$, $n = 23$). In *S. siberica*, the length of the pellets was similar, irrespective of the depth (Mann-Whitney U test, $p > 0.1$, $n = 37$) and time of day (Fig. 4, Mann-Whitney U test, $p > 0.1$, $n = 69$). The proportion of *S. siberica* with food inside was 96–100 %, irrespective of the depth and time of day. The proportion of *L. macrurus* with food was around 50 % in the day and increased to 90 % at night (Fig. 5).

Feeding activity of *L. macrurus* based on gut pigment fluorescence analysis was lower during the daylight hours than at night (Fig. 6). The observed difference in gut pigment contents between day and night was significant (Mann-Whitney U test, $p < 0.05$, $n = 22$). The gut pigment content of *S. siberica* was lowest in mid-afternoon (14:30) (Fig. 6); however, the difference between mean daytime and nighttime values was insignificant (Mann-Whitney U test, $p > 0.1$, $n = 19$).

The pigment content of a fecal pellet of *L. macrurus* equaled 1/3 of the gut pigment content when the gut pigment content was both low and high. The pigment content of a *S. siberica* fecal pellet equaled 1/2 the amount of pigment in the gut. The gut passage time in the two species was similar (Table 2).

The amount of pigment ingested in 24 h and daily rations obtained through herbivory by *S. siberica* were five times higher than by *L. macrurus* (Table 3).

The pigment ingestion rate of *S. siberica* measured in incubation experiments was similar to that of *L. macrurus*: 254 ± 14 ($n = 3$) and 231 ± 14 ($n = 4$) ng Chl *a* ind^{-1} day^{-1}, accordingly (Mann-Whitney *U* test, $p > 0.05$).

Grazing impact

The grazing impact of *L. macrurus* and *S. siberica* was assessed as total Chl *a* and phytoplankton organic carbon ingested by the respective populations at the studied stations (Table 4). Maximum grazing (17–20 %) was recorded in the area of the southern periphery of the frontal zone. The lowest impact on Chl *a* and primary production was obtained for the estuarine frontal zone stations. In the freshwater area (st. 125-15, 125-16) and southern periphery of the estuarine frontal zone (st. 125-14, 125-17), the population of *S. siberica* was responsible for 80–90 % of the grazing impact. In the estuarine frontal zone (st. 125-13, 125-12), grazing of the population of *L. macrurus* accounted for 44–63 % of the total impact.

Metabolism

Oxygen consumption and ammonia excretion of *S. siberica* CV (7.83 ± 0.56 µlO_2 ind^{-1} day^{-1}, 0.22 ± 0.042 µg N ind^{-1} day^{-1}, $n = 3$) were higher than in *L. macrurus* females (5.02 ± 0.36 µlO_2 ind^{-1} day^{-1}, 0.15 ± 0.07 µg N ind^{-1} day^{-1}, $n = 3$). The specific rates of respiration (0.074 and 0.087 µlO_2 µg C^{-1} day^{-1}) and excretion (0.002 µg N µg C^{-1} day^{-1} for both species) as well as the metabolic O:N ratio were similar (44.1 and 41.3 by atoms).

Table 3 Feeding rates of *L. macrurus* females and *S. siberica* CV

Species/stage	W_c	*I*	*R*	R/W_c (%)
S. siberica CV	130.2 ± 46.3 (5)	329.2	15.1	11.6
L. macrurus female	118.5 ± 37.7 (5)	67.6	3.1	2.6

W_c, body carbon (µg C ind^{-1}); I, daily pigment ingestion (ng Chl *a* ind^{-1} day^{-1}); R, daily ration (µg C ind^{-1} day^{-1})

Body state

Both copepods contained considerable lipid reserves. Total volume of the lipid sacs in *S. siberica* and *L. marcurus* females did not differ significantly: 40.0 ± 38.0 mm^3 $\times 10^{-3}$, $n = 33$, and 26.9 ± 27.8 mm^3 $\times 10^{-3}$, $n = 37$ (Mann-Whitney *U* test, $p = 0.156$). However, patterns of the frequency distribution of lipid sacs of various volumes in *S. siberica* and *L. macrurus* were different. In the former, it was flat (low excess), while in the latter, there was a pronounced peak (high excess) (Fig. 7). Around 10 % of the *S. siberica* population was without visible lipid sacs, but all of the *L. macrurus* contained lipid sacs.

