

# First observation of krill spawning in the high Arctic Kongsfjorden, west Spitsbergen

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**Abstract** In the past, two euphausiid species prevailed in the high Arctic Kongsfjorden, the arcto-boreal *Thysanoessa inermis* (Kroeyer, 1846) and *Thysanoessa raschii* (Sars, 1964). Both were considered expatriates from the Barents Sea or Norwegian Sea and non-reproductive due to low temperatures. The macro-zooplankton of the fjord has been studied as a component in an ecosystem context since 2006, including baseline investigation of distribution and functional performance of key species. In recent years, three additional krill species were regularly detected in the fjord and are the focus of an intensive long-term study. Of these species, *Thysanoessa longicaudata* (Kroeyer, 1846) and *Meganctiphanes norvegica* (Sars, 1857) are typical for the boreal Atlantic whereas *Nematoscelis megalops* (Sars, 1883) has a broad distribution in temperate to subtropical provinces. Their occurrence in the Kongsfjorden clearly indicates increasing Atlantic influence. During the 2011 campaign, *T. raschii* was observed spawning in the field for the first time and showed development up to the naupliar stage in the laboratory. Should more evidence of reproduction be encountered in any of the five krill species in the Kongsfjorden in the future, it will be taken as an indication of a changing environment concerning temperature and food web composition.

**Keywords** High Arctic · Climate change · Krill · *Thysanoessa* · Reproduction

## Background and previous findings

Although only 86 species of Euphausiids are recorded worldwide, they are pivotal components of ecosystems at all latitudes (Mauchline 1980). Most species are truly pelagic and are consumers of phyto- and zooplankton constituting strong links within food chains reaching from primary producers, other meso-zooplankton, squid, fish, seals, birds to toothed and baleen whales. Accordingly, krill are suited as indicators of changes in food web composition from a bottom-up as well as a top-down perspective (Hempel 1970).

The most charismatic species is the Antarctic krill, a truly stenothermic, polar species of the Southern Hemisphere, *Euphausia superba*. This species had 20 mio years to evolve within the Antarctic ring ocean. The Arctic is much younger and far less secluded with access to and input from the North Atlantic and North Pacific waters. Accordingly, a real Arctic equivalent of the Antarctic krill as a true polar species does not exist. Instead, boreo-arctic species prevail, namely *Thysanoessa inermis* (Kroeyer, 1846) and *Thysanoessa raschii* (Sars, 1964), *T. inermis* being considered the continental slope species and *T. raschii* the neritic species (Mauchline 1980).

Euphausiids are not abundant in the high Arctic. However, eggs, larvae and adults of *T. inermis* have been recorded from net catches at eight stations along two Atlantic transects: one close to the north coast of Spitsbergen (NW–NE) and the other to the south-east (Timofeev 1993). Timofeev determined ontogenetic status and size of the specimens and found sequential increase in development and size, generally from the south to the north, interpreted as transport by currents during development. Eggs were non-fertile in *T. inermis*. However, he encountered developing eggs and nauplii of *T. raschii* at one

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single station as high as 80°N, north-east of Spitsbergen, and interpreted this as further indication of advection from the south. Timofeev concluded that krill spawns in the North Atlantic, that is the Barents Sea and is then transported into the Arctic Atlantic and the polar basin by currents that include the northernmost extension of the Gulf Stream. From current trajectories, he back-calculated that the possible breeding grounds in the Barents Sea would be close to Bear Island at 74°N; 19°E. Furthermore, Timofeev (1993) confirmed that *T. inermis* were non-reproductive in the high Arctic due to the low temperatures, and thus formed pseudo-populations, being ex-patriates from the North Atlantic (Lomakina 1978).

