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ORIGINAL PAPER

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

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Abstract *Limnocalanus macrurus* is an important member of the zooplankton communities of the Siberian shelf seas. During the cruise, Boris Petrov 1999, in August/September to the southern Kara Sea and the Ob and Yenisej estuaries, its abundance and vertical distribution were investigated. In adults, salinity tolerance, egg production, feeding and lipid composition were studied. *L. macrurus* occurred in water with salinities ranging from 1.7 to >33 without clear preference, as revealed from salinity-tolerance experiments. The dominance of adults and their high wax-ester content, as well as the lack of egg production and feeding activity, suggest that the population was in the pre-overwintering condition. Wax esters allow *L. macrurus* to survive long starvation periods and to reproduce in times of little food availability, but through its potential carnivory, it should be able to replenish its diet by preying on other zooplankton. Morphology and swimming behaviour of *L. macrurus* resemble the omnivorous copepod *Metridia longa*, which, however, is mainly found in the open ocean. The overall lipid composition and the mode of lipid storage also point to an omnivorous feeding behaviour. However, the high proportion of the marker fatty acid 16:1(*n*-7) suggests that *L. macrurus* strongly exploited the existent phytoplankton bloom, consisting mainly of diatoms. A striking characteristic of its lipids is the high level of the 20:1(*n*-7) fatty alcohol in addition to the 18:1(*n*-7) fatty acid and alcohol. It is the first copepod species known to produce such high amounts of 20:1(*n*-7) alcohol. Since this alcohol and the corresponding fatty acid are not abundant in any prey, this long-chain monounsaturated wax-ester moiety has to be produced de novo. Owing to these particular lipid characteristics in its distribution, feeding, and life-cycle strategy, *L. macrurus* can be described as a very versatile and opportunistic copepod.

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Introduction

The calanoid copepod *Limnocalanus macrurus* 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 Arctic coastal waters of Canada, Russia 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).

In the Laptev and Kara Seas, it is a dominant component of the zooplankton communities (Vinogradov et al. 1995a, 1995b; Lischka et al. 2001; Fetzer et al. 2002). These shelf seas are characterized by an extreme seasonality of freshwater inflow through Siberian rivers. In early summer, a large plume of low-saline water spreads out on top of oceanic water, extending the brackish-water region far away from the river mouths. The marine distribution of *L. macrurus* seems to be closely related to freshwater admixture, since it is found only rarely on the shelf break of the Laptev and Kara Seas and is absent in the Barents Sea and the Arctic Ocean proper (Kosobokova et al. 1998; Kosobokova and Hirche 2000). In the light of increasing river discharge to the Arctic Ocean (Peterson et al. 2002), the habitat of *L. macrurus* may be extended in the future.

Complete studies of the life-cycle of *L. macrurus* are only available from freshwater lakes. In Lake Michigan, the reproductive period lasts from November to May and seems to be timed so that the new generation develops in spring during high abundance of prey, which consists of crustacean microzooplankton and net phytoplankton (Vanderploeg et al. 1998). A similar life-cycle was described for *L. macrurus* in a high-Arctic lake by Roff and Carter (1972), where first nauplii appeared at the beginning of December. However, in Resolute Lake,

the reproductive phase was shifted by as much as 6 months (Roff 1972).

Survival of long periods of unfavourable food conditions and reproduction in the winter is made possible by a large lipid content in autumn, which accounted for up to 67% dry mass in *L. macrurus* (Vanderploeg et al. 1998). In Lake Michigan, Cavaletto et al. (1989) found wax esters to contribute 57–80% to total lipids, similar to many high-latitude herbivorous *Calanus* species. Accordingly, Vanderploeg et al. (1998) suggested that *L. macrurus* retained a marine Arctic lipid and life-cycle strategy. It is considered an omnivore with a strong carnivorous tendency. Predation on nauplii and copepodites (C) starts when it becomes a CIV (Warren 1985). In a lake on northern Ellesmere Island, van Hove et al. (2001) reported adult *L. macrurus* preying upon the smaller copepod *Drepanopus bungei*.

Detailed fatty-acid and alcohol compositions have been used to determine trophic relationships and to identify feeding behaviour and food preferences of zooplankton species (e.g. Falk-Petersen et al. 1990; Graeve et al. 1994a). This approach has a high potential since dietary fatty acids from primary producers are conserved and incorporated into lipids by copepods. However, copepods are also themselves important producers of particular fatty acids and alcohols (reviewed by Sargent and Henderson 1986; Dalsgaard et al. 2003). Fatty acids and alcohols of *L. macrurus* have not hitherto been determined.

