

Stable isotopic compositions of overwintering copepods in the arctic and subarctic waters and implications to the feeding history

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Abstract

Highly abundant zooplankton dominated by copepods was found in the upper 200 m water column off the west of Spitsbergen in winter, although copepods in high-latitude environments during the overwintering period are known to reside in deep waters. We examined the possible feeding activities of these surface dwelling, overwintering copepods through their stable isotope compositions ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$), and their internal lipids. The differences in the $\delta^{15}\text{N}$ values ($\delta^{15}\text{N}$ enrichment factor) between the particulate organic matter (POM) at the surface layers and the dominant copepods in winter showed that the averaged $\delta^{15}\text{N}$ enrichment factor in *Calanus glacialis* (+2.7‰) and *Metridia longa* (+2.8‰) were higher than that in *Calanus finmarchicus* (+1.7‰). This suggests that *C. glacialis* and *M. longa* might be occasional omnivorous feeders, because the $\delta^{15}\text{N}$ enrichment factor of these two copepods were relatively close to the previously reported value (e.g. $+3.4 \pm 1.1$ ‰, [Geochim. Cosmochim. Acta 48 (1984) 1135]) for a stepwise increase of the value with the food chain. The estimated lipid isotopic ratios ($\delta^{13}\text{C}$) of *C. finmarchicus* and *M. longa* tended to decrease with the decreasing lipid contents (lipid carbon/total carbon), suggesting that some lipid components with heavy isotopes were removed from the total lipids. The isotopic changes of lipids with the lipid contents probably reflect the metabolic processes of lipid utilization of arctic and subarctic copepods during the overwintering period.

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1. Introduction

Copepods, for example *Calanus finmarchicus*, spend the winter period at depths below 600 m in the Norwegian Sea (Østvedt, 1955). They were mainly observed as copepodite V (CV) in the Greenland Sea, and as CIV and CV in the Barents Sea in

winter (Smith, 1988; Hirche, 1989; Pedersen et al., 1995). Several workers showed that copepods do not feed during the overwintering period. This is based on observations of their empty stomachs (Conover, 1962), low digestive activities (Tande and Slagstad, 1982), the reduction of mid gut epithelium (Hallberg and Hirche, 1980) and the lack of faecal pellet production (Ussing, 1938). Copepods are known to consume their own stored lipids in oil sacs for basal metabolic activities in winter, and for reproduction in early spring (Sargent and Falk-Petersen, 1988).

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Recent studies indicated that the overwintering populations of *C. finmarchicus* often occur in surface waters (Bathmann et al., 1990; Hirche, 1991; Baliño and Aksnes, 1993; Pedersen et al., 1995). However, it has not been satisfactorily explained why overwintering copepod populations remain abundant in surface layers (Pedersen et al., 1995). A highly abundant zooplankton population dominated by copepods was found in surface waters off the west of Spitsbergen in January 1999 (Sasaki et al., 2001). The maximum standing stock reached about 3 g DW m^{-2} (Sasaki et al., 2001), and the observed abundance was quite high compared with those in other arctic sea areas. For example, the maximum abundance in winter was a little lower than the average standing stocks in the Barents Sea during the phytoplankton productive seasons from spring to summer ($2\text{--}20 \text{ g DW m}^{-2}$, Rey et al., 1987; Skjoldal et al., 1987). The surface abundance in winter was almost equivalent to a highly dense population in deep layers in late fall ($6\text{--}9 \text{ g DW}$

m^{-2} , Hirche, 1991), which would have overwintered there. If both surface and deep dwelling copepods that had overwintered occur in spring, the integrated abundance of these copepods can affect spring phytoplankton productivity. Nevertheless, little information is available about the ecology of surface dwelling copepod populations during the overwintering period, primarily because of difficulties of sampling in high latitudes in winter.

