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ORIGINAL PAPER

Ten years after: krill as indicator of changes in the macro-zooplankton communities of two Arctic fjords

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Abstract A macro-zooplankton study from 1996 was repeated in 2006 and focused on euphausiid species as indicators of advection and warming effects in Kongsfjorden, West Spitsbergen, Svalbard. The influence of warmer Atlantic water in Kongsfjorden was indicated by the findings of three additional euphausiid species of typically Atlantic origin, relative to the previous study 10 years ago. The predominant presence of *Thysanoessa inermis* in Hornsund suggested persisting cold conditions in this more southerly, but more Arctic influenced fjord. In this species, moult stage analysis showed that trophic effects can override temperature forcing. Histology and lipid analysis suggest that reproductive activity should be monitored as an indication of warming and possibly a shift in food web composition.

Keywords Arctic fjords · Macro-zooplankton · Euphausiids · Krill · Moulting · Lipids · Global warming

Introduction

The European part of the Arctic, where Atlantic water (AW) meets Arctic water (ArW), currently is the subject of intensive studies investigating the ecosystem consequences of climate change. The northernmost extent of the Gulf Stream flows along the west coast of the Svalbard

archipelago, transporting southern species into the polar waters. Ongoing warming effects are expected to lead to an increasing number of eurythermal species able to persist in an Arctic environment (Ellingsen et al. 2008). Consequently, there is a necessity in current research not only simply to describe the changes but also to discuss causalities and consequences for the observed composition of faunal assemblages in a food web context. This will allow assessing impacts of the amplification of warming effects from single species to Arctic communities.

In the pelagic realm, macro-zooplankton is important as food for top predators such as fish and birds. Typical inhabitants of high-latitude waters are certain krill species. Euphausiids are moreover good indicators of change due to their central position within marine food webs worldwide (Hempel 1970). Different water masses tend to contain a characteristic krill fauna and therefore the different species are suited as water mass indicators and facilitate climatic comparisons when considering specialised krill species from different regions (Buchholz 2003).

Macro-zooplankton sampling is dependent on specialised equipment and taxonomic expertise. Accordingly, analyses of the larger plankton are often not included in routine environmental and plankton surveys of specific regions. One of the few early studies in the Arctic is found in Weslawski et al. (2000). The area investigated was Kongsfjorden, one of the glacial west coast fjords of Spitsbergen of the archipelago of Svalbard. The macro-zooplankton community was dominated by Euphausiacea (*Thysanoessa inermis* and *Thysanoessa raschii*), Amphipoda (*Themisto libellula*) and Pteropoda (*Limacina helicina*). Other taxa were of minor importance. A cruise of the Polish RV Oceania in 2006 gave the opportunity to do a macro-zooplankton repeat survey after exactly a decade using the same equipment, particularly a 1-m² Tucker trawl

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specialised for macro-plankton. Furthermore, the cruise was scheduled to investigate in parallel another fjord further south with a very different hydrographic regime: due to currents, the Hornsund is far more influenced by Arctic, i.e. colder waters than Kongsfjorden (Swerpel 1985; Weslawski et al. 1988; Hop et al. 2002; Svendsen et al. 2002; Weslawski et al. 2006; Ellingsen et al. 2008). In comparing both areas, an emphasis was laid on krill. Currently, other recent zooplankton studies may serve as reference for zooplankton generally, partly integrating macro-zooplankton of both fjords (Kwasniewski et al. 2003; Walkusz et al. 2003; Walkusz 2007; Kedra 2008). Piwosz et al. (2009) reported on the different productivity of Kongsfjorden compared to Hornsund in terms of phytoplankton.

The occurrence of krill species and their distribution were studied in conjunction with physiological parameters with the aim to differentiate temperature from trophic effects in krill of both fjords. Growth through moulting and coupled reproductive processes were analysed and evaluated as indication of the trophic environment and production conditions of the two fjords. Histological analysis of reproductive cycles and of accumulation of lipid reserves was started to find further relations to the trophic regime of the fjords, at least to record the summer situation in 2006. However, a major aim of this study was to lay the basis for future repeated sampling of the area and to identify a suited indicator of change, i.e. euphausiid species, to follow the development in the frame work of more encompassing biodiversity and foodweb studies. The current ‘snapshot’ of the two fjords compared may then be used to elucidate ongoing trends and effects of global change in Arctic waters (ACIA 2005).

Materials and methods

Sampling areas and locations

The two fjords studied (Fig. 1) are the northernmost and the southernmost larger fjord systems of the west coast of Spitsbergen. Kongsfjorden (KF) and Hornsund (HS) are located at 79° and 77°N, respectively, some 220 km apart. Both are open fjords; Kongsfjorden is approx. 30 km long and approx. 10 km wide, whereas Hornsund is approx. 30 km long and approx. 6–20 km wide. Both have a larger western outer part and a smaller eastern inner part separated by an inner sill of 30 and 50 m depth, respectively. The western outer parts are approx. 300 and 200 m deep, respectively, and the inner parts are up to 140 and 90 m deep, respectively. Stations were chosen in the case of Kongsfjorden as repeats of the 1996 study close to Polish station K3 in the western fjord and K7 in the eastern, inner

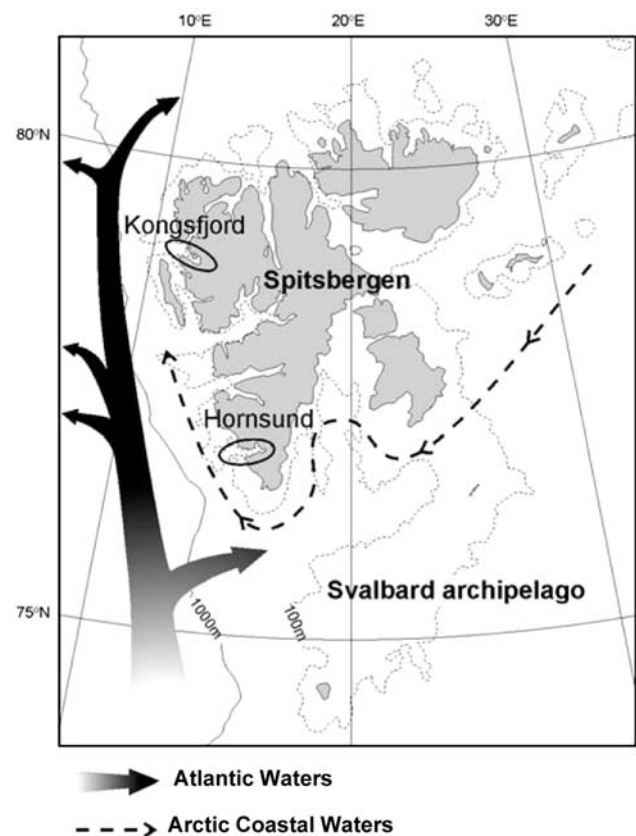


Fig. 1 Map of Svalbard indicating principal currents; Spitsbergen with locations of Kongsfjorden and Hornsund (circles)

fjord; correspondingly in Hornsund close to Polish stations H4 (outer) and H3 (inner). Exact positions of the current study are shown in Table 1.