Here we present data on the distribution, population structure, egg production and lipid pattern of *L. macrurus* in the Kara Sea collected in September 1999. In order to understand the mechanisms controlling the distribution of this euryhaline species in the estuarine and marine environment of Arctic marginal seas, experiments of salinity tolerance were conducted. The fatty-acid and alcohol composition will help to elucidate life-cycle and feeding strategies.

Materials and methods

Sampling

Samples were collected at 24 stations during a cruise with RV "Akademik Boris Petrov" from 26 August to 9 September 1999 to the southern Kara Sea (Fig 1). For zooplankton sampling, a Nansen closing net was used (0.442 m^2 catching area, 150 µm mesh size; 0.5 m s^{-1} hauling speed) below and above the pycnocline, which was determined from CTD profiles. At shallow stations (< 10 m depth) in the Ob and Yenisej estuaries, the net frame was mounted with a non-closing, short net of 1 m length. For determination of distribution and abundance, samples were preserved in 4% borax-buffered formaline. All specimens were counted.

Salinity tolerance

Two salinity-tolerance experiments with *L. macrurus* were set up directly on board after collection. In each experiment, a complete Nansen-net tow was split into nine parts and incubated in Plexiglas

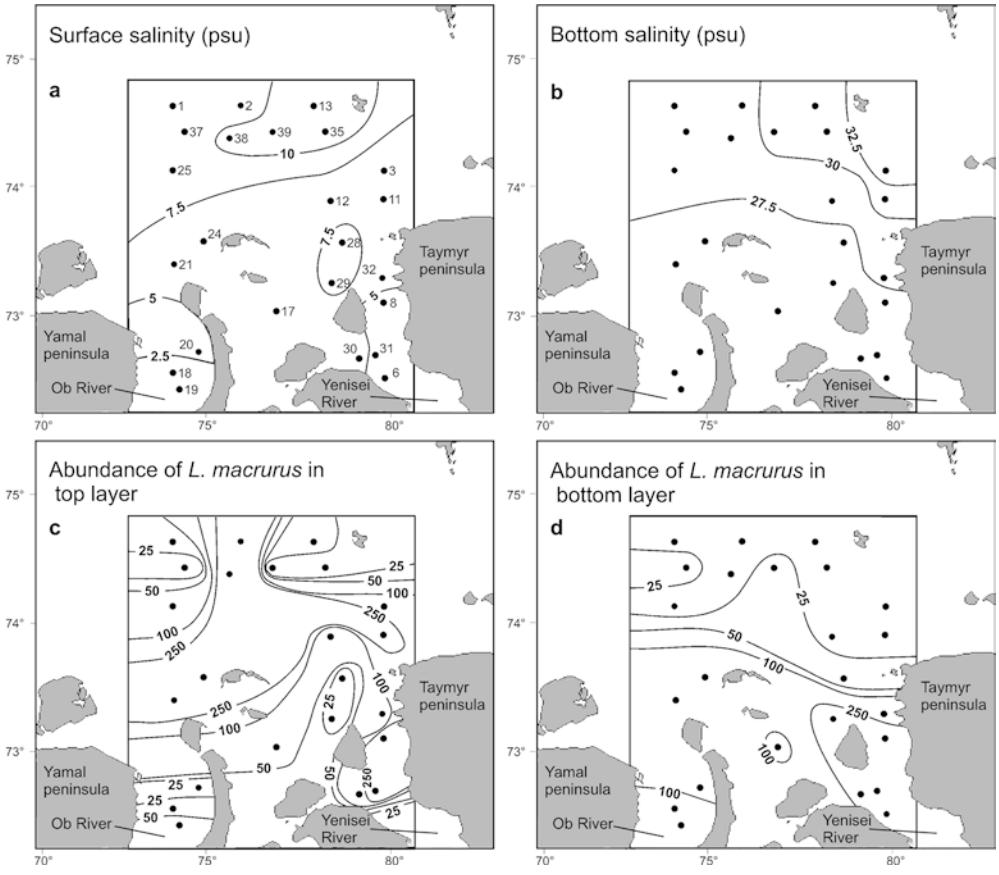

Fig. 1a–d Distribution of salinity and abundance of *Limnocalanus macrurus* in the Kara Sea. Surface (**a**) and bottom (**b**) salinity; abundance of *L. macrurus* in top (**c**) and bottom layer (**d**). Station numbers are given in the surface salinity plot