Gonads of *L. macrurus* females could be compared to the G 2 of *Calanus* spp. reproductive stage (Niehoff and Hirche 1996). The ovary, diverticula and oviducts were well developed, and the oocytes increasing in size could be recognized (Fig. 8). Gonads of *S. siberica* were underdeveloped and hardly recognizable under a microscope.

Discussion

The highest concentrations of *L. macrurus* (4780 ind m^{-3}) and *S. siberica* (5750 ind m^{-3}) in the Ob Estuary were found in a narrow near-bottom layer in September 1993 (Vinogradov et al. 1995). Recalculation for the whole water column resulted in values of 16,000 ind m^{-2} (*L. macrurus*) and 19,000 ind m^{-2} (*S. siberica*). Flint (Flint et al. 2010) reported a maximum abundance of 26,200 and 7320 ind m^{-2}, respectively, for *L. macrurus* and *S. siberica.* Our results for *L. macrurus* and *S. siberica* are similar

Table 2 Gut passage time in *S. siberica* CV and *L. macrurus* females (with low and high initial gut contents)

Species/stage	*G*	G_{fp}	*t*	*T*
S. siberica CV	15.40 ± 3.09 (3)	7.30 ± 1.45 (4)	0.66 ± 0.21 (5)	1.32
L. macrurus female	3.37 ± 1.38 (3)	1.05 ± 0.02 (2)	0.43 ± 0.18 (5)	1.30
L. macrurus female	9.02 ± 0.45 (3)	2.96		

Means and SD are given. Number of replicates in parentheses

G (ng ind^{-1}), gut pigment content; G_{fp} (ng Chl *a* pellet^{-1}), fecal pellet pigment content; *t* (h), time interval between successive defecations; *T* (h), gut passage time

Table 4 Grazing impact of *L. macrurus* and *S. siberica*

Station	Chl *a*	PP	E_{chl}			E_c			E_{chl}/Chl *a*, %	E_c/PP (%)
			L. macrurus	*S. siberica*	Total	*L. macrurus*	*S. siberica*	Total		
125-16	95.9	208	0.061	5.414	5.47	2.8	249.0	251.8	5.7	121.1
125-15	42.2		0.015	4.943	4.96	0.7	227.4	228.1	11.7	
125-14	39.2		1.208	5.413	6.62	55.6	249.1	304.6	16.9	
125-17	43.2	350	0.396	8.074	8.47	18.2	371.4	389.6	19.6	111.3
125-13	40.3		0.637	0.800	1.44	29.3	36.8	66.1	3.6	
125-12	26.9	170	0.175	0.104	0.28	8.1	4.8	12.9	1.0	7.5

Calculation is based on the total abundance of copepods in the water column (Fig. 3)

Chl *a*, mean chlorophyll concentration at the studied stations, mg Chl *a* m^{-2}; PP, primary production, mg C m^{-2} day^{-1}; E_{chl} and E_c, grazing in terms of Chl *a*, mg Chl *a* m^{-2} day^{-1} and carbon, mg C m^{-2} day^{-1} respectively