Gear and tows

The Tucker trawl is a rectangular mid-water zooplankton trawl and designed to be used on small ships. The single net is mounted along two bars which are released by wire-messengers operating a double action mechanism that is opening the net by sliding the bottom bar downwards along two stays at the sides, and then closed again at a defined depth by releasing the top bar. The effective mouth area is defined in the Tucker trawl by presenting a 1 m² mouth

Table 1 Positions of sampling

| Area | Station codes | Latitude | Longitude |
|----------------|----------------|----------|-----------|
| Kongsfjorden W | KF1–6/KF9 + 10 | 78°55.8N | 12°04.1E |
| Kongsfjorden E | KF7–8 | 78°57.4N | 12°25.0E |
| Hornsund W | HS8 | 76°58.8N | 15°42.2E |
| Hornsund E | HS3 | 77°00.0N | 16°25.6E |

opening to the water column while under tow, at a nominal 45° actual mouth pitch angle. The mesh size used was 1 mm Dacron. The net was deployed from the Polish RV Oceania from the stern at 2 kn; opening and closing positions and tow path length were determined by GPS. Depth of the net was determined by a 200 m-depth gauge (Hydrobios). Depth, temperature and salinity were recorded in parallel with a Seabird—CTD.

Post catch, krill were maintained in aerated sea-water at 4°C until analysed. Before moult staging, live krill was sexed, state of thelycum and presence of spermatophores noted, and total length determined from the forward rim of the eyes to the tip of the telson, rounded to the lower millimetre. All staged specimens were preserved, either at –20°C for total lipid determination or in 10% buffered formalin in filtered sea water for histology.

To document species composition a standardised population sample was taken at each location and completely fixed in 4% buffered formalin.

Moult staging

The moult-staging system adopted here for the five krill species was derived from Drach's method as previously established for euphausiids (Buchholz 1982; Buchholz 1991; Buchholz et al. 2006). Staging was done on a live preparation of the uropods. According to Drach's system based on changes in the integument, the crustacean moult cycle is divided into moult stages (MS) grouped in two periods, which are separated by the actual moult (Ecdysis), i.e. the post-moult period, with MS A, B and C and the pre-moult period starting at apolysis with MS D0, D1, D2 and D3. Detailed moult stages were scored and later grouped for physiological analyses.

Lipid stages

While moult staging fresh material and handling the live animals, a translucent mass was frequently observed underneath the transparent carapace which had the appearance of a fat deposit. Accordingly, approx. 300 of the 500 specimens moult staged were also scored for the size of this mass. In the course of the determinations, five categories could be distinguished and were named Lipid stages LS 0–4, where LS 0 corresponded to “no mass” visible and LS 4 to “filling the complete available space of the thorax plus part of the first abdominal segment”, while LS 1 was up to a third, LS 2 around half, LS 3 more than three quarters of the thoracic cavity filled. In order to verify the proximate composition of the deposit, lipids were determined gravimetrically in a subset of whole animals.

Lipid determination

For gravimetric lipid determination according to Hagen (2000), whole freeze-dried and weighed krill were extracted twice in 4 ml di-chloro-methane/methanol 2:1. The extract was dried under nitrogen gas for 1 h and weighed. Lipid values were given as $\text{mg} \times \text{mg}^{-1}$ DW. Lipids measured were regressed against the lipid stages LS 0–4 resulting in a highly significant fitted line with parameters: $y = 2.72x + 1.49$ ($r^2 = 0.751$, $P < 0.0001$, $n = 25$).

Histology

For specific demonstration of lipid material krill specimens fixed in 10% formalin in seawater were rinsed in water for some hours, infiltrated with 20% sucrose in PBS, embedded in 3% gelatine/PBS and immediately frozen in liquid nitrogen. Sagittal kryosections were stained with Oil red and Hemalaun.

Statistics

The statistics package GraphPad Prism 5 was used for all calculations.

Results

Hydrography

From the extensive data set of CTD casts during the expedition, four diagrams were selected to illustrate the temperature of typical water masses in the two fjords west and east of the respective sills (Fig. 2).

In the western part of Kongsfjorden temperature was up to 5°C higher in the upper 20 m of the water column than in western Hornsund and almost double as high the next 120 m down. The eastern Kongsfjorden showed water temperatures between 2 and 5°C down to 50 m depth, whereas they were only 1–3°C in eastern Hornsund. Temperatures of 0°C were reached around 73 or 80 m depth, respectively. Salinity was <34 at all measured depths decreasing to less than 33 in the upper 40 m of both inner and outer fjords. The surface layer of the upper 10 m is generally less saline due to glacier run-off, and this also is reflected in the characteristic dent of the isotherms close to the surface indicating the cooler melt water (Fig. 2).

With respect to the origin of the predominant water masses, the Kongsfjorden profiles show the following: There is a thick melt-water influenced top zone followed by the Atlantic water/fjord water mixing zone extending to the bottom. The smooth curve is matched by the salinity gradient (data not shown), indicating that the inner fjord is

