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## Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea

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### ABSTRACT

The diets of krill and amphipods were examined using light microscopy on field-collected specimens from 2004 to 2005 from the Marginal Ice Zone of the northwestern Barents Sea, north and east of Spitsbergen. Stomach content analyses indicate dominant krill species to have a filter-feeding mode, whereas amphipods seem to be mainly raptorial feeders. The dominant krill, *Thysanoessa inermis*, is primarily regarded as an herbivore feeding mostly on diatoms. Alternatively, *Thysanoessa longicaudata* fed occasionally on calanoid copepods in addition to being a suspension feeder on phytoplankton. The largest of the krill species, *Meganyctiphanes norvegica*, showed a mixed diet with regular feeding on calanoid copepods and phytoplankton.

The degree of carnivory varied between stations and was determined by examining the size and shape of the mandible of copepods. *M. norvegica*, with a total length of between 26 and 41 mm, had up to two copepods in their stomachs, with a mandible width of the copepods varying from 32 to 154 μm, corresponding, respectively, to a computed prosome length of 0.3 and 2.6 mm. *Themisto libellula* fed primarily on C3 and C4 copepodite stages of *Calanus glacialis* and *Calanus hyperboreus*, and up to three copepods were found in the stomach contents of *T. libellula*. *Themisto abyssorum* fed on herbivorous and omnivorous prey such as copepods and appendicularians. The presence of *Metridia* spp. and appendicularians, e.g., *Oikopleura vanhoffeni* in the diet of *T. abyssorum* may indicate feeding in the deeper layers (>200 m).

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### 1. Introduction

Zooplankton may have a number of different feeding modes such as filtering, raptorial feeding, and scraping for food from surfaces. Zooplankton organisms are known to utilise a wide variety of food items, including algae, copepods and other zooplankton, and detritus. Recent studies indicate that individual zooplankton such as krill may change from an herbivorous diet to carnivory or vice versa, depending on the availability of different food sources (Mauchline and Fisher, 1969; Kaartvedt et al., 2002; Båmstedt and Karlson, 1998).

Studies in the Northeast Atlantic show that krill predation may contribute significantly to the mortality of *Calanus finmarchicus* (Båmstedt and Karlson, 1998). Investigations by Sullivan et al. (1975), Karlson and Båmstedt (1994), Nakagawa et al. (2001), and Giesecke and González (2004) show that by examining the size and the shape of mandibles of copepods one can determine the degree of carnivory in predators. Copepod mandibles, which are made of silica and chitin, are easily recognised under both light

and electron microscopy. The shape, size, and the number of mandibles can be used to identify and quantify copepods consumed by a predator.

The primary production in the Marginal Ice Zone (MIZ), though comparatively high, may be limited to a shorter season than in waters further south. The production of ice algae starts 1–2 months earlier than the pelagic production. These blooms fuel the energy flow in the arctic ice edge ecosystem and the carbon fixed by algae is transferred up the food chain mainly as lipids (Falk-Petersen et al., 1990; Scott et al., 1999).

More recently, studies from coastal and fjord areas in Norwegian waters on gut content of krill (*Thysanoessa* spp. and *Meganyctiphanes norvegica*) by light microscopy have answered important questions, such as the relative importance of carnivory (Båmstedt and Karlson, 1998; Kaartvedt et al., 2002), regional and diurnal differences in diet (Lass et al., 2001), or seasonal differences (Kaartvedt et al., 2002). The present study supplements information on krill diet from MIZ from the Barents Sea, where only a few studies have been carried out.

Lipid biomarkers have been used as tracers to evaluate trophic levels of Arctic zooplankton in the recent years (Scott et al., 1999; Falk-Petersen et al., 2000a; Auel et al., 2002) Though several

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studies dealing with trophic analysis of pelagic zooplankton in the MIZ based on lipid content are available (Dalsgaard et al., 2003 and references therein), rather few studies are done on microscopic investigations on their diet. Combined information on trophic patterns of zooplankton by fatty acid (FA) or stable isotope analyses and traditional method of stomach content analyses may provide a more comprehensive picture of trophic levels of these organisms.

The present study is part of a large project “Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climate change” (CABANERA), which was initiated in 2003. The objectives of this study were twofold: (a) provide regressions and keys/images to assess copepod carnivory, and (b) study trophic interactions of krill and amphipods from the MIZ.

## 2. Materials and methods

Krill and amphipods caught by the Methot Isaac Kidd (MIK) during two cruises to MIZ in the Barents Sea in 2004 and 2005 were used for diet studies (Fig. 1, Table 1). Due to the ice cover, it was not possible to tow the MIK and, only vertical hauls were taken in 2004 and 2005. As microscopy-based diet studies are very time consuming, only selected stations where species overlapped were considered. MIK is a ring trawl with a 2-m-diameter ring and a 14-m-long net. The forepart of the net was coarser with a 1.2-mm mesh size and the 1.5-m-long cod end of the net was equipped with a 500- $\mu$ m net.

To evaluate the relative abundance of larger copepods, 4%-formaldehyde-preserved MIK samples taken in 2004 and 2005 (see Dalpadado et al., 2008) were analysed.

For diet studies, krill and amphipods caught by MIK were stored in a freezer at  $-20^{\circ}\text{C}$  during the cruise and transferred to a  $-80^{\circ}\text{C}$  freezer right after the cruise. Each stomach was carefully removed and the contents were closely examined under a light microscope. In each individual, the stomachs were classified according to their degree of filling described by Nakagawa et al. (2001).

The stomach filling was defined as follows:

- stage 0—empty,
- stage 1—<25% full,
- stage 2—25–50% full,
- stage 3—50–75% full,
- stage 4—75–100% full.

The prey items were grouped into different categories: (a) diatoms/dinoflagellates, (b) copepods (presence of mandibles and appendages), and (c) other. Images of plankton in the stomachs were taken regularly to facilitate the identification process. The length of the prey organisms was measured with an image analysis system when the state of digestion permitted. After accessing the contents qualitatively, each individual was primarily grouped as a herbivore (H), a carnivore (C), or feeding on a mixture of herbivorous and carnivorous diet (HC).