Minagawa and Wada (1984) demonstrated that the differences in the $\delta^{15}\text{N}$ values between prey and predator ($\delta^{15}\text{N}$ enrichment factor) in marine environments could be $+3.4 \pm 1.1\text{‰}$. DeNiro and Epstein (1981), Fry (1988), Hobson and Welch (1992), and Hobson et al. (1995) also showed the enrichment formulae of ca. $3\text{--}4\text{‰}$ in land and marine ecosystems. The $\delta^{15}\text{N}$ enrichment factor between particulate organic matter (POM) collected in surface layers ($0\text{--}50 \text{ m}$) and copepods ($0\text{--}ca. 200 \text{ m}$) in the Barents Sea in spring were about $+4\text{‰}$ (Sasaki et al., 2001),

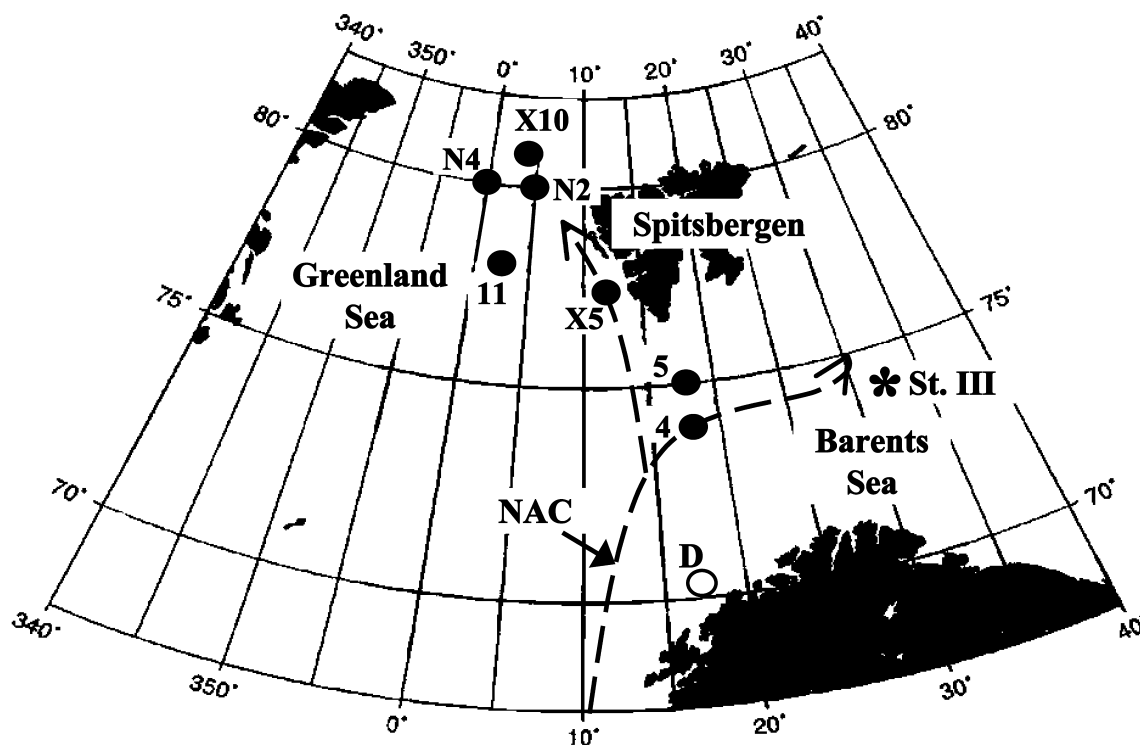


Fig. 1. Location of sampling sites of the Norwegian Atlantic Water in September and March 1994 (○), the west of Spitsbergen in January 1999 (●), and the Barents Sea in May 1998 (*). Dotted arrow indicates the simplified Norwegian Atlantic Currents (Loeng, 1989).

which were almost coincident with the previously reported values. In the waters off the west of Spitsbergen in winter, the $\delta^{15}\text{N}$ enrichment factor between POM without phytoplankton and copepods was about +3.2‰, which was almost the same as that in spring (Sasaki et al., 2001). They suggested that part of the copepods in winter might depend on POM, but not phytoplankton. However, this suggestion is apparently contradictory to the previous studies showing that copepods do not feed in winter. The isotopic values suggested by Sasaki et al. (2001) were very variable, because the analyzed zooplankton sample contained various copepods. The present study examines the specific isotopic enrichment of two dominant copepod groups (*Calanus* spp. and *Metridia* spp.) collected in surface layers in winter, and the seasonal variability in stable isotope compositions of the main body tissues and lipids of these copepods. We aim at confirming the possibility that stable isotope compositions ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) reflect feeding behaviors and histories of overwintering copepods in the arctic and subarctic waters.