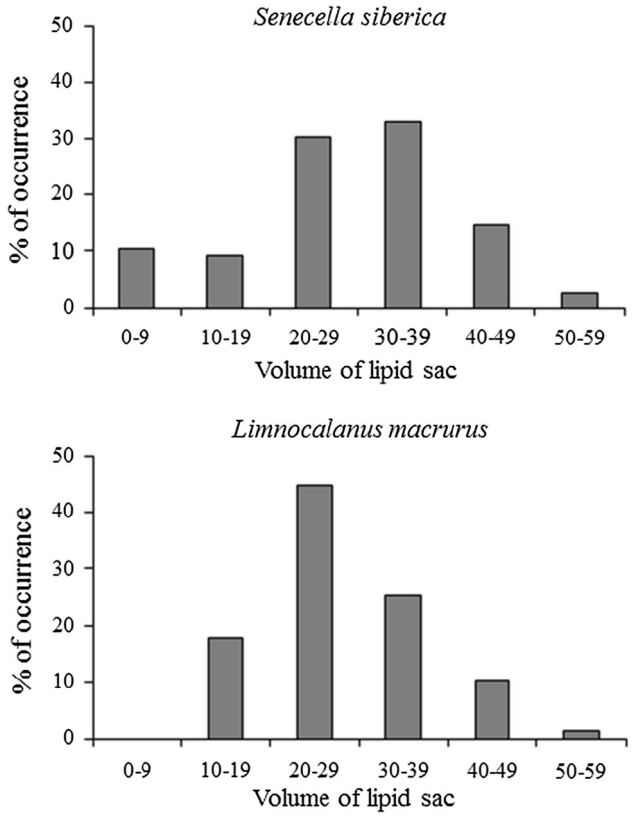

Fig. 7 Frequency distributions of the volume of the lipid sacs ($mm^3 \times 10^{-3}$) in *S. siberica* and *L. macrurus*

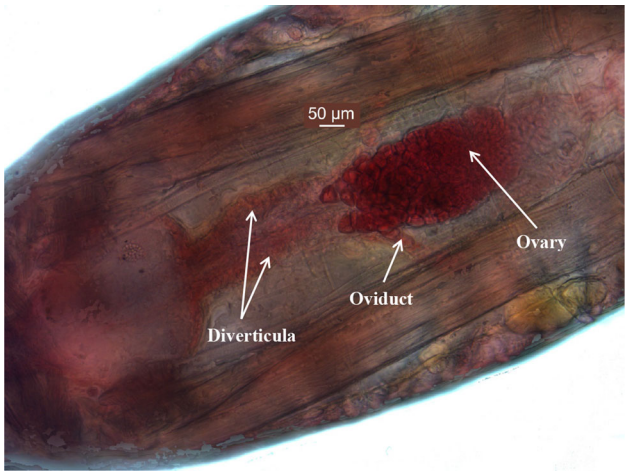

Fig. 8 State of gonad development of *L. macrurus* females

(22,000 and 23,000 ind m^{-2}, respectively). A general pattern in the spatial distribution of these species could be revealed comparing the data obtained in September of 1993, 2007 and 2013. According to Vinogradov et al. (1995), maximum concentrations of *L. macrurus* and *S. siberica* were found at the hydrochemical front. In September 2007, dense aggregations of these copepods were found within a narrow (<10 miles) area of maximum latitudinal gradients of salinity (Flint et al. 2010). Our data point to a maximum abundance of both species at st. 125-14/17, where an intrusion of saline water into the near-bottom layer was recorded for the first time along the transect. Abundance maxima of various zooplankton taxa confined to narrow frontal areas have been previously recorded (Flint et al. 2002; Flint 2004).

The distribution of the two species within the studied area differed noticeably. *S. siberica* predominantly inhabited the freshwater zone. Their abundance was an order of magnitude lower in the estuarine frontal zone where the surface salinity was higher than 1. On the contrary, the abundance of *L. macrurus* was high in the estuarine frontal zone and considerably decreased in the freshwater zone at salinity values <0.4. A similar pattern was described in September 2007 (Flint et al. 2010). These results clearly demonstrate the dependence of the distribution patterns of the two species on hydrographic conditions. According to the correlation analysis, the only factor that influences the

distribution of *S. siberica* is the surface salinity. The wide range of salinity tolerance of *L. macrurus* from 1.7 to >30 (Chislenko 1972; Hirche et al. 2003) provides the species with a high distribution potential. *L. macrurus* inhabited freshwaters with salinity less than 0.4 (this study) as well as waters with salinity typical of the Kara Sea shelf (Fetzer et al. 2002). Hydrographic conditions seem to be similarly comfortable for both species at the frontal border within the southern periphery of the frontal zone (Flint et al. 2010). Our results on the vertical distribution of *L. macrurus* suggest that these copepods perform diel vertical migrations (DVMs). In the daytime, most of the population (75 %) stayed in the lower water layer, while at night, a portion of the population (both adult females and males) ascended into the upper water layer while the rest stayed below the pycnocline. A similar pattern of the DVM was described for *L. macrurus* in Weslemkoom Lake in southern Ontario (Carter and Goudie 1986). However, the DVM pattern varied among the other three studied lakes because of the different level of predation pressure (Carter and Goudie 1986). These authors also reported the DVM (although with a considerably lower amplitude) in *S. calanoides*. Since we have no data on the vertical distribution of *S. siberica* at night, we cannot state whether these copepods were performing DVM or not. Unlike *L. macrurus*, *S. siberica* was homogeneously distributed within the water column in the daytime. These differences in the daytime vertical distribution could be related to the different patterns of predator avoidance. Predation risk for copepods from visual predators could be expected to decrease in turbid water (Salonen et al. 2009). *Senecella calanoides* is an extremely fast swimmer (Ramcharan et al. 1985), and this may enable the copepod to avoid capture by planktivorous fishes whose feeding efficiency could be reduced in turbid waters. Slower *L. macrurus* (Wong and Sprules 1986) could reduce the predation risk by visual predators by descending to the most turbid deeper layers (Fig. 2) during daytime. In the Ob and Yenisei Estuaries, the most important visual predators are the commercial white fish (*Coregonus sardinella and C. muksun*). One of the main components of their diet is *L. macrurus* (Pirozhnikov 1950, 1955; Kuklin 1980).

