SHORT COMMUNICATION

Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*

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Abstract The pelagic amphipods *Themisto abyssorum* and *Themisto libellula* represent important links between the herbivore zooplankton community and higher trophic levels of the Arctic marine food webs. Large double structured eyes of both of these hyperiid species are assumed to be used for visual prey detection. However, no information is available on the feeding strategies of these visually searching predators for the period of the polar night, a time of year with no or very low levels of daylight. Here, we report on the stomach and gut content of both *Themisto* species collected during a January expedition around Svalbard (78° to 81°N). Results indicate that *T. abyssorum* and *T. libellula* feed actively during the Arctic winter. The major food source of both amphipods consisted of calanoid copepods, most frequently *Calanus finmarchicus*.

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Introduction

Two species of the hyperiid genus *Themisto*, *T. libellula*, a typical Arctic species and its subarctic-boreal congener *T. abyssorum*, occur in the open waters of the northern polar regions (Dunbar 1957; Koszteyn et al. 1995; Dalpadado et al. 2001; Dalpadado 2002). Both are epipelagic predators and considered to be visual feeders. In their adult life stage, both feed on smaller mesozooplankton (e.g., Dalpadado et al. 2008) and act themselves as prey for marine vertebrates, for example, polar cod, little auk and seals (Wing 1976; Falk-Petersen et al. 1987, 2004, 2009; Scott et al. 1999; Auel et al. 2002; Marion et al. 2008; Renaud et al. 2012). Thus, both represent links between herbivore zooplankton and higher trophic levels in the Arctic marine food web.

Previous studies of their feeding ecology have focused on the larger one of the two, *T. libellula* (Auel et al. 2002; Dalpadado et al. 2008; Marion et al. 2008; Noyon et al. 2011, 2012). Findings included an increased storage of lipids of *T. libellula* in late summer and a diet dominated by copepodid stages III–IV of *Calanus* spp. (Scott et al. 1999; Dale et al. 2006). *T. abyssorum* on the other hand is known to have a more diverse diet including omnivorous prey such as appendicularians (Dalpadado et al. 2008).

Most of these investigations are based on spring or summer data. To our knowledge, there is no published information on the food sources and feeding strategies of these predators during the Arctic winter. This period of the year, defined here as the time period when the Sun is more than 12° below the horizon, is perceived by humans as being continuously dark. Difficulties of obtaining winter samples in the Arctic Ocean are the likely reason for this scarce information (Dalpadado et al. 2008; Berge et al. 2009). Thus, a good seasonal coverage is essential for a full

understanding of zooplankton annual routines (Varpe 2012), including their feeding activity and potential role as predators, for instance on overwintering copepods.

The aim of this study was to identify whether the pelagic amphipods *T. abyssorum* and *T. libellula* feed during the Arctic polar night and if they do, what their dominant prey is.

Materials and methods

Investigation areas

Themisto abyssorum and *T. libellula* were collected during the ARCTOS Marine ecological research cruise with *R/V Helmer Hanssen* at sampling sites in Rijpfjorden (80°18′N, 22°16′E), Sofiadjupet (81°44′N, 14°17′E) and Isfjorden (78°16′N, 15°33′E), Svalbard, from January 12 to January 18, 2012. The area around the archipelago of Svalbard is characterized as a transition zone between Atlantic and Arctic waters, with the West Spitsbergen Current as the

main pathway of Atlantic water into the Arctic Ocean, running at its western coast. This is where the sampling site of Isfjorden is located, which is strongly influenced by the inflowing Atlantic water masses (Nilsen et al. 2008). North–west of Svalbard an eastward turning branch of the West Spitsbergen Current flows along the continental slope (Rudels et al. 1999) and keeps this area around the Sofiadjupet, the "Whalers Bay," mostly ice free during winter time. Rijpfjorden is a broad shallow fjord located along the northern coast of Nordaustlandet and dominated by colder Arctic water.