2. Materials and methods

2.1. Sampling

Zooplankton was collected in three different areas of the arctic and subarctic waters (Fig. 1). The samples in March and September 1994 were obtained using MOCNESS net (mesh size 180 μm) from station D located in waters off the coast of northern Norway during the R/V *Jan Mayen* OMEX cruise (Halvorsen and Tande, 1999; Wassmann et al., 1999). The sampling depths were 50–100 m. The samples in January 1999 were obtained using a NORPAC net (North Pacific Standard net; 330 μm in mesh size) in the upper 200 m from seven stations located in the waters off the west of Spitsbergen during the R/V *Ivan Petrov* cruise (Ito, 1999). The samples in May 1998 were obtained using MOCNESS net in the upper 100 m from St. III located in the Barents Sea during the R/V *Jan Mayen* ALV-II cruise (Reigstad et al., 2002). All samples collected were preserved with neutralized formalin. Part of the copepod samples used in this study was the same taken in May 1998 and January 1999 by Sasaki et al. (2001).

2.2. Stable isotopic analysis

Relatively large copepods (>2 mm in prosome length) were removed out from preserved zooplankton samples, and classified into two major copepod groups, *Calanus* spp. and *Metridia* spp. (Table 1). Since some copepodite stages of *Calanus* and *Metridia* could not be precisely identified, three copepod samples were regarded as *Calanus* spp. CIV (January), *Calanus* spp. CV (January), and *Metridia* spp. CV (May). More than 80% of the *Calanus* spp. CV in abundance collected in January could be composed of *C. finmarchicus*, and the rest were *Calanus glacialis*. The *Metridia* spp. collected in May included *Metridia longa* and *Metridia lucens*.

The copepods in each group were divided into two fractions, one of which was exposed to chloroform/methanol (2:1, v/v) solution for 24 h to remove their lipids. The two fractions were then regarded as copepods with lipids and copepods without lipids. The carbon isotopic ratios of animal samples are known to be affected by the internal lipids that often make the carbon isotopic ratios of lower value than expected (McConnaughey and McRoy, 1979). One sample consisted of at most 12 individuals (350 μg to 1.8 mg DW). Each sample with copepods was dried in

Table 1
List of zooplankton analyzed

Date	Site	Zooplankton
Sept. 1994	Nordvestbanken, northern Norway	<i>C. finmarchicus</i> CIV <i>C. finmarchicus</i> CV <i>C. finmarchicus</i> CVI <i>M. lucens</i> CVI
Jan. 1999	off the west of Spitsbergen	<i>Calanus</i> spp. CIV <i>Calanus</i> spp. CV <i>C. finmarchicus</i> CVI <i>C. glacialis</i> CVI <i>M. longa</i> CVI
Mar. 1994	Nordvestbanken, northern Norway	<i>C. finmarchicus</i> CV <i>C. finmarchicus</i> CVI <i>M. longa</i> CVI
May 1998	Barents Sea	<i>C. finmarchicus</i> CIV <i>C. finmarchicus</i> CV <i>C. finmarchicus</i> CVI <i>Metridia</i> spp. CV <i>M. longa</i> CVI

More than 80% of *Calanus* spp. CIV, CV collected in January 1999 were composed of *C. finmarchicus*. *Metridia* spp. CV in May 1998 included *M. longa* and *M. lucens*.