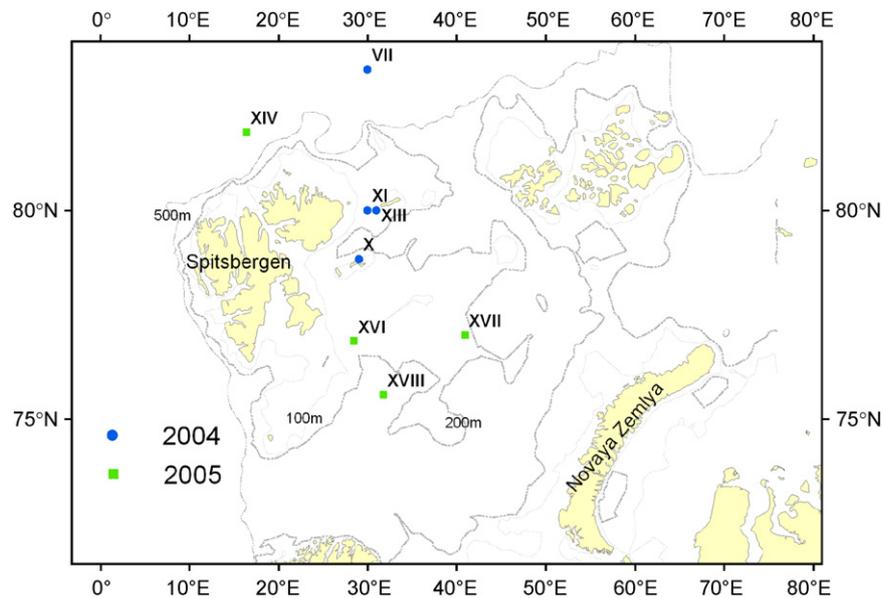


Fig. 1. Location of zooplankton stations with MIK in the MIZ during July 2004 and May 2005.

Table 1

Station information on CABANERA cruises carried out in 2004 and 2005

Year	St. no.	Month	Lat. N	Lon. E	Bottom depth (m)	Sampling depth (m)
2004	VII	7	82°23.898'	29°34.200'	3500	1000–0
	X	7	79°26.316'	28°47.730'	ca. 310	300–0
	XI	7	79°56.982'	30°15.408'	ca. 240	230–0
	XIII	7	80°07.868'	30°46.344'	ca. 200	180–0
2005	XIV	5	81°24.60'	16°24.00'	2052	1000–0
	XVI	5	77°06.00'	28°27.60'	203	193–0
	XVII	5	77°15.00'	40°55.80'	ca. 270	260–0
	XVIII	5	75°41.40'	31°46.80'	343	330–0

The ratio of phytoplankton to zooplankton (mainly copepods) was subjectively assessed after microscopic examination. If the amount of phytoplankton was very dominant (approximately >80% of the volume measured by eye), the individuals were classified as herbivores. The same applied for carnivores, if >80% of the stomach content consisted of zooplankton. If the contents had a mixed diet where the above given limits did not apply, these individuals were classified as feeding on a mixture of herbivorous and carnivorous diet. The classification of “digested green” in stomachs was used when much digested brownish/green pigments were present, and it was not possible to visually detect whether the food source was obtained from direct feeding on phytoplankton or remains of gut contents of copepods.

When examining the diet of krill and amphipods we found a variety of different shapes and sizes of mandibles in the stomachs. Mandibles would provide us with information not only of the species of copepods eaten but also of their size and stage of development. The mandible investigations in this study supplement the work of Karlson and Båmstedt (1994). We extend this study to several copepod species, e.g., *Calanus hyperboreus*, *Calanus glacialis*, and *Pareuchaeta norvegica*, in the Barents Sea and provide morphometric information of mandibles and regressions, which aids to quantify predation on copepods.

Copepod species and stages were sorted, and their prosome length and total length were measured to the nearest 0.05 mm. Copepod samples for mandible examination were from 2003 to 2004 CABANERA cruises (Dalpadado et al., 2008). The mandibles of each copepod were dissected out for further investigation. The mandibles were prepared for light-microscope studies, first by lightly staining in methylene blue and then by mounting them in gum-chloral. The size (L1, mandible width given in Karlson and Båmstedt, 1994) and mandible shape for each copepod species and stage were recorded and images of the mandible were taken. In addition, copepods in the MIK samples from 2004 to 2005 were analysed for relative abundance estimations. The copepod species were identified and their number in the whole sample was counted.

### 3. Results

#### 3.1. Shape and size of mandibles

Fig. 2 gives drawing images of mandibles of five different copepod species, *C. finmarchicus*, *C. hyperboreus*, *C. glacialis*, *Metridia longa*, and *P. norvegica*. The size and shape differed between the copepod species and stages. *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* had similar-shaped mandible blade (MB), though with different complexity of the tooth structure. These three species can be separated using the MB width, with *C. hyperboreus* generally having larger MBs than *C. finmarchicus* and *C. glacialis* (Table 2). For copepodite stages C4 and CV, the average MB widths were 121, 143; 139, 183; and 199, 242  $\mu\text{m}$ ; respectively, for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus*.

Concerning *M. longa*, the mandibles were generally smaller for copepodite stages C4 (104  $\mu\text{m}$ ) and C5 (130  $\mu\text{m}$ ) than for the *Calanus* species. However, the MB of adult females was much larger and comparable to *Calanus* spp. measured in this study (Table 2). The tooth edge of the MB of *M. longa* was more rounded and less complex in all stages, and hence can be easily distinguished from the *Calanus* species. The shape and tooth edge of the MB of *P. norvegica* were very characteristic, with deeper curved teeth at the MB edge, and can be easily distinguishable under a light microscope (Fig. 2). The shape of the mandible

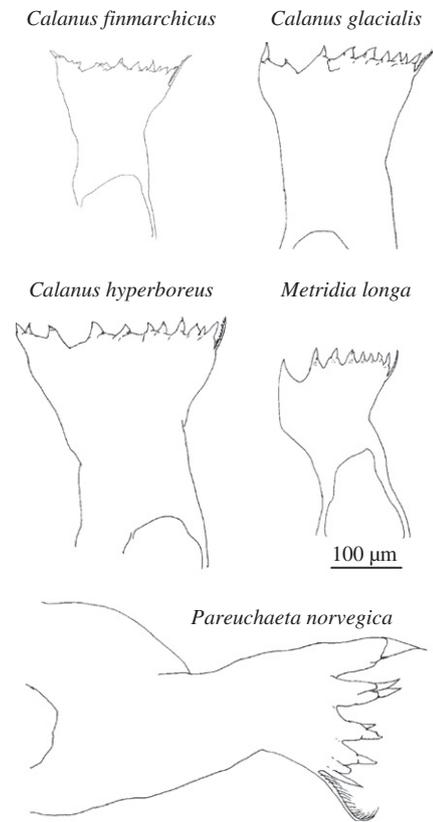


Fig. 2. Drawing images of mandibles of copepodite stage 5 (C5) for five copepod species.

