

Mar Biol (2007) 150:443–454
DOI 10.1007/s00227-006-0359-4

RESEARCH ARTICLE

Seasonal lipid dynamics of the copepods *Pseudocalanus minutus* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard)

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Received: 23 November 2005 / Accepted: 10 May 2006 / Published online: 23 June 2006
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Abstract Seasonal lipid dynamics of various developmental stages were investigated in *Pseudocalanus minutus* and *Oithona similis*. For *P. minutus*, the dominance of 16:1($n-7$), 16:4($n-3$) and 20:5($n-3$) fatty acids indicated a diatom-based nutrition in spring, whereas 22:6($n-3$), 16:0, 18:2($n-6$) and 18:1($n-9$) pointed to a flagellate-based diet during the rest of the year as well as omnivorous/carnivorous low-level feeding during winter. The shorter-chain fatty alcohols 14:0 and 16:0 prevailed, also reflecting biosynthetic processes typical of omnivores or carnivores. Altogether, the lipid signatures characterized *P. minutus* as an opportunistic feeder. In contrast, *O. similis* had consistently high amounts of the 18:1($n-9$) fatty acid in all stages and during all seasons pointing to a generally omnivorous/carnivorous/detritivorous diet. Furthermore, the fatty alcohol 20:1($n-9$) reached high percentages especially in adult females and males, and feeding on *Calanus* faecal pellets is suggested. Fatty alcohols, as wax ester moieties, revealed significant seasonal variations in *O. similis* and a seasonal trend towards wax ester accumulation in autumn in *P. minutus*. *P. minutus* utilized its lipid deposits for development in the copepodite stages III and IV and for gonad

maturation in CV and females during the dark season. However, CVs and females depended on the spring phytoplankton bloom for final maturation processes and reproduction. *O. similis* fueled gonad maturation and egg production for reproduction in June by wax esters, whereas reproduction in August/September co-occurred with the accumulation of new depot lipids. Both species revealed significantly higher wax ester levels in deeper (>50 m) as compared to surface (0–50 m) dwelling individuals related to a descent prior to overwintering.

Introduction

The calanoid copepod *Pseudocalanus minutus* (Krøyer) is widespread in arctic-boreal regions, whereas the cyclopoid *Oithona similis* (Claus) is found throughout the world's oceans. Both species sometimes occur in extremely high abundances (e.g. Corkett and McLaren 1978; Gallienne and Robins 2001; Nielsen and Andersen 2002). It is a well-known fact that life cycles especially of herbivorous pelagic species vary with the latitude, as the period of phytoplankton availability shortens the more polar they live. Living under arctic conditions therefore requires specific adaptations to cope with food paucity during the long, dark winter season.

The accumulation of large lipid reserves especially by herbivorous zooplankton during the highly productive spring–summer algal bloom is a characteristic feature in polar marine systems (Hagen 1999; Lee et al. 2006). Lee et al. (1971a) and Lee and Hirota (1973) pointed to a substantial increase of lipid and wax ester levels in epipelagic copepods from the (sub)tropics to

Communicated by O. Kinne, Oldendorf/Luhe

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high latitudes, and emphasized the high percentages of wax esters in copepods from polar regions.

Neutral lipids, mainly in the form of wax esters, are known to function as storage lipids, which may enable the animals to survive the winter season with a reduced metabolism at the cost of their internal energy reserves (Lee et al. 1971a, 1971b; Clarke 1983; Kattner and Hagen 1995). Hence, the lipid composition can indicate the nutritional state of zooplankters (Båmstedt et al. 1990), and many studies have therefore focused on the lipid biochemistry of various marine species (e.g. Hagen 1988; Hagen et al. 1993; Falk-Petersen et al. 2001). Furthermore, fatty acid trophic markers allow to conclude on dietary relationships integrated over a longer time scale (e.g. Graeve et al. 1994a; Auel et al. 2002; Dalsgaard et al. 2003).

Very few studies exist on the lipids of small-sized copepods such as *P. minutus* and *O. similis*. Norrbin et al. (1990) investigated the lipid class and fatty acid compositions of *Pseudocalanus acuspes* in the north Norwegian Balsfjorden, Kattner and Krause (1989) carried out seasonal examinations on lipids of *Pseudocalanus elongatus* from the North Sea, and Kattner et al. (2003) presented the only existing study on the fatty acid and alcohol compositions of *O. similis* from Antarctic regions. No studies are available on the lipid biochemistry of *P. minutus* and *O. similis* in Arctic regions. Therefore, in the Arctic Kongsfjorden (79° N) on Svalbard, the fatty acid and alcohol compositions and their quantities were investigated in the two copepod species on a seasonal basis, and the amount of fatty alcohols served to estimate storage lipids (wax esters). The objective of this work was to elucidate life-cycle strategies and feeding habits of these two species in a high-latitude environment.

Materials and methods

Stratified zooplankton samples were collected in the Arctic Kongsfjorden (Ny Ålesund, Svalbard, 78° 57' N 11° 50' E, Fig. 1) between August 1998 and May 1999 with a modified Apstein closing net (100 µm mesh size, 0.2 m² mouth opening) (for details see Lischka and Hagen 2005).

Pseudocalanus minutus and *Oithona similis* were sorted alive as soon as possible after capture in a cooled laboratory (ca. 0°C). Following sorting according to species and stages, individuals were immediately placed in dichloromethane : methanol (DCM : MeOH) [2:1(v/v) + 0.01% butylhydroxytoluene (BHT) as antioxidant] contained in glass vials with a Teflon cap. The specimens were shock-frozen in liquid nitrogen and

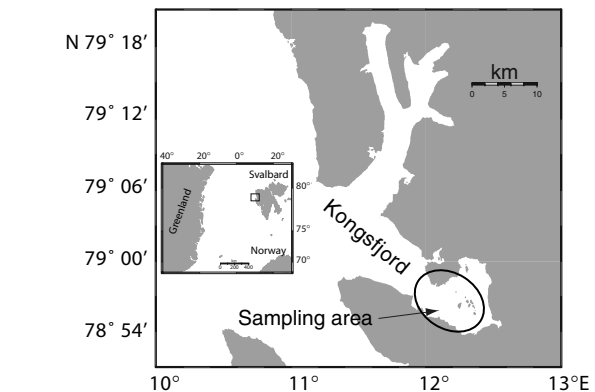


Fig. 1 Svalbard Archipelago with Kongsfjorden and sampling area

finally stored in a freezer at -80°C until analysis. 5–170 specimens of *P. minutus*, and 20–70 specimens of *O. similis* were pooled for each sample to ensure sufficient lipid mass for the analyses. To determine the fatty acid compositions, total lipids were first extracted with dichloromethane:methanol [2:1(v/v)] according to Hagen (2000). A known amount of the fatty acid 23:0 was added as internal standard to all but 14 samples (which were analyzed first) to calculate total amounts of fatty acids and fatty alcohols in $\mu\text{g ind}^{-1}$. Afterwards, lipids were hydrolyzed and the fatty acids converted to their methyl ester derivatives (FAME) in methanol containing 3% concentrated sulphuric acid at 80°C for 4 h (Kattner and Fricke 1986). After cooling, 4 ml deionized water was added and FAME were extracted with hexane (3×2 ml), analyzed in a gas chromatograph (HP 6890A) equipped with a DB-FFAP column (30 m length, 0.25 mm inner diameter and 0.25 µm film thickness) using temperature programming and helium as carrier gas. FAME were detected by flame ionization and identified by comparing retention times with those obtained from a standard mixture. All peaks smaller than 0.5% were omitted from calculations. Due to some impurities in the samples, unknown peaks, which could not be identified as fatty acids/alcohols by mass spectrometer, were omitted from calculations (in case of *O. similis* results comprise eight fatty acids and four fatty alcohols). The total lipid mass was calculated as the sum of fatty acids and alcohols ($\mu\text{g ind}^{-1}$), which is a slight underestimation of the real value, because sterols and the phosphobase of phospholipids are not taken into consideration. The percentage of fatty alcohols was used for a rough estimate of the wax ester levels, which could not be quantified by the usual Iatroscan method, due to very low concentrations below the detection limit.