Table 2

Stable carbon isotopic values for *C. finmarchicus*

Date	Stage	Copepods with lipids	Copepods without lipids
		$\delta^{13}\text{C}$ (‰) \pm SD	$\delta^{13}\text{C}$ (‰) \pm SD
Sept.	CIV	-24.5 ± 0.2	-22.8 ± 0.3
	CV	-24.4 ± 0.5	-23.7 ± 0.3
Jan.	CV	-24.9 ± 1.4	-22.3 ± 0.8
Mar.	CVI	-23.4 ± 1.0	-22.4 ± 0.8
May	CVI	-22.9 ± 0.5	-21.9 ± 0.2

CV in January indicates *Calanus* spp. CV. SD indicates standard deviation.

an aluminum dish at 60 °C for 24 h. They were used for determination of the carbon and nitrogen contents, and their stable isotopic compositions were measured using an ANCA/GSL mass spectrometer (Europa Scientific). The results were expressed as conventional $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, where the ratio of the sample is compared to that of a standard,

$$\delta X (\text{‰}) = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \times 1000,$$

where X is ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The standards were calibrated by PDB and atmospheric nitrogen. The analytical errors for nitrogen and carbon were $\pm 0.1 \text{‰}$ and $\pm 0.3 \text{‰}$, respectively.

The relative lipid contents (lipid carbon/total carbon) and $\delta^{13}\text{C}$ values of the lipids derived from the copepods were calculated using measured values and the following equations,

$$\text{Lipid carbon/Total carbon (\%)} = \text{Wb/Wc} \times 100,$$

$$\delta^{13}\text{C}_{\text{b}} (\text{‰}) = (\text{Wc} \cdot \delta^{13}\text{C}_{\text{c}} - \text{Wa} \cdot \delta^{13}\text{C}_{\text{a}})/\text{Wb},$$

where Wa is the carbon contents of copepods without lipids, Wc is the carbon contents of copepods with lipids, and $\text{Wb} (= \text{Wc} - \text{Wa})$ is the carbon contents of lipids, $\delta^{13}\text{C}_{\text{a}}$ is the carbon isotope value of copepods without lipids, $\delta^{13}\text{C}_{\text{b}}$ is the carbon isotope value of lipids, and $\delta^{13}\text{C}_{\text{c}}$ is the carbon isotope value of copepods with lipids. The data of $\delta^{15}\text{N}$ of POM was referred from Sasaki et al. (2001).

3. Results

The $\delta^{13}\text{C}$ values of *C. finmarchicus* apparently showed the marked difference between copepods with lipids and without lipids (Table 2). The $\delta^{13}\text{C}$ values of *C. finmarchicus* without lipids were higher than those with lipids. The difference between the

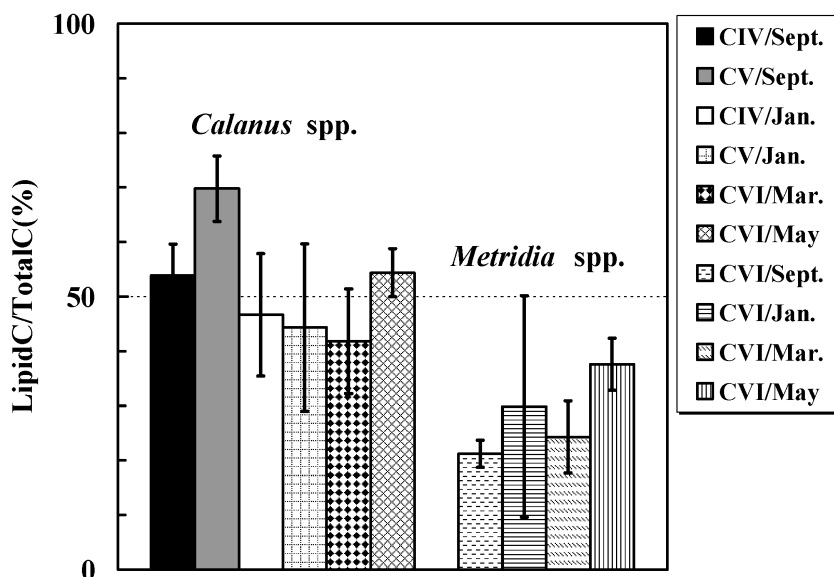


Fig. 2. Variability of relative lipid contents of *Calanus* spp. (left), and *Metridia* spp. (right). Bars indicate standard deviations (SD). More than 80% of *Calanus* spp. in abundance was composed of *C. finmarchicus*.