Sampling and processing

Profiles of temperature, salinity and density at each sampling site were measured vertically using a Sea-Bird Electronics SBE 9 CTD sonde throughout the total water column. Water masses have been classified according to Baczewska et al. (2012) and references therein (Table 1). Daily data on down-welling irradiance (PAR, μmol m^{-2} s^{-1}) during the research cruise were provided from

Table 1 Station and amphipod composition data at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

Station position	Rijpfjorden 80°18′N, 22°16′E	Isfjorden 78°16′N, 15°33′E	Sofiadjupet 81°44′N, 14°17′E
Sampling date	January 13, 2012	January 17, 2012	January 15, 2012
Time interval (UTC)	1104–1232 hours	1957–2300 hours	0713–0900 hours
Bottom depth (m)	278	269	2257
Sampling depth (m)/water mass[b]	20/meltwater	30/meltwater	30/meltwater
Salinity (PSU)/temperature (°C)	34.24/0.36	34.34/−0.36	33.98/−1.85
	75/Arctic water	60/meltwater	500/Arctic deep water
	34.41/0.68	34.23/−1.12	34.95/1.52
	225/Arctic water	225/mixed Fram Strait water	1200/Arctic deep water
	34.57/−1.26	34.63/1.89	34.91/−0.26
Average PAR (μmol m^{-2} s^{-1} ± SD)[a]	Day (0700–1900 hours): 6.49 ± 4.08	–	–
	Night (1900–0700 hours): 7.58 ± 6.03		
Themisto abyssorum			
Depth (m)/density (ind 1,000 m^{-3})	20/60.6	30/0.4	0–1200/13.3
	75/169.3	60/2.9	–
	225/23.1	225/1.8	–
Size (total body length in mm ± SD)	11.9 ± 2.6	12.7 ± 1.7	
Themisto libellula			Absent
Depth (m)/density (ind 1,000 m^{-3})	20/16.1	30/5.1	–
	75/25.7	60/3.9	–
	225/6.7	225/0.0	–
Size (total body length in mm ± SD)	26.0 ± 5.5	22.7 ± 4.5	–

[a] Average down-welling irradiance PAR (μmol m^{-2} s^{-1} ± SD) measured during day—and nighttime hours from January 13 to January 17, 2012 at the Rijpfjorden Weather Station (80°13′N, 22°28′E) with an Iridium interface with CR1000 datalogger and Kipp & Zonen PAR LITE Quantum Sensor

[b] Dominant water mass at the three sampling sites and respective depths. Classification based on temperature and salinity (see Baczewska et al. 2012 and references therein)

SD standard deviation

the Rijpfjorden Weather Station (80°13′N, 22°28′E) using a Kipp&Zonen PAR LITE Quantum Sensor on an Iridium Satellite System. A total of 12 Methot Isaac Kidd (MIK) hauls (3.14 m^2 opening, 1.5 mm mesh size) were carried out. The net was trawled for 10 min at a speed of ~1.5 knots. Three depth intervals were sampled (20, 75 and 225 m in Rijpfjorden and 30, 60 and 225 m in Isfjorden) by doing separate hauls at each depth. Deck lights were switched on for the handling of the net winch, but these did not illuminate the net or the sampling area. Due to ice cover, no MIK tow was possible at Sofiadjupet. Instead, samples were collected using a vertically hauled WP3 net (1 m^2, 1.0 mm mesh size, 0–1,200 m depth). At Sofiadjupet, only *T. abyssorum* was present in the net. Live individuals were immediately sorted from the catch and transferred into buckets with cold seawater. To avoid post-capture feeding, all examined specimens were immediately separated from other zooplankton after the samples were collected on deck. The collected specimens were identified according to species and stage, and total body length was measured to the nearest millimeter (from the anterior side of the head to the tip of the third pair of uropods (Dunbar 1957)). After identification, all specimens were deep-frozen alive at -55 °C as soon as possible (at latest within 4 h of capture) and transferred into a −80 °C freezer after the cruise. Subsamples of 44 adult individuals of *T. abyssorum* (size range 8–15 mm) and 17 adult individuals of *T. libellula* (size range 20–32 mm) were selected for stomach and gut content analysis.