Statistics

One-way ANOVA was performed to test for significant seasonal differences in relative fatty acid quantities and the total relative amount of fatty alcohols. Data obtained from the different sampling events were grouped according to seasons as follows: May samples were categorized as “spring”, those from August/September as “summer”, those from November as “autumn” and those from February/March as “winter”. For the detection of differences in the amounts of fatty alcohols between water depths, samples were grouped in a shallow water (0–50 m) and a deep-water group (>50 m). All percentage data were Arcsine-transformed and then tested for normal distribution and homogeneity of variances before performing the ANOVA. In case of unequal variances, a Welch-ANOVA was used. Tukey–Kramer post-hoc tests were applied for multiple comparisons of group means. All analyses were conducted using the software package JMP for Macintosh (Version 5.1). Multivariate statistics using the PRIMER program (Clarke and Warwick 1994, Plymouth Marine Laboratory, UK) were performed for the detection of seasonal and stage-specific similarities in fatty acid compositions. For untransformed data Bray–Curtis similarities were calculated and an analysis of similarities (ANOSIM) was performed. The similarity pattern was illustrated using multi-dimensional scaling (MDS) plots. To reveal the contribution of single fatty acids to the dissimilarity between groups, SIMPER analyses were done. Here, the average dissimilarity is given on a scale between 0 and 100, where 0 means no dissimilarity between groups and 100 stands for total dissimilarity (Clarke and Warwick 1994). The contribution of single fatty acids to the dissimilarity is given as percentage of total fatty acids (average abundance). Due to the low number of replicates of each stage, all statistics were done at species level, not differentiating between stages. Significance level for all statistics was $P < 0.05$.

Results

Seasonal variability of fatty acids and fatty alcohols

Pseudocalanus minutus

In general, fatty acid compositions of different stages of *P. minutus* did not change much during the seasons (Table 1). However, one-way ANOSIM indicated that the composition in spring was significantly different from that in summer and winter ($n=48$, Fig. 2a).

According to SIMPER analyses the five fatty acids predominantly contributing to seasonal dissimilarities were: 20:5($n=3$), 18:1($n=9$), 16:1($n=7$), 22:6($n=3$) and 16:0 (Table 2).

Furthermore, one-way ANOSIM revealed significant differences in fatty acid compositions between females and copepodids III and IV (CIII, CIV) as well as between copepodids V and III (CV, CIII) ($n=47$, Fig. 2b). According to SIMPER analyses, the fatty acids predominantly responsible for these dissimilarities were 22:6($n=3$), 18:1($n=9$), 16:1($n=7$), 20:5($n=3$) and 16:0 (Table 3).

One-way ANOVA of single fatty acids showed that 16:4($n=1$) was significantly higher in spring ($P=0.0009$), 18:2($n=6$) was significantly lower in spring than in all other seasons ($P < 0.0001$), 20:4($n=3$) was significantly lower in spring than in winter ($P=0.0338$), 20:5($n=3$) was significantly higher in spring than in summer and winter ($P < 0.0001$) and 22:6($n=3$) was significantly higher in autumn than in the other seasons ($P < 0.0001$).

According to one-way ANOVA based on all stages, no significant variation in the amount of fatty alcohols (respectively, wax esters) was found between seasons ($P=0.5249$). However, in the overwintering individuals (CIII, CIV and CV) a slight general trend emerged that fatty alcohols (and, therefore, wax esters) increased late in the year and they showed a subsequent decline towards the end of the overwintering period (Fig. 3). *P. minutus* did not utilize storage lipids to the same extent to molt from CV to adult females in May as compared to February/March, since the amount of fatty alcohols hardly changed during this time (Fig. 3, see Lischka and Hagen 2005 for stage development). Following molting and reproduction, females made use of their remaining wax esters by the end of summer (no fatty alcohols detected in September). Furthermore, one-way ANOVA of fatty alcohols revealed that individuals from below 50 m had significantly higher amounts as compared to those caught in the surface layer (0–50 m, $P=0.0056$).

Fatty alcohol levels (as percent of total fatty acids and alcohols) varied during the year in females from 0 to 30%, in CV from 25 to 42%, in CIV from 20 to 31% and in CIII from 16 to 31%. Males had 38% fatty alcohols in May. The shorter-chain fatty alcohols 14:0 (24–48%) and 16:0 (25–59%) clearly predominated during all seasons (Table 1).

Total lipid (sum of fatty acids and fatty alcohols) varied year-round from 4–9 $\mu\text{g ind}^{-1}$ in females, 3–8 $\mu\text{g ind}^{-1}$ in CV, 0.5–2.2 $\mu\text{g ind}^{-1}$ in CIV and 0.6–1.9 $\mu\text{g ind}^{-1}$ in CIII. It was 4.5 $\mu\text{g ind}^{-1}$ in males which only occurred in spring (Fig. 3).

Table 1 *Pseudocalanus minutus*: fatty acid and fatty alcohol compositions (mass %) in the different stages during the four seasons (F females, M males, CV, CIV, CIII copepodite stages, Mn mean, SD standard deviation, for n=2 both measurements are listed (I, II))—traces (<0.5%)