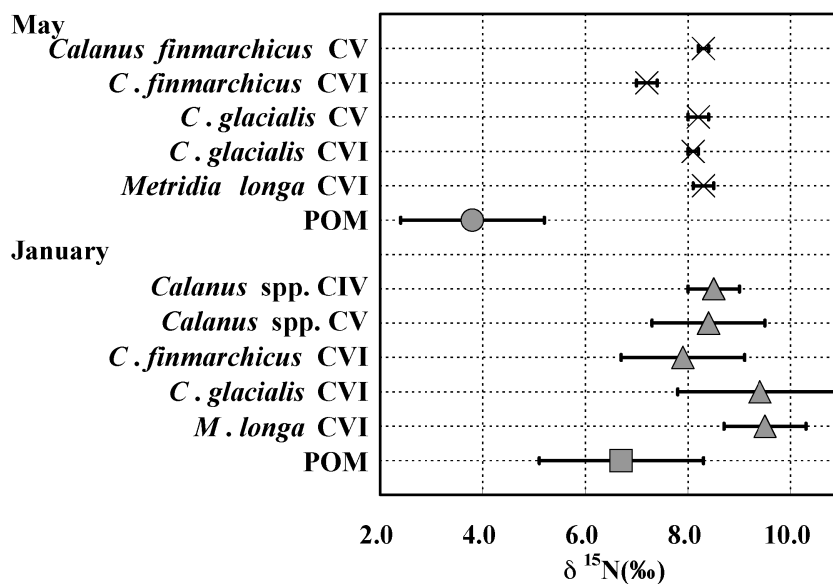


Fig. 3. Variability of $\delta^{15}\text{N}$ values of copepods without lipids and POM. Bars indicate SD. More than 80% of *Calanus* spp. in abundance was composed of *C. finmarchicus*.

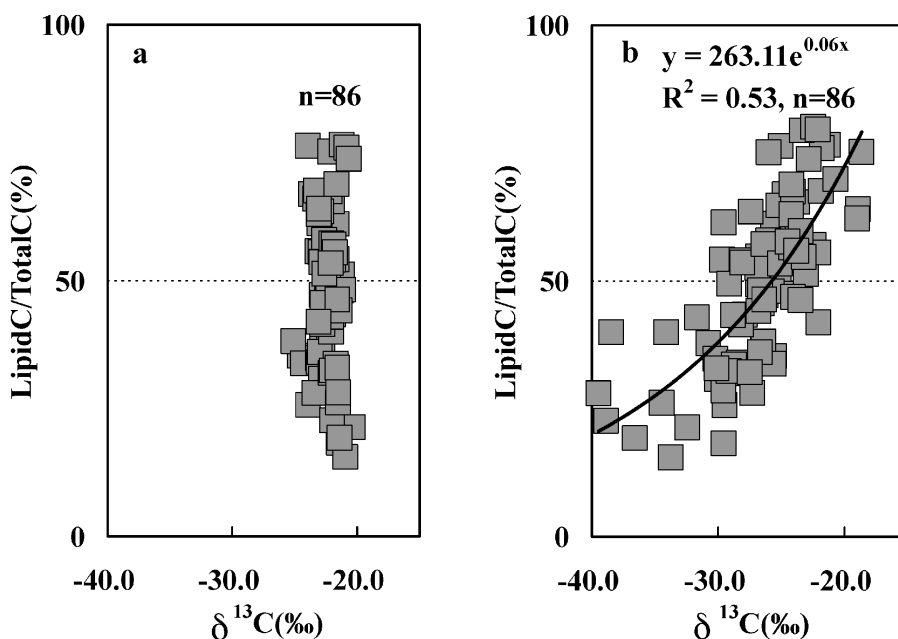


Fig. 4. (a) Variability of $\delta^{13}\text{C}$ values of body tissues without lipids and relative lipid contents of *C. finmarchicus*. Only winter samples include *C. finmarchicus* and *C. glacialis* CIV and CV. (b) Variability of $\delta^{13}\text{C}$ values of lipids and relative lipid contents of *C. finmarchicus*. Only winter samples include *C. finmarchicus* and *C. glacialis* CIV and CV.

two sample types was relatively large in January (2.6‰), with the maximum standard deviations (Table 2).

