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ORIGINAL PAPER

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Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords

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Abstract Population structure, growth and body composition (wet-, dry-, ash weight and total lipid) of the Arctic pelagic amphipod *Themisto libellula* were studied in four fjords on West Spitsbergen, Svalbard, from July to December 2000 and in April 2002. In one of the fjords, Kongsfjorden, growth of *T. libellula* was calculated as the change in mean length of the 0+ cohort from July to December. The young were released from the brood pouches in early spring (March–April). Summer growth was 3.5 mm $month^{-1}$, whereas growth during the autumn was only 0.6 mm $month^{-1}$. The size frequency distributions indicated a 2–2.5 year life-span. The size structure of the population in Hornsund, the southernmost fjord on Spitsbergen, indicated a delayed time of spawning. The storage of lipids in *T. libellula* occurred during late summer and towards the winter, when the food items contain the maximum amount of stored lipids.

Introduction

Themisto libellula (Lichtenstein 1822) is widely distributed in the Arctic (Bowman 1960) and regarded as a good indicator of Arctic water (Dunbar 1946, 1957; Koszteyn et al. 1995; Dalpadado 2002). This pelagic hyperiid amphipod is important in Arctic marine pelagic food webs and is characterized as carnivorous, feeding primarily on copepods (Wing 1976), occasionally cannibalistic and possibly consuming phytoplankton as juveniles (Dunbar 1946; Bowman 1960). Thus *T. libellula* forms a key link between smaller zooplankton and higher trophic levels. This amphipod is an important food for marine vertebrates such as polar cod (*Boreogadus saida*) and little auks (*Alle alle*) (Lydersen et al. 1989; Lønne and Gulliksen 1989; Lønne and Gabrielsen 1992), as well as ringed and harp seals (*Phoca hispida* and *P. groenlandica*) (McLaren 1958; Lydersen et al. 1991).

Life history parameters of *T. libellula* have been reported from studies around the marginal seas of the Arctic. In the European Arctic water, a 3-year life-span has been suggested (Koszteyn et al. 1995), whereas a 2-year life-span was suggested in the Barents Sea by Dalpadado (2002) and in Hudson Bay and southeast of Baffin Island by Dunbar (1957). However, Wing (1976) suggested a 1-year life cycle for *T. libellula* in the Alaskan costal waters. Newly released juveniles from the brood pouches have a length of approximately 2–4 mm (Dunbar 1957; Wing 1976; Dalpadado 2002), and the peak release of juveniles is in spring/early summer (March–May) (Wing 1976; Percy 1993; Dalpadado 2002). Sexual maturation occurs at a body-length between 19 and 29 mm (Dunbar 1946; Bowman 1960; Percy 1993).

The objectives of this study were: (1) to outline the size structure and growth of *T. libellula* in different fjords on Spitsbergen with emphasis on Kongsfjorden, and (2) determine the body composition in terms of wet weight, dry weight, ash and total lipid contents of *T. libellula* of the age group 0+ in Kongsfjorden.

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Material and methods

Study area

The investigation of *T. libellula* was carried out in fjords on Spitsbergen from July to December 2000 and in April 2002 (Table 1; Fig. 1). In summer 2000, samples were

Table 1 *Themisto libellula*: sample date, station designations, position and gear used, July–December 2000 and April 2002

Date	Station	Position	Gear
Kongsfjorden			
7/23/2000	K5	78°53′N 12°28′E	TT
7/24/2000	K2	78°58′N 11°44′E	TT
7/23/2000	K0	79°03′N 11°08′E	TT
7/27/2000	B8	78°55′N 09°35′E	TT
Van Mijenfjorden			
7/29/2000	V3	77°45′N 15°14′E	TT
7/29/2000	V5	77°49′N 16°38′E	TT
Hornsund			
7/31/2000	H1	76°57′N 15°20′E	TT
7/31/2000	H2	77°00′N 16°02′E	TT
7/31/2000	H3	77°00′N 16°02′E	TT
Kongsfjorden			
9/19/2000	K2	78°58′N 11°44′E	TT
9/19/2000	K2	78°58′N 11°44′E	PT
9/20/2000	K0	79°03′N 11°08′E	TT
Wijdefjorden			
9/20/2000	W3	79°06′N 16°01′E	TT
9/20/2000	W3	79°06′N 16°01′E	PT
9/21/2000	W1	79°50′N 15°14′E	TT
Kongsfjorden			
12/4/2000	K2	78°58′N 11°44′E	TT
12/4/2000	K0	79°03′N 11°08′E	TT
Kongsfjorden			
4/18/2002	K15	79°01′N 10°54′E	TT