Stomach and gut content analysis

At the home laboratory, the stomach and gut of each individual were carefully removed and placed in a solution of glycerin in water. The degree of fullness was classified according to Nakagawa et al. (2000) and Dalpadado et al. (2008), with stage 0: empty, stage 1: <25 % full, stage 2: 25–50 % full, stage 3: 51–75 % full and stage 4: 76–100 % full. The prey items were examined under a light microscope and grouped into different categories based on the work of Dalpadado et al. (2008) and modified by the inclusion of the groups: amphipod appendages, fecal pellets, eggs and the parasite *Ganymedes themistos*:

1) Copepods (with the presence of mandibles and/or appendages)
2) Amphipods (presence of appendages)
3) Dinoflagellates
4) Fecal pellets/digested green
5) Eggs
6) Parasite *Ganymedes themistos* (Prokopowicz et al. 2010)
7) Unidentified

When whole prey individuals were found, their total body length was measured. All encountered copepod mandibles were photographed and their size was recorded to the nearest micrometer (mandible width L1, given in Karlson and Båmstedt (1994)) using an inverted microscope (Zeiss IM40, magnification 60–400×) and the image analysis system AxioVision40 V4.7.1 (Carl Zeiss Imaging Solution GmbH). All copepod mandibles were identified to species and stage level when possible (Table 3), following the results of Karlson and Båmstedt (1994) and Dalpadado et al. (2008).

Results

Stomach and gut content: *Themisto abyssorum*

Thirty-two out of forty-four analyzed specimens of *T. abyssorum* possessed a full or partly filled stomach and gut (Fig. 1). In 16 cases, their diet consisted predominantly of copepod residues (Table 2). This included mandibles (Fig. 2a), antennae, fragments of prosomes and other body parts in various stages of digestion. Adult female and male individuals with a total body length of 11–15 mm had up to two copepods in their stomachs. The mandible width of the exclusively calanoid copepods varied from 50 to 175 μm. Examination of the mandibles showed that *Calanus finmarchicus* was the main prey species of *T. abyssorum* at Isfjorden and Sofiadjupet (Table 3). The copepodite stages CII, CIII, CV and adults of this species were identified. At Rijpfjorden, two of the three mandible samples were damaged and could not be identified to species level. Their blade widths of 140 and 138 μm indicate that they belonged to *C. finmarchicus* CV or *C. glacialis* CIII and CIV.

Other food components included fecal pellets and a gregarine parasite, which we identified as *Ganymedes* spp.
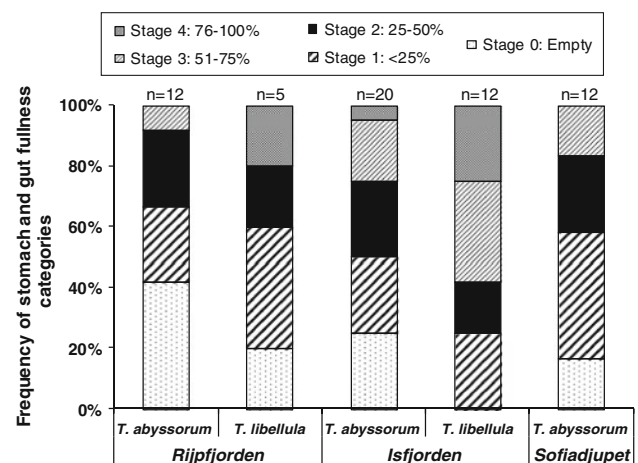
Fig. 1 Degree of gut fullness in percent for the hyperiid amphipod *Themisto abyssorum* and *Themisto libellula* at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