The lipid contents of *Calanus* spp. were highest in September, and decreased from September through March (ANOVA $p < 0.01$) (Fig. 2). The lipid contents of *Metridia* spp. were primarily less than those of *Calanus* spp. in all seasons, and no obvious seasonal change was found (Fig. 2). Microscopic observations revealed that no gut content was found in January, particularly for *C. finmarchicus*, and that the relative sizes of the oil sacs of *M. longa* and *M. lucens* were a little smaller than those of *Calanus* spp.

The averaged $\delta^{15}\text{N}$ value of *C. finmarchicus* CVI was significantly higher than those of POM in May (the difference of 3.4‰, t -test $p < 0.01$), and the same formula of *Calanus* spp. CV (mostly *C. finmarchicus* CV) in January was higher than those of POM (1.7‰, $p < 0.01$) (Fig. 3). The averaged $\delta^{15}\text{N}$ of *C. glacialis* CVI was 2.7‰ higher than those of POM in January ($p < 0.05$) (Fig. 3). The averaged $\delta^{15}\text{N}$ value of *M. longa* CVI was 4.5‰ higher than those of

POM in May ($p < 0.01$), and the same formula was higher than those of POM in January (2.8‰, $p < 0.05$) (Fig. 3).

The variability of $\delta^{13}\text{C}$ values of body tissues without lipids and the relative lipid contents of *Calanus* spp. (mostly *C. finmarchicus*) are shown in Fig. 4a. The $\delta^{13}\text{C}$ values of the *Calanus* spp. body tissues were in the range from about -21‰ to -23‰ , and the lipids contents greatly fluctuated from 20% to 80%. The estimated $\delta^{13}\text{C}$ values of the lipids showed a large variation from -20‰ to -30‰ or less, which was quite different from those of the body tissues (Fig. 4b). Although there was a large fluctuation, the $\delta^{13}\text{C}$ values of the lipids tended to decrease with decreasing lipid contents. The $\delta^{13}\text{C}$ values of the *Metridia* spp. body tissues did not show a marked change as much as *Calanus* spp., even if the lipid contents decreased (Fig. 5a). The relationship between the relative lipid contents and lipid isotopic values of *Metridia* spp. were apparently similar to that of *Calanus* spp. The $\delta^{13}\text{C}$ values of the lipids of *Metridia* spp. also decreased with decreasing lipid contents (Fig. 5b).

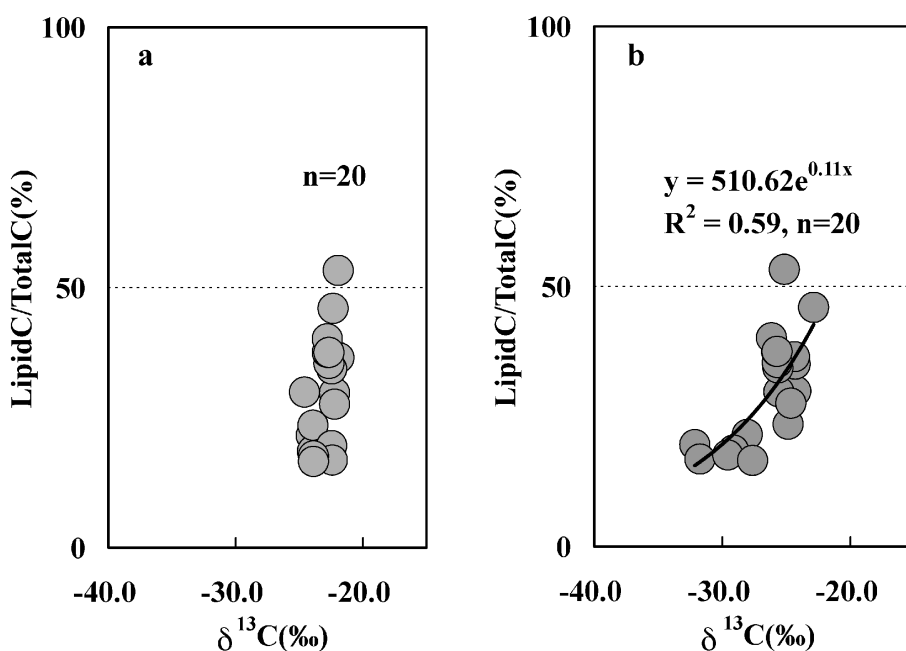


Fig. 5. (a) Variability of $\delta^{13}\text{C}$ values of body tissues without lipids and relative lipid contents of *M. longa*. (b) Variability of $\delta^{13}\text{C}$ values of lipids and relative lipid contents of *M. longa*. Fall samples include *M. lucens*.