Table 2

Information on mandible blade width (MB  $\mu\text{m}$ ) for different copepod species and copepodite stages (C) from 2003 to 2004 CABANERA cruises

Species	Mandible blade width ( $\mu\text{m}$ )				
	Stage	N	Minimum	Maximum	Mean
<i>C. finmarchicus</i>	C1	7	31.3	41.1	37.8
	C2	7	58.3	65.9	63.2
	C3	10	72.4	89.3	81.5
	C4	9	107.5	132.9	121.4
	C5	10	124.5	180.2	143.2
<i>C. glacialis</i>	C4	3	139.0	140.0	139.3
	C5	6	181.0	186.0	183.2
	C6F	6	209.0	227.0	218.0
	C6M	1	191.0	191.0	191.0
<i>C. hyperboreus</i>	C3	8	133.1	155.9	145.4
	C4	10	188.5	215.3	199.7
	C5	2	239.9	244.4	242.1
	C6F	1	362.0	362.0	362.0
<i>M. longa</i>	C1	4	52.9	61.7	55.8
	C2	5	64.8	71.4	67.8
	C3	3	82.8	88.6	86.3
	C4	7	98.5	108.0	104.2
	C5F	2	129.9	131.3	130.6
	C5M	2	140.4	140.4	140.4
<i>P. norvegica</i>	C6F	10	170.4	195.4	180.3
	C2	2	59.3	61.7	60.5
	C4F	2	115.6	129.2	122.4
	C5F	2	175.3	188.0	181.6
C6F	1	247.0	247.0	247.0	

of all copepod species was relatively uniform throughout the development of copepodite stages (C1–C6), though the tooth complexity amplified with ontogeny.

The regression equations between MB width and body size of copepods are given in Table 3. Fig. 3 shows the relationships between MB width (MB μm) and Prosome (PL μm) for filter-feeding copepods (*C. finmarchicus*, *C. hyperboreus*, *C. glacialis*, *M. longa*) versus carnivores (*P. norvegica*). A paired *t*-test carried out on pooled data for all stages for the different species shows that the regressions between MB and PL are significantly different between *P. norvegica* and the rest of the copepod species (Fig. 3). *Pareuchaeta* spp. is mainly a carnivore (Fleddum et al., 2001), whereas the other calanoid copepod species are mainly regarded as suspension feeders (Melle et al., 2004). These regression equations given in Table 2 and Fig. 3 were used in order to calculate the copepod size consumed by planktivorous zooplankton.

**Table 3**  
Regressions showing the relationships, mandible blade (MB) width versus prosome length (PL) of copepods, from 2003 to 2004 CABANERA cruises

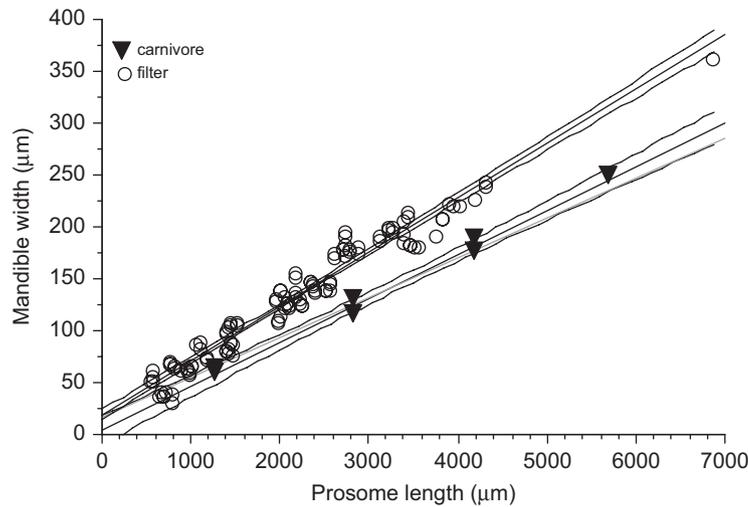
Species	Regression	N	R <sup>2</sup>	P-value
<b>Individual</b>				
<i>C. finmarchicus</i>	MB = 0.311+0.059PL	43	0.973	<0.001
<i>C. glacialis</i>	MB = 0.670+0.054PL	16	0.950	<0.001
<i>C. hyperboreus</i>	MB = 40.921+0.048PL	21	0.982	<0.001
<i>M. longa</i>	MB = 23.419+0.057PL	33	0.988	<0.001
<i>P. norvegica</i>	MB = 4.290+0.042PL	7	0.993	<0.001
<b>Pooled</b>				
Suspension feeders	MB = 19.57+0.052PL	113	0.960	<0.001
Carnivores	MB = 4.290+0.042PL	7	0.993	<0.001

3.2. Diet composition of krill and amphipods

We have examined the diet of three krill species (*Thysanoessa inermis*, *Thysanoessa longicaudata*, and *M. norvegica*) and two amphipod species (*Themisto abyssorum* and *Themisto libellula*). Among all the species examined in this study, *T. inermis* showed a diet that in most cases could be classified as a main herbivore (Table 4). However, in some cases a minor amount of dinoflagellates was observed in the diet. Many dinoflagellate species are heterotrophic; so when krills are feeding on them, it has an omnivorous feeding mode.

Next to *T. inermis*, *T. longicaudata* fed most often on phytoplankton, while occasionally preying on copepods (stations VII and XVII). Alternatively, the largest of the krill species, *M. norvegica*, preyed often on calanoid copepods in addition to phytoplankton. This is clearly evident from the data shown (Table 4). Therefore, this species was classified as a HC, with the degree of carnivory varying between stations. *M. norvegica* of total length 26–41 mm had up to two copepods in their stomachs, with a mandible width of copepods varying from 32 to 150 μm. This species fed on a mixture of calanoid copepods.

Most of the samples from the stations were taken between dusk and dawn (except for station XIV—taken in the middle of the day) and the krill had stomach filling which varied from 2 to 4. Diatoms were the most numerous phytoplankton found in the stomachs of krill. The most dominant diatoms were *Thalassiosira* spp.; however, at some northern stations (stations VII and XIV), pennate diatoms (*Fragilariopsis*, *Pseudonitzschia*, and *Navicula* spp.) were also abundant. In addition, lorica of tintinnids were found in *M. norvegica* (station XIV), and in most krill stomachs, detritus material was also present.