| Stage | Spring | | | | | | Summer | | | | | | Autumn | | | | | | Winter | | | | | | | | | | | | | | | |
|-----------------------|--------|------|------|------|------|------|--------|------|------|------|------|------|--------|-----|------|------|------|------|--------|------|------|------|------|------|------|------|------|------|------|------|-----|---|---|---|
| | CIII | CIV | CV | II | F | M | CIII | CIV | CV | F | F | CIII | CIV | CV | F | CIII | CIV | CV | F | CIII | CIV | CV | F | | | | | | | | | | | |
| | n=1 | n=2 | n=2 | n=3 | n=3 | n=1 | n=6 | n=4 | n=6 | n=3 | n=1 | n=1 | n=1 | n=1 | n=1 | n=5 | n=5 | n=5 | n=5 | n=5 | n=5 | n=5 | n=3 | | | | | | | | | | | |
| Fatty acids | I | II | I | II | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | Mn | SD | | | | | | | | | | |
| 14:0 | 3.3 | 2.7 | 1.1 | 2.4 | 2.1 | 1.3 | 3.2 | 1.6 | 1.6 | 3.1 | 1.4 | 1.4 | 1.3 | 0.9 | 3.3 | 1.0 | 1.3 | 1.2 | 1.4 | 1.2 | 1.4 | 1.4 | 1.4 | 0.8 | 1.7 | 0.8 | 2.4 | 2.2 | 3.3 | 0.6 | | | | |
| 14:1(n-5) | 7.6 | 3.4 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | | |
| 15:0 | - | - | - | - | - | - | 0.8 | 0.7 | 1.3 | 0.9 | 0.3 | 0.5 | 1.0 | 1.1 | - | - | - | - | 0.7 | - | - | - | - | - | 0.5 | 0.5 | 0.2 | 0.4 | 1.1 | 2.4 | - | | | |
| 16:0 | 17.8 | 17.0 | 14.2 | 9.3 | 13.0 | 10.7 | 1.6 | 7.9 | 15.9 | 5.6 | 5.4 | 4.1 | 16.7 | 1.5 | 10.4 | 8.4 | 7.6 | 8.4 | 7.6 | 12.7 | 1.1 | 11.3 | 1.9 | 10.3 | 8.1 | 11.3 | 1.9 | 10.3 | 8.1 | 15.2 | 2.3 | | | |
| 16:1(n-9) | - | - | - | - | - | - | 2.6 | 1.6 | 3.0 | 2.2 | 0.7 | 1.1 | 1.9 | 2.0 | 1.1 | 0.9 | 1.3 | 0.7 | 0.8 | 0.7 | 0.8 | 0.7 | 1.0 | 0.6 | 0.9 | 3.6 | 0.5 | 0.9 | 3.6 | 0.5 | - | - | | |
| 16:1(n-7) | 3.8 | 8.6 | 14.1 | 18.4 | 11.4 | 17.3 | 1.7 | 16.4 | 4.4 | 2.4 | 6.0 | 1.7 | 14.6 | 7.0 | 8.1 | 6.7 | 8.5 | 8.9 | 6.3 | 1.3 | 10.7 | 2.6 | 12.2 | 7.4 | 13.3 | 1.6 | 13.3 | 1.6 | - | - | - | - | | |
| 16:2(n-4) | 2.7 | - | 1.0 | 1.3 | 0.7 | 0.6 | 1.5 | - | - | - | - | - | - | - | - | 3.4 | 1.7 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | |
| 17:0 | - | - | - | - | - | - | 0.8 | 1.3 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| 16:3(n-4) | - | - | - | 1.5 | 1.3 | 0.8 | 0.7 | 1.0 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| 16:4(n-1) | - | - | 2.5 | 4.6 | 3.9 | 3.3 | 0.3 | 3.8 | - | - | 1.3 | 2.7 | 0.8 | 0.9 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| 18:0 | 9.4 | 5.0 | 2.7 | - | 1.3 | 0.5 | 0.5 | - | 5.0 | 3.4 | 3.5 | 3.3 | 1.3 | 1.7 | 6.6 | 2.7 | 3.0 | 1.8 | 4.8 | 3.5 | 2.1 | 2.3 | 1.0 | 2.7 | 3.9 | 6.4 | 0.8 | 6.4 | 0.8 | - | - | - | - | |
| 18:1(n-9) | 19.0 | 21.0 | 15.2 | 19.9 | 23.0 | 29.3 | 6.0 | 39.4 | 27.0 | 6.2 | 26.6 | 3.9 | 34.4 | 2.5 | 21.4 | 15.9 | 30.8 | 31.7 | 39.5 | 26.0 | 8.4 | 31.4 | 2.8 | 39.6 | 7.4 | 38.3 | 6.1 | 38.3 | 6.1 | - | - | - | - | |
| 18:1(n-7) | - | - | 4.0 | 2.9 | 2.7 | 2.5 | 0.7 | - | 1.1 | 0.9 | 1.9 | 0.2 | 1.7 | 0.2 | 1.7 | 1.5 | 1.4 | 1.3 | 1.1 | 1.8 | 0.4 | 1.5 | 0.9 | 0.7 | 1.0 | 1.5 | 1.3 | 1.5 | 1.3 | - | - | - | - | |
| 18:2(n-6) | 3.4 | - | 1.9 | 0.9 | - | 0.5 | 0.6 | - | 3.5 | 1.0 | 3.3 | 0.6 | 2.2 | 0.5 | 7.3 | 8.2 | 2.7 | 2.4 | 2.3 | 2.3 | 2.1 | 2.3 | 0.3 | 2.1 | 1.2 | 4.3 | 1.1 | 4.3 | 1.1 | - | - | - | - | |
| 20:1(n-9) | 5.0 | - | - | - | - | - | - | - | 1.6 | 1.9 | 1.0 | 1.2 | - | - | 2.0 | 3.4 | 1.2 | 1.1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| 20:4(n-3) | 13.6 | - | - | - | - | - | - | - | 2.9 | 2.4 | 1.0 | 1.2 | 2.1 | 0.9 | 0.9 | 1.5 | 2.8 | 3.2 | 2.9 | 2.6 | 3.4 | 2.2 | 0.7 | 3.6 | 2.3 | 1.6 | 2.8 | 1.6 | 2.8 | - | - | - | - | |
| 20:5(n-3) | 6.8 | 25.9 | 26.9 | 28.1 | 25.5 | 22.6 | 3.0 | 20.0 | 12.3 | 3.6 | 13.8 | 3.2 | 16.3 | 4.4 | 13.2 | 9.0 | 16.3 | 16.4 | 12.2 | 15.3 | 4.1 | 15.9 | 2.1 | 11.9 | 2.8 | 7.8 | 4.8 | 7.8 | 4.8 | - | - | - | - | |
| 18:5(n-3) | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| 22:5(n-3) | - | - | - | - | - | - | - | - | 2.5 | 5.1 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 22:6(n-3) | 5.8 | 15.8 | 14.8 | 12.0 | 14.3 | 10.5 | 0.8 | 8.5 | 18.4 | 6.0 | 18.5 | 4.2 | 13.9 | 4.4 | 14.3 | 12.0 | 19.0 | 19.7 | 18.1 | 22.1 | 6.7 | 17.7 | 4.3 | 11.2 | 1.8 | 4.8 | 2.6 | 4.8 | 2.6 | - | - | - | - | |
| Fatty alcohols | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14:0 | 36.2 | 45.3 | 41.3 | 43.1 | 51.9 | 47.2 | 1.1 | 46.0 | 40.8 | 7.2 | 44.7 | 4.7 | 48.2 | 1.8 | 23.9 | 20.9 | 40.1 | 41.2 | 48.4 | 36.5 | 6.6 | 39.0 | 5.7 | 34.7 | 19.8 | 43.4 | 5.5 | 43.4 | 5.5 | - | - | - | - | |
| 16:0 | 22.5 | 44.4 | 46.9 | 53.0 | 45.2 | 50.2 | 2.0 | 54.0 | 46.9 | 8.7 | 46.9 | 6.2 | 46.8 | 1.8 | 25.4 | 22.1 | 51.5 | 52.6 | 47.5 | 48.3 | 3.7 | 50.0 | 2.9 | 59.0 | 23.1 | 44.7 | 3.1 | 44.7 | 3.1 | - | - | - | - | |
| 18:0 | 30.4 | 10.3 | 6.1 | - | - | 0.9 | 1.5 | - | 9.3 | 10.1 | 7.5 | 7.0 | 1.8 | 2.1 | 11.2 | 9.7 | 5.1 | 2.6 | 2.4 | 7.7 | 3.3 | 3.5 | 2.9 | 2.1 | 2.7 | 10.6 | 4.5 | 10.6 | 4.5 | - | - | - | - | |
| 18:1(n-7) | 11.0 | 0.0 | 5.7 | 3.9 | 2.9 | 1.8 | 1.7 | - | 1.0 | 1.6 | 1.0 | 2.0 | 3.2 | 1.6 | 6.2 | 5.7 | 3.3 | 3.6 | 1.8 | 7.4 | 4.9 | 7.5 | 1.8 | 4.2 | 3.4 | 1.4 | 2.5 | 1.4 | 2.5 | - | - | - | - | |
| Proportion | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Fatty acids | 80.2 | 74.9 | 77.9 | 68.5 | 71.1 | 70.8 | 2.7 | 62.1 | 78.3 | 3.8 | 76.1 | 3.9 | 63.7 | 5.3 | 88.5 | 11.4 | 69.0 | 69.5 | 60.7 | 82.1 | 3.5 | 72.2 | 4.5 | 68.3 | 14.3 | 59.7 | 16.6 | 59.7 | 16.6 | - | - | - | - | |
| Fatty alcohols | 19.8 | 25.1 | 22.1 | 31.5 | 28.9 | 29.2 | 2.7 | 37.9 | 21.7 | 3.8 | 23.9 | 3.9 | 36.3 | 5.3 | 11.5 | 11.4 | 31.0 | 30.5 | 39.3 | 17.9 | 3.5 | 27.8 | 4.5 | 31.7 | 14.3 | 25.8 | 9.0 | 25.8 | 9.0 | - | - | - | - | |