TT = Tucker trawl, *PT* = Pelagic trawl

taken from Kongsfjorden, Van Mijenfjorden and Hornsund. In autumn 2000, samples were taken from Kongsfjorden and Wijdefjorden. Additional samples were obtained from Kongsfjorden in winter 2000 and in April 2002. Both population structure and body composition were studied in Kongsfjorden in July, September and December 2000. For the other fjords, only population structure was studied.

Kongsfjorden is an open fjord with no sill (Fig. 1), and with strong advection involving relatively warm and saline Atlantic water between the shelf and the fjord (Loeng 1991; Svendsen et al. 2002). Modifications through local processes and mixing with cold Arctic water result in transformed Atlantic water in West Spitsbergen fjords (Svendsen et al. 2002)

Hornsund is the southernmost fjord of Svalbard (Fig. 1). It is under the direct influence of both Atlantic water from the West Spitsbergen Current (WSC) and cold costal water from the South Cape Current (SCC) (Swerpel 1985). The fjord is described as a cold fjord because of the persistently large influence of cold Arctic water. It has a high pelagic production, is rich in large plankton, and provides good feeding grounds for sea birds (Weslawski et al. 1991).

Van Mijenfjorden is situated on the West Spitsbergen coast, north of Hornsund (Fig. 1). The fjord is divided into two basins by sills. The mouth of the fjord is partly blocked by the rocky island, Akseløya, which reduces water exchange between the fjord and the shelf (Gulliksen et al. 1985).

Wijdefjorden is the longest fjord on Spitsbergen (Fig. 1). It has a deep inner basin that is rather isolated

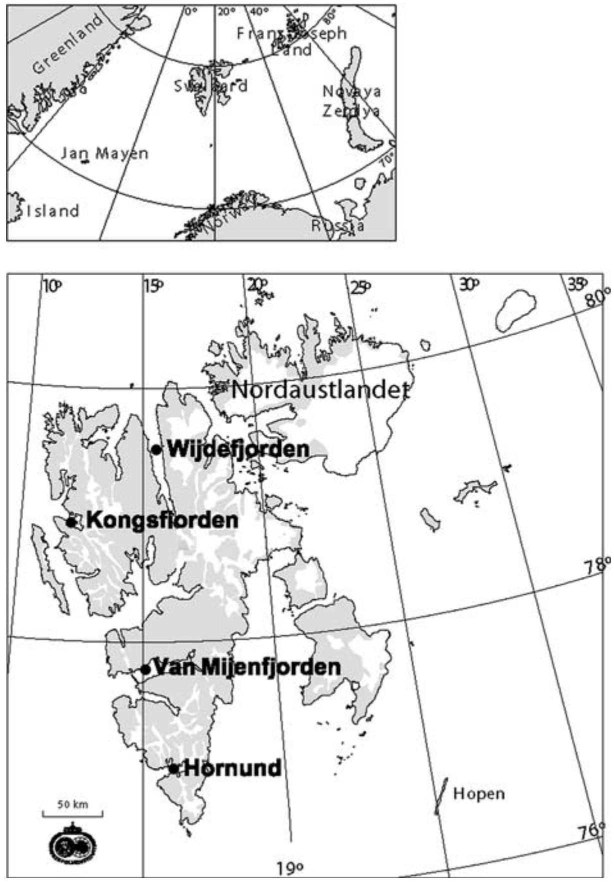

Fig. 1 Map of Svalbard with sampling locations (*filled circle*)

from the rest of the fjord by a shallow sill. The WSC, which transports relatively warm Atlantic water to the north of Svalbard, also influences this fjord.

Sampling

Samples were collected during four cruises (Table 1): in 2000 mid-summer (July) with RV *Oceania*, in autumn (September) and winter (December) with RV *Jan Mayen*, and in spring (April 2002) with RV *Lance*. A Tucker trawl with 1.4 m^2 mouth opening and 1 mm mesh size was used to collect the amphipods for the present study. The trawl was towed horizontally for 15 min at two knots for each sample. Two hauls were taken on each station; one haul for the population dynamics study and one haul for body composition study. In addition, a pelagic trawl was used for sampling during the cruise in autumn. The opening of the pelagic trawl was 11 × 40 m and the mesh size in the cod end was 4 mm. The trawl was towed with a speed of three knots for 30 min. Individuals used for the body composition study were picked from a bucket of seawater, and carefully dried off before being packed, in tens, in small plastic bags and frozen at −20°C. Samples for population dynamics were fixed with 4% formaldehyde in seawater buffered with hexamine.