The predation threat likely affects other aspects of these copepod activities, such as the feeding activity. In *L. macrurus,* the gut pigment content as well as size of food pellets and the proportion of copepods with food in their guts were significantly lower during the daytime hours. Another possible reason for the reduced daytime feeding activity of this species could be a lower Chl *a* concentration in the near-bottom layers where *L. macrurus* spent the day. *S. siberica* did not demonstrate any of these patterns.

The daily pigment ingestion rates calculated from the gut pigment content are within the range of values reported for these species in the previous studies on zooplankton feeding in the Ob and Yenisei Estuaries. According to Arashkevich et al. (2010), the amount of pigment ingested by *L. macrurus* adults and *S. siberica* CVs in the Ob Estuary in September was 37–39 ng Chl *a* ind^{-1} day^{-1} and 180–306 ng Chl *a* ind^{-1} day^{-1}, respectively. In the Yenisei Estuary, *L. macrurus* ingested 59 ng Chl *a* ind^{-1} day^{-1} and *S. siberica* CV 345 ng Chl *a* ind^{-1} day^{-1} during the same period (Drits et al. 2015). However, Hirche et al. (2003) reported the lack of feeding activity in *L. macrurus* females collected in the same regions in August–September, suggesting that the population was already in a pre-overwintering condition. Pigment ingestion rates of *S. siberica* obtained in the food removal experiments (254 ng Chl *a* ind^{-1} day^{-1}) were close to those measured by the gut fluorescence method (329 ng Chl *a* ind^{-1} day^{-1}). This indicates that the chlorophyll was not degraded below phaeophytin in the process of digestion. The difference was considerably higher in *L. macrurus*: ingestion rates assessed in the food removal experiments (231 ng Chl *a* ind^{-1} day^{-1}) were 3.3 times higher than the gut fluorescence data (67.6 ng Chl *a* ind^{-1} day^{-1}). Several reasons for such a considerable difference between the results of different methods could be suggested. First, *L. macrurus* demonstrated a tendency toward predatory feeding (Warren 1985; Nero and Sprules 1986). Low feeding on phytoplankton could be supplemented with a high level of carnivory in nature, while in the experimental bottles, the concentration of prey might be too low. However, we did not find copepod or other prey remnants in the guts of *L. macrurus* from the sea. Second, the diel feeding rhythm of *L. macrurus* could be altered in the experiment where copepods were incubated in the dark. The daily ingestion (166 ng Chl *a* ind^{-1} day^{-1}) calculated on the basis of maximum nocturnal values of the gut contents (9.0 ng Chl *a* ind^{-1}) at st. 125-13 is close to the values obtained in the food removal experiments (233 ng Chl *a* ind^{-1} day^{-1}). Third, there is still a possibility that in *L. macrurus*, unlike *S. siberica*, chlorophyll was degraded during the digestion process.