Table 2 Diet composition (% contribution of prey by numbers) for the hyperiid amphipod *Themisto abyssorum* and *Themisto libellula* at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

Prey item	Rijpfjorden T. abyssorum	T. libellula	Isfjorden T. abyssorum	T. libellula	Sofiadjupet T. abyssorum
Copepoda (fragments)	75.8	42.5	53.6	78.9	32.5
Amphipoda (fragments)	–	10.0	–	–	–
Dinoflagellates (whole)	0.7	–	0.4	0.8	–
Fecal pellets/digested green (fragments)	10.7	43.8	34.0	17.1	27.0
Eggs, full and empty (whole)	12.1	–	3.2	0.1	9.5
Ganymedes spp. (whole)	–	3.7	3.6	0.5	20.0
Unidentified (fragments)	0.7	–	5.2	2.7	11.0
Number of guts analyzed	12	5	20	12	12
Mean volume of gut content (mm^3)	0.8	1.4	1.1	4.2	1.1
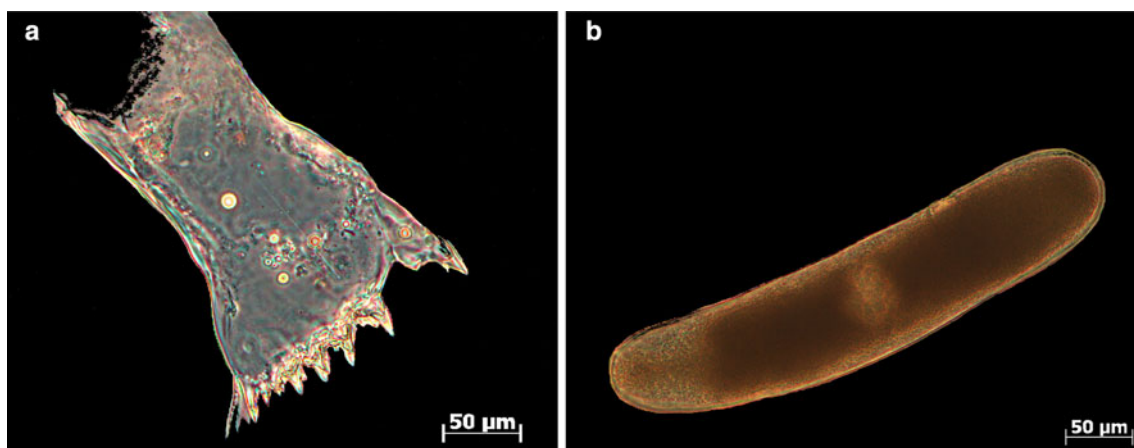
Fig. 2 Stomach and gut contents identified from winter samples of *Themisto abyssorum*; **a** mandible *Calanus finmarchicus* CV; **b** marine gregarine trophozoite *Ganymedes*

according to its morphological structure (Fig. 2b). The stages of digestion varied from moderately digested material with good recognizable features of the preferred prey such as prosomes of calanoid copepods to heavily digested material consisting mainly of fecal pellets in the fore- and midgut of *T. abyssorum*. Individuals with empty stomach were also present at all stations; most of them, however, from the cold Arctic, Rijpfjorden (Table 2).

Stomach and gut content: *Themisto libellula*

In contrast to *T. abyssorum*, almost all examined individuals of *T. libellula* possessed a (partly) filled stomach and gut at the sampling sites Rijpfjorden and Isfjorden (Table 2; Fig. 1). Similar to its congener, its diet also consisted mainly of calanoid copepods, with up to three copepods per analyzed amphipod. This included CIV, CV or adult stages of *C. finmarchicus* (Fig. 3a), *C. hyperboreus* and *Metridia longa* (Table 3) with mandible widths from 117 to 240 µm. While adult female individuals of

T. libellula with a total body length from 25 to 28 mm also possessed copepod appendages in their guts, intact mandibles were only found in the male specimens (total body length from 20 to 32 mm).