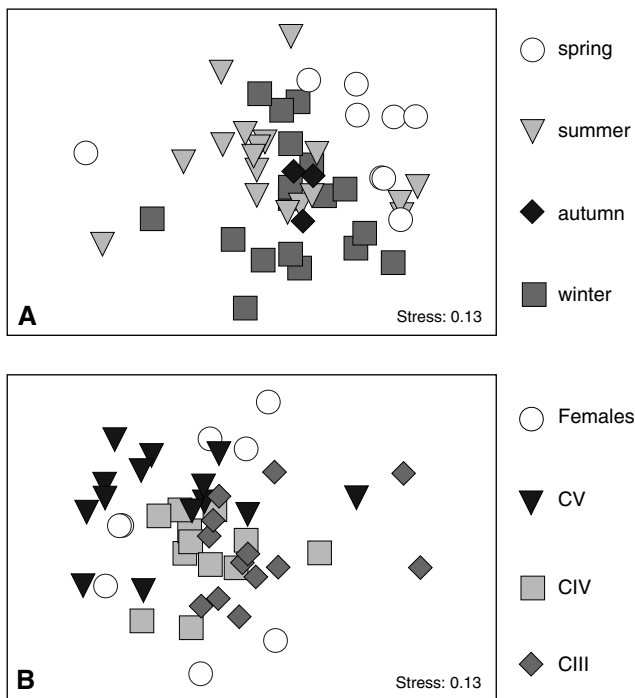


Fig. 2 Fatty acid compositions of *P. minutus*: **a** 2-dimensional MDS configuration for seasons (*spring, summer, autumn, winter*), **b** MDS configuration for copepodid stages (*Females, CV, CIV, CIII*)

Table 2 *Pseudocalanus minutus*: SIMPER analysis showing average dissimilarities (Av Diss) of fatty acid compositions between seasons as well as average abundances (Av Ab, %) of the five predominant fatty acids accounting for dissimilarities between seasons

| | SIMPER | | | | |
|--------------------|--------|-------------|--------------------|--------|------|
| | Spring | Summer | Spring | Winter | |
| Av Diss | 31.0 | | 29.9 | | |
| | Av Ab | Av Ab | Av Ab | Av Ab | |
| Fatty acids | | Fatty acids | | | |
| 20:5(<i>n</i> -3) | 22.3 | 14.6 | 18:1(<i>n</i> -9) | 25.0 | 33.3 |
| 18:1(<i>n</i> -9) | 25.0 | 27.8 | 20:5(<i>n</i> -3) | 22.3 | 13.2 |
| 16:1(<i>n</i> -7) | 13.8 | 8.8 | 22:6(<i>n</i> -3) | 11.4 | 14.9 |
| 22:6(<i>n</i> -3) | 11.4 | 17.0 | 16:1(<i>n</i> -7) | 13.8 | 10.3 |
| 16:0 | 12.4 | 13.1 | 16:0 | 12.4 | 12.1 |

Oithona similis

The fatty acid compositions of different stages of *O. similis* were generally very similar between seasons (Table 4). However, one-way ANOSIM of fatty acid compositions between seasons showed that those in spring and summer were significantly different to winter composition, whereas there were no significant differences between spring, summer and autumn, and

autumn and winter, respectively (*n*=38, Fig. 4a). According to SIMPER analyses, the most important fatty acids accounting for dissimilarities between seasons were: 18:1(*n*-9), 22:6(*n*-3), 16:0, 18:0, 20:5(*n*-3) and 18:2(*n*-6) (Table 5). One-way ANOSIM of fatty acid compositions among stages revealed no significant discrepancies (Fig. 4b).

One-way ANOVA for differences in relative amounts of specific fatty acids between seasons found significant changes in 16:0 (higher in spring than in winter, *P*=0.0268), 16:1(*n*-9) (lower in spring than during all other seasons, *P*=0.0012), 18:1(*n*-9) (lower in summer than in winter, *P*=0.0057) and 18:2(*n*-6) (lower in spring than in winter, *P*=0.0098).

One-way ANOVA of the amount of total fatty alcohols (respectively, wax esters) based on all stages revealed significant seasonal variations (*P*=0.0007): spring was characterized by lower values than those detected in summer and autumn, and summer values were higher as compared to the winter data (Fig. 5). Furthermore, significantly higher fatty alcohol levels were observed in deeper waters (>50–max. 350 m) than in the surface samples (0–50 m, *P*=0.0371).

During the year fatty alcohol levels (percentage of total fatty acids and alcohols) varied in *Oithona* females between 26 and 65%, in copepodids V between 17 and 65%, in CIV between 12 and 31% and in males between 9 and 40% (Fig. 5). Predominant fatty alcohols were 14:0 (0–31%), 16:0 (7–71%), 18:0 (4–32%) and 20:1(*n*-9), which occurred in very high amounts (0–82%) (Table 4).

Total lipid (sum of fatty acids and fatty alcohols) varied between 0.3 and 0.9 µg ind⁻¹ in females, 0.2 and 1.5 µg ind⁻¹ in CV, 0.3 and 1.0 µg ind⁻¹ in CIV and 0.6 and 0.9 µg ind⁻¹ in males (Fig. 5).

Discussion

Pseudocalanus minutus

The fatty acid composition of *P. minutus* points to a diatom-based diet in spring and a flagellate/dinoflagellate-based diet during summer, autumn, and winter. Typical diatom marker fatty acids such as 16:1(*n*-7), 16:4(*n*-1) and 20:5(*n*-3) dominated in spring, whereas the flagellate/dinoflagellate marker 22:6(*n*-3) and 16:0 as well as 18:2(*n*-6) had a higher share during the other seasons pointing to a more omnivorous feeding during this time (Reuss and Poulsen 2002; Dalsgaard et al. 2003 and references therein). 18:2(*n*-6) and 16:0 were found in substantial amounts of total lipids in particulate matter and were related to an omnivorous