cylinders with mesh (330 μm) false bottoms. Cylinders were then suspended in 3-l poly-methyl-pentene beakers containing filtered seawater from the site of collection. During one experiment with samples from sts. 11 and 13, salinity was increased every 24 h by 5 psu starting from 10 up to 40. The second experiment with samples from st. 29 started at a salinity of 20. Every 24 h in one half of the beakers, salinity was increased in steps of 5 psu from 20 to 40, whereas in the other half, salinity was decreased by 5 psu from 20 to zero. Dead specimens were counted and removed every day. The rest were transferred with the Plexiglas cylinders to fresh seawater with adjusted salinity. Specimens in three beakers were used as controls, with constant salinities of 10 and 20, respectively. Dead specimens in the controls were counted and subtracted from the experimental data.

Feeding experiments

Feeding experiments with *L. macrurus* were carried out on board and, in addition, specimens were transported to the home laboratory in Bremerhaven. There, about 1 month after collection, feeding experiments were set up again using mixed phytoplankton cultures grown from Kara Sea inoculates and nauplii of *Artemia salina*. Single female *L. macrurus* were incubated in 10-ml cell wells at 4°C (according to the in-situ temperature) with a dense culture of phytoplankton, containing mainly the brackish-water diatoms *Asterionella formosa* and *Cyclotella* sp. from the same waters as the copepods (Larionov and Kodina 2000). After 24 h, the wells were inspected for faecal pellets. In a second experiment, ten *Artemia* nauplii were added to one female in each cell well. In addition, one experiment was set up with 50 females incubated in 2 l of filtered seawater containing 50 nauplii. Due to the low temperatures, the nauplii were sinking to the bottom after several hours. After 24 h, the water was filtered over a 50-μm sieve and searched for faecal pellets.

Egg production

For egg-production measurements, 42–48 females of *L. macrurus* were sorted directly after capture. Single females were incubated in cell wells containing 10 ml filtered seawater at in-situ temperature in dim light for 24 h. Cell wells were checked for eggs usually every 3 h to account for cannibalism. At 1 station, in addition, 100 females were incubated in Plexiglas cylinders with mesh (330-μm) false bottoms to separate eggs from females. Cylinders were suspended in 3-l poly-methyl-pentene beakers containing filtered seawater.

Dry mass and lipids

Ten to 15 *L. macrurus* (total number of samples: 8 for females, 9 for males, 3 for CV) were sorted into pre-weighed aluminium trays and stored at −20°C. In the laboratory, they were dried at 60°C for 24 h and weighed on a microbalance.

Two samples of females and 1 of males (20 individuals each) were sorted at sts 11 and 13 immediately after collection and preserved in dichloromethane:methanol (2:1, by volume). Samples were stored at −30°C until analysis. Lipids were extracted essentially according to the method of Folch et al. (1957). The fatty-acid and alcohol compositions were determined by gas chromatography (Kattner and Fricke 1986). Lipids were hydrolysed in methanol containing 3% concentrated sulphuric acid, and fatty acids were converted to methyl esters by transesterification at 80°C for 4 h. Fatty-acid methyl esters and free alcohols were then simultaneously analysed with a gas liquid chromatograph (Chrompack 9000) on a 30 m×0.25 mm i.d. wall-coated open tubular column (film thickness: 0.25 μm; liquid phase: DB-FFAP) using temperature programming. Fatty acids and alcohols were identified with standard mixtures and, if necessary, additional confirmation was carried out by GC-MS. The structure of the alcohols, especially 20:1(*n*-7), was additionally determined by GC-MS after thin-layer chromatographic separation from fatty-acid methyl esters on silica gel (Kattner et al. 1998). The proportion of wax esters of total lipid was calculated according to their molecular structure using the areas of the fatty acids and alcohols as obtained by GC analysis (Kattner and Krause 1987).