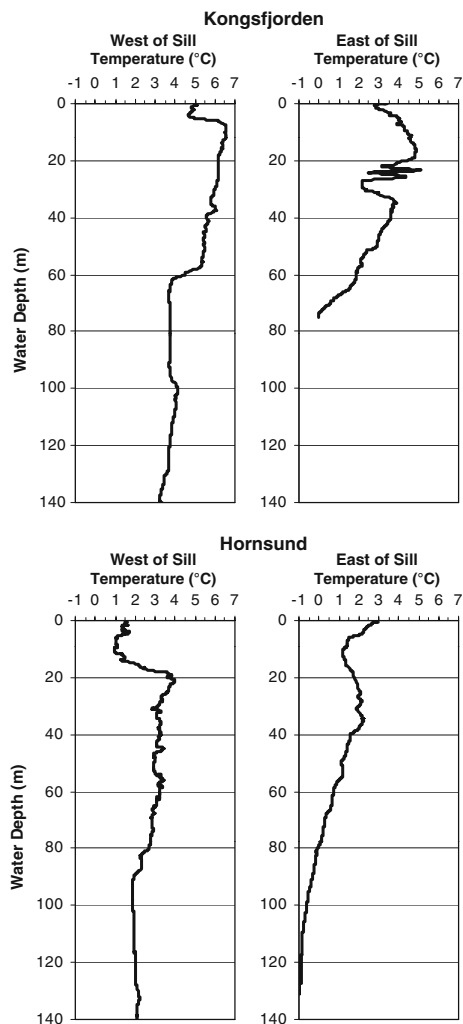
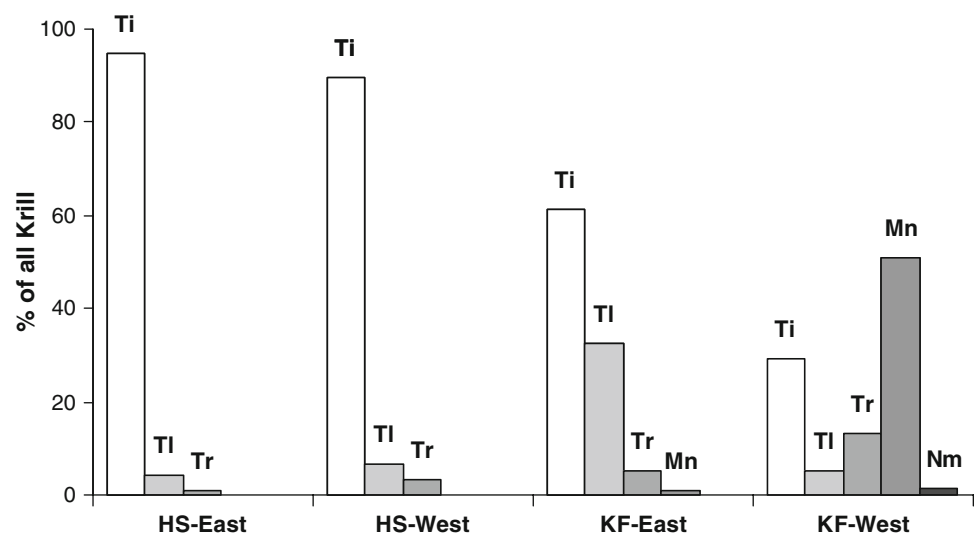


Fig. 2 Temperature profiles of mid-Kongsfjorden (top, left, off Ny Alesund; west of sill) and inner Kongsfjorden (top, right; east of sill), outer Hornsund (bottom, left; west of sill) and inner Hornsund (bottom, right; east of sill) between 22 and 30 July 2006

Fig. 3 Species distribution of euphausiids in percent, east and west of sill in Hornsund (HS) and Kongsfjorden (KF). *Ti* *Thysanoessa inermis*, *Tl* *Thysanoessa longicaudata*, *Tr* *Thysanoessa raschii*, *Mn* *Meganyctiphanes norvegica*, *Nm* *Nematoscelis megalops*. (HS-E $n = 113$; HS-W $n = 59$; KF-E $n = 407$; KF-W $n = 229$)



much less influenced by Atlantic intrusions but is more glacier water dependent. With respect to temperature, the whole water columns at Hornsund are generally 3–5°C colder than those of Kongsfjorden waters at both the inner and outer fords. This reflects predominant Atlantic impact in the Kongsfjorden in the north and Arctic water input in the Hornsund in the south (see “Discussion”). Basically, the hydrography recorded at the two fjords has roughly a similar pattern: warmer and high salinity Atlantic influenced waters in the western parts and colder low salinity glacier run-off influenced water in the inner eastern parts.

Populations

At all locations, the most numerous of the euphausiids caught were three *Thysanoessa* species, namely *T. inermis*, a coastal species (Mauchline and Fisher 1969), followed by *T. longicaudata*, considered an oceanic species (Mauchline and Fisher 1969) and *T. raschii*, a neritic one (Mauchline and Fisher 1969).

Among the *Thysanoessa inermis* specimens of Kongsfjorden were five specimens identified as *T. inermis neglecta*.

Further species with boreal Atlantic provenance were encountered. First, *Meganyctiphanes norvegica* occurred in larger numbers. However, in the population sample west of the Kongsfjorden sill 97% of the total 117 *M. norvegica* were juveniles of 10–16-mm length. The imbalance between adult and juvenile *M. norvegica* was also observed in an analysis of fresh krill on board, where *M. norvegica* appeared in combined catches at station KF4-6: 132 of 312 krill were *M. norvegica* (42.3%) with a modal length of 14 mm usually corresponding by size to year class 0. There were only three adults >22 mm.

Second, five adult female and four adult male specimens of the truly Atlantic *Nematoscelis megalops* were identified

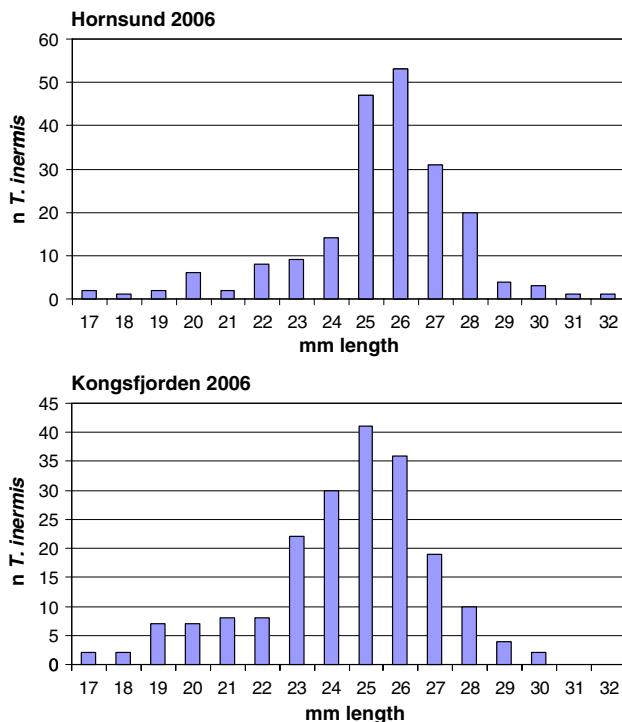


Fig. 4 *Thysanoessa inermis*, length–frequency, Hornsund versus Kongsfjorden, all krill measured alive immediately post catch

in the population sample west of the sill in Kongsfjorden corresponding to 3.1% of all analysed krill >10 mm. No *Nematoscelis* was found in the eastern part of Kongsfjorden nor in Hornsund.

In *Thysanoessa inermis*, the length–frequency distributions (Fig. 4) in the two fjords were tested for size differences, where females from Hornsund were significantly larger than Kongsfjorden females, by 1 mm ($t = 3.488$, $P < 0.001$, $n = 285$). The comparison of the males gave the same result ($t = 3.148$, $P < 0.002$, $n = 156$). Therefore, the average size of Hornsund specimens was larger than at Kongsfjorden.