Table 3 *Pseudocalanus minutus*: SIMPER analysis showing average dissimilarities (Av Diss) of fatty acid compositions between stages as well as average abundances (Av Ab, %) of the five predominant fatty acids accounting for dissimilarities between stages (F females, CIII, CIV, CV copepodite stages)

| | SIMPER | | | | | | | |
|--------------------|--------|-------|--------------------|-------|-------|--------------------|-------------|------|
| | F | | CIII | | CIV | | CV | |
| Av Diss | 31.5 | | 26.9 | | 26.9 | | 30.3 | |
| | Av Ab | Av Ab | Av Ab | Av Ab | Av Ab | Av Ab | Av Ab | |
| Fatty acids | | | Fatty acids | | | | Fatty acids | |
| 22:6(<i>n</i> -3) | 10.5 | 18.9 | 18:1(<i>n</i> -9) | 28.3 | 27.6 | 18:1(<i>n</i> -9) | 34.8 | 26.3 |
| 18:1(<i>n</i> -9) | 28.3 | 26.3 | 22:6(<i>n</i> -3) | 10.5 | 17.7 | 16:1(<i>n</i> -7) | 13.4 | 5.3 |
| 16:1(<i>n</i> -7) | 14.1 | 5.3 | 20:5(<i>n</i> -3) | 15.9 | 16.9 | 22:6(<i>n</i> -3) | 13.1 | 18.9 |
| 20:5(<i>n</i> -3) | 15.9 | 13.3 | 16:1(<i>n</i> -7) | 14.1 | 9.1 | 16:0 | 9.0 | 14.4 |
| 16:0 | 14.0 | 14.4 | 16:0 | 14.0 | 13.2 | 20:5(<i>n</i> -3) | 15.9 | 13.3 |

feeding mode by Scott et al. (2002). In Kongsfjorden, during the spring phytoplankton bloom diatoms and the haptophyte *Phaeocystis pouchetii* predominate in open waters, whereas diatoms prevail at the underside of the ice (Hop et al. 2002). In summer and early autumn, the chrysophyte *Dinobryon balticum* increases in abundance together with flagellates and dinoflagellates (Okolodkov et al. 2000). Among stages,

females and CIIIs/CIVs as well as CVs and CIIIs showed significant variations based on ANOSIM. Here, SIMPER analyses suggest that females and CVs fed mainly on diatoms, since the respective marker fatty acids 16:1(*n*-7) and 20:5(*n*-3) were high. In CIII and CIV, however, the flagellate marker 22:6(*n*-3) dominated. 18:1(*n*-9) also contributed strongly to dissimilarity between these stages, since it had higher

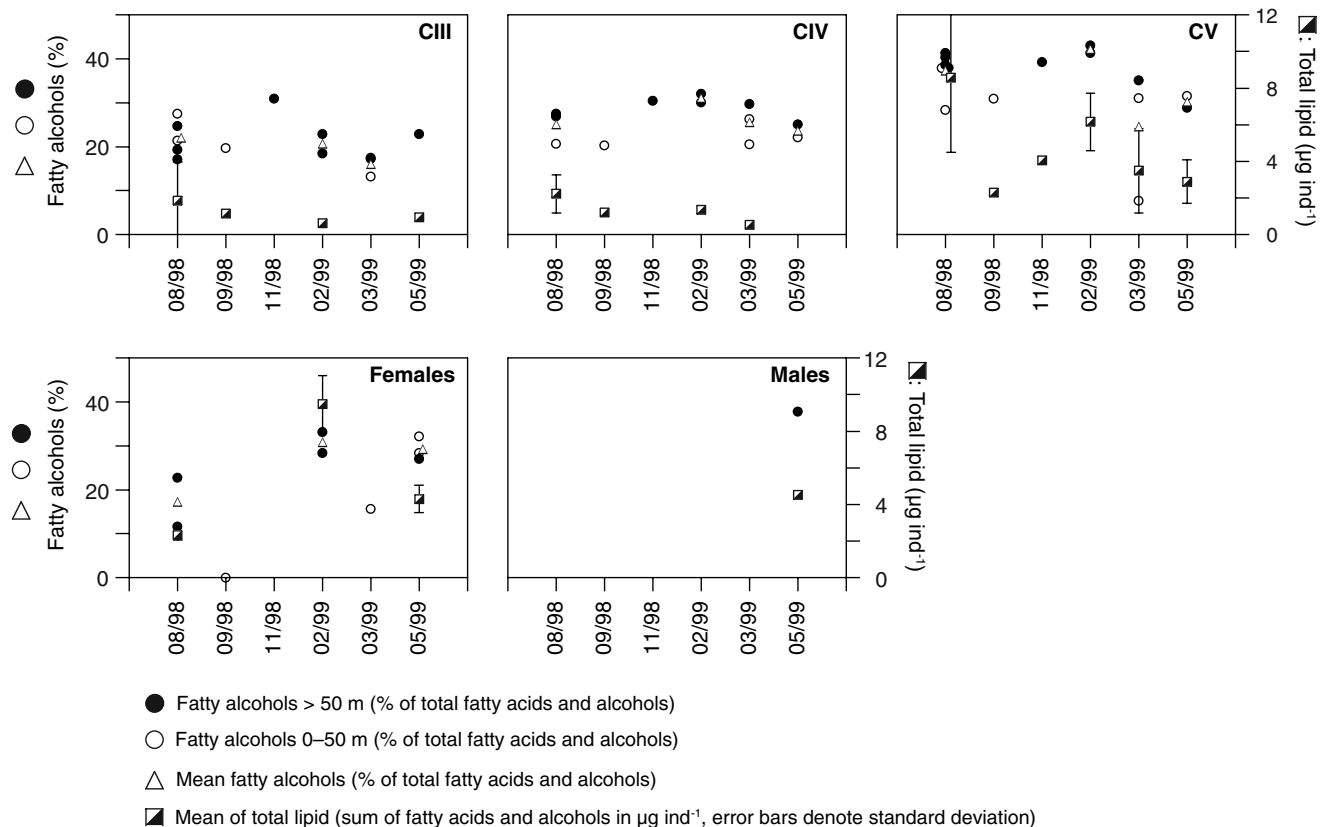


Fig. 3 *Pseudocalanus minutus*: relative fatty alcohol amount (% of total fatty acids and alcohols) in 0–50 m, >50 m and mean value, as well as total mass of fatty acids and fatty alcohols ($\mu\text{g ind}^{-1}$) during the various sampling months

Table 4 *Oithona similis*: fatty acid and fatty alcohol compositions (mass %) in the different stages during the four seasons (F females, M males, CV, CIV copepodite stages, Mn mean, SD standard deviation, for n=2 both measurements are listed (I, II))—traces (<0.5%)