4. Discussion

The Norwegian Atlantic Current (NAC) is one of the dominating currents in the present study area. A branch of NAC flows into the northern Greenland Sea, west of Spitsbergen, and meets with the Arctic current (AC) that comes from the Arctic Ocean (Loeng, 1989). Another branch of the NAC flows into the Barents Sea, and also meets with the AC (Loeng, 1989). The zooplankton populations (e.g. *C. finmarchicus*) are transported with the NAC into waters off the west of Spitsbergen and the Barents Sea, as suggested by Jashnov (1970), Conover (1988) and Mumm (1993). Although the dominant copepods collected in this study derive from three different locations, they originated most probably from the same waters (NAC), and possibly have comparable seasonal life cycles. Copepods begin to descend into deep layers in summer (Østvedt, 1955), and do not feed during the overwintering period (Hallberg and Hirche, 1980). Copepods, such as CIV or CV of *C. finmarchicus*, are believed to depend on stored lipids in winter (Båmstedt and Ervik, 1984). The main component of stored lipids is wax ester in later copepodites (Kattner et al., 1989), most of which are invested in reproductive processes during winter to early spring (Sargent and Falk-Petersen, 1988).

The $\delta^{13}\text{C}$ values of *Calanus* spp. without lipids are higher than those of copepods with lipids (Table 2). The difference in the carbon isotopic values must be caused by removing lipids, because the carbon isotopic values of lipids are generally lower than those of major constituents, such as proteins (Deines, 1980). No direct evidence was obtained for the large fluctuation in the lipid isotopic value in winter (Table 2), but the fluctuation would be caused by the variable consumption of lipid storage during the starvation period. The lipid content of *Metridia* spp. was primarily smaller than that of *Calanus* spp. in all seasons (Fig. 2), which is consistent with the former report of Hopkins et al. (1984) who suggested that *C. finmarchicus* were more dependent on stored lipids than *M. longa*. Falk-Petersen et al. (1987) also showed that *M. longa* had a lower percentage of neutral lipids than *C. finmarchicus*.

The $\delta^{15}\text{N}$ enrichment factor between the POM with phytoplankton and copepods in May was about +3.4‰ for *C. finmarchicus* CVI and +4.5‰ for

M. longa CVI (Fig. 3). The difference between the POM without phytoplankton and copepods in January was about +2.8‰ for *M. longa* CVI, and +2.7‰ for *C. glacialis* CVI, which were higher than the same formula for *C. finmarchicus* CV (+1.7‰, Fig. 3). According to the $\delta^{15}\text{N}$ enrichment factor (ca. 3–4‰) with a trophic level rise in the food chain reported by Minagawa and Wada (1984) and Hobson and Welch (1992), the present results indicate that the two copepod groups mainly fed on phytoplankton in May. However, the differences of $\delta^{15}\text{N}$ between POM without phytoplankton and copepods in January were apparently lower than those in May (Fig. 3). *M. longa* and *C. glacialis* have higher values (ca. 2.8‰) of $\delta^{15}\text{N}$ difference than *C. finmarchicus*, and the values are in a lower (2.4‰) of the enrichment factor of Minagawa and Wada (1984). It suggests that the former copepods would be more dependent on POM than the latter in January. Sasaki et al. (2001) showed that the $\delta^{15}\text{N}$ enrichment factor between the POM and copepods irrespective of the composition was +3.2‰ in winter. Those winter samples should include the *C. glacialis* that were relatively high in the nitrogen isotopic values (maximum value was 13‰) estimated in this study. The high nitrogen isotope values of *C. glacialis* could have brought about the unexpectedly high average values found by Sasaki et al. (2001).