Other items found in the guts included fecal pellets and the gregarine *Ganymedes* spp. (Fig. 3b), probably *Ganymedes themistos* at both fjords. Also, varying stages of digestion of the diet were seen, with a higher amount of heavily digested material (fecal pellets, Fig. 3c) at the sampling site of Rijpfjorden (Table 2). Due to the larger size of *T. libellula*, the mean gut content of this Arctic species was nearly three times higher compared with *T. abyssorum*, with an amount of 2.8 and 1.0 mm^3, respectively.

Discussion

Within polar ecosystems, sampling conditions are harsh and the investigation of zooplankton winter life cycle strategies is a challenge in the total darkness of the polar

Table 3 Information on all encountered copepod mandibles in the digestive tract content of the analyzed hyperiids *Themisto abyssorum* and *T. libellula*

Species	Sex	Total body length (mm)	Wet weight (mg)	Mandible blade width (μm)	Species	Stage
Rijpfjorden						
T. abyssorum	M	13	25.1	140	*Calanus* spp.	–
T. abyssorum	F	10	22.4	146	*C. finmarchicus*	CV
T. abyssorum	F	11	31.1	138	*Calanus* spp.	–
Isfjorden						
T. abyssorum	M	11	30.4	175	*C. finmarchicus*	Adult
T. abyssorum	F	15	58.3	50	*C. finmarchicus*	CII
T. libellula	M	27	176.3	185	*Metridia longa*	CIV
				174	*C. finmarchicus*	Adult
T. libellula	M	20	74.3	122	*C. finmarchicus*	CIV
				117	*C. finmarchicus*	CIV
T. libellula	M	23	130.9	240	*C. hyperboreus*	CV
				135	*C. finmarchicus*	CV
				185	*C. finmarchicus*	Adult
Sofiadjupet						
T. abyssorum	F	14	40.7	78	*C. finmarchicus*	CIII
				144	*C. finmarchicus*	CV
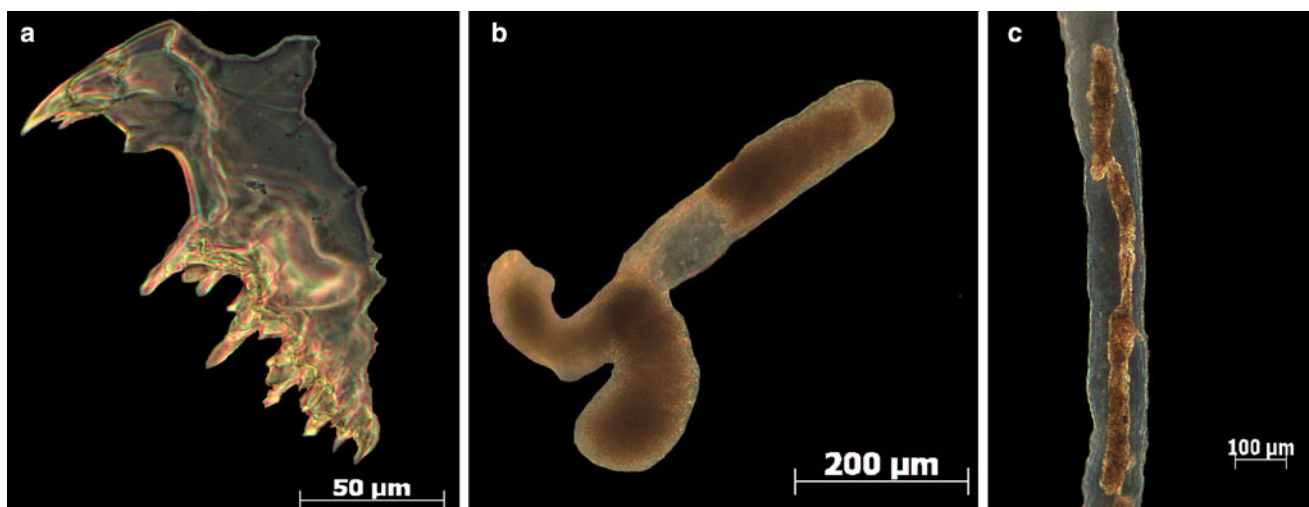
Fig. 3 Stomach and gut contents identified from winter samples of *Themisto libellula*; **a** mandible *Calanus finmarchicus* adult; **b** marine gregarine trophozoite *Ganymedes*; **c** fecal pellet in mid-gut segment