| Stage | Spring | | | | | | Summer | | | | | | Autumn | | | | | | Winter | | | | | | | | | | | | |
|-----------------------|--------|-------|------|------|------|------|--------|------|------|------|------|------|--------|------|------|------|------|------|--------|------|------|------|------|------|------|------|------|------|------|------|--|
| | CIV | CV | F | II | I | M | CV | F | Mn | SD | Mn | SD | F | II | I | M | CIV | CV | F | Mn | SD | Mn | SD | CIV | CV | F | Mn | SD | | | |
| | n=2 | n=2 | n=2 | n=2 | n=2 | n=1 | n=4 | n=6 | n=4 | n=1 | n=2 | n=1 | n=2 | n=4 | n=1 | n=3 | n=1 | n=2 | n=5 | n=3 | n=1 | n=2 | n=3 | n=1 | n=2 | n=5 | n=3 | n=1 | n=2 | n=5 | |
| Fatty acids | I | II | I | II | I | II | Mn | Mn | SD | Mn | SD | F | II | I | Mn | SD | Mn | SD | F | Mn | SD | Mn | SD | CIV | CV | F | Mn | SD | | | |
| 14:0 | 7.0 | 10.9 | 4.0 | 4.3 | 9.9 | 6.6 | 7.0 | 8.1 | 2.6 | 8.0 | 3.0 | 8.1 | 3.0 | 7.3 | 4.6 | 4.5 | 8.5 | 1.7 | 8.8 | 6.0 | 1.9 | 6.3 | 1.5 | 6.9 | 3.5 | 3.2 | 3.0 | 3.0 | 3.0 | 3.0 | |
| 16:0 | 30.2 | 30.1 | 20.6 | 30.1 | 28.9 | 26.9 | 30.8 | 25.6 | 1.4 | 23.0 | 3.8 | 25.6 | 3.8 | 21.9 | 19.1 | 22.0 | 25.7 | 2.1 | 28.4 | 23.6 | 3.2 | 21.3 | 3.4 | 26.3 | 1.9 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | |
| 16:1(n-9) | 4.9 | 4.7 | 1.6 | - | - | - | - | 3.9 | 3.2 | 3.7 | 1.6 | 3.9 | 1.6 | 3.1 | 2.7 | 3.5 | 4.6 | 1.4 | 5.2 | 4.8 | 1.1 | 4.0 | 0.9 | 2.2 | 2.4 | 1.1 | 1.1 | 1.1 | 1.1 | 1.1 | |
| 16:1(n-7) | - | 3.6 | 8.1 | - | - | - | - | 8.6 | 8.6 | 5.4 | 2.2 | 2.6 | 2.2 | - | 2.8 | 2.0 | 2.4 | 1.8 | - | 2.4 | 2.6 | 1.8 | 2.0 | - | - | - | - | - | - | - | |
| 18:0 | 14.2 | 13.3 | 5.4 | 9.6 | 7.9 | 9.9 | 15.8 | 13.6 | 3.5 | 7.0 | 10.6 | 10.4 | 10.6 | 6.9 | 15.2 | 10.5 | 3.1 | 12.2 | 9.7 | 1.8 | 8.4 | 1.7 | 12.6 | 1.5 | 1.8 | 1.8 | 1.8 | 1.8 | 1.8 | 1.8 | |
| 18:1(n-9) | 20.9 | 23.4 | 21.2 | 26.1 | 19.2 | 21.2 | 27.2 | 17.8 | 10.8 | 14.0 | 10.2 | 17.8 | 10.2 | 35.6 | 38.5 | 32.2 | 21.5 | 3.9 | 16.9 | 28.0 | 7.7 | 35.9 | 3.5 | 25.7 | 2.5 | 7.7 | 7.7 | 7.7 | 7.7 | 7.7 | |
| 18:1(n-7) | - | 3.8 | 2.9 | - | - | - | - | 1.5 | 1.5 | 1.3 | 1.7 | 1.5 | 1.7 | - | 2.6 | 2.8 | 3.4 | 0.4 | 3.6 | 1.4 | 1.3 | 1.7 | 1.6 | 1.7 | 1.7 | 1.7 | 1.7 | 1.7 | 1.7 | 1.7 | |
| 18:2(n-6) | 5.5 | - | 2.7 | - | - | 6.5 | 6.1 | 3.8 | 2.7 | 3.5 | 2.3 | 3.8 | 2.3 | 5.8 | 3.0 | 3.6 | 3.4 | 2.3 | 14.6 | 6.8 | 4.6 | 6.1 | 2.8 | 10.0 | 10.7 | 4.6 | 4.6 | 4.6 | 4.6 | 4.6 | |
| 20:5(n-3) | 7.2 | 5.7 | 16.7 | 11.4 | 15.1 | 13.0 | 4.7 | 7.7 | 7.7 | 12.5 | 2.6 | 7.7 | 2.6 | 5.4 | 8.4 | 5.1 | 6.8 | 3.1 | 3.6 | 10.8 | 8.5 | 6.0 | 2.5 | 5.1 | 2.9 | 8.5 | 8.5 | 8.5 | 8.5 | 8.5 | |
| 22:6(n-3) | 10.3 | 4.5 | 16.9 | 18.5 | 19.1 | 16.0 | 8.3 | 15.4 | 7.3 | 21.7 | 4.6 | 15.4 | 4.6 | 10.5 | 11.5 | 9.1 | 13.2 | 7.0 | 6.8 | 6.5 | 6.1 | 8.4 | 3.9 | 9.6 | 4.9 | 6.1 | 6.1 | 6.1 | 6.1 | 6.1 | |
| Fatty alcohols | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14:0 | 26.9 | - | 22.3 | 36.5 | - | - | - | 5.5 | 3.8 | 3.4 | 8.4 | 5.5 | 8.4 | - | 10.5 | 16.0 | 4.8 | 3.2 | 7.4 | 26.4 | 2.7 | 19.9 | 5.2 | 5.0 | 3.2 | 2.7 | 2.7 | 2.7 | 2.7 | 2.7 | |
| 16:0 | 28.3 | 100.0 | 40.0 | 63.5 | 10.1 | 25.4 | 26.7 | 6.8 | 8.1 | 6.8 | 9.8 | 6.8 | 9.8 | 38.1 | 42.0 | 39.2 | 8.4 | 6.4 | 9.5 | 55.3 | 14.5 | 48.7 | 8.5 | 10.8 | 6.2 | 14.5 | 14.5 | 14.5 | 14.5 | 14.5 | |
| 18:0 | 44.8 | - | 8.2 | - | 7.5 | - | 31.9 | 3.7 | 4.2 | 6.0 | 9.1 | 6.0 | 9.1 | 11.1 | 6.0 | 12.5 | 6.3 | 4.2 | 9.6 | 10.1 | 8.8 | 13.2 | 5.4 | 7.0 | 4.7 | 8.8 | 8.8 | 8.8 | 8.8 | 8.8 | |
| 20:1(n-9) | - | - | 25.8 | - | 82.4 | 74.6 | 41.4 | 13.2 | 13.2 | 81.5 | 25.3 | 77.9 | 25.3 | 50.8 | 41.5 | 32.3 | 78.0 | 10.9 | 73.5 | 8.2 | 7.8 | 11.8 | 14.2 | 76.2 | 10.5 | 7.8 | 7.8 | 7.8 | 7.8 | 7.8 | |
| 20:1(n-7) | - | - | 3.7 | - | - | - | - | 3.8 | 3.5 | 4.6 | 2.1 | 3.8 | 2.1 | - | - | - | 2.5 | 2.9 | - | - | - | 6.3 | 14.2 | 0.9 | 2.1 | - | - | - | - | - | |
| Proportion | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Fatty acids | 78.9 | 94.7 | 78.1 | 86.6 | 62.4 | 84.8 | 81.3 | 49.8 | 13.7 | 44.0 | 17.0 | 49.8 | 17.0 | 69.5 | 68.9 | 67.6 | 52.4 | 16.6 | 60.8 | 79.0 | 13.3 | 70.4 | 5.9 | 56.9 | 16.9 | 13.3 | 13.3 | 13.3 | 13.3 | 13.3 | |
| Fatty alcohols | 21.1 | 5.3 | 21.9 | 13.4 | 37.6 | 15.2 | 18.7 | 50.2 | 13.7 | 56.0 | 17.0 | 50.2 | 17.0 | 30.5 | 31.1 | 32.4 | 47.6 | 16.6 | 39.2 | 21.0 | 13.3 | 29.6 | 5.9 | 43.1 | 16.9 | 13.3 | 13.3 | 13.3 | 13.3 | 13.3 | |