Moult and reproduction

To assess and compare the potential for growth between locations or seasonally, the relationship between the numbers of “moult active” to “moult inactive” specimens was determined. The moult active fraction consists of krill actually involved in the immediate preparation for moult, ecdysis itself or the early consolidation of the cuticle directly post-moult. The immediate pre-ecdysial stage D3 and the post-ecdysial stages A and B are characterised by a soft exo-skeleton and are of fixed duration because a sequence of highly coordinated processes, e. g. resorption and fast completion of the endocuticle, have to follow each other (Buchholz and Buchholz 1989). This phase (D3 + A + B) has been found to comprise 15% of a moult

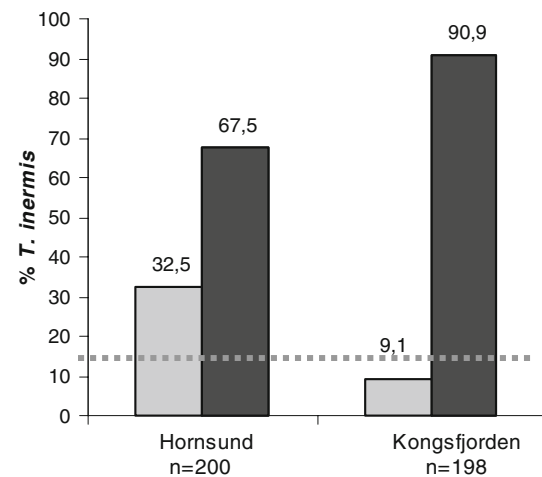


Fig. 5 Overall moult activity in *Thysanoessa inermis*, Hornsund versus Kongsfjorden. Grey bars depict ‘moult active’ and black bars ‘moult inactive’ specimens; Dotted line expected percentage of ‘moult active’ krill (see text)

cycle, meaning that if random moulting is going on in a population, 15% of the krill can be expected to be found in that phase (Buchholz et al. 2006). Accordingly, this percentage is a measure for moult and thus growth activity. As demonstrated in Fig. 5, >30% of *T. inermis* from Hornsund were involved in ecdysis indicating that moulting occurred twice as often as expected. In contrast, in Kongsfjorden, moult activity was approx. one-third lower than expected.

A contingency test using the Chi-square distribution gave a highly significant difference between the fjords when all male and female specimens scored for stages “moult active” or “moult inactive” (ref. Fig. 5) were compared ($n = 398$, $\chi^2 = 143.4$, $df 1$, $P < 0.0001$).

Furthermore, when the seven detailed moult stages taken from the same data set are considered, moult activity may be interpreted from their detailed sequence with higher resolution.

In fact, the moult inactive krill in the Kongsfjorden were found in stages C and D2, which are both ‘resting stages’ (Buchholz et al. 2006). In C, moult processes may have come to a standstill, at ‘intermoult’, while the cuticle is hard and the epidermis inactive (Fig. 6 a). In D2 the cuticle bears the new epi- and exocuticle underneath the old one, ready for the next moult to be initiated. Apparently, moult activity had almost ceased in the Kongsfjorden krill, confirming the observation taken from Fig. 5. In contrast, approx. 30% of *T. inermis* in Hornsund were found in the early stages of A and B, i.e. a large part of the population had just completed a moult (Fig. 6b). This finding may also indicate synchronicity of moulting in the particular krill swarm sampled. Likewise had a krill swarm in the inner Hornsund, sampled before on two consecutive days, indicated moult synchronicity (Fig. 6c, d): On the first day, the

larger part of the swarm was found directly involved in moulting (stages D3, A, B) or almost ready for ecdysis (D2). The following day, the number of D2-krill had diminished and the recently moulted krill (D3, A, B) had advanced to the predominant stage C. Accordingly, a progression of stages was notable within these 2 days. Furthermore, the high percentage of moult active stages on 21.07.06 at the eastern and on 26.07.06 at the western location indicated synchronicity in the swarms sampled in Hornsund (Fig. 6).

Lipids and histology

The specimens analysed for moult and lipid stages were used to relate the lipid stages to the location, i.e. Hornsund versus Kongsfjorden and to the stages of the moult cycle.

Figure 7a shows a schematic drawing delineating the position of the lipid deposit by a dotted line corresponding to the maximal extent in LS 4. Open spaces are occupied by stomach, hepatopancreas, muscle, and heart. Figure 7b shows the saddle-shaped mass seen from the side (opaque homogeneously stained area), filling the thorax to the largest extent, tapering out frontally towards the eyes and reaching caudally into the first abdominal segment matching the drawing.

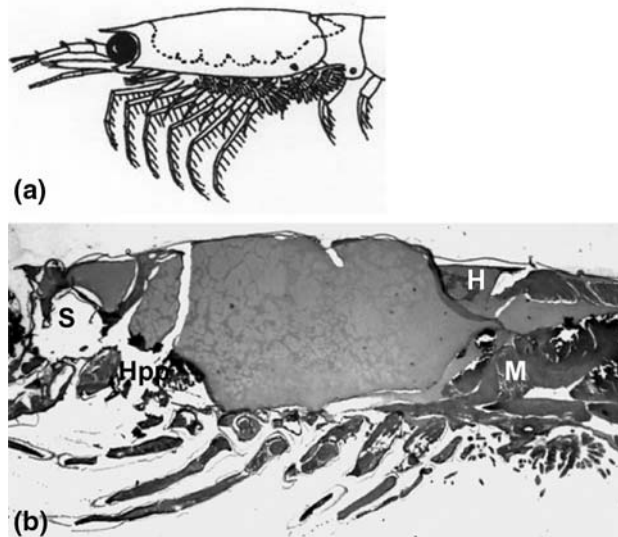


Fig. 7 *Thysanoessa inermis*, cephalothorax, a schematic drawing with position of lipid deposit (dotted line) at lipid stage LS 4 corresponding to b sagittal kryosection stained with Oil red, Hemalaun. H Heart, Hpp hepatopancreas, M muscle, S stomach

In Fig. 8, the distribution of lipid stages LS 0–4 encountered in *T. inermis* of Hornsund (top, n = 129) and Kongsfjorden (bottom, n = 162) showed different patterns