MB = 19.579 + .052 \* PL; R<sup>2</sup> = 0.956 (filter)  
 MB = 4.290 + .042 \* PL; R<sup>2</sup> = 0.993 (carnivore)

Paired *t*-test  
 Hypothesized difference between regressions = 0

	Mean Diff.	DF	t-Value	P-Value
MB VS PL-Total	-2089.689	119	-20.630	<0.0001
MB VS PL -Carnivore	-3055.800	6	-5.212	0.0020
MB VS PL -Filter	-2029.841	112	-20.413	<0.0001

**Fig. 3.** Regressions between mandible width (MB) and prosome length (PL) for filter feeders (*C. finmarchicus*, *C. hyperboreus*, *C. glacialis*, *M. longa*) and carnivores (*P. norvegica*). Broken lines indicate the 95% confidence intervals. The paired *t*-test values on regressions between MB versus PL are given for the total, carnivores, and filter feeders.

**Table 4**  
Diet composition of major krill species from 2004 and 2005 cruises in the Marginal Ice Zone

Year	St. no.	Date	Month	Time	Species	TL (mm)	DF	Phytoplankton	Zooplankton	Copepod iden.	Copepod no.	Other	Mode
2004	VII	24	7	330	<i>M. norvegica</i>	29	4	Diatoms/dinoflagellate					H
2004	VII	24	7	330	<i>T. inermis</i>	25	3	Diatoms/dinoflagellate					H
2004	VII	24	7	330	<i>T. inermis</i>	32	3	Diatoms/dinoflagellate					H
2004	VII	24	7	330	<i>T. inermis</i>	26	4	Diatoms/dinoflagellate					H
2004	VII	24	7	330	<i>T. longicaudata</i>	15	0						
2004	VII	24	7	330	<i>T. longicaudata</i>	12	2	Diatoms/dinoflagellate	Copepods	Appendages			HC
2004	X	28	7	2300	<i>M. norvegica</i>	41	4	Diatoms/digested green	Copepods	Mandible	1		HC
2004	X	28	7	2300	<i>M. norvegica</i>	26	4	Diatoms	Copepods	Mandible	2		HC
2004	X	28	7	2300	<i>M. norvegica</i>	36	4	Digested green	Copepods	Appendages			C
2004	X	28	7	2300	<i>M. norvegica</i>	39	4	Digested green	Copepods	Appendages			HC
2004	X	28	7	2300	<i>T. inermis</i>	24	2	Diatoms					H
2004	X	28	7	2300	<i>T. inermis</i>	23	4	Diatoms					H
2004	X	28	7	2300	<i>T. inermis</i>	22	4	Diatoms					H
2004	X	28	7	2300	<i>T. inermis</i>	17	3	Diatoms					H
2004	X	28	7	2300	<i>T. longicaudata</i>	12	2	Diatoms/digested green					H
2005	XIV	20	5	415	<i>M. norvegica</i>	24	3	Diatoms/dino cysts	Copepods	Mandible	2	Tintinnids	HC
2005	XIV	20	5	415	<i>M. norvegica</i>	29	3	Diatoms	Copepods	Appendages			HC
2005	XIV	20	5	415	<i>M. norvegica</i>	29	4		Copepods	Appendages			C
2005	XIV	20	5	415	<i>M. norvegica</i>	26	4	Diatoms	Copepods	Appendages		Tintinnids	HC
2005	XIV	20	5	415	<i>M. norvegica</i>	23	3	Diatoms	Copepods	Appendages		Tintinnids	HC
2005	XIV	20	5	415	<i>M. norvegica</i>	17	2	Diatoms					H
2005	XIV	20	5	415	<i>M. norvegica</i>	19	2	Diatoms					H
2005	XIV	20	5	415	<i>M. norvegica</i>	29	3	Diatoms	Copepods	Appendages			HC
2005	XIV	20	5	415	<i>M. norvegica</i>	26	3	Diatoms	Copepods	Mandible	1	Tintinnids	HC
2005	XIV	20	5	415	<i>T. inermis</i>	18	2	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	19	1	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	17	1	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	27	3	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	23	1	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	21	3	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	25	2	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	22	0						
2005	XIV	20	5	415	<i>T. inermis</i>	26	4	Diatoms					H
2005	XIV	20	5	415	<i>T. inermis</i>	24	0						
2005	XIV	20	5	415	<i>T. longicaudata</i>	12	0						
2005	XIV	20	5	415	<i>T. longicaudata</i>	11	0						
2005	XIV	20	5	415	<i>T. longicaudata</i>	15	3					Tintinnids	C
2005	XIV	20	5	1530	<i>T. longicaudata</i>	15	2	Diatoms					H
2005	XIV	20	5	1530	<i>T. longicaudata</i>	15	2	Diatoms					H
2005	XIV	20	5	1530	<i>T. longicaudata</i>	14	1	Diatoms					H
2005	XIV	20	5	1530	<i>T. longicaudata</i>	14	2	Diatoms					H
2005	XIV	20	5	1530	<i>T. longicaudata</i>	13	2	Diatoms					H
2005	XVI	26	5	1930	<i>M. norvegica</i>	24	4	Diatoms	Copepods	Mandible	1		HC
2005	XVI	26	5	1930	<i>M. norvegica</i>	27	1	Digested green					H
2005	XVI	26	5	1930	<i>M. norvegica</i>	33	3	Diatoms/digested green					H
2005	XVI	26	5	1930	<i>M. norvegica</i>	36	3		Copepods	Mandible	2		C
2005	XVI	26	5	1930	<i>M. norvegica</i>	35	3		Copepods	Mandible	2		C
2005	XVI	26	5	1930	<i>T. inermis</i>	23	4	Diatoms/dinoflagellate					H
2005	XVI	26	5	1930	<i>T. inermis</i>	20	4	Diatoms					H
2005	XVII	28	5	415	<i>T. longicaudata</i>	15	0						
2005	XVII	28	5	415	<i>T. longicaudata</i>	16	0						
2005	XVII	28	5	415	<i>T. longicaudata</i>	11	0		Copepods	Mandible	1		C
2005	XVII	28	5	415	<i>T. longicaudata</i>	15	2	Diatoms					H
2005	XVII	28	5	415	<i>T. longicaudata</i>	14	2	Digested green					
2005	XVIII	31	5	330	<i>M. norvegica</i>	28	4	Diatoms	Copepods	Mandible	2	Tintinnids	C
2005	XVIII	31	5	330	<i>M. norvegica</i>	33	4	Diatoms	Copepods	Mandible	2	Tintinnids	HC
2005	XVIII	31	5	715	<i>M. norvegica</i>	28	0						
2005	XVIII	31	5	330	<i>M. norvegica</i>	22	4	Diatoms	Copepods	Appendages			HC
2005	XVIII	31	5	330	<i>T. inermis</i>	23	3	Diatoms/dino cysts					H
2005	XVIII	31	5	330	<i>T. inermis</i>	22	3	Diatoms					H
2005	XVIII	31	5	330	<i>T. inermis</i>	20	2	Diatoms					H
2005	XVIII	31	5	330	<i>T. inermis</i>	24	1	Diatoms					H
2005	XVIII	31	5	715	<i>T. inermis</i>	24	4	Diatoms					H
2005	XVIII	31	5	715	<i>T. inermis</i>	24	1	Digested green					
2005	XVIII	31	5	715	<i>T. inermis</i>	26	1	Digested green					
2005	XVIII	31	5	330	<i>T. inermis</i>	24	3	Diatoms					H
2005	XVIII	31	5	715	<i>T. inermis</i>	22	4	Diatoms					H
2005	XVIII	31	5	715	<i>T. longicaudata</i>	12	2	Diatoms					H
2005	XVIII	31	5	715	<i>T. longicaudata</i>	12	2	Diatoms					H