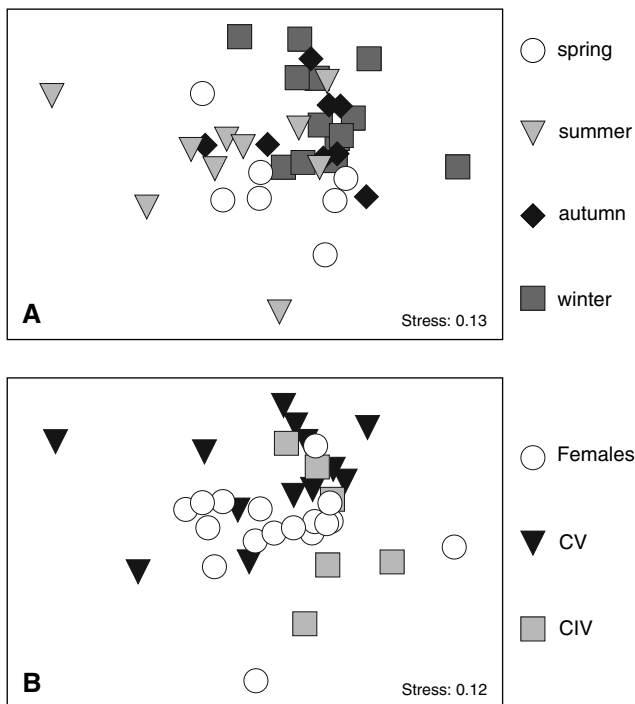


Fig. 4 Fatty acid compositions of *O. similis*: **a** 2-dimensional MDS configuration for seasons (*spring, summer, autumn, winter*), **b** MDS configuration for copepodite stages (*Females, CV, CIV*)

average abundances in females and CV, as well as in winter for all stages. This may suggest additional winter-feeding especially of the older stages (CV and females). 18:1(*n*–9) is important in particulate matter (Kattner et al. 1983) and used as a general marker for carnivorous and omnivorous feeding (Sargent and Henderson 1986; Falk-Petersen et al. 1990; Graeve et al. 1994b, 1997). It was also found in high amounts in *Pseudocalanus* spp. from late summer (up to 30% of total fatty acids) by Peters et al. (2004), who suggested the need of additional opportunistic winter-feeding. Omnivorous feeding of overwintering individuals is also known from *P. minutus* and *P. acuspes* in northern Norway (Poulet 1974; Norrbin 1987 cited in Norrbin et al. 1990).

Although lipid classes have not been investigated due to low total lipid concentrations, the generally high portion of fatty alcohols allows the conclusion that wax esters are the major lipid class in *P. minutus*, which is in accordance with the findings by Fraser et al. (1989), Kattner and Krause (1989), and Norrbin et al. (1990). Furthermore, due to this fact, changes in fatty acid compositions reflect mostly variations in wax ester compositions, which also include biomarker fatty acids.

For copepodids IV and V of *P. minutus* higher amounts of fatty alcohols were found in specimens

Table 5 *Oithona similis*: SIMPER analysis showing average dissimilarities (Av Diss) of fatty acid compositions between seasons as well as average abundances (Av Ab, %) of the five predominant fatty acids accounting for dissimilarities between seasons

| | SIMPER | | | | |
|--------------------|--------|--------|--------------------|--------|------|
| | Spring | Winter | Summer | Winter | |
| Av Diss | 24.31 | | 27.56 | | |
| | Av Ab | Av Ab | Av Ab | Av Ab | |
| Fatty acids | | | | | |
| 18:1(<i>n</i> –9) | 23.0 | 30.2 | 18:1(<i>n</i> –9) | 16.3 | 30.2 |
| 22:6(<i>n</i> –3) | 13.6 | 8.4 | 22:6(<i>n</i> –3) | 17.9 | 8.4 |
| 16:0 | 29.4 | 23.8 | 20:5(<i>n</i> –3) | 9.6 | 6.7 |
| 20:5(<i>n</i> –3) | 9.5 | 6.7 | 18:0 | 10.9 | 10.3 |
| 18:2(<i>n</i> –6) | 2.2 | 7.8 | 18:2(<i>n</i> –6) | 3.7 | 7.8 |

from deeper layers as compared to surface samples. Apparently, individuals with still insufficient storage lipids for overwintering remained in surface layers, thus prolonging their feeding period. Levels of storage lipids have been considered to determine the overwintering depth (Irigoiien 2004).

For *P. minutus* in Kongsfjorden, a 1-year life cycle was recently described with CIII, CIV and to a lesser extent CV overwintering at depth below 100 m (Lischka and Hagen 2005). The corresponding lipid data indicate a trend of wax ester accumulation in summer and autumn in copepodids III, IV and V and a progressive decline of these lipids towards the end of the overwintering period. This illustrates that winter survival and stage succession (CIII to CV) towards the end of the overwintering period was supported by wax ester reserves. This is in contrast to other primarily herbivorous calanoids using wax esters primarily for reproduction and not overwintering (e.g. Hagen and Schnack-Schiel 1996; Scott et al. 2000).

Surprisingly, CVs and females in May exhibited nearly the same high wax ester levels (approximately 60%). This suggests that development to adult females, including final stages of gonad maturation and reproduction, depended on external food supply from the spring phytoplankton bloom, which starts usually in May (Wiktor 1999; personal observation). Feeding on ice-algae may also be possible, which is known for *Pseudocalanus* spp. (Bedo et al. 1990; Conover and Huntley 1991), since spring sampling in May occurred in ice-covered waters. In contrast, *P. acuspes* from temperate waters depends on lipid reserves for final gonad maturation (Norrbin et al. 1990), whereas *P. minutus* in Kongsfjorden relies on the spring phytoplankton for molting to females and final maturation of gonads.

If wax ester accumulation is compared with dry mass data from formaline-preserved samples of *Pseudocalanus*

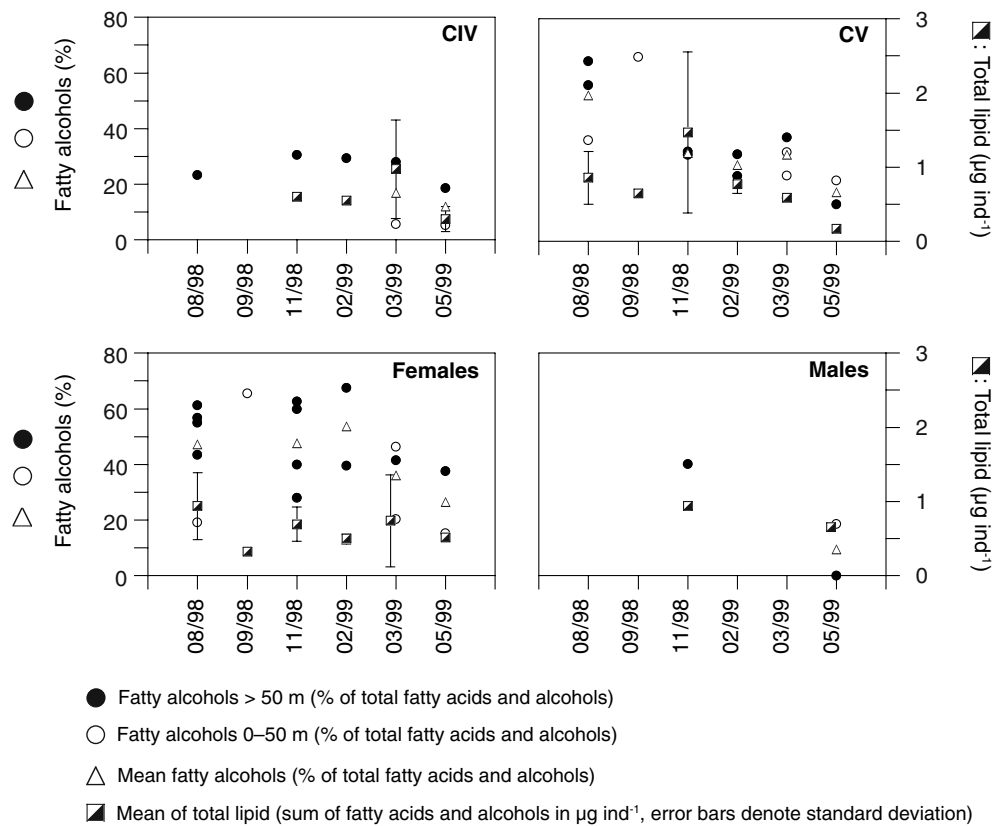


Fig. 5 *Oithona similis*: relative fatty alcohol amount (% of total fatty acids and alcohols) in 0–50 m, >50 m and mean value, as well

as total mass of fatty acids and fatty alcohols (µg ind⁻¹) during the various sampling months

spp. stages (Conover and Huntley 1991), a similar trend is found. Dry mass also increases during the course of the year, although the mass increment between April and August in stage CIII is larger (twofold), while in stage CV it is not as pronounced (about 22%). However, it should be kept in mind that changes in dry mass are not necessarily directly associated with the lipid dynamics, but may rather be explained by different increases in individual size in a developing population or different condition of cohorts. (Lipid data can also be biased since they may dissolve in formaline-preserved samples.) However, interpretation on basis of such different datasets have to be taken with care.