Results

Hydrography

A general description of the hydrographic conditions and zooplankton community during this study was published previously (Amon and Köhler 2000; Stephansev and Shmelkov 2000; Fetzer et al. 2002). Therefore the hydrography is only briefly described here. The depth range of the 24 stations 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. Surface salinity in the inner parts of Ob Bay had a minimum value of almost 2, which slowly increased to 10 towards the outer parts, and at the southernmost station in the Yenisej River, salinity was 2.7. Surface temperature ranged from 3.5 to 7°C in both rivers and their estuaries. At the northernmost stations, where the influence of the colder marine water masses became more dominant, the surface temperature decreased to 2.9°C. The bottom temperatures showed constant values between 0° and 1.9°C. A strong pycnocline, which was located between 5 and 13 m depth with an average thickness of about 3 m, separated the low saline waters from the deeper oceanic layer that reached far into the rivers below the pycnocline. The sea ice in the Kara Sea starts to break up in June (Blanchet et al. 1995). During our cruise, the sea was completely free of ice. River runoff exhibits a large seasonal signal, with the maximum discharge occurring usually in June (Pavlov and Pfirman 1995).

Abundance and distribution

L. macrurus was among the most abundant copepods of the zooplankton population (mean 10.6%) in the study area. It was present at 96% of all stations. At sts. 13 and 38, it contributed 30% of total zooplankton abundance. Maximum concentration was 5,990 individuals m^{-3} (st. 8). The population was dominated by adults, with females more abundant than males; copepodites V made up 6.3%; younger CI–CIV were found only at a very low percentage (Table 1) at five stations in Ob Bay and north of it (sts. 18, 19, 20, 21, 24). No eggs were produced during egg-production experiments, explaining the lack of nauplii and young copepodites. However, female gonads were well developed.

Females probably did not feed anymore during this late sampling season, as shown by the feeding experiments in which females did not produce faecal pellets. However, specimens were actively swimming in their containers.

Table 1 *Limnocalanus macrurus* in the Kara Sea. Stage composition as percent of all stages (mean of all stations) and dry mass (mean and standard deviation, SD)

Stage	Stage composition %	Dry mass (μg) Mean ± SD
C I	0.2	
C II	0.2	
C III	0.2	
C IV	0.2	
C V	6.3	83 ± 72
Female	54.5	193 ± 65
Male	38.6	147 ± 35

The distribution patterns of *L. macrurus* above and below the pycnocline and the surface and bottom salinities are presented in Fig. 1. This species was found over a wide salinity range from 1.7 to 33.3. The surface abundance maxima (Fig. 1c) in the north were in close areas to minima. Thus, at st. 38 we found 317 ind. m^{-3} as opposed to 5 ind. m^{-3} at st. 37 and 3 ind. m^{-3} at st. 39. Distribution in the bottom layer (Fig. 1d) was less variable than in the top layer. From the abundance maxima at sts. 29 and 8 in the wake of the Yenisej River, abundances decreased rapidly towards the north. Similarly, in the eastern part, higher numbers in the outer estuary of the Ob River decreased sharply to the north around 74°N.

In the abundance of *L. macrurus*, there was no clear trend in any of the water layers, although it seems that the species is less abundant at the lowest and highest salinities (Fig 2). Regarding vertical distribution, *L. macrurus* was more abundant in the upper layer at 11 stations and more in the deep layer at 7 stations (Fig. 3). At 3 stations abundance was similar, and at 5 stations (2, 11, 13, 29, 38) differences in vertical distribution were enormous, with several hundred specimens in one layer and almost none in the other. Thus, 507 ind. m^{-3} in the upper layer contrasted with 13.6 in the lower layer at st. 29. Stations with maxima in the upper or lower layer were sometimes closely spaced, e.g. st. 39 (maximum in lower layer) and st. 38 (maximum in upper layer). Therefore, no clear spatial trend with regard to these extreme stations could be detected.

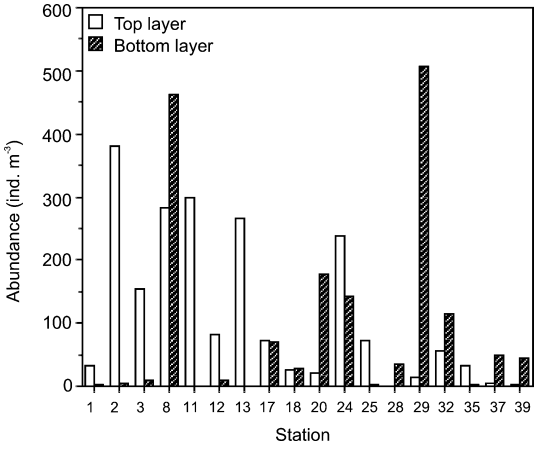

Fig. 2 Vertical distribution of *Limnocalanus macrurus* from stations with vertically separated hauls