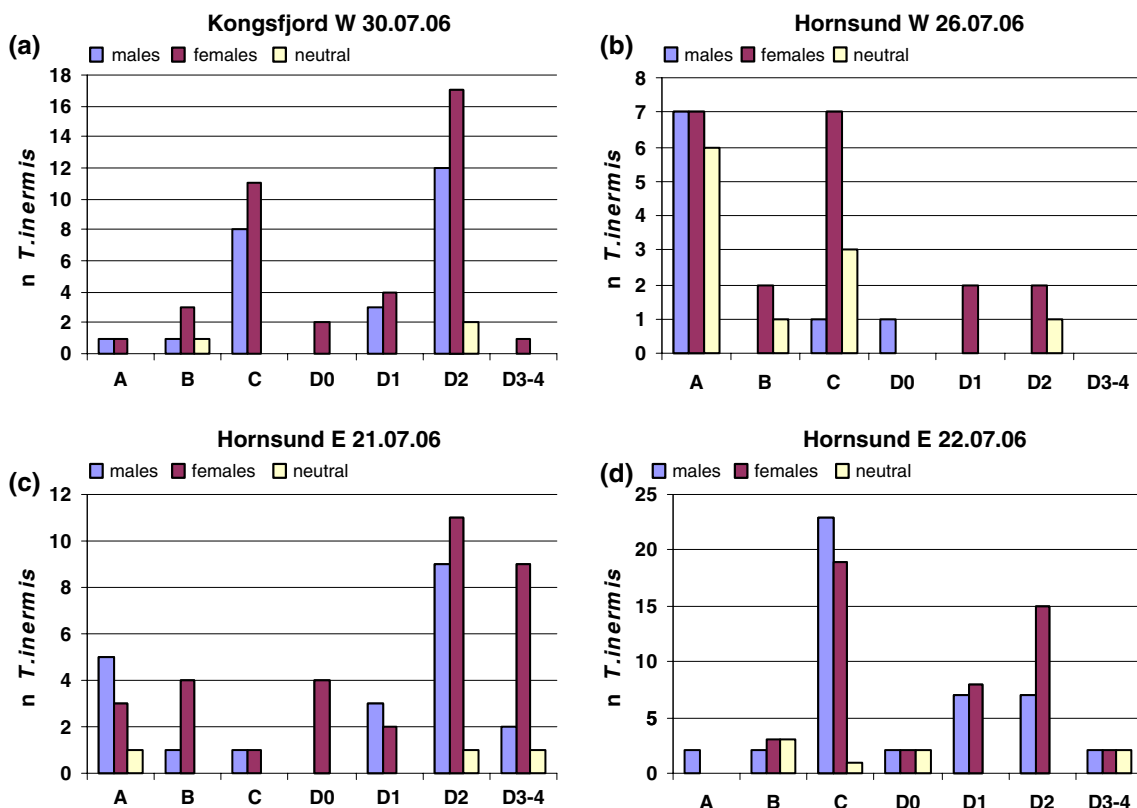


Fig. 6 Detailed moult stages (A–D3) in *Thysanoessa inermis*, a Kongsfjorden versus b Hornsund and c, d Hornsund on two consecutive days (W west of sill; E east of sill)

of visible lipid mass. A contingency test using the Chi-square distribution gave a significant difference between the fjords, when all male and female specimens scored for the five lipid stages were compared ($n = 291$, $\chi^2 = 9.940$, $df 4$, $P = 0.041$). In Hornsund little difference between the stages was noted, whereas in Kongsfjorden either high amounts (LS 3 and LS 4) or no lipid (LS 0) was found.

Lipid stage distributions of females and males from either fjord were not statistically different but the overall stage patterns of the two fjords were. In Hornsund, krill showed a rather uniform percentage of lipid stages determined. In contrast, in Kongsfjorden, a steady increase is seen from LS 1 towards maxima at LS 4. An initial maximum occurs within stage LS 0.

Furthermore, consecutive accumulation of visible lipid mass within the cephalothorax was observed in females at different moult stages and scored for frequency of lipid stages 0 and 4 (Fig. 9, *T. inermis*). The main moult stages were used corresponding to stages A and B for immediate post-moult, C for inter-moult, the three pre-moult stages D0, D1, D2 and finally stage D3 at the immediate pre-moult stage.

The highest percentages of LS 4 were found in moult stages C and D0. Stage C is the phase with the longest and most intensive reserve accumulation, apparently including the lipids described, continuing into early pre-moult. Subsequently, the steady decrease over D1 and D2 towards immediate pre-moult, D3, indicated possible liberation of lipid reserves. Such reserves are necessary to help fuel the construction of the new cuticle underneath the old one. The

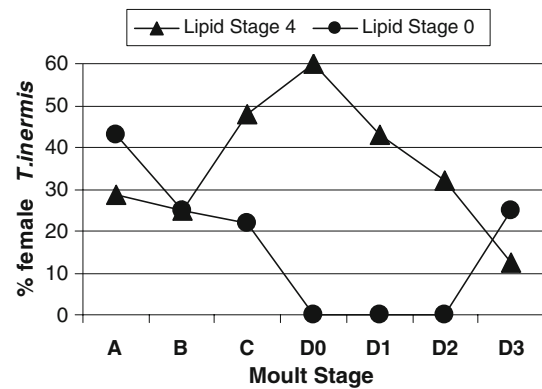


Fig. 9 *Thysanoessa inermis*: visible lipid mass within the thorax in female *T. inermis* of Hornsund at different moult stages and scored for frequency of lipid stages LS 0 and LS 4; $n = 42$

continuation of low values into the early pre-moult stages A and B is brought about by the continuing necessity of consolidation of the new endo-cuticle. The course of the occurrence of the lowest Lipid stage LS 0 is almost exactly the reverse, supporting the increasing accumulation of lipids during post-moult and increasing demand during the pre-moult phase.

Discussion

Fjords as “magnifying glasses”

There is not much doubt currently but a “general agreement that the Arctic Ocean at present is in a transition towards a new, warmer state”. This is cited from a recent comprehensive evaluation of the physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden by Hop et al. (2006). Walczowski and Piechura (2006) and Cottier et al. (2007) give further examples relevant to the study area.