Diet composition of individuals is classified as (a) diatoms/dinoflagellates (b) copepods and (c) other. DF = degree of stomach filling, H = Herbivore, C = Carnivore, HC = mixture of herbivore & carnivore, TL = Total length.

**Table 5**  
Diet composition of hyperiid amphipods from 2004 and 2005 cruises in the Marginal Ice Zone

Year	St. no.	Date	Month	Time	Species	TL (mm)	DF	Phytoplankton	Zooplankton	Copepod iden.	Copepod no.	Other	Mode
2004	VII	24	7	330	<i>T. abyssorum</i>	13	4		Copepods	Mandible	1		C
2004	VII	24	7	330	<i>T. abyssorum</i>	12	3		Copepods	Appendages	1		C
2004	VII	24	7	330	<i>T. abyssorum</i>	16	3		Copepods	Appendages		Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	10	4					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	12	4		Copepods	Appendages		Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	10	4					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	11	3					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	14	3					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	11	3					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	12	4					Appendicularia	C
2004	VII	24	7	330	<i>T. abyssorum</i>	16	4		Copepods	Whole	2		C
2004	X	28	7	2300	<i>T. libellula</i>	20	4		Copepods	Mandible	2		C
2004	X	28	7	2300	<i>T. libellula</i>	22	1		Copepods	Appendages			C
2004	X	28	7	2300	<i>T. libellula</i>	21	4		Copepods	Mandible	3		C
2004	X	28	7	2300	<i>T. libellula</i>	15	2	Diatoms/digested green	Copepods	Appendages			HC
2004	X	28	7	2300	<i>T. libellula</i>	15	2	Diatoms/digested green					H
2004	X	28	7	2300	<i>T. libellula</i>	26	4		Copepods	Mandible	2		C
2004	X	28	7	2300	<i>T. libellula</i>	19	4		Copepods	Mandible	2		C
2004	XI	29	7	2400	<i>T. abyssorum</i>	12	3	Diatoms/digested green					H
2004	XI	29	7	2400	<i>T. abyssorum</i>	9	3					Appendicularia	C
2004	XI	29	7	2400	<i>T. abyssorum</i>	11	3					Appendicularia	C
2004	XI	29	7	2400	<i>T. abyssorum</i>	11	3					Appendicularia/tintinnids	C
2004	XI	29	7	2400	<i>T. abyssorum</i>	9	3					Appendicularia/tintinnids	C
2004	XI	29	7	2400	<i>T. libellula</i>	19	4		Copepods	Mandible	3		C
2004	XI	29	7	2400	<i>T. libellula</i>	25	3		Copepods	Mandible	3		C
2004	XI	29	7	2400	<i>T. libellula</i>	29	4		Copepods	Mandible	1		C
2004	XI	29	7	2400	<i>T. libellula</i>	19	4		Copepods	Mandible	1		C
2004	XI	29	7	2400	<i>T. libellula</i>	20	3		Copepods	Appendages		Tintinnids	C
2004	XI	29	7	2400	<i>T. libellula</i>	17			Copepods	Mandible	2		C
2005	XIV	20	5	1530	<i>T. libellula</i>	15	0						
2005	XIV	20	5	1530	<i>T. libellula</i>	16	0						
2005	XIV	20	5	1530	<i>T. libellula</i>	32	0						
2005	XIV	20	5	1530	<i>T. libellula</i>	20	3		Copepods	Appendages			C
2005	XIV	20	5	415	<i>T. abyssorum</i>	10	3		Other				H
2005	XIV	20	5	415	<i>T. abyssorum</i>	12	2	Digested green					
2005	XIV	20	5	415	<i>T. abyssorum</i>	10	2	Diatoms					H
2005	XIV	20	5	415	<i>T. abyssorum</i>	12	3		Other				C
2005	XIV	20	5	415	<i>T. abyssorum</i>	11	3		Other				C
2005	XVI	26	5	1930	<i>T. libellula</i>	26	2		Copepods	Appendages			C
2005	XVI	26	5	1930	<i>T. libellula</i>	29	4		Copepods	Appendages			C
2005	XVI	26	5	1930	<i>T. libellula</i>	28	2		Copepods	Appendages		Tintinnids	C
2005	XVI	26	5	1930	<i>T. libellula</i>	20	4		Copepods	Appendages		Tintinnids	C
2005	XVI	26	5	1930	<i>T. libellula</i>	19	4		Copepods	Mandible	1	Tintinnids	C
2005	XVI	26	5	1930	<i>T. libellula</i>	18	4		Copepods	Mandible	1		C
2005	XVI	26	5	1930	<i>T. libellula</i>	18	3		Copepods	Appendages		Tintinnids	C
2005	XVII	28	5	415	<i>T. libellula</i>	32	4		Copepods	Mandible	1		C
2005	XVII	28	5	415	<i>T. libellula</i>	30	4		Copepods	Mandible	1		C
2005	XVII	28	5	415	<i>T. libellula</i>	29	3		Copepods	Mandible	1		C
2005	XVII	28	5	415	<i>T. libellula</i>	29	3		Copepods	Appendages			C
2005	XVII	28	5	415	<i>T. libellula</i>	30	4		Copepods	Mandible	1		C
2005	XVII	28	5	415	<i>T. libellula</i>	26	4		Copepods	Appendages			C
2005	XVII	28	5	415	<i>T. abyssorum</i>	15	2	Diatoms/digested green					H
2005	XVII	28	5	415	<i>T. abyssorum</i>	15	3	Diatoms/digested green	Copepods	Appendages			HC
2005	XVII	28	5	415	<i>T. abyssorum</i>	16	3	Diatoms/digested green	Copepods	Appendages			HC
2005	XVII	28	5	415	<i>T. abyssorum</i>	13	1	Diatoms/digested green					H
2005	XVII	28	5	415	<i>T. abyssorum</i>	16	2	Diatoms/digested green					H

Diet composition of individuals is classified as (a) diatoms/dinoflagellates, (b) copepods, and (c) other. DF = degree of stomach filling, H = herbivore, C = carnivore, HC = mixture of herbivore & carnivore, TL = Total length.