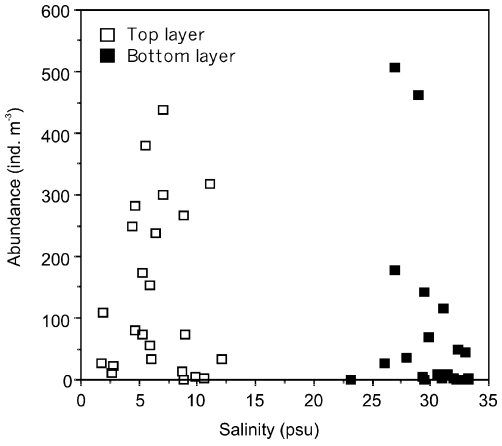

Fig. 3 Abundance of *Limnocalanus macrurus* from two layers versus salinity of surface and bottom waters

Salinity tolerance

According to its distribution pattern described above, *L. macrurus* is a euryhaline species. All males and females collected at a salinity of 10 survived successive increase of salinity in steps of 5 until 40 (Fig 4a). In contrast, 40% of the specimens collected at a salinity of 20 died at 40 (Fig. 4b). At decreasing salinity, mortality increased abruptly between 5 and 0. As *L. macrurus* was also found, although in low numbers, at stations with salinities down to 1.7, the lower salinity limit seems to be

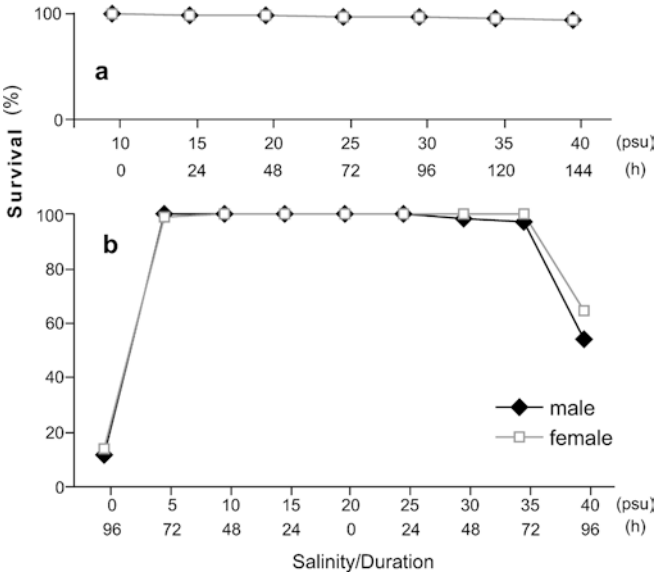

Fig. 4a, b Survival rate of adult *Limnocalanus macrurus* collected at 10 psu at increasing salinities (**a**) and collected at 20 psu at increasing and decreasing salinites (**b**)

close to zero. At st. 6 with the lowest overall salinity in the whole water column (surface 2.6 and bottom 3.0), 10.4 ind. m^{-3} were counted, and at st.18 (surface 1.7 and bottom 26.1) 25 ind. m^{-3}.

Dry mass and lipid composition

The dry mass of adults and CV *L. macrurus* is given in Table 1. Females had the highest dry mass, ranging from 102 to 295 μg (mean of 193 μg). The dry mass of males was slightly lower (92–186 μg), being 147 μg on average. CV stages had only half of the mass of adults (mean of 83 μg).

The fatty-acid and alcohol compositions were determined for females and males. The proportions of wax esters and fatty acids/alcohols were very similar in both sexes, and therefore in Table 2 only mean values are presented. The lipids of *L. macrurus* were dominated by wax esters, accounting on average for 87.1% of total lipid. Major fatty acids were 16:1(*n*-7), the 18:1 isomers (*n*-9) and (*n*-7), 20:5(*n*-3) and 22:6(*n*-3), composing 72% of total fatty acids. Minor components were 16:0, 20:1(*n*-9), 20:4(*n*-3), 22:5(*n*-3), 18:4(*n*-3) and 18:2(*n*-6). The alcohols were dominated by 16:0, accounting for half of the total. Significant proportions with more than 10% were detected for 14:0, 18:1(*n*-7) and 20:1(*n*-7) alcohols. The fatty acids and alcohols of the (*n*-7) family with 16–20 carbon atoms contributed high proportions (ca. 30%) to the total fatty acids and alcohols, respectively.