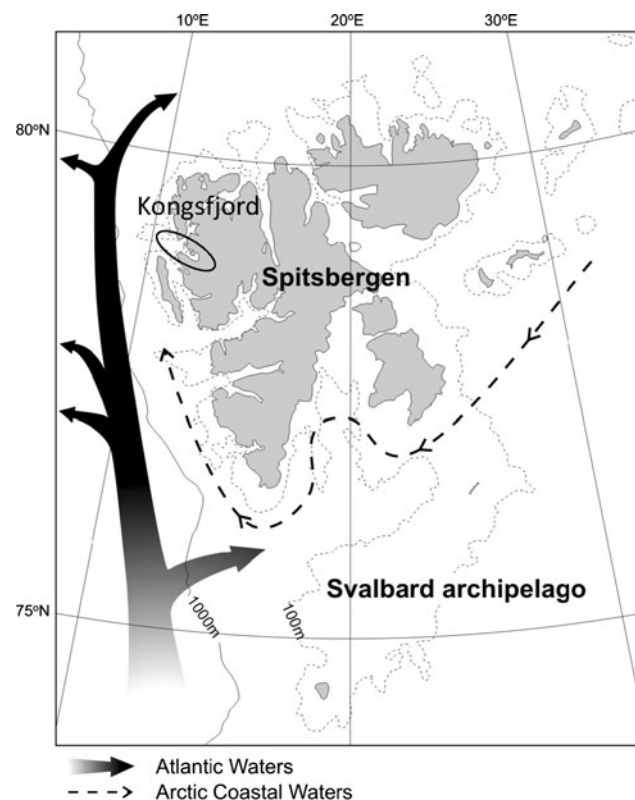
In a later investigation, eggs, nauplii and calytopis larvae of *T. raschii* were found in net catches in the Laptev Sea on the continental slope at 79°N; 105°E (Timofeev 2000). The author concluded that the coexistence of these life stages was an indication of a closed reproductive cycle. Favourable feeding conditions might have induced maturation and spawning, overcoming the constraints of low temperatures close to 0 °C. Advection from the warmer Atlantic was considered impossible in view of the long distance of 2,000 km from the western Barents Sea to these Siberian waters.

Dalpadado and Skjoldal (1991) described *T. inermis* and *T. raschii* and their spawning grounds in the Barents Sea in detail. The dominant species were *T. inermis* and the oceanic *Thysanoessa longicaudata* (Kroeyer, 1846) at densities of 0.6 vs. 0.4 ind m<sup>-3</sup> of adult krill, whereas the neritic *T. raschii* appeared only in smaller numbers. Spawning time in all three species was May–June coinciding with the spring phytoplankton bloom (Dalpadado and Skjoldal 1996). *Meganctiphanes norvegica* (Sars, 1857) also occurred but not in a reproductive state. The northernmost spawning ground of *M. norvegica* was identified as the continental slope of the Norwegian Sea close to but below the polar circle (Dalpadado 2006). A thorough summary of 30 years of records of krill stocks in the Barents Sea (Eriksen and Dalpadado 2011) showed that krill has considerably increased in biomass, particularly over the last decade. This refers predominantly to the oceanic species *T. inermis* but also to *M. norvegica*. Concomitantly, increasing temperatures may have enhanced both primary and secondary production (Ellingsen et al. 2008), particularly along the western Barents Sea, which is the region of northward Atlantic transport, that is to the Spitsbergen area. Krill stocks appear to profit from an enhanced trophic environment. However, population dynamics of the Barents Sea krill is strongly controlled by fish, particularly the capelin (Eriksen and Dalpadado 2011).

In the well-studied high Arctic Kongsfjorden, north-west Spitsbergen (79°N; 12°E, Fig. 1; see Hop et al. 2002), the occurrence of five krill species has regularly been

recorded since 2006, when an initial macro-zooplankton study of 1996 (Weslawski et al. 2000) was repeated (Buchholz et al. 2010). Krill density increased between 2006 and 2011 in both the oceanic *T. inermis* and the neritic species *T. raschii* with an increase in *T. inermis* from 0.1 to 0.3 ind m<sup>-3</sup> (Buchholz et al. 2010 and Buchholz unpubl.). The increase in krill density is probably caused by an increasing influx of Atlantic waters to the fjord. The ‘atlantification’ of the Kongsfjorden may further be affirmed by the recent record of the oceanic krill species, *T. longicaudata*, *M. norvegica* and the subtropical *Nematoscelis megalops* (Sars, 1883) (Buchholz et al. 2010). Due to longer retention time of water and plankton communities in the fjord, it is a well-suited observatory anticipating changes of the larger scale oceanic system (loc. cit.).