Large samples were sub-sampled by splitting the samples into two or more by a box-type plankton splitter (Motoda 1959). Body length of *T. libellula* was measured (to the nearest mm) from the anterior margin of the head to the end of the uropod. Individuals < 12 mm were classified as juveniles. Animals in the size class 12–19 mm could be either classified as male, based on segmentation and length of the first antenna (Dunbar 1957), or female, and are referred to as sub-adults (Fig. 2). Population composition and sex ratio (F:M) calculations are based on adults with reliable antenna characteristics, and immatures (< 20 mm) as a group including juveniles and sub-adults. Females with eggs in the marsupium were also noted.

Body composition

The frozen individuals were slowly thawed in seawater at a temperature close to 0°C. Each individual was length measured, carefully blotted on filter paper to remove excess seawater and weighed (0.1 mg) in small aluminum trays (WW). Samples were dried in an oven at 60°C for 24 h and then cooled to room temperature before weighing (DW). Ash weight (AW) was measured on a full size range of specimens. Individuals were burned in a muffle oven at 540°C for 8 h, and cooled to room temperature prior to weighing. Total lipid was extracted from dried tissue of whole individuals (Folch et al. 1957). The dried tissue was put into a tube and gently crushed before adding 3 ml chloroform/methanol (2:1). After about 30 min, the mixture was centrifuged at 4,000 rpm for 10 min. The lipophilic phase was transferred into a 15 ml centrifuge tube and extracted twice with 3 ml of chloroform/methanol (2:1) resulting in approximately 9 ml of solution in the tube. After diluting to 10 ml, a salt solution (2 ml 9‰ NaCl) was added and the sample spun for 10 min at 3,000 rpm. The upper water phase was removed with a suction pipette. Each sample was dried for 24 h at 50°C, and then weighed (0.1 mg) in room temperature for determination of total lipid.

Data analyses

Size frequency distributions were used to determine the population structure and cohort(s) in the fjords. Samples