Data on the metabolism rates of *L. macrurus* were mostly obtained on the copepods from the lakes. Roff (1973) studied the influence of various environmental parameters on the oxygen consumption of *L. macrurus* from the two Arctic lakes, Cornwallis Island Char Lake and Resolute Lake. On the basis of the equation obtained (Roff 1973), we calculated the respiration rate of the adult females at 8 °C. It appeared to be considerably lower than that measured in our experiment (1.61 μlO_2 ind^{-1} day^{-1} and 5.02 μlO_2 ind^{-1} day^{-1}, respectively). However, the comparison is hampered by the differences in weight: the dry weight of *L. macrurus* adults from the lakes (27 μg ind^{-1}) is much lower than that of *L. macrurus* from

the Kara Sea (147–193 μg ind^{-1}) (Hirche et al. 2003). Such a pronounced difference in weight is related to the existence of small- and large-sized forms of *L. macrurus*. The small form inhabits the lakes of the high Arctic (Roff 1973; Appolonio and Saros 2013). The large form was found in Lake Michigan (Vanderploeg et al. 1998) as well as in the Kara Sea (Hirche et al. 2003; our data). Populations of both small- and large-sized *L. macrurus* were found in the Baltic Sea (Viitasalo et al. 1985). The respiration rate of *L. macrurus* adults (226 μg ind^{-1} DW, our data) calculated with an equation from Ikeda et al. (2001) equaled 6.04 μl O_2 ind^{-1} day^{-1}, which is close to our experimental data (5.02 μl O_2 ind^{-1} day^{-1}). The respiration rates of *S. siberica* CV (282 μg ind^{-1} DW, our data), calculated in the same way, equaled 6.44 μl O_2 ind^{-1} day^{-1}, which is also rather close to our measurements (7.83 μl O_2 ind^{-1} day^{-1}). The ammonia excretion rate of these species (0.38–0.41 μg N ind^{-1} day^{-1}, Ikeda et al. 2001) was not much different from 0.15 to 0.22 μg N ind^{-1} day^{-1} in this study. Our results on the O:N ratio for both species were close to 40, which indicates that the metabolism was based on about equal proportions of protein and lipid (Mauchline 1998).

Metabolic expenditures converted from O_2 to carbon units (RQ = 0.97, Ikeda et al. 2001) made up 4.07 μg C ind^{-1} day^{-1} in *S. siberica* and 2.61 μg C ind^{-1} day^{-1} in *L. macrurus*. Assuming assimilation of phytoplankton of 0.6 (Mauchline 1998), energy intake by *S. siberica* not only covered the metabolic requirements, but also enabled the copepods to develop gonads and accumulate lipids. Meanwhile, herbivorous feeding of *L. macrurus* hardly met the metabolic demands. As there are no data on seasonal changes in the population abundance and demography of these copepods in the Ob Estuary, we cannot place our results within the context of their life cycles with certainty. We suggest that in September the populations of the two species were at different phases of the seasonal cycle. The population of *L. macrurus* was more advanced as it consisted predominantly of adult females and males, while in *S. siberica*, the dominant stage was CV. The frequency distribution of the size classes of the lipid sacs suggests that the population of *S. siberica* was at the stage of active lipid accumulation, as individuals without an oil sac comprised 10 % of all CVs and 6 % of females, and, on the other hand, specimens with large lipid depots were also found. At the same time, all adults of *L. macrurus* contained oil sacs with a well-defined peak (45 % of adults with a relatively high lipid content). *L. macrurus* was almost ready for reproduction, which is known to occur in the winter-spring (Vanderploeg et al. 1998). The *S. siberica* population was at a stage of molting into adults and lipid accumulation. Development of the gonads confirms this suggestion: the few *S. siberica* females present contained small underdeveloped gonads (stage G1), while gonads of *L. macrurus* females were larger and more developed. Copepods of the species *Calanus* are known to use lipid depots for the final stages of oocyte development (Niehoff and Hirche 1996). If *L. macrurus* had already accumulated large lipid reserves, developed their gonads and performed the initial stages of oocyte development, could it be possible that their feeding need not be at the maximum rate? *S. siberica*, on the other hand, had to molt into adults, and adults had to develop gonads and accumulate lipids—all these activities require a high energy input. Could *S. siberica* under such a high energy demand neglect the diel feeding rhythm to feed at maximum rates around the clock?