In contrast, in boreal fringe seas of the NE Atlantic, *Thysanoessa* populations seem to diminish at more southern locations like the Kattegat (0.5 ind m<sup>-3</sup> in Buchholz and Boysen-Ennen 1988) referring to an intensive study on *M. norvegica* (Tarling et al. 1999) at the so-called Läsö-Deep, where accompanying *Thysanoessa* were no longer recorded. The same observation applies to the Swedish Gullmarsfjord, where *Thysanoessa* was regularly found in the late 1980s but was no longer detected in a study by



**Fig. 1** Map of Svalbard indicating principal currents; Spitsbergen with location of Kongsfjorden (circle)

Buchholz et al. (2006). Possibly, vanishing *Thysanoessa* at these southern locations and increasing krill numbers in the Barents Sea and further north are indicating a similar northern shift of these species as was documented in zooplankton communities dominated by calanoid copepods (Hatun et al. 2009).

### New findings

The probability of the various krill species colonizing new northern habitats and completing their full life cycle there will be assessed in the AWIPEV project KOP 124 on the Kongsfjorden krill population (<http://ssf.npolar.no/pages/database.htm>; Buchholz 3451). By its closeness to the entrance of the Arctic basin and with its research base at Ny Ålesund, the Kongsfjorden system provides the opportunity to observe the effects of increasing influence of warmer Atlantic waters on a long-term scale. Our current studies focus on the growth and reproduction of krill caught in the Kongsfjorden, flanked by eco-physiological investigations, that is energy storage and turnover measurements including experimentation on thermal and trophic requirements. The species recently encountered in the fjord, each with very different temperature and nutritional background, are considered as a natural experiment of adaptive capacity. The range of adaptability is taken as an indication of the species' possible persistence in the area in view of rapid climate change.

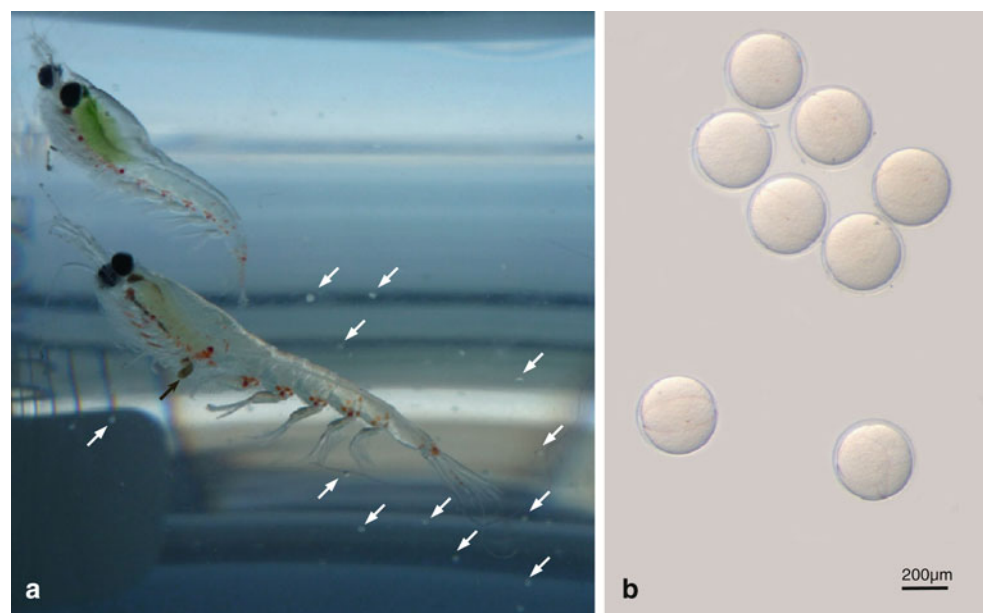
In 2010 and 2011, krill was caught in the Kongsfjorden with the same Tucker trawl as described in Buchholz et al. (2010), but using the work boat 'Teisten' chartered from Kings Bay at Ny Ålesund. While in June 2010 a blue