Fjords have frequently been used as model oceans (Buchholz et al. 2006). They often carry typical features of adjacent seas but retain characteristics for longer periods than the open sea. Therefore, ecological phenomena can be noticed when initially developing at a small scale. In this sense, fjords may serve as ‘magnifying glasses’ for focused observations. The two fjords compared both have an outer and an inner part, i.e. a volume flushed regularly and a more secluded part where observations on similar communities and abiotic conditions may be continued for longer times. However, these inner fjords are prone to silt and fresh water input from surrounding glaciers which may change the oceanic conditions drastically, facts to be taken into account. Of the two, Kongsfjorden has intensively been studied (Hop et al. 2006) and it can well serve as the basis of the decadal comparison. Hornsund is less well

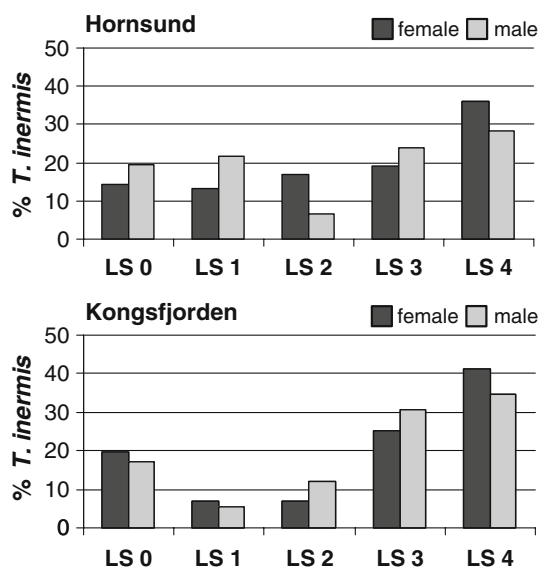


Fig. 8 *Thysanoessa inermis*, frequency of lipid stages LS 0–LS 4 at Hornsund (top, $n = 129$) and Kongsfjorden (bottom, $n = 162$) indicating the accumulation of visible lipid mass within the thorax. LS 0 No lipid, LS 4 lipid mass reaching into first abdominal segment

described, but is under long-term observation by the Polish station near the mouth of the fjord (Weslawski et al. 1988). The latter fjord is clearly more Arctic-influenced as it is in the reach of the Arctic coastal waters (Sörkapp current) which flow around the southern tip of Spitsbergen, coming from the north from the cold northern Barents sea (Dalpadado et al. 2008a, 2008b). The warmer West-Spitsbergen current flows well westward bringing warmer Atlantic waters towards the area of Kongsfjorden and beyond. The occurring krill species are used to indicate possible changes, both in the composition of water masses and within the plankton community. The combined analysis of abiotic and biotic data is intended to set a baseline for further long-term studies.

Populations

“Origin of Species”: species composition and implications

Two species of krill were found in the macro-zooplankton of Kongsfjorden in July 1996 (Weslawski et al. 2000). These were *T. inermis* which occurred at densities of 50 specimens/100 m³ and *T. raschii* at 1.3 specimens/100 m³. East of the sill, separating inner and outer parts of the fjord, the same order of magnitude of occurrence is seen for *T. inermis* in the current work (Table 2), whereas *T. raschii* shows the previous density. In *T. inermis*, large inter-annual fluctuations are reported by Walkusz (2007). Dalpadado (personal communication) found seasonal differences in *T. inermis* of two orders of magnitude, with high numbers in May and low numbers in August and October, when the latter match the krill density reported here. This difference may be associated with strong predation pressure on krill, particularly by capelin and polar cod which may deplete krill stocks early in the year. Mauchline (1980) considers *T. inermis* as boreal-Arctic and *T. raschii* as Arctic-boreal; however, Falk-Petersen et al.

(2000) convincingly define *T. inermis* as the most northern Arctic species according to its lipid composition.

In the present study, three species are ‘new’ in comparison to the 1996 data in Kongsfjorden (Weslawski et al. 2000). However, among these, *T. longicaudata* and *M. norvegica* have been recorded occasionally, but not quantified (Hop et al. 2002; Kwasniewski et al. 2003; Walkusz et al. 2003). Both species are considered boreal-Atlantic. *Nematoscelis* is a new record: Three adult female specimens of *N. megalops* were identified in the population sample west of the sill at Kongsfjorden. Another total of two female and four male adult *N. megalops* were encountered in the other catches west of the sill, which makes it roughly 3% of all analysed krill >10 mm, whereas these were found neither in eastern Kongsfjorden nor in any part of Hornsund. The exclusive occurrence of the species in the outer Kongsfjorden clearly indicates its Atlantic provenance.

When the euphausiids are considered as water mass indicators, the relative proportion of species composition may indicate either Atlantic or Arctic water input (Fig. 3). In the inner (HS-E) and outer (HS-W) parts of the Hornsund fjord *T. inermis* dominates and shows a similar proportion as it was the case in Kongsfjorden a decade ago, i.e. 50:1 *T. inermis* versus *T. raschii*. Such a proportion may reflect the Arctic situation which is still typical for Hornsund, but has changed in Kongsfjorden. In Kongsfjorden we found five species of krill, and not only *N. megalops* is clearly indicative of Atlantic input but also *T. longicaudata* is considered an oceanic Atlantic species which is now found in larger proportions in the inner part, possibly as a consequence of the plankton trap, *sensu* Weslawski et al. (2000). Noteworthy is the occurrence of a swarm of juvenile *M. norvegica* which were probably advected into the fjord with Atlantic water but theoretically (see also below) could have been spawned there in April/May and would then be at their expected size as residents

Table 2 Number of krill specimens relative to volume fished ($n \times 100 \text{ m}^{-3}$), Kongsfjorden (KF) versus Hornsund (HS), between 22 and 30 July, 2006

| Location Station no. | Kongsfjorden Overall $n \times 100 \text{ m}^{-3}$ | East of sill KF8 $n \times 100 \text{ m}^{-3}$ | West of sill KF1 $n \times 100 \text{ m}^{-3}$ | Hornsund Overall $n \times 100 \text{ m}^{-3}$ | East of sill HS3 $n \times 100 \text{ m}^{-3}$ | West of sill HS8 $n \times 100 \text{ m}^{-3}$ |
|-------------------------|--|--|--|--|--|--|
| <i>T. inermis</i> | 7.02 | 12.04 | 2.75 | 4.50 | 13.18 | 1.93 |
| <i>T. longicaudata</i> | 3.19 | 6.36 | 0.49 | 0.25 | 0.62 | 0.15 |
| <i>T. raschii</i> | 1.15 | 1.06 | 1.23 | 0.08 | 0.12 | 0.07 |
| <i>M. norvegica</i> | 2.66 | 0.15 | 4.80 | – | – | – |
| <i>N. megalops</i> | 0.07 | – | 0.12 | – | – | – |
| All krill ≥ 10 mm | 14.09 | 19.60 | 9.39 | 4.84 | 13.92 | 2.15 |
| Not specified <10 mm | 14.07 | 27.02 | 3.04 | 0.23 | 0.25 | 0.22 |

All krill ≥ 10 mm: all larger krill identified by species. Not specified: <10 mm: small krill not differentiated by species

of the fjord area. Clearly, the open fjords will be flushed several times so that species proportions change during the seasons. However, three species of Kongsfjorden are of Atlantic origin and the dominance of Arctic *T. inermis* as well as the almost complete lack of the other ‘Atlantic species’ in Hornsund stands for the prevailing Arctic input. Nevertheless, the different species compositions in the fjords are not necessarily indicative of a decadal trend, but may be the consequence of interannual variation and anticipate a warmer future environment. 2006 was exceptionally warm with strong Atlantic inflow and elevated core temperatures in the centre of the West Spitsbergen Current (Walczowski and Piechura 2006). Clearly, there is a need for regular monitoring to discriminate between variability and trends.