night—a time period when the sun is continually located more than 12° below the horizon. During this study, the only light source at all sampling sites was (beside the ship's deck lights) star and moonlight, with a mean irradiance of 6–7 PAR (Table 1, measured at the Rijpfjorden Weather Station). This is 100× less compared with the period of the midnight sun with a mean irradiance of ∼600–700 PAR.

With the onset of shorter daylight periods in fall, many zooplankton species such as calanoid copepods are known to descend to deeper waters and enter a state of winter dormancy (diapause) (e.g., Hirche 1991, 1996; Kosobokova 1999; Wold et al. 2011). Other species such as the

carnivorous hyperiid *Themisto* have been suggested to maintain their active mode of life also during the winter (e.g., Dale et al. 2006). However, evidence on their feeding strategy has been missing.

Our study suggests active feeding in both species during the polar night. The food items identified consisted predominantly of calanoid copepods and did not differ substantially between the sampling sites. With adult and CV stages of *C. finmarchicus* found in the diet of both species (Table 3), our results indicate at least a partial overlap in terms of food sources. *T. libellula* also seemed to prey upon other copepod species such as *C. hyperboreus*

and *Metridia longa*. The traditional analysis of digestive tract contents is used in numerous studies to give a first insight into the feeding modes of different species, including fish and zooplankton (e.g., Dalpadado et al. 2008). While the stomach and gut content analysis is expected to provide reliable qualitative results regarding the kind of prey, the semi-quantitative estimates using this method have to be treated with caution as predation rates may be over- or underestimated. This is due to the variable physical properties and thus differing digestion rate of the prey contents. In this study, the digestive tract content of both investigated amphipods showed moderately to advanced stages of digestion. With the known average digestion rate of *Themisto* to be 7.5–13 hours (Pakhomov and Perissinotto 1996; Marion et al. 2008), we suggest that our results present a good qualitative assessment of the recent food uptake of *T. abyssorum* and *T. libellula* during the polar night.

Our results stand in contrast to two studies, which compared the feeding modes of *T. abyssorum* and *T. libellula* in Arctic waters during summer and fall (Auel et al. 2002; Dalpadado et al. 2008). Both studies suggested that their diet differed, with extensive feeding on copepods by *T. libellula* (also shown by, for example, Scott et al. (1999), Marion et al. (2008), Noyon et al. (2011, 2012)) and a broader food spectrum for *T. abyssorum*. The latter has been shown to possess a mixed diet by preying upon copepods as well as other zooplankton groups such as appendicularians (Dalpadado et al. 2008). The authors concluded that this mixed diet of *T. abyssorum* is a possible consequence of its broad vertical distribution in the water column (reaching down to 2,000 m depth) and its association with warmer, Atlantic water (Koszteyn et al. 1995; Dalpadado 2002). Our study showed a rather similar diet composition with a clear dominance of calanoid copepods, indicating no difference in prey selectivity among the two species during winter. The diet appeared to be complemented by intraspecific cannibalism as well as the feeding on dinoflagellates. With the latter, however, it remains unclear if the amphipods fed directly upon them or if they were digested with the copepod prey. Also, the origin of the ingested eggs remains unclear (Table 2).