Oithona similis

The fatty acid and alcohol compositions of the various *O. similis* stages in our studies are in agreement with the predominant fatty acids described for *O. similis* adult males and females from the Antarctic (Kattner et al. 2003). Consistently high percentages of 18:1(*n*–9) fatty acids in all stages and during all seasons point to a generally omnivorous/carnivorous/detritivorous diet (Dalsgaard et al. 2003 and references therein). Accord-

ingly, Kattner et al. (2003), based on its lipid composition, described *O. similis* to feed opportunistically on a great variety of organisms. In addition, the predominance of 22:6(*n*–3) over 20:5(*n*–3), as well as the low portions of 16:1(*n*–7) and 18:1(*n*–7) rather suggest a flagellate-based diet (Graeve et al. 1994a). *Oithona* spp. is known to be an omnivore including herbivorous, carnivorous, detritivorous and coprophagous feeding (Lampitt and Gamble 1982; Paffenhöfer 1993 and references therein; Gonzáles and Smetacek 1994).

Wax esters of adult males and females consisted predominantly of the long chain 20:1(*n*–9) alcohol, whereas copepodids V and IV had mainly 14:0 and 16:0 alcohols (except for summer CVs). Kattner et al. (2003) and Obermüller (1999) also found the 20:1(*n*–9) alcohol in similarly high amounts in *O. similis* (20–80% in females). The predominance of the 20:1(*n*–9) alcohol is a characteristic feature of herbivorous calanoid copepods, which biosynthesize this alcohol de novo (Lee et al. 1971b; Sargent and Henderson 1986), and as yet there is no evidence of other copepods also having this ability. The origin of the 20:1(*n*–9) alcohol in *O. similis* adults is not clear. Ingestion of the 20:1 alcohol via *Calanus* nauplii

seems unlikely, since these are too large as prey (Eaton 1971), although they may store lipid droplets (Lee et al. 2006). Another possibility could be feeding on *Calanus* faecal pellets or even fish faecal pellets. Prahl et al. (1984, 1985) found considerable amounts of 20:1 and 22:1 alcohols in faecal pellets of *Calanus helgolandicus* fed an unialgal diet of *Dunaliella primolecta* (green alga), as well as in faecal pellets of different fish species fed *C. helgolandicus*. Similarly, Harvey et al. (1987) reported the 20:1 alcohol in faecal pellets of *C. helgolandicus* fed a dinoflagellate (*Scrippsiella trochoidea*). However, Reigstad et al. (2005) did not find experimental evidence for *O. similis* feeding on *Calanus* faecal pellets. *O. similis* may also be able to biosynthesize 20:1 alcohols de novo or via elongation of shorter-chain saturated precursors of dietary origin. However, according to Kattner et al. (2003), it is unlikely that small copepods are able to produce these fatty alcohols de novo. Hence, the origin of these long-chain alcohols remains a matter of conjecture.

At times, fatty alcohols and thus wax esters seemed to play an important role in all stages of *O. similis*, although it is not a diapausing species and therefore does not depend on primary production, but stays active and reproduces the whole year (Fransz 1988). Kattner et al. (2003) also found high-wax ester levels in the adult males of *O. similis* from Antarctic waters (70%). Generally, high wax ester levels are indicated by clearly visible large lipid droplets, especially in the November specimens (personal observation). Similarly, Fransz (1988) observed large oil globules in epipelagic copepods from the Weddell Sea (Antarctica) including *O. similis*. A continuous decrease in the amounts of fatty alcohols of all stages during the overwintering period, with significantly lower values in spring than in summer, suggests that *O. similis* survived the winter at least partly using internal lipids as energy reserves. Year-round feeding has been deduced from the absence of wax esters in other copepod species (Lee 1974; Sargent et al. 1981; Hagen et al. 1993), and the accumulation of wax esters is usually linked to a seasonal feeding pattern (Falk-Petersen et al. 1987; Scott et al. 1999). The high wax ester deposits in *O. similis* from Kongsfjorden strongly support the results of Kattner et al. (2003) from the Antarctic. Thus, *O. similis* in Kongsfjorden is not typical in this respect, since it feeds omnivorously but produces wax esters. Our results showed maximum wax ester levels in summer, which continuously decreased during the dark season, until they reached a minimum in spring. Reproduction in *O. similis* in Kongsfjorden peaks rather late in June and August/September

(Lischka and Hagen 2005). The low fatty alcohol levels in spring (May) indicate that molting, as well as gonad maturation and egg production in June, was probably fueled at least partially by storage lipids, whereas in August/September wax ester accumulation co-occurred with reproductive processes. Furthermore, wax ester levels were significantly lower in surface-dwelling individuals than in specimens from deeper layers. Hence, the surface specimens may have extended feeding activities in the epipelagic zone to accumulate sufficient lipid deposits and then descend to overwintering depth (see above).

In conclusion, the fatty acid compositions of *P. minutus* showed stronger seasonal variations as compared to *O. similis*. In *P. minutus* diatom marker fatty acids dominated in spring. During the other seasons, flagellate/dinoflagellate markers prevailed and especially in winter an omnivorous feeding mode developed. In contrast, in *O. similis* fatty acids characteristic of omnivorous/carnivorous feeding as well as for feeding on flagellates/dinoflagellates dominated year-round. The characteristic food preferences of the two species were also reflected in the fatty alcohol compositions. In *P. minutus* shorter-chain alcohols prevailed, typical of smaller mainly herbivorous/omnivorous copepods (e.g. Kattner and Hagen 1995; Albers et al. 1996). Adults of *O. similis* showed striking amounts of the 20:1($n-9$) alcohol, which may be related to a coprophagous feeding mode. Variations in wax ester levels were more pronounced in *O. similis*. While *P. minutus* seemed to use these lipid reserves for overwintering and stage development in CIII and CIV, the final stages of gonad maturation and reproduction in females and CV were also supported by the spring phytoplankton bloom. *O. similis* fueled winter survival of all stages as well as gonad maturation and peak reproduction in June by lipid reserves, whereas in August/September reproduction and replenishment of lipid reserves co-occurred.

Acknowledgments We thank UNIS on Svalbard, especially Dr. Ole-Jørgen Lønne, for all support during the sampling period. Petra Wencke and Janna Peters from the Marine Zoology in Bremen are gratefully acknowledged for their invaluable support and help during the lipid analyses and fruitful discussions of the data. Dr. Martin Graeve (Alfred Wegener Institute, Bremerhaven) is acknowledged for identifying unknown peaks by GC-MS. Thanks are also due to Dr. Dieter Piepenburg (Institute for Polar Ecology, Kiel) for statistical advice and to Dr. Holger Auel (Marine Zoology, Bremen) for critical comments on the manuscript. We also thank two anonymous reviewers for their comments on the manuscript. The 1-year sampling period on Svalbard was supported by the Deutsche Forschungsgemeinschaft (HA 1706/4-1).

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