In contrast to krill, amphipods showed a more carnivorous type of diet (Table 5). Of the two amphipods, the larger (>19 mm) *T. libellula* fed almost exclusively on calanoid copepods, which appears to be the most important carbon source in the MIZ, in May and July. The width of the MBs in the stomachs ranged from 65 to 373  $\mu\text{m}$ , which corresponds to the computed prosome lengths of 1–6.7 mm (Table 6). Copepodite stages C3 and C4 of *C. glacialis* were especially numerous in the stomachs. *T. abyssorum* on the other hand showed a mixed diet. *T. abyssorum* seems to feed on copepods and other zooplankton organisms such as appendicularians (stations VII and XI). From the large size of

appendicularians tails (>6 mm) found in the stomachs and the high numbers of *Oikopleura vanhoeffeni* caught in the MIK (not shown), we deduce the stomach content to be *O. vanhoeffeni*. Occasionally phytoplanktons also were found in the diet of *T. abyssorum*.

Examination of the mandibles showed that a mixture of copepods was present in the stomachs of amphipods (Table 6). These include, *C. hyperboreus*, *C. glacialis*, *C. finmarchicus*, and *M. longa*. Among the calanoid copepods, *C. glacialis* and *C. hyperboreus* were most frequently observed, which reflects the copepods found in the water column (Table 7). Abundances

**Table 6**  
Information on copepods preyed by krill & amphipods

Species	TL (mm)	St.	MB (μm)	Species	PL (mm)	Stage
<i>M. norvegica</i>	41	X	61	<i>Calanus</i> spp.	0.88	C1
<i>M. norvegica</i>	26	X	140	<i>Metridia longa</i>	2.37	C5
<i>M. norvegica</i>		X	32	<i>Calanus</i> spp.	0.34	C1
<i>T. libellula</i>	20	X	130	<i>C. glacialis</i>	2.18	C4
<i>T. libellula</i>		X	148	<i>C. glacialis</i>	2.52	C4
<i>T. libellula</i>	21	X	209	<i>C. glacialis</i>	3.67	C6
<i>T. libellula</i>		X	169	<i>C. glacialis</i>	2.91	C4
<i>T. libellula</i>		X	148	<i>C. glacialis</i>	2.53	C4
<i>T. libellula</i>	26	X	143	<i>C. glacialis</i>	2.43	C4
<i>T. libellula</i>		X	154	<i>C. glacialis</i>	2.63	C4
<i>T. libellula</i>	19	X	158	<i>C. glacialis</i>	2.71	C4
<i>T. libellula</i>		X	84	<i>C. finmarchicus</i>	1.32	C3
<i>T. libellula</i>	25	XI	147	<i>C. glacialis</i>	2.50	C4
<i>T. libellula</i>		XI	136	<i>C. glacialis</i>	2.29	C4
<i>T. libellula</i>		XI	146	<i>C. glacialis</i>	2.47	C4
<i>T. libellula</i>	29	XI	109	<i>C. finmarchicus</i>	1.79	C4
<i>T. libellula</i>	19	XI	81	<i>C. glacialis</i>	1.26	C2
<i>T. libellula</i>		XI	113	<i>C. glacialis</i>	1.87	C3
<i>T. libellula</i>		XI	140	<i>C. glacialis</i>	2.37	C4
<i>T. libellula</i>	19	XI	84	<i>C. glacialis</i>	1.32	C2
<i>T. libellula</i>	17	XI	130	<i>C. glacialis</i>	2.18	C3
<i>T. libellula</i>		XI	137	<i>C. glacialis</i>	2.31	C4
<i>M. norvegica</i>	24	XIV	150	<i>C. glacialis</i>	2.56	C4
<i>M. norvegica</i>		XIV	145	<i>C. finmarchicus</i>	2.46	C5
<i>M. norvegica</i>	26	XIV	109	<i>Metridia longa</i>	1.79	C4
<i>M. norvegica</i>	24	XVI	154	<i>Calanus</i> spp.	2.63	C4
<i>M. norvegica</i>	36	XVI	53	<i>Metridia longa</i>	0.73	C1
<i>M. norvegica</i>		XVI	97	<i>Calanus</i> spp.	1.56	C2
<i>T. libellula</i>	32	XVII	262	<i>C. hyperboreus</i>	4.66	C6
<i>T. libellula</i>	29	XVII	180	<i>Metridia longa</i>	3.12	C6
<i>T. libellula</i>	30	XVII	373	<i>C. hyperboreus</i>	6.75	C6
<i>T. libellula</i>	19	XVI	152	<i>Metridia longa</i>	2.59	C5
<i>T. libellula</i>	18	XVI	65	<i>C. glacialis</i>	0.96	C1
<i>M. norvegica</i>	28	XVIII	121	<i>C. hyperboreus</i>	2.01	C3
<i>M. norvegica</i>		XVIII	90	<i>C. hyperboreus</i>	1.43	C2
<i>M. norvegica</i>	33	XVIII	114	<i>C. hyperboreus</i>	1.88	C3
<i>M. norvegica</i>		XVIII	118	<i>C. hyperboreus</i>	1.96	C3
<i>T. abyssorum</i>	13	VII	133	<i>Metridia longa</i>	2.24	C5
<i>M. norvegica</i>	35	XVI	92	<i>C. glacialis</i>	1.47	C2
<i>M. norvegica</i>		XVI	189	<i>C. hyperboreus</i>	3.29	C4

Copepod species, stage determination is based on information and regressions from Figs. 1 and 2, Table 3 and from literature (Kwasniewski et al., 2003). TL = total length of krill, MB = mandible blade width, PL = prosome length.