Assemblages of lipid-rich calanoid copepods were present throughout the water column at the three sampling sites in January (personal observations), thus being available as a food source for *Themisto*. These populations were sampled with a multinet (Hydrobios, 0.25 m² opening, mesh size 200 μm) at five depths (260, 200, 100, 50 and 20 m) and will be analyzed for mesozooplankton species composition, vertical and size distribution (to be reported in a separate publication). The highest densities of *Themisto* were observed within the upper 75 m of the water column (Table 1). Therefore, the hyperiids may play a role

in the control of mesozooplankton communities also during the Arctic winter.

The presence of the gregarine trophozoite *Ganymedes* spp., probably *G. themistos*, in both amphipod species was unexpected. While this parasite has been previously recorded and was newly described from *T. libellula* samples collected in the Canadian Arctic (Prokopowicz et al. 2010), to our knowledge our study is the first to document its appearance in *T. abyssorum* (Fig. 2b). Leander (2008) described the group of marine gregarines as single-celled, host-specific organisms, which inhabit the intestines of invertebrates and can reach large sizes. Because of this host specificity, we recognize the necessity to genetically compare the parasites in order to reach a reliable conclusion if the same species (*G. themistos*) infects both *Themisto* species. In our study, most amphipod individuals, which contained *Ganymedes* in their digestive tract also had other food items (including copepod mandibles) present. Therefore, we agree with Prokopowicz et al. (2010) that this trophozoite infection does not seem to have a significant impact on the feeding and survival of *T. libellula*. Furthermore, we suggest that the same is also true for its congener *T. abyssorum*.

Our findings of active feeding raise questions concerning the mechanism that enables these supposedly visual predators to hunt during the polar night. A characteristic feature of hyperiid amphipods are the large, double structured eyes which possess special upward-pointing regions covering a narrow field of view (Land 1989, 2000). Land (2000) suggested that these regions are an adaptation to the task of detecting small objects against the dim down-welling light in the water column. As little down-welling light is available at high latitudes during the Arctic winter (with the exception of the periodic moonlight events), this part of the eye structure may only play a small part in the active foraging strategy of *Themisto* during this time of the year if at all. The lower part of the eyes is considered to be used to detect bioluminescent sources, whose brightness would show only little variation with depth (Land 1989, 2000). We found one specimen of a bioluminescent copepod in the digestive tract of the analyzed amphipods, *Metridia longa* (Table 3). There is the opportunity that *Metridia* itself could provide background illumination, a concept suggested for other visual predators, for example, polar cod (*Boreogadus saida*) (Benoit et al. 2010). Berge et al. (2012) recently documented the presence of small bioluminescent dinoflagellates retaining metabolic rates that enable them to produce light also during the polar night. It is a possibility that *Themisto* uses this illumination to actively prey on copepods. Beside the visual aspect, feeding modes of hyperiids may also depend on mechanical, tactile and olfactory stimuli. Carnivorous zooplankton including copepods of the genus *Euchaeta*, scyphozoan

jellyfish and siphonophores have been shown to use tactile stimuli over vision, tracking the vertical movements of their prey. This enables them to prey upon zooplankton equally well under darkness and daylight conditions (Hays 2003). However, because of the lack of investigations it still remains unclear to what degree tactile or other impulses such as olfactory or mechanical ones are important in the feeding strategy of *Themisto*. Our observations of active feeding during dark conditions suggest that alternatives to visual search may be more important than previously acknowledged. We suggest further studies, including controlled laboratory investigations, of the potential role of tactile or other prey search mechanisms in *Themisto* spp. in order to understand to what extent a pelagic predator relies on visual search.

Conclusion

Our results showed that the Arctic hyperiids *T. abyssorum* and *T. libellula* are active raptorial feeders during the polar night. The most important prey items consisted of calanoid copepods such as *Calanus finmarchicus*. In addition, we present first evidence of a marine gregarine infection within the hyperiid *Themisto abyssorum*.