Table 2 *Limnocalanus macrurus* in the Kara Sea. Fatty-acid and alcohol composition [mass% of total fatty acids and alcohols, respectively; mean and standard deviation *SD*, number of samples (*in parentheses*) and wax-ester proportion in % of total lipid]

Fatty acids	Mean ± SD (3)
14:0	0.8 ± 0.2
15:0	0.0 ± 0.1
16:0	4.3 ± 0.9
16:1(*n*-7)	19.6 ± 1.9
16:1(*n*-5)	0.4 ± 0.2
16:2(*n*-4)	0.5 ± 0.4
16:3(*n*-4)	0.3 ± 0.2
16:4(*n*-1)	0.1 ± 0.1
18:0	0.5 ± 0.3
18:1(*n*-9)	16.2 ± 1.6
18:1(*n*-7)	12.6 ± 1.1
18:2(*n*-6)	2.2 ± 0.5
18:3(*n*-3)	1.1 ± 0.2
18:4(*n*-3)	2.3 ± 0.2
20:1(*n*-9)	4.2 ± 0.4
20:1(*n*-7)	1.4 ± 0.2
20:4(*n*-6)	1.4 ± 0.1
20:4(*n*-3)	3.8 ± 0.2
20:5(*n*-3)	12.9 ± 2.3
22:1(*n*-11)	0.5 ± 0.4
22:1(*n*-9)	0.3 ± 0.3
22:1(*n*-7)	0.3 ± 0.1
22:5(*n*-3)	2.4 ± 0.3
22:6(*n*-3)	10.7 ± 1.8
24:1	1.3 ± 0.2
Alcohols	
14:0	14.3 ± 3.2
16:0	48.6 ± 1.0
16:1(*n*-7)	3.3 ± 0.4
18:1(*n*-9)	3.0 ± 0.3
18:1(*n*-7)	13.7 ± 1.2
20:1(*n*-9)	2.4 ± 0.6
20:1(*n*-7)	13.1 ± 2.3
22:1(*n*-11)	1.5 ± 0.3
Wax ester proportion of total lipid	87.1 ± 2.3

Discussion

During our study in the southern Kara Sea, *L. macrurus* was present at all but one station, and made up on average 10.6% of total zooplankton abundance. At some stations it reached up to 30%. Similarly, in the very shallow part of the Laptev Sea close to the rivers Lena and Yana, it also built the bulk of zooplankton abundance and biomass (up to 64% total biomass; Lischka et al. 2001). Regional distribution patterns and salinity tolerance experiments could not provide a clear picture of the factors controlling its distribution. Although it is assumed to be a brackish-water species (Vinogradov et al. 1995a, 1995b; Lischka et al. 2001), it was found in this study at many stations with high oceanic salinities. We also could not detect any trend in the vertical distribution. Interannual variability is strikingly high; thus, in 1997 *L. macrurus* accounted for only 0.5% of total zooplankton in samples collected in the same area at a similar time of year (Fetzer et al. 2002).

The predominance of adults indicates that the population is close to its overwintering state. Abramova (1999) described the overwintering population in the Laptev Sea as consisting only of adults, similar to lake populations (Vanderploeg et al. 1998). In contrast to many other polar species, the new generation moves through all copepodite stages to adult without diapausing (Vanderploeg et al. 1998). The preparation for overwintering is also indicated by the enormous lipid content of the adults. Seasonal variation in lipid classes of *L. macrurus* from Lake Michigan has been determined by Cavaletto et al. (1989) and Vanderploeg et al. (1998). They found large stores of lipids (67% dry mass) and wax esters constituting 10–80% of total lipids. Total lipids, wax esters and oil sac continued to build in the adults throughout the summer and autumn until the maximum was reached before reproduction in winter (Vanderploeg et al. 1998). Their observations correlate well with the high wax-ester content in adults collected in September during our study.