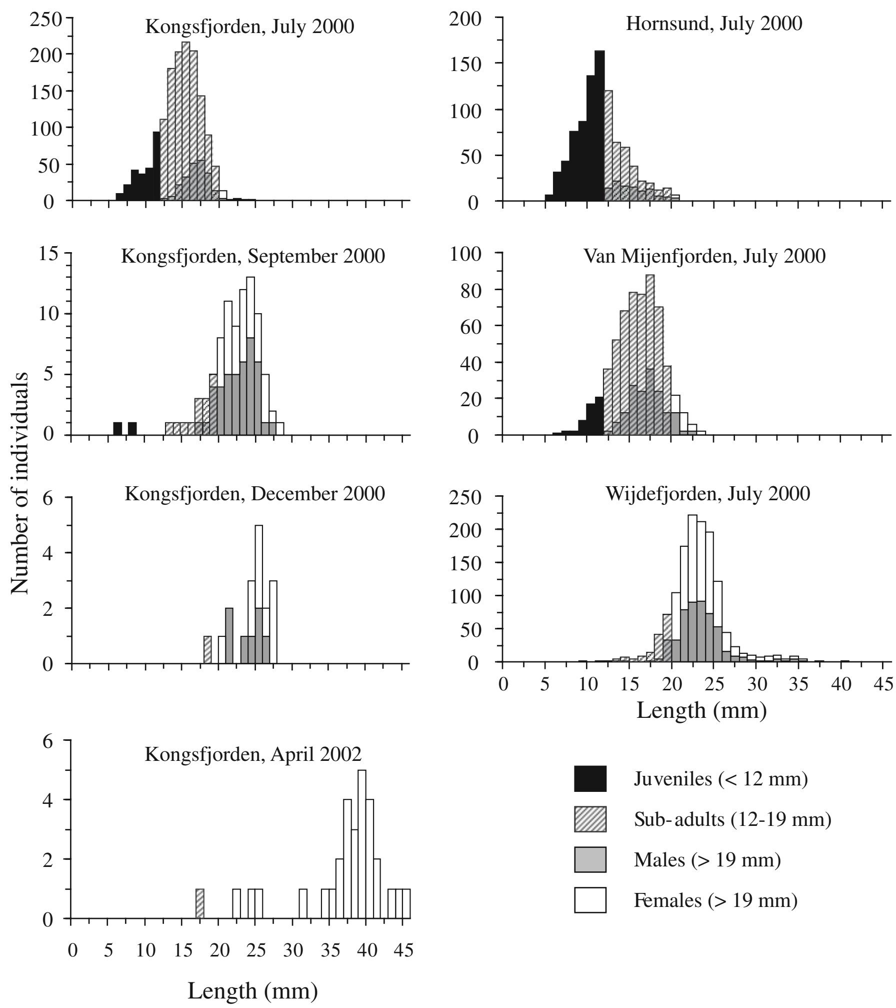

Fig. 2 *Themisto libellula*. Length frequency distribution from different Spitsbergen fjords, from July to December 2000 and April 2002. Note the differences in scales on the *y*-axes. The *hatched bars* indicate sub-adults with uncertain sex characteristics

were pooled from all stations in each fjord on the same cruise. The mean lengths (±SD) of each cohort were used to calculate growth between months. Back calculation of growth was performed to determine the time of release from the brood pouches. In Wijdefjorden, evidently more than one cohort existed, and to derive the cohorts from size-frequency data, a distribution mixture analysis program "MIX" was used (MacDonald and Green 1988). Maximum likelihood estimates from the grouped data were derived (MacDonald and Pitcher 1979). The program was run in an interactive mode, by stepwise optimization of certain variables.

Individuals representing the 0+ cohort in length from July to December were used for the body composition survey. The mean total body lengths for individuals were 16 mm in July, 20 mm in September and 24 mm in December. Length–weight data for body composition (wet weight, dry weight, total lipid and ash weight) were represented by the regression equation:

$\log W = \log a + b (\log L)$, where W = weight and L = total length, $\log a$ is the intercept and b the slope of the regression line. Each regression was tested for significance by ANOVA ($P = 0.05$). In order to eliminate length as a variable when comparing populations with different means length, a standardized animal of length 18 mm was used; it was represented in the population between July and December in Kongsfjorden. The change in each body composition variable was then calculated by regression for the different time periods, based on the standardized animal. Percent total lipid of dry weight and percent ash weight of dry weight were also calculated for the respective months.

Results

Population dynamics

The length–frequency histograms for *T. libellula* showed three distinct cohorts for the period July–December 2000 and April 2002 (Fig. 2). The most pronounced peak that appeared in all samples was stated to be the 0+ cohort in 2000. In Wijdefjorden, some larger individuals were also present, representing the 1+ cohort. Samples from Kongsfjorden in April 2002 showed a peak of a cohort that was considered to be the 2+ cohort.

In Kongsfjorden, the cohort of the year (0+) had a mean length of 14.2 (±2.9) mm in July (Table 2). This cohort had increased to a mean length of 22.0 (±4.0) mm in September and to 23.7 (±2.6) mm in December. In April 2002, the cohort 2+ had a mean length of 36.4 (±6.4) mm.

Hornsund and Van Mijenfjorden also showed distinct 0+ cohorts in July with mean lengths of 11.2 (±2.9) mm and 15.0 (±2.8) mm, respectively (Table 2).

The two cohorts (0+ and 1+) of the population in Wijdefjorden in September had mean lengths of 22.0 (±2.8) mm and 32.0 (±2.6) mm, respectively (Table 2).

In Kongsfjorden, the 0+ cohort grew to 7.8 mm from July to September, which corresponds to a growth rate of 3.9 mm $month^{-1}$. From September to December the same cohort grew to 1.7 mm, or 0.6 mm $month^{-1}$ during the autumn (Table 2). In Wijdefjorden, the difference between mean length of cohort 0+ and 1+ was 10.0 mm in September. Assuming a full year between these two groups, this implies a monthly growth rate of 0.8 mm.