References

Auel H, Harjes M, da Rocha R, Stubing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374–383

Baczewska A, Blachowiak-Samolyk K, Angel M (2012) Distribution of pelagic Ostracoda (Crustacea) inhabiting the waters around Svalbard (Arctic Ocean: 76°36–81°50 N). Hydrobiologia 688: 75–92

Benoit D, Simard Y, Gagne J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. Polar Biol 33:1505–1520

Berge J, Cottier F, Last KS, Varpe Ø, Leu E, Soreide J, Eiane K, Falk-Petersen S, Willis K, Nygard H, Vogedes D, Griffiths C, Johnsen G, Lorentzen D, Brierley AS (2009) Diel vertical migration of Arctic zooplankton during the polar night. Biol Lett 5:69–72

Berge J, Båtnes AS, Johnsen G, Blackwell SM, Moline MA (2012) Bioluminescence in the high Arctic during the polar night. Mar Biol 159:231–237

Dale K, Falk-Petersen S, Hop H, Fevolden SE (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol 29:1063–1070

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656–666

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876–895

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266–2274

Dunbar MJ (1957) The determination of production in the northern seas: a study of the biology of *Themisto libellula* Mandt. Can J Zool 35:797–819

Falk-Petersen S, Sargent JR, Tande KS (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. Polar Biol 8:115–120

Falk-Petersen S, Haug T, Nilssen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res 23:43–50

Falk-Petersen S, Mayzaud P, Kattner G, Sargent J (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5:18–39

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163–170

Hirche HJ (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. Polar Biol 11:351–362

Hirche HJ (1996) Diapause in the marine copepod *Calanus finmarchicus*. Ophelia 44:129–143

Karlson K, Båmstedt U (1994) Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Mar Ecol Prog Ser 108:79–89

Kosobokova KN (1999) The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. Polar Biol 22:254–263

Koszteyn J, Timofeev S, Weslawski JM, Malinga B (1995) Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in the European Arctic Seas. Polar Biol 15:85–92

Land MF (1989) The eyes of hyperiid amphipods: relations of optical structure to depth. J Comp Physiol Sensory Neural Behav Physiol 164:751–762

Land MF (2000) On the functions of double eyes in midwater animals. Philos Trans R Soc Lond Ser B-Biol Sci 355:1147–1150

Leander BS (2008) Marine gregarines: evolutionary prelude to the apicomplexan radiation? Trends Parasitol 24:60–67

Marion A, Harvey M, Chabot D, Brethes JC (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system Canada. Mar Ecol Prog Ser 373:53–70

Nakagawa Y, Endo Y, Taki K (2000) Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan. Plankton Biol Ecol 48:68–77

Nilsen F, Cottier F, Skogseth R, Mattsson S (2008) Fjord–shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic Water in Isfjorden, Svalbard. Continent Shelf Res 28:1838–1853

Noyon M, Narcy F, Gasparini S, Mayzaud P (2011) Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. Mar Biol 158:883–892

Noyon M, Narcy F, Gasparini S, Mayzaud P (2012) Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). Mar Biol 159:805–816

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudi* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91–100

Prokopowicz AJ, Rueckert S, Leander BS, Michaud J, Fortier L (2010) Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp n. (Apicomplexa, Eugregarinorida). Pol Biol 33:1339–1350

Renaud P, Berge J, Varpe Ø, Lønne O, Nahrgang J, Ottesen C, Hallanger I (2012) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biol 35:401–412

Rudels BJ, Friedrich H, Quadfasel D (1999) The Arctic circumpolar boundary current. Deep-Sea Res II 46:1023–1062

Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biol 21:65–70

Varpe Ø (2012) Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. J Plankton Res 34: 267–276

Wing BL (1976) Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan waters. Northwest Fisheries Center Processed Report, Seattle

Wold A, Darnis G, Soreide JE, Leu E, Philippe B, Fortier L, Poulin M, Kattner G, Graeve M, Falk-Petersen S (2011) Life strategy and diet of *Calanus glacialis* during the winter-spring transition in Amundsen Gulf, south-eastern Beaufort Sea. Polar Biol 34:1929–1946