The present study is among the few that have attempted to estimate the grazing impact on autotrophic phytoplankton in estuaries of the large Siberian Arctic rivers. The zooplankton grazing impact estimated with the gut fluorescence method was 1–2 % of the phytoplankton standing stock in the Ob Estuary at the end of September (Arashkevich et al. 2010). Drits et al. (2015) reported average zooplankton grazing rates of about 1–8 % of the phytoplankton standing stock in the Yenisei Estuary in September, with the highest values of 12–14 % associated with local zooplankton aggregations at hydrological fronts. Our results on the daily grazing impact of the two dominant copepod species on autotrophic phytoplankton of 1–12 % with maximum values of 20 % at the southern boundary of the estuarine frontal zone were close to the estimates cited above. The organic carbon consumption of only two species, *L. macrurus* and *S. siberica* (110–120 % of primary production), is similar to the 110 % reported for the total zooplankton community in the freshwater zone by Arashkevich et al. (2010). In the estuarine frontal zone, the daily grazing impact of *L. macrurus* and *S. siberica* decreased to 7 % of the primary production, which is considerably lower than the total zooplankton grazing of 300 % reported previously (Arashkevich et al. 2010). This discrepancy likely results from the inter-annual differences in primary production rates. Primary production was only 11 mg C m^{-2} at the end of September 2007 (Arashkevich et al. 2010), while it was more than an order of magnitude higher (170 mg C m^{-2}) at the beginning of September (present study). Besides, Arashkevich et al. (2010) used a C:Chl *a* ratio of more than 300 obtained by relating chlorophyll directly to the particulate organic carbon in the water samples. This suggests that living phytoplankton cells constituted only a small portion of the suspended matter, which makes a direct comparison of the two estimates hardly possible.

Based on the zooplankton distribution within a narrow local maximum in the southern periphery of the Ob Estuary frontal zone, Flint et al. (2010) concluded that the aggregations of herbivorous mesoplankton form a specific

pelagic "biofilter" in the Ob Estuary. This "filter" accumulates allochthonous organic matter, mainly phytoplankton transported by the river, and considerably accelerates sedimentation via the fecal pellet flux in shallow areas. Flint et al. (2010) attempted to estimate zooplankton grazing within the aggregations on the basis of the plankton abundance, ingestion rates (Arashkevich et al. 2010) and C:Chl *a* ratio. However, the resulting value of total consumption (more than 300 % of the phytoplankton biomass in terms of carbon) considerably overestimates the impact, because, as mentioned above, the C:Chl *a* ratio was obtained for total particular organic matter. Using the data by Flint et al. (2010) on zooplankton abundance in the area of local aggregations and data on zooplankton ingestion rates (Arashkevich et al. 2010), we re-calculated the daily grazing impact to 15 % of autotrophic phytoplankton, with *L. macrurus* having a contribution of more than 80 % to this grazing. According to our direct estimations, the grazing impact of the two species in the area of their aggregations reached 20 % of the phytoplankton biomass, which indicates an efficient transformation of energy in this area and thus supports the idea of a "biofilter" coinciding with the zone of maximum gradients.

Conclusion

The two co-occurring copepods, *L. macrurus* and *S. siberica*, dominate the zooplankton community in the high-gradient environment of the Ob Estuary. They differ in various aspects of their ecology. While a part of the differences (horizontal and vertical distribution, diel feeding rhythms and feeding activity) is most likely connected with the differential preference for certain hydrophysical conditions (e.g., salinity), another part (demographical structure, volume of lipid reserves, state of gonad development) is likely related to the different phase of the seasonal development of the two populations.

The populations of *L. macrurus* and *S. siberica* play a major role in the functioning of the pelagic "biofilter" in the Ob Estuary in September. Their daily grazing impact made up one-fifth of the phytoplankton biomass and more than 100 % of primary production. During the study period, *S. siberica* was responsible for the main part of the total grazing impact (up to 90 %). We expect that an inversion in the relative grazing impact of two species could occur inter-annually, at different periods of the productive season and local habitats.

Acknowledgments We thank the crew of the RV "Professor Stockman" for help in the field work. The study was supported by RSCF grant #14-16-00681 to MVF (organization and carrying out the expedition to the Kara Sea), RSCF grant #14-05-00095 (proceeding of samples), RFBR grant #13-04-00613 and grant #16-05-00037 to AFP (feeding experiments, analysis of lipid content, gonad development of copepods). We are grateful to Prof. T.E. Whitledge and three anonymous reviewers for valuable comments and improving the English.