In Kongsfjorden, immatures were much more abundant in July (99%) than in September (19%) (Table 2). In December, only 6% immatures were present. For individuals of 20 mm and longer, the sex ratio was quite stable with 1.0 in September and 1.4 in December, but with a dominance of females in July based on a sex ratio of 2.5. Only one female (21.0 mm) with juveniles in the marsupium was recorded in September. In Hornsund, immatures also dominated the population with 99%. The sex ratio was 1.0 for the mature individuals represented by only six individuals 20 mm and longer. The population in Van Mijenfjorden consisted of 93% immatures in July. Females carrying juveniles in the marsupium were present ($n = 5$). Most of the immatures (> 95%) were in the sub-adult category, except for Kongsfjorden and Hornsund in July, with 10 and 42% juveniles, respectively.

A relatively even sex ratio of 1.5 was observed for the population in Wijdefjorden in September. There were only a few immatures (12%) present in the population.

Table 2 *Themisto libellula*: population composition (%), sex ratio female/male (F:M) and mean length ± SD (mm) of age class based on size-frequency distributions from Spitsbergen fjords during July–December 2000 and April 2002

Fjord	Month	Year	*n*	Immatures (%)	Females (%)	Males (%)	Females w/egg (%)	Sex ratio (F/M)	Age class 0+ (mm)	Age class 1+ (mm)	Age class 2+ (mm)
Kongsfjorden	July	2000	1,461	98.6	1.0	0.4	0.0	2.5	14.2 ± 2.90		
Kongsfjorden	September	2000	88	19.0	40.0	41.0	1.1	1.0	22.0 ± 4.00		
Kongsfjorden	December	2000	18	6.0	55.0	39.0	0.0	1.4	23.7 ± 2.60		
Kongsfjorden	April	2002	32	3.0	97.0	0.0	0.0				36.4 ± 36.4
Hornsund	July	2000	896	99.0	0.5	0.5	0.0	1.0	11.2 ± 2.90		
Van Mijenfjorden	July	2000	600	93.0	4.3	2.7	0.7	1.6	15.0 ± 2.80		
Wijdefjorden	September	2000	1,321	11.5	52.5	36.0	1.9	1.5	22.0 ± 2.80	32.0 ± 2.60	

n is the number of individuals (females w/eggs are in percentage of all females in the sample). Immatures include juveniles (< 12 mm), and sub-adults (12–19 mm) with uncertain sex

Females ($n = 24$) with eggs in the marsupium represented 2% of the total number of females in the sample (Table 2).

Body composition

For all months, there was a positive relationship that existed between length and wet- and dry-weight and total lipid (ANOVA, $P < 0.05$; Table 3). Ash weight was significantly related to length in July but not in September.

The estimated growth, of a standardized animal, was positive for wet- and dry-weight and total lipid from July to September (Fig. 3). Wet weight increased from 50.1 mg in July to 51.9 in September but decreased to 47.2 mg in December. Dry weight showed a similar increase from 11.2 mg in July to 13.7 mg in September and decreased to 11.9 mg in December. Total lipid content increased from 2.6 mg in July to 4.1 mg in September and further up to 4.5 in December. Percent total lipid of dry weight decreased from 30.7% in July to 25.1% in September and decreased further to 21.9% in December, whereas the percent ash weight decreased from 27 to 24% between July and September (Table 4).

Discussion

Population dynamics

Relatively little is known about when *T. libellula* is mating and how long the broods are kept in the brood pouch. Females dominated in Kongsfjorden in July and one gravid female appeared in the sample in September. Females with broods were also observed in Wijdefjorden in September, but no broods were left in April. Thus, females probably mature during their first year and mate during autumn and winter. The broods are then released from the brood pouches during early spring. Back-calculated growth rate for July–September indicates that *T. libellula* releases its broods in March–April. This is supported by Dunbar (1957) and Dalpadado (2002), who found newly released 2–3 mm long juveniles during March–April in the Canadian Arctic and the Barents Sea, respectively. The strategy of releasing broods to match with the spring bloom is likely an adaptation to the strong seasonality in food supply in the Arctic (Clarke 1992). This may be valid for the initial release of juveniles. The reproductive strategy for Arctic zooplankton may also include large eggs, which allow for the larva to proceed to an advanced stage before hatching (Clarke 1992). An alternative strategy applied by amphipods is to let the broods hatch in the brood pouch before being released as self-reliant individuals. This is in agreement with females carrying broods already in September, even though the release of the broods may occur half a year later in March–April. Population studies of *T. libellula* in Canadian Arctic waters (Dunbar 1957; Percy 1993) and Southeast Alaska (Wing 1976) showed that the peak release of juveniles occurs in spring/early summer. A later release in the Canadian Arctic may be due to delayed blooms related to the melting of sea ice, which occurs later than in Svalbard fjords.