There is some debate as to some euphausiid species representing a group of subspecies (Berkes 1977; Lomakina 1978). Among the *Thysanoessa* of Kongsfjorden five specimens were identified as *T. inermis neglecta*. With decreasing body size, morphological analysis alone is not sufficient to distinguish *T. longicaudata* from the *T. inermis neglecta* form. The degree of eye constriction varies as well as the length of the sixth pleon segment, which quite often is almost as long as the combined 4th and 5th segments, but not longer and may lack the posterior spine typical for *T. inermis*. The bristles on the elongated second thoracic leg (if preserved) seem to show no consistent differences between the species. The presently developed bar-coding method for euphausiids (Bucklin et al. 2006) may be an appropriate device for clarification. In our case, the five *T. inermis neglecta* specimens were unified with *T. inermis* because this form may be considered a neotenic form of adult *T. inermis* (sensu Lomakina 1978).

Environmental forcing

Topography and currents

According to Weslawski et al. (2000), marine waters in Kongsfjorden flow inward along the south coast, in the inner part glacier melt water flows on top and outwards along the north side of the fjord. The macro-zooplankton encompasses good swimmers which can hold their position against currents; this is particularly so for the krill species which are transported inward until they meet the fresh water which they normally tend to avoid by active swimming but will be ‘trapped’ in the inner part towards the end of the fjord. A net inward transport of zooplankton is also described by Basedow et al. (2004). The plankton trap described for Kongsfjorden may apply to Hornsund as well. Nevertheless, it is difficult to verify the probability of having sampled a specific population repeatedly, particularly with respect to judgement on whether the time of

residence allows for full reproductive cycles to occur in the fjords. The recordings of zooplankton backscatter with moored ADCP-current metres (Cottier et al. 2007; Basedow et al. 2004) may be helpful for future interpretation and assessments of zooplankton dynamics.

Timofeyev (1993) gives some calculations on possible sources of krill being transported along the Atlantic current from the south. He finds that recruitment in the south, e.g. in the vicinity of Bear island (Barents sea) may be possible, and current-driven transport to the north would make all life stages appear in the vicinity or even north of Svalbard. However, krill would not be able to complete maturation or to become fertile in the north due to the thermal constraint. We extended such assessments of transport, applied them to all five krill species we found in Kongsfjorden and it led us to underline that, at least, all of the krill species are suitable indicators of the presence of Atlantic waters as far north as to the marginal ice zone (MIZ) (Dalpadado et al. 2008a). The performance of complete reproduction may, however, be a matter of changing environmental conditions (see below).

Salinity and feeding conditions

In Kongsfjorden, Weslawski and Legezynska (1998) reported mass mortality of zooplankton due to melt water runoff. In soft-bottom samples large quantities of dead copepods and amphipods were found but no krill. The latter probably reflects the euryhalinity of krill species in general: Aarset and Torres (1989) report that *Euphausia superba* is an osmoconformer in the salinity range of 25–45, similar to *M. norvegica* (Forward and Fyhn 1983) in the salinity range of 24–40 with the lower lethal limit occurring between 20 and 24. *Euphausia pacifica* is cited to tolerate 21 in the laboratory. In the Sandsfjord in southern Norway, *T. raschii* generally ascended close to the surface at night (Kaartvedt and Svendsen 1990), where maximum numbers of individuals were often found in the 5–0 m depth interval. In this interval salinity decreased rapidly from 30 to 16. In conclusion, krill are osmoconformers and they are euryhaline, i.e. they are little dependent on salinity changes. This corresponds to their occurrence in neritic and tidal areas as well as to their typical vertical migration behaviour in areas where often steep vertical salinity gradients prevail. Concerning the situation in the Kongsfjorden inner part, they are probably far less influenced by melt water than other zooplankton—which show high mortality—and can thus stay and persist in this area. Accordingly, the possible concentrating effect in the inner fjords is not counteracted by fresh-water-caused mortality for krill: on the contrary, the inner fjord may be an attractive location for krill, since it is the area with the highest sedimentation rate including detritus. The latter is

to a large extent of biogenic origin (Hop et al. 2006) and *T. inermis* and *T. raschii* are known to feed on detritus including algal material at least in northern Norway (Falk-Petersen et al. 2000). Krill was also found feeding just above the sea floor in the organically enriched nepheloid layer often found closely above the bottom where pine pollen were indicative of detritus (Lass et al. 2001, and own observations by ROV). Therefore, if both, diatoms and zooplankton perish in large quantities, detrital material and moribund plankton may be a suitable food source for krill in the fjords. Accordingly, the inner fjord area may mean a niche for krill where competitors cannot intrude, due to salinity constraints. A combination of lipid and dual stable isotope analysis can help to verify this hypothesis in a food web context.

Temperature and hydro-climate

In Kongsfjorden, there are pronounced temperature and salinity gradients brought about by seawater and freshwater input and a complicated current system (Hop et al. 2002, 2006). The Hornsund situation is much less well known but currents may follow similar patterns. Recent work confirms the relative separation of the eastern inner parts of Kongsfjorden (Basedow et al. 2004). Furthermore, the ongoing warming in Kongsfjorden is pronounced and the zooplankton community structure is changing (Walkusz et al. 2003; Walkusz 2007; Kedra 2008). The winter 2005–2006, preceding the sampling in summer for the present study, was a particularly warm one in Kongsfjorden and may thus shed some light on the warmer conditions to come (Walczowski and Piechura 2006). However, fjord temperatures are determined by complex interannual influences, not only by the magnitude of Atlantic inflow, but also by the dimension of glacial melt-water and the duration and dynamics of the winter and spring ice situation (Hop et al. 2006). Accordingly, simple hypotheses to directly relate short-term Atlantic input and macrozooplankton species composition are questionable. With respect to the trophic environment, diatoms dominate the spring phytoplankton blooms, whereas later the importance of flagellates increases which are known to be ingested by krill (Keck et al. 1999). This initial study on the krill species as indicators of environmental change may help to support a future monitoring of the Kongsfjorden system.