References

Appolonio S, Saros JE (2013) The freshwater copepod *Limnocalanus macrurus* in the Canadian Arctic Archipelago: numbers, weights and respiration observed in September 1961–July 1962. Arctic 66:37–42

Arashkevich EG, Drits AV, Timonin AG (1996) Diapause in the life cycle of *Calanoides carinatus* (Krøyer) (Copepoda, Calanoida). Hydrobiologia 320:197–208

Arashkevich EG, Flint MV, Nikishina AB, Pasternak AF, Timonin AG, Vasilieva JV, Mosharov SA, Soloviev KA (2010) The role of zooplankton in transformation of organic matter in the Ob Estuary, on the shelf and in the deep regions of the Kara Sea. Oceanology 50:780–792

Carter JCH, Goudie KA (1986) Diel vertical and horizontal distribution of *Limnocalanus macrurus* and *Senecella calanoides* (Copepoda:Calanoida) in lakes of Southern Ontario in relation to planktivorous fish. Can J Fish Aquat Sci 43:2508–2515

Cavaletto JF, Vanderploeg HA, Gardner WS (1989) Wax esters in two species of freshwater zooplankton. Limnol Oceanogr 34:785–789

Chislenko LL (1968) Nomograms for determination of weight of aquatic organisms by size and body shape. Nauka, Leningrad **(in Russian)**

Chislenko LL (1972) Species composition and distribution of zooplankton ecological groups in the Yenisei Bay. Issled Fauny Morey 12:228–238 **(in Russian)**

Davies KTA, Ryan A, Taggart CT (2012) Measured and inferred gross energy content in diapausing *Calanus* spp. in a Scotian shelf basin. J Plankton Res 34:614–625

Deubel H, Engel M, Fetzer I, Gagaev S, Hirche H-J, Klages M, Larionov V, Lubin P, Lubina O, Nöthig E-M, Okolodkov Y, Rachor E (2003) The southern Kara Sea ecosystem: phytoplankton, zooplankton and benthos communities influenced by river run-off. In: Stein R, Fahl K, Futterer DK, Galimov EK, Stepanets OV (eds) Siberian river run-off in the Kara Sea. Elsevier, Amsterdam, pp 237–265

Drits AV, Arashkevich EG, Nikishina AB, Nikishina AB, Sergeeva VM, Soloviev KA (2015) Feeding of dominant mesozooplankton species and their grazing impact on autotrophic phytoplankton in Yenisei Estuary in Autumn. Oceanology 55:573–582

Fetzer I, Hirche HJ, Kolosova EG (2002) The influence of freshwater discharge on the distribution of zooplankton in the southern Kara Sea. Polar Biol 25:404–415

Flint MV (2004) Role of the shelf frontal zones in formation of biological production in the Bering Sea. DSci dissertation, Institute of Oceanology, Moscow

Flint MV, Sukhanova IN, Kopylov AI, Poyrkov SG, Whitledge TE (2002) Plankton distribution associated with frontal zones in the vicinity of the Pribilof Islands. Deep Sea Res II 49:6069–6093

Flint MV, Semenova TN, Arashkevich EG, Sukhanova IN, Gagarin VI, Kremenetskiy VV, Pivovarov MA, Soloviev KA (2010) Structure of the zooplankton communities in the region of the Ob River's estuarine frontal zone. Oceanology 50:766–779

Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol Oceanogr 17:805–815

Futterer DK, Galimov EM (2003) Siberian river run-off into the Kara Sea: characterization, quantification, variability and

environmental significance. In: Stein R, Fahl K, Futterer DK, Galimov EK, Stepanets OV (eds) Siberian river run-off in the Kara Sea. Elsevier, Amsterdam, pp 1–8

Hirche HJ, Fetzer I, Graeve M, Kattner G (2003) *Limnocalanus macrurus* in the Kara Sea (Arctic Ocean): an opportunistic copepod as evident from distribution and lipid patterns. Polar Biol 26:720–726

Hirche HJ, Kosobokova KN, Gaye-Haake B, Harms I, Meon B, Nöthig E-M (2006) Structure and function of contemporary food webs on Arctic shelves: a panarctic comparison. The pelagic system of the Kara Sea—communities and components of carbon flow. Prog Oceanogr 71:288–313