The high wax-ester content of *L. macrurus* is similar to many herbivorous calanoid copepods (e.g. Lee 1975; Sargent and Henderson 1986; Kattner and Hagen 1995). Wax esters are important energy-storage compounds, which enable copepods to survive long periods of starvation and provide energy for reproduction. *L. macrurus* follows a similar reproductive strategy to

Calanus hyperboreus and *C. glacialis* in the Arctic Ocean and on Arctic shelves, which spawn in winter (Sars 1903; Conover 1988; Hirche and Kattner 1993; Hirche and Niehoff 1996). With regard to lipid accumulation and composition, *C. hyperboreus* seems to be best adapted to the extreme Arctic environment. It has the highest lipid content and highest proportions of wax esters with the most energy-rich moieties, i.e. high amounts of long-chain monounsaturated fatty acids and alcohols with 20 and 22 carbon atoms (Albers et al. 1996). *C. glacialis* contains less lipids of high caloric value, but still more than *L. macrurus*. The lipid composition of *L. macrurus* is, however, more similar to omnivorous copepods like *Metridia longa* or *Rhincalanus gigas* (Graeve et al. 1994a; Albers et al. 1996), due to shorter-chain lipid moieties dominated by 14, 16 and 18 carbon chain length, and especially by the alcohols 14:0 and 16:0. Another difference from *C. glacialis* is the structure of the oil sac, which in the *Calanus* species is one structure extending over the whole cephalothorax, whereas in *L. macrurus* four oil sacs surround the intestines (Vanderploeg et al. 1998). While many *Calanus* species spend the winter in a diapause as described by Hirche (1996, 1997), the physiological state of *L. macrurus* during winter has not yet been described. Lipids are drawn down to extremely low levels (10%) during the reproductive period in winter (Vanderploeg et al. 1998), but this does not exclude food uptake. For a carnivore or omnivore that preys on items as large as diaptomid copepodites (Warren 1985), food should be available all winter long. However, in our preliminary feeding experiments, females were not feeding on phytoplankton or *Artemia* nauplii in autumn, although they kept on cruising continuously.

In our adult *L. macrurus*, the high level of fatty acids and alcohols of the (*n*-7) family with 16–20 carbon atoms is striking. High proportions of the 16:1(*n*-7) fatty acid are well documented in marine herbivorous copepods, especially in the high-Arctic *C. glacialis* (e.g. Tande and Henderson 1988; Hirche and Kattner 1993; Scott et al. 2002). These high levels are attributed to feeding on diatoms, which are extremely rich in this fatty acid (e.g. Kates and Volcani 1966; Ackman et al. 1968; Graeve et al. 1994b). During our study, a phytoplankton bloom covered large parts of the southern Kara Sea, with a high proportion of diatoms (Larionov and Kodina 2000; Deubel et al. 2003). Obviously, *L. macrurus* had used these diatoms, although it was described as an omnivore with a tendency to carnivory (Vanderploeg et al. 1998). Alternatively, the 16:1(*n*-7) fatty acid could originate from feeding on herbivorous copepods rich in this fatty acid due to grazing on diatoms (Tande and Henderson 1988; Kattner et al. 1989). *L. macrurus* further elongates 16:1(*n*-7) to 18:1(*n*-7) and 20:1(*n*-7) fatty acids and, by reduction, to its major monounsaturated fatty alcohols (Table 2). This two-step elongation to 20:1(*n*-7) is exceptional. *L. macrurus* is the first copepod species known to produce such high amounts of 20:1(*n*-7) alcohol. In addition, the high proportions of the 18:1(*n*-7) fatty acid and alcohol are also unusual.

The overall lipid composition of *L. macrurus* points to an omnivorous feeding behaviour comparable to another Arctic copepod, *M. longa*. The fatty-acid and alcohol composition of that species is characterized by short-chain moieties but it contains less wax esters. Significant amounts of the long-chain monounsaturated fatty acids and alcohols, 20:1(*n*-9) and 22:1(*n*-11), in *M. longa* were attributed to feeding on herbivorous calanids rich in these components. This is a major difference from *L. macrurus*, which contains considerable amounts of the 20:1(*n*-7) alcohol. This alcohol and the corresponding fatty acid are non-existent or only trace components in most marine organisms studied so far. Thus, they are most likely produced by *L. macrurus* and therefore imply herbivory. Not only the habitus and feeding patterns but also the mode of lipid storage suggest that *L. macrurus* occupies an intermediate position between typical omnivorous and herbivorous species. Owing to this adaptation, *L. macrurus* is one of the more opportunistic and versatile marine and freshwater copepods.

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