**Table 7**  
Abundance (no/m<sup>2</sup>) of copepod species in MIK during 2004 and 2005 CABANERA cruises

St. no.	<i>C. hyperboreus</i>	<i>C. glacialis</i>	<i>C. finmarchicus</i>	<i>Metridia</i> spp.	<i>Pareuchaeta</i> spp.	Sum
<b>2004</b>						
VII	482	10	133	77	51	753
X	187	974	172	110	48	1490
XI	292	1080	72	71	12	1527
XIII	25	382	36	0	4	447
<b>2005</b>						
XIV	1631	9	149	81	311	2180
XVI	43	27	3	1	42	115
XVII	1727	634	192	145	65	2763
XVIII	138	33	31	21	36	259

of copepods, based on MIK from the same stations as krill and amphipods, indicate that *C. hyperboreus* dominated in most stations in 2005, whereas *C. glacialis* dominate the stations in 2004 (Table 7). Though the carnivorous copepod *Pareuchaeta* spp. was present *in situ*, this species was not found in the stomachs of

krill and amphipods except on one occasion, which was probably owing to their larger body size. In station VII, *T. abyssorum* had fed on a smaller (C2) stage of *Pareuchaeta* spp.

#### 4. Discussion

Many studies have shown that occurrence of copepod mandibles in predator stomachs could be used as a powerful tool for identifying and quantifying the predation on copepods (Karlson and Båmstedt, 1994; Kaartvedt et al., 2002; Giesecke and González, 2004). The mandible shape, size, and tooth structure are closely associated with the feeding mode of copepods. In this study we found the carnivorous feeders (*P. norvegica*) to have relatively smaller mandibles than the herbivorous feeders (*Calanus* spp.). Giesecke and González (2004) report that the carnivorous copepods with their smaller mandibles and thus having greater agility are able to capture mobile prey effectively.

The specific mean length  $L_1$  of mandible width observed in this study for stages CI–CIII of *C. finmarchicus* was smaller than the ones reported by Karlson and Båmstedt (1994), while for stage CIV the MB width was slightly higher, and for C5 the values are similar. The mean mandible size of *M. longa* given in Karlson and Båmstedt (1994) fits well with the descriptions and size given in the current study for stage CVI (adult females). No specific pattern in the difference in mandible size between the two studies for *C. finmarchicus* was observed. The different results obtained in mean mandible size in the two studies may reflect regional differences, as the samples from Karlson and Båmstedt (1994) are from southern part of Norway (60°N) whereas the current study is from the Barents Sea (75°N). One should expect that for a given species, individuals in colder waters to be larger in size and therefore have larger mandible width than the ones in warmer waters, but these differences may not be clearly seen as the estimates also may depend on the sample size as well as the number of individuals examined within a development stage, e.g., early stage CI or late CI stage.

In the current study we found *T. inermis* to be the most herbivorous among the krill species investigated, feeding almost exclusively on diatoms at most stations in May and July. In positioning krill at different trophic levels by using lipid studies and isotope analyses, Falk-Petersen et al. (2000a) and Tamelander et al. (2008) placed *T. inermis* as a true herbivore. Studies on Pacific krill show that during spring “diatom” bloom, euphausiid species change to a phytoplankton diet. However, when phytoplankton concentrations are low, krills switch their diet mainly to copepods (Ponomareva, 1966).

Recent studies indicate that the heterotrophic prey contributed significantly to the total ingested carbon in several krill species (Buchholz et al., 1995; Båmstedt and Karlson, 1998; Lass et al., 2001; Kaartvedt et al., 2002; Nakagawa et al., 2002). Falk-Petersen et al. (2000a), in studying trophic levels of *M. norvegica* and *T. longicaudata* by measuring lipid content, concluded that they have more of a carnivorous nature and feed mostly on copepods. Virtue et al. (2000) observed *M. norvegica* from the northeast study to have high levels of copepod FA tracers. The present study indicates that the contribution by copepods, especially in *M. norvegica*, is often quite high compared to autotrophy, and that the larger *M. norvegica* (>30 mm) fed on up to two copepods within a restricted period. High feeding rates have been found both in experiments and in the field when there is abundant zooplankton food with rates of 1 and 2 copepods ind<sup>-1</sup> h<sup>-1</sup> (Båmstedt and Karlson, 1998).

We also found phytoplankton in the stomach content of *M. norvegica*, with the degree of autotrophy varying with degree

of heterotrophy. Though we have not quantified the relationship between autotrophy and heterotrophy, the stomach analysis in this study shows that *M. norvegica* that have fed on several copepods usually have less phytoplankton in their stomachs, and vice versa. Some of these phytoplanktons may have come from the copepods ingested, but some also may have been from the filtering. Studies by Lass et al. (2001) on stomach content analysis of *M. norvegica* show an omnivorous feeding behaviour, though their results showed that krill from the Clyde Sea had a more herbivorous (mainly central diatoms) diet than the ones taken in Kattegat. Their study also indicates that the krill fed in the upper layers at night on epipelagic plankton. Their observations support our findings that *M. norvegica* are opportunists, feeding on whatever they may find.

With their specialised filter-feeding basket, krill may be able to filter several litres per hour, more water than previously thought (Skjoldal et al., 2004). Phytoplankton is digested more quickly than hard-bodied zooplankton and may pass through the stomach more rapidly. This may underestimate the role of phytoplankton in the stomachs of krill. In this study, most of the of *T. longicaudata* examined had empty stomachs and only on two occasions we found this species to feed on copepods. Thus, the results on the feeding mode of this species are inconclusive. Based on the information we have, the feeding pattern of the three krill species from the MIZ could be ranked as having a more herbivorous to a more carnivorous diet, *T. inermis* → *T. longicaudata* → *M. norvegica*, mainly in line with results from other areas of north Atlantic (Båmstedt and Karlson, 1998; Lass et al., 2001; Kaartvedt et al., 2002).

Skjoldal et al. (2004) indicate that the ecological role of amphipods is of importance in the North Atlantic. In considering predator–prey interactions between fish (herring and blue whiting) and *Themisto* and between *Themisto* and *Calanus*, these authors claim that *Themisto* play a dual role as being both a competitor for food and a prey of herring and blue whiting. Several studies have shown the importance of Arctic amphipod *T. libellula* as prey for the polar cod, harp seals, and sea birds in the central Arctic waters of the Barents Sea (Lønne and Gulliksen, 1989; Nilssen et al., 1992). Close to the Polar Front, *Themisto* species are an important food source for 0–2 group cod and capelin (Panasenko, 1981; Dalpadado and Bogstad, 2004).