Physiology as indication of environmental forcing

Moult and reproduction

Concerning moult activities, the situation in *T. inermis* is different in Kongsfjorden with respect to Hornsund (Figs. 5, 6); the krill in Hornsund still actively moults

whereas in Kongsfjorden moulting has subsided or ceased possibly due to seasonal effects or more precisely the end of the growth season had been reached in Kongsfjorden. It is known, however, that moulting in krill can be trophically induced (Buchholz et al. 2006). Intermediate phytoplankton blooms have been seen to occur in Hornsund during summer and until early autumn due to the input of land or glacial run-off nutrients and a stabilised water column that had persisted for some time (J Wiktor, IOPAS, personal communication). To such a transitional nutritionally improved situation krill may have reacted by allocating the energy input immediately into moult and growth. Such a fast response is known from other krill species, like *M. norvegica* in the Scottish Clyde sea (Tarling and Cuzin-Roudy 2003) or *E. superba* in oceanic Antarctic waters (Buchholz et al. 1996). Furthermore, indications of synchronised moulting observed in Hornsund may count as confirmation of the response. If such an inductive situation was met in the colder Hornsund, this could mean that a temporary enhancement of the trophic environment would have overridden the thermal constraint in the fjord. Accordingly, as exemplified in the warmer and cooler fjord, temperature effects should be evaluated in conjunction with trophic influences and not mono-causally.

Moult and reproductive processes are coupled (Cuzin-Roudy and Buchholz 1999). It is therefore sensible to monitor for signs of reproductive activity in parallel to moult stage analysis. This was done by histological analysis in *T. inermis* from both fjords (to be published elsewhere). In fact, in all species studied, different stages of egg maturation were evident, albeit at a low level, not being indicative of contemporary spawning. A more thorough, seasonally oriented sampling would have been necessary to reveal a temporal sequence of egg maturation. However, so far, the three *Thysanoessa* species are not considered fertile in the Arctic, presumably as a consequence of the low temperature constraint (Timofeyev 1993; Dalpadado et al. 2008a, b). The latter authors stated that the MIZ associated with low temperatures may be a barrier for reproduction in krill. Vice versa, the presence of a full reproductive cycle may be considered as an indication of warming and possibly a shift in food web composition and thus as a possible effect of the Atlantification of the area. Kongsfjorden may be a well suited observatory to follow such a development. Considering reproductive activity in comparison of the species, *T. inermis* and *T. raschii* are found to reproduce regularly in the Norwegian Balsfjorden at 69°N, but not *M. norvegica* (Falk-Petersen and Hopkins 1981). The same holds for northern Iceland at 66°N (Astthorsson 1990). Einarsson (1945) considered that the northern spawning limit of *M. norvegica* coincides with the 5°C isotherm at 100 m depth and the often so called ‘Northern krill’ may thus stay an ‘expatriate’ to the Arctic

and would probably be among the last to start breeding in the Arctic. The specific lipid spectrum supports this notion (Falk-Petersen et al. 2000). Less is known about *N. megalops*, but its predominant southern occurrence from Iceland waters down to the subtropical Atlantic suggests the same.

Lipids and location

In Hornsund, the overall even distribution of lipid stages (Fig. 8) may indicate an ongoing dynamic process: moult activity is still high. Accordingly, lipid reserves have to be mobilised for growth processes, e.g. resorption of the old cuticle, construction and consolidation of the new one, or lipid cannot be accumulated to the same extent. Nevertheless, the frequent occurrence of the LS 4 stage indicates the highest lipid mass, possibly as an overwintering reserve.

In contrast, in Kongsfjorden, concurrent with low moult activity (Fig. 5) the predominance of higher lipid stages indicates preferred allocation of energy into winter fat deposits. According to Falk-Petersen et al. (2000), *T. inermis* is characterized by accumulating considerable lipid deposits for overwintering on the one hand, but also for fuelling the start into the next productive season in spring. Although only females have to prepare for oocyte maturation, it is interesting to note that also males show the same lipid accumulation, confirming the necessity to deposit overwintering reserves.

Lipids and moult

Female krill which are actively moulting in Hornsund (Fig. 9) show also a clear relation to the storage of lipids and/or fat reserves: maximum percentages correspond to the middle stages of the moult cycle while the zero-values follow the opposite run of the curve.

The percentage of high lipid accumulation values increases after moult towards stage C = inter-moult which is known as the predominant phase of reserve accumulation (Buchholz 1991).

A further increase is seen at the initiation of the next pre-moult phase at D0 after which a steady decrease is seen towards the immediate pre-ecdysis stage D3. This pattern may be taken as an indirect confirmation of active moult preparation because it follows the effective physiological needs during the moult cycle: during the feeding phase fat reserves are being continuously accumulated which are depleted again while krill expends energy in building a second cuticle in preparation for the coming moult. This phase corresponds to stages D2 and D3.

The values of LS 0 confirm this conclusion: in the immediate moult stages, i.e. shortly before and after ecdysis: A, B and D3, respectively, show completely

depleted reserves probably due to the liberation of fat reserves needed for the energy cost of the moult processes (Buchholz and Buchholz 1989).

On more general, ecological terms, there seems to be a competing mechanism within long-term processes. On one hand there is the storage of over-wintering reserves; on the other hand, even late in the season, lipid reserves previously stored may be liberated again to fuel bouts of moult and growth. Much is known about differential phases of lipid accumulation and storage, lipids as trophic markers as well as seasonal condition indices (Falk-Petersen et al. 2000). The lipid stages described briefly here are easily discerned after some training. Used as indicators they may be helpful in the comparison of lipid dynamics in *T. inermis* on the level of season, location or latitude. The five stages LS 0–LS 4 may be completed by a further and last stage LS 5, corresponding to “maximal extension” and characterized by the lipid mass extending the carapace of the specimen.

Conclusions and outlook

Climatic relevance

The increasing Atlantic influence in Kongsfjorden may be reflected in the presence of three more euphausiid species characteristic for the boreal Atlantic. In contrast, Hornsund retains a prevailing Arctic influence with *T. inermis* as an Arctic indicator. Apparently, in the colder fjord trophic effects can override temperature forcing. Consequently, warming effects should be studied in the context of integrated food web analysis. Full reproductive activity may serve as an indication of progressing Atlantic influence: If krill reproduce, this may point to a regime shift from Arctic conditions to a boreal situation. A regular monitoring—as it is intended in fact at least in Kongsfjorden—should help to verify these hypotheses.

Biochemical implications

In order to separate temperature constraints from nutrition effects, further biochemical analysis may help. In future seasonal studies, lipid composition may elucidate exemplary functions like lipid allocation as overwintering reserve versus functions as reservoir to fuel vitellogenesis. Stable isotope composition in krill may clarify the significance of fresh-water versus Atlantic water input and may be helpful to assess residence times of water masses and krill as indicators in the fjords at the same time.

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