The carbon isotopic values of the body tissues (without lipids) of *Calanus* spp. were relatively stable compared with those of the lipids (Fig. 4a). However, the carbon isotopic values of the lipids of *Calanus* spp. tended to decrease with decreasing lipid contents (Fig. 4b), although the regression curve had a weak significance ($R^2=0.53$, $n=86$) due to the large fluctuations. If this correlation is accepted, the isotopic change of lipids suggests that some lipid components with heavy isotopes were selectively removed from the total lipids during the overwintering period. Previous reports on lipid compositions and isotope values showed that plants and mammals include many kinds of lipids, such as wax ester and triacylglycerol, and each lipid component can have a specific isotope value (Naraoka et al., 1994; Collister et al., 1994). The change in lipid isotopic values can be due to a difference in the synthesizing and mobilization processes of each lipid component. Although the organic chemical processes associated with changes of the lipid isotopic values have not yet been fully under-

stood, the present results of lipid isotopic values probably reflect processes of lipid utilization in copepods.

Since *C. finmarchicus* mainly feed on phytoplankton during phytoplankton productive periods, and then starve during the rest of the year (Tande, 1982; Hirche, 1983), their body tissue is considered to basically synthesize from spring to summer. Because of this, the isotopic values of the body tissue are rather stable, because the body tissue would be derived from the same carbon source, such as phytoplankton. The stored lipids, such as wax esters, are also synthesized from spring to summer (Falk-Petersen et al., 1987) using phytoplankton carbon. But the lipids are continuously utilized as an energy source. This results in the qualitative alteration of lipids during starvation periods (Sargent and Falk-Petersen, 1988), represented by the decrease of lipid isotopic values.

Although relatively fewer numbers of samples of *Metridia* spp. were analyzed than *Calanus* spp., the relationship between the relative lipid contents and lipid isotopic values of the former was primarily similar to that of the latter (Figs. 4b and 5b). Less distinct isotopic changes of the stored lipids in *Metridia* spp. may be attributed to less pronounced lipid utilization processes than *Calanus* spp., and then to their low dependency on the stored lipids.

If the isotopic variation with the lipid contents reflects the metabolic processes of stored lipids, it may point at a difference in the overwintering strategies of *Calanus* spp. and *Metridia* spp. For example, *C. finmarchicus* feeds only on phytoplankton in a phytoplankton-productive period, and depends on the stored lipids during an overwintering period (Tande, 1982; Hirche, 1983), while *M. longa* may not depend entirely on the lipids, and live on a variety of foods (Båmstedt et al., 1985). Grønvik and Hopkins (1984) suggested that *M. longa* overwinters in an active state compared with *C. finmarchicus*. Falk-Petersen et al. (1987) suggested that *M. longa* has a more carnivorous feeding habits than the essentially herbivorous *C. finmarchicus*. A less distinct change in the lipid contents associated with the lipid isotope values of *Metridia* spp. is probably concomitant with a relatively low dependency on their stored lipids.

The present results can not conclusively explain why surface dwelling copepods occur during winter. Pedersen et al. (1995) suggested that these winter

copepods could never descend during late summer or early fall, and have been brought up to the surface in highly turbulent waters, and then trapped and maintained in these layers. It is now commonly accepted that an important adaptive value of vertical migration is to reduce predation risks from visually guided predators (Zaret and Suffern, 1976; Ohman, 1988; Aksnes and Giske, 1990). Dale et al. (1999) showed that *C. finmarchicus* appeared to overwinter in waters with a low abundance of planktivorous fish. Surface dwelling copepods in the marginal ice zone in winter observed in this study might stay under the ice to escape from predators.

In conclusion, our results confirm that surface dwelling *C. finmarchicus* did not feed on POM in winter, but utilized lipids stored as oil sacs, while *M. longa* and *C. glacialis* might overwinter with occasional feedings. The lipid isotopic values of *Calanus* spp. tended to decrease with decreasing relative lipid contents, and those of *Metridia* spp. showed less distinct changes in lipid isotope values. The isotopic changes of lipids with the relative lipid contents probably reflect the difference in the metabolic processes of lipid utilization of overwintering copepods in the arctic and subarctic waters.

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