Studies in the European Arctic suggest that *T. libellula* has a life span of 2–3 years (Koszteyn et al. 1995; Dalpadado 2002). In the Canadian Arctic, *T. libellula*

Table 3 *Themisto libellula*

	n	b	SE	Lower CI	Upper CI	a	r^2	F
Wet weight								
July	125	2.684	0.111	2.463	2.904	−1.669	0.82	579.33*
September	62	3.293	0.155	2.982	3.604	−2.418	0.88	449.64*
December	18	2.843	0.241	2.332	3.354	−1.895	0.90	138.98*
Combined	205	2.825	0.063	2.700	2.950	−1.833	0.91	1991.60*
Dry weight								
July	125	2.689	0.124	2.444	2.934	−2.326	0.79	470.48*
September	62	3.226	0.225	2.776	3.675	−2.912	0.78	206.31*
December	18	3.313	0.360	2.550	4.076	−3.085	0.84	84.74*
Combined	205	3.154	0.079	2.999	3.310	−2.863	0.89	1601.19*
Total lipid								
July	93	1.654	0.174	1.307	2.000	−1.654	0.50	89.94*
September	52	2.964	0.429	2.103	3.826	−3.110	0.49	47.81*
December	18	3.890	0.882	2.020	5.759	−4.489	0.55	19.46*
Combined	163	2.005	0.122	1.763	2.247	−1.869	0.62	268.01*
Ash weight								
July	26	2.556	0.308	1.921	3.191	−2.709	0.74	69.00*
September	8	1.880	0.613	0.380	3.381	−1.861	0.61	9.40*
Combined	34	2.462	0.242	1.969	2.955	−2.595	0.76	103.40*

Regression equation for body composition of weight (mg) against length (mm), given by the equation: $\log W = \log a + b (\log L)$, where a = regression constant, b = slope, W = weight (mg), L = length (mm), n = number of individuals, SE = standard error of slope, lower and upper limits of 95% confidence interval for slope, r^2 = coefficient of determination and F = Fisher's value

*Regression explains significant part of the variation between length and weight ($P < 0.05$)

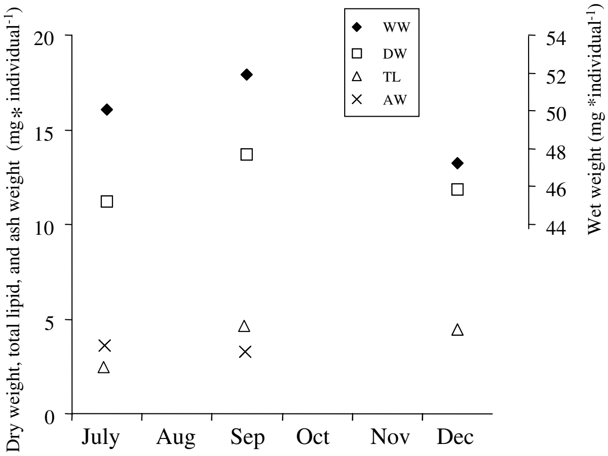

Fig. 3 *T. libellula* in Kongsfjorden, July–December 2000. Body mass changes over time, based on a standardized animal of 18 mm, calculated from length to weight regression equations representing wet weight (*WW*), dry weight (*DW*), total lipid (*TL*) and ash weight (*AW*). Weights are expressed as mg per individual on two axes

generally has a life-span of 2 years (Dunbar 1957), although a 1-year or 15-months life cycle may occur in a small proportion of the population. In Alaskan costal waters, a 1-year life-span has been suggested (Wing 1976). The present study in Spitsbergen fjords is comparable to the two previous studies in the European Arctic. With a relatively high growth rate, the amphipods grow to about a mean length of 25 mm during the first year, and then the growth decreases towards and during the next years. Samples taken in Kongsfjorden in April 2002 showed that *T. libellula* can have three cohorts. Thus, we conclude that *T. libellula* in fjords of Spitsbergen live through two spawning seasons with a life-span up to 3 years.