Holm-Hansen O, Lorenzen CJ, Holmes RW, Strickland JDH (1965) Fluorometric determination of chlorophyll. J Cons Perm Int Explor Mer 30:3–15

Ikeda T, Kanno Y, Ozaki K, Shinada A (2001) Metabolic rates of epipelagic copepods as a function of body mass and temperature. Mar Biol 139:587–596

ICES Zooplankton Methodology Manual (2000) Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (eds). Elsevier, Amsterdam

Kuklin AA (1980) Feeding of *Coregonus muksun* in Yenisei. Sbornik nauchnykh trudov GosNIORKX 158:87–90 **(in Russian)**

Lisitzin AP (1995) The marginal filter of the ocean. Okeanologia 34:671–682 **(in Russian)**

Mackas DL, Bohrer RN (1976) Fluorescence analysis of zooplankton gut contents and investigation of diel feeding patterns. J Exp Mar Biol Ecol 25:77–85

Mauchline J (1998) The biology of calanoid copepods. Academic Press, London

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol Oceanogr 45:569–579

Miller CB, Morgan CA, Prahl FG, Sparrow MA (1998) Storage lipids of the copepod *Calanus finmarchicus* from Georges Bank and the Gulf of Maine. Limnol Oceanogr 43:488–497

Nero RW, Sprules WG (1986) Predation by the three glacial opportunists on natural zooplankton communities. Can J Zool 64:57–64

Niehoff B, Hirche H-J (1996) Oogenesis and gonad maturation in the copepod *Calanus finmarchicus* and the prediction of egg production from preserved samples. Polar Biol 16:601–612

Pirozhnikov PL (1950) On the feeding of white fish in the estuarine regions. Zool Zhurnal 29:140–146 **(in Russian)**

Pirozhnikov PL (1955) Foraging and foraging relations in fish in the estuarine regions of the Laptev Sea. Voprosy ikhtyologii 3:140–185 **(in Russian)**

Ramcharan CW, Sprules WG, Nero RW (1985) Notes on the tactile feeding behaviour of *Mysis relicta* Loven (Malacostraca: Mysidacea). Verh Int Ver Theor Angew Limnol 22:3215–3219

Roff JC (1973) Oxygen consumption of *Limnocalanus macrurus* Sars (Copepoda: Calanoida) in relation to environmental conditions. Can J Zool 5:877–885

Roff JC, Carter JHC (1972) Life cycle and seasonal abundance of the copepod *Limnocalanus macrurus* Sars in high arctic lake. Linmol Oceanogr 17:363–370

Salonen M, Urcho L, Engstrom-Ost J (2009) Effect of turbidity and zooplankton availability on the condition and prey selection of pike larvae. Boreal Environ Res 14:981–989

Solorzano L (1969) Determination of ammonia in natural water by the phenolhypochlorite method. Limnol Oceanogr 14:799–801

Steemann Nielsen E (1952) The use of radioactive carbon (C^{14}) for measuring organic production in the sea. J Cons Perm Int Explor Mer 18:117–140

Tande KS, Hopkins CCE (1981) Ecological investigations of the zooplankton community of Balsfjorden, northern Norway: the genital system in *Calanus finmarchicus* and the role of gonad development in overwintering strategy. Mar Biol 63:159–164

Vanderploeg HA, Cavaletto JF, Liebig JR, Gardner WS (1998) *Limnocalanus macrurus* (Copepoda:Calanoida) retains a marine arctic lipid and life strategy in Lake Michigan. J Plankton Res 20:1581–1597

Viitasalo M, Koski M, Pellikka K, Johansson S (1985) Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. Mar Biol 123:241–250

Vinogradov ME, Shushkina EA, Lebedeva LP, Gagarin VI (1995) Mesoplankton of the East Kara Sea and the Ob and Yenisei river estuaries. Oceanology 34:646–652

Warren GJ (1985) Predaceous feeding habits of *Limnocalanus macrurus*. J Plankton Res 7:537–552

Wong CK (1984) A study of the relationships between the mouthparts and food habits in several species of freshwater calanoid copepods. Can J Zool 62:1588–1595

Wong CK, Sprules WG (1986) The swimming behavior of the freshwater calanoid copepods *Limnocalanus macrurus* Sars, *Senecella calanoides* Juday and *Epishura lacustris* Forbes. J Plankton Res 8:77–90