This study confirms the findings of other studies that have dealt with lipid biomarkers, in that adult *T. libellula* feed extensively on copepods (Auel et al., 2002; Dalsgaard et al., 2003 and references therein). The zooplankton abundance is dominated by *Calanus* species (*C. glacialis* and *C. hyperboreus*) in the high Arctic waters of the Barents Sea and thus available as the main prey of *T. libellula*. *T. libellula* is a relatively epipelagic species (<50 m), whereas *T. abyssorum* is usually restricted to mesopelagic layers (>200 m; Dalpadado et al., 2001; Auel et al., 2002).

In contrast, the deeper-living *T. abyssorum* may be feeding on more carnivorous copepods and other omnivorous and carnivorous zooplankton (Wing, 1976; Scott et al., 1999; Auel et al., 2002). Results from this study demonstrate that the food of *Themisto* species may differ, with the largest *T. libellula* feeding principally on copepods and *T. abyssorum* feeding on copepods as well as omnivorous zooplankton such as appendicularians, e.g., *O. vanhoeffeni*. In high latitudes (Beaufort Sea and Canada Basin), *O. vanhoeffeni* can be observed from the surface to deeper waters (1200 m), thus occupying several water masses of the entire water column (Raskoff et al., 2005). The highest abundance of *O. vanhoeffeni* was restricted between 300 and 700 m, with peak distributions associated to temperature maxima of the water column (Raskoff et al., 2005). *O. vanhoeffeni* is a suspension feeder with omnivorous habits (Deibel et al., 1992).

The present study indicates that within a station the diet compositions were rather uniform, indicating that they feed on what is available. Nakagawa et al. (2001) found that *Euphausia pacifica*, which has a similar life span as *T. inermis*, changes its diet according to ambient food conditions in waters northeast of Japan.

Studies by Falk-Petersen et al. (2000b) show that ice algae are predominated by diatoms, whereas open waters often contain flagellates. Scott et al. (1999) separated ice algae into two categories in the MIZ of the Barents Sea, one dominated by assemblages of *Melosira arctica* and the other dominated by *Nitzschia frigida* and associated diatoms. In station XI in 2004, *Thalassiosira* blooms were dominant. This was also reflected in the stomachs of krill by having large numbers of frustules of *Thalassiosira*. Falk-Petersen et al. (2000b), also showed that *Thalassiosira* and *Chaetoceros* spp. were two of the dominant phytoplankton from the central Arctic.

At the station furthest north, dinoflagellate cysts and ice algae *Nitzschia* spp. were also important constituents, and were found in the stomach contents of krill. Grazing on ice diatoms released into the water column by ice melting could explain the finding of these algae in krill stomachs. Stable carbon isotope composition showed that most energy assimilated by zooplankton from the MIZ originated from pelagic primary production, but when ice algae were abundant, these also contributed to zooplankton energetics (Tamelander et al., 2008). Mumm et al. (1998) also indicated that in spring, ice algae constitute a reliable food source for zooplankton in the underlying water column.

Krill are known to feed in the upper layers at night. Simmard et al. (1986) and Nakagawa et al. (2003) indicate that krill descend rapidly to deeper layers (50–250 m) just after satiation. Nakagawa et al. (2003) feeding activity might be low during daytime irrespective of its prey abundance. In common with many other zooplanktons the night feeding may be associated with being less conspicuous for its predators in the dark. We usually caught very little krill in the upper layers (see Dalpadado et al., 2008). Adult krills seem to restrict themselves mostly to Atlantic waters in the deeper layers (>100 m), irrespective of the time of the day. This may indicate that though they feed in the upper layers (indicated by phytoplankton species in their diet), they do migrate rapidly to their preferred waters and stay deep most of the time.

Stomach content analyses from this study indicate dominant krill species to have more phytoplankton in their stomachs and therefore a filter-feeding mode, feeding mainly on phytoplankton, filtering with their well-developed filter-feeding baskets. In contrast, amphipods seem to be mainly feeding on copepods and thus are raptorial feeders, capturing with their strongly developed maxillipeds. The observations made by this study seem to be consistent with feeding ecology studies of the lipid and stable isotope analyses reported for krill and amphipod species from the central Arctic (Dalsgaard et al., 2003 and references therein).

Copepod mandibles observed in the stomachs of krill and amphipods were mainly from calanoid copepods such as *C. glacialis*, *C. hyperboreus*, *C. finmarchicus*, and *M. longa*. Calanoid copepod species are regarded mainly as suspension feeders (Melle et al., 2004), and results from this study indicate that the krill and amphipod carnivory in the MIZ are mainly carried out on herbivorous copepods. In the central Arctic Ocean the biomass of meso-zooplankton was dominated by large copepods *C. hyperboreus* and *C. glacialis* (present study; Mumm et al., 1998). Another abundant arctic copepod is *M. longa* (Melle et al., 2004), which can be up to 4 mm in prosome length. *M. longa* is a deeper-living species than *Calanus* spp. (>100 m) and is known to be quite important, both in abundance and biomass in the central Arctic (Mumm et al., 1998). Krill and amphipods may prey on these copepods in the deeper layers. Due to the rather coarse mesh size

in MIK, small organisms such as the various stages of *C. finmarchicus* were not caught in quantitatively correct numbers, and therefore the copepod abundances given in this study may be underestimated.

The meso-zooplankton production in the central Arctic is much higher than previously indicated (Mumm et al., 1998). These authors claim that the reason for high secondary production in this region is most likely due to the fact that more primary production is available to secondary production than previously considered and also that the nutritional demands of zooplankton is lower than assumed in the past. The reason given above seems to indicate that the competition for food may not be great among krill species in the MIZ.

Traditional stomach content analyses may be biased due to the differential digestion rates of various prey types in the stomachs of zooplankton. The hard parts of prey such as mandibles of copepods may remain longer and may lead to an overestimation of predation on copepods. In addition, this method provides mainly qualitative information on recent feeding patterns. Nevertheless, results from this study not only show for example that *T. inermis*, *M. norvegica*, *T. libellula*, and *T. abyssorum* from the same station had different feeding modes, but also provide information on the dominant phytoplankton and zooplankton species predated on by these in the MIZ. Despite its shortcomings, the traditional stomach analyses seem to provide valuable data on feeding ecology to other trophic marker techniques such as lipid and isotope analyses.

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