The samples from Van Mijenfjorden and Kongsfjorden, taken in July, had similar mean lengths of the 0+ cohort of 14–15 mm. Hornsund differed from the other fjords in July with a shorter mean length of the 0+ cohort of 11 mm. Hornsund is more influenced by cold Arctic water because of the South Cape Current (Weslawski et al. 1991) which can result in later release of broods as well as slower growth. Auel and Werner (2003) sampled *T. libellula* in Fram Strait during August 2000. They found individuals ranging from 10 to 17 mm

Table 4 *Themisto libellula:* percent total lipid (TL) of dry weight (DW) from July to December 2000, and percent ash weight (AW) of dry weight from July and September 2000, Kongsfjorden, Svalbard

	Percent TL/DW			Percent AW/DW		
	n	Mean	SD	*n*	Mean	SD
July	93	30.70	8.6	26	27.19	5.94
September	53	25.10	10.94	8	23.73	3.20
December	18	21.90	7.39			

All weights are to nearest 0.1 mg

to be most abundant and stated that individuals in this group represented the 1+ age group. This is in disagreement with our study, where the same length group was assigned to the 0+ age group. The mean length of the 0+ age group *T. libellula* in Kongsfjorden in September was 22 mm. This is larger than the mean total length of the 0+ cohort by late August in the Canadian Arctic (17 mm; Percy 1993), which may be due to later release of juveniles related to the delayed production peak of the colder waters.

Growth from July to September of the age group 0+ was estimated as 3.9 mm month^{-1}, and in late autumn it was estimated as 0.6 mm month^{-1}. Growth rates from Frobisher Bay, Arctic Canada, ranged from 3.5 to 6.8 mm month^{-1} during summer (Percy 1993). Results from Alaskan costal waters (Wing 1976) display a similar growth pattern for *T. libellula*, with fast growth rate during late summer and decreased rates towards the winter. Seasonal vertical migration of *T. libellula* has been revealed in the Alaskan costal waters (Wing 1976) and in the Central Arctic Ocean (Grainger 1985). In these areas, *T. libellula* was most concentrated in the upper layers during summer, and descended to below 200–300 m during autumn and winter. Sampling of *T. libellula* in Kongsfjorden in December resulted in very few individuals compared to similar sampling efforts earlier in the year. The variation in abundance in Kongsfjorden can partly be explained by physical factors. There is significant seasonal and inter-annual variability of advected water masses, which influence the abundance and composition of zooplankton in the fjord (Basedow et al. 2004; Cottier et al. 2005).

Body composition

Wet weight increased from July to September, before decreasing markedly between September and December. Dry weight increased more (2.5 mg) than total lipid (1.5 mg) from July to September, although the percentage increase was larger for lipids. The ash weight was relatively high and stable throughout the period. Falk-Petersen (1981) found that the lipid level of krill in northern Norway increased with size, and Falk-Petersen et al. (1987) reported that the highest lipid levels in both krill and *Calanus* species were recorded in late autumn. The same can be seen for *T. libellula* in Kongsfjorden, where the lipid level increased with size, with the highest levels recorded in September–December. Arctic zooplankton store energy, as lipids, for overwintering and reproduction (Lee 1975; Falk-Petersen et al. 1987, 1990). High lipid levels are present in Arctic *Calanus* species, the main prey of large *T. libellula*, during August–September in Kongsfjorden (Scott et al. 2000, 2002). Falk-Petersen (1981) also determined that krill in a sub-arctic fjord decrease their relative amount of lipids during winter, mainly because of decreased food quality as well as allocation of energy to the growth of gonads. In our study, the lipid level in *T. libellula* was still high in

December. As a carnivorous species, its growth pattern is more similar to the carnivorous krill *Meganyctiphanes norvegica*, which feed throughout the winter (Falk-Petersen 1985). This krill species had a lipid content ranging from 20 to 30% of the dry weight, which was similar to our findings for *T. libellula*. Previous studies of *T. libellula* from the northern Fram Strait and the Barents Sea have also shown a high lipid content of 39% in June and 38% in July–August (Scott et al. 1999; Auel et al. 2002).

Conclusion

From the present work it can be concluded that *T. libellula* from Spitsbergen fjords release its brood in March–April just before the vernal spring bloom, grows fast to maturation within the first year, and has a life-span of up to 3 years. With its relatively high lipid level (20–30%), this amphipod is a valuable energy source for higher trophic levels throughout the year.

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References

Auel H, Werner I (2003) Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. J Exp Mar Biol Ecol 296:183–197

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

Basedow SL, Eiane K, Tverberg V, Spindler M (2004) Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). Estuar Coast Shelf Sci 60:113–124

Bowman TE (1960) The pelagic amphipod genus *Parathemisto* (Hyperiidea: Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc US Nat Mus 112:343–392

Clarke A (1992) Reproduction in the cold: Thorson revisited. Invertebr Reprod Dev 22:175–184

Cottier F, Tverberg V, Inall M, Svendsen H, Nilsen F, Griffiths C (2005) Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. J Geophys Res 110, C12005. DOI 10.1029/2004JC002757

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

Dunbar MJ (1946) On *Themisto libellula* in Baffin Island coastal waters. J Fish Res Board Can 6:419–434

Dunbar MJ (1957) The determinants of production in northern seas; a study of the biology of *Themisto libellula*, Mandt. Can J Zool 35:343–391

Falk-Petersen S (1981) Ecological investigation on the zooplankton community of Balsfjorden, northern Norway: seasonal changes in body weight and main biochemical composition of *Thysanoessa inermis* (Kroyer), *T. raschii* (M. Sars), and *Meganyctiphanes norvegica* (M. Sars) in relation to environmental factors. J Exp Mar Biol Ecol 49:103–120

Falk-Petersen S (1985) Growth of the euphausiids *Thysanoessa inermis*, *Thysanoessa raschii*, and *Meganyctiphanes norvegica* in a Subarctic fjord, north Norway. Can J Fish Aquat Sci 42:14–22

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

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Proceedings of the 24th European marine biological symposium, Aberdeen University Press, Aberdeen pp 315–333

Folch J, Lees M, Stanley HS (1957) A simple method for the isolation and purification of total

Grainger EH (1985) Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey L, Alexander V (eds) Proceedings of the sixth conference of the Comité Arctique International, 13–15. Brill EJ, New York, pp 48–60

Gulliksen B, Holte B, Jakola KJ, Gray JS (1985) The soft bottom fauna in Van Mijenfjord and Raudfjord, Svalbard. Marine biology of polar regions and effects of stress on marine organisms. Proceedings of the 18th European marine biology symposium, Norway, pp 199–215

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

Lee RF (1975) Lipids in arctic zooplankton. Comp Biochem Physiol 51B:263–266

Loeng H (1991) Features of the physical oceanographic conditions of the Barents Sea. Polar Res 10:5–18

Lønne OJ, Gabrielsen GW (1992) Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. Polar Biol 12:685–692

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1973) in ice covered waters. Polar Biol 9:187–191

Lydersen C, Gjertz I, Weslawski JM (1989) Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. Polar Res 25:107–114

Lydersen C, Angantyr LA, Wiig Ø, Øristland T (1991) Feeding habits of northeast Atlantic harp seal (*Phoca groenlandica*) along the summer ice edge of the Barents Sea. Can J Fish Aquat Sci 48:2180–2183

MacDonald PTM, Green PEJ (1988) User's guide to program MIX: an interactive program for fitting mixtures of distribution. Ichthus data system, Hamilton, Ontario, Canada

MacDonald PTM, Pitcher J (1979) Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J Fish Res Board Can 36:987–1001

McLaren IA (1958) The biology of the ringed seal (*Phoca hispida*, Schreber) in the eastern Canadian Arctic. Bull Fish Res Board Can 118:97

Motoda S (1959) Devices of simple plankton apparatus. Mem Fac Fish, Hokkaido University 7:73–94

Percy JA (1993) Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula*, Mandt. Polar Biol 13:131–139

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

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2000) Lipid and life strategies of *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. Polar Biol 23:510–516

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2002) Species differences, origins and functions of fatty alcohols and fatty acids in the wax ester and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. Mar Ecol Prog Ser 235:127–134

Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowiski M, Azzolini R, Bruland O, Wiencke C, Winther J-G, Dallmann W (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Res 21:133–166

Swerpel S (1985). The Hornsund fiord: water masses. Pol Polar Res 6:475–496

Weslawski JM, Jankowski A, Kwasniewski S, Swerpel S, Ryg M (1991) Summer hydrology and zooplankton in two Svalbard fjords. Pol Polar Res 12:445–460

Wing BL (1976) Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan coastal waters. Northwest Fish Cent Proc Rep, March 1976. US Nat Mar Fish Serv