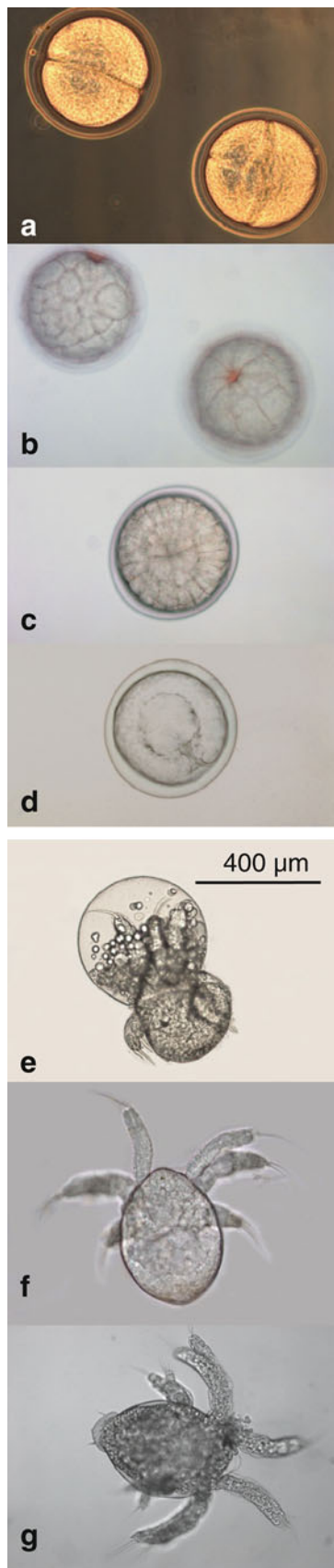
shimmer in *Thysanoessa* specimens was only seen in the freshly captured individuals and could not be further analysed, in June 2011 some individuals could be transferred to the laboratory before the colour had completely faded and spawning krill, *Thysanoessa raschii*, caught in an Arctic fjord was subsequently observed for the first time (Fig. 2). A group of 3 + 1 female *T. raschii* (22–23 mm, one 26 mm long) had been isolated from other krill immediately after the catch and were observed spawning an average of 45 eggs and 52 eggs, respectively. To avoid loss of spawned eggs during the catch, the last steps of maturation and the complete spawning will have to be investigated in the laboratory. Fertility of the eggs was obvious, because most of them started cleavage shortly after being spawned and had reached the gastrula stage within 12 h. Of the 136 eggs retrieved, 67, that are roughly 50 %, had developed to 1st or 2nd nauplia at 4 °C after 5 days (Fig. 3). Eggs of female *T. raschii* with 22–23 mm body length had a mean diameter of 390.5 µm, SD 13.2,  $n = 21$ . Egg sizes in the Laptev Sea were smaller at 350–375 µm and 325–350 µm in the Barents Sea (Timofeev 2000). The body length of the 2nd nauplia ranged from 475 to 525 µm (mean  $500 \pm 25$  µm,  $n = 5$ ), and the width from 313 to 338 µm (mean  $328 \pm 11$  µm,  $n = 5$ ). Nauplii found in the Laptev Sea were slightly smaller at 425–500 µm (Timofeev 2000).

A sample of 20 female *T. raschii* measured had a body length of  $23.8 \pm 1.1$  mm (anterior rim of eyes to tip of telson). Accordingly, they would fall into the range of sizes at reproduction (22.6–24.0 mm) in the Barents Sea (Dalpadado and Skjoldal 1991).

The spawning location was the inner fjord, where 17 'blue' *T. raschii* were collected in a catch of 70 females. Spawning krill are easily detected in a catch as the ovary is

**Fig. 2** **a** Photograph of spawning krill, *Thysanoessa raschii*, in a beaker. Note the carapace inflated by eggs, brown spermatophores ventrally (black arrow), green hepatopancreas, floating eggs (white arrows). **b** Freshly spawned eggs under the dissecting microscope. Note the plane of first and second cleavage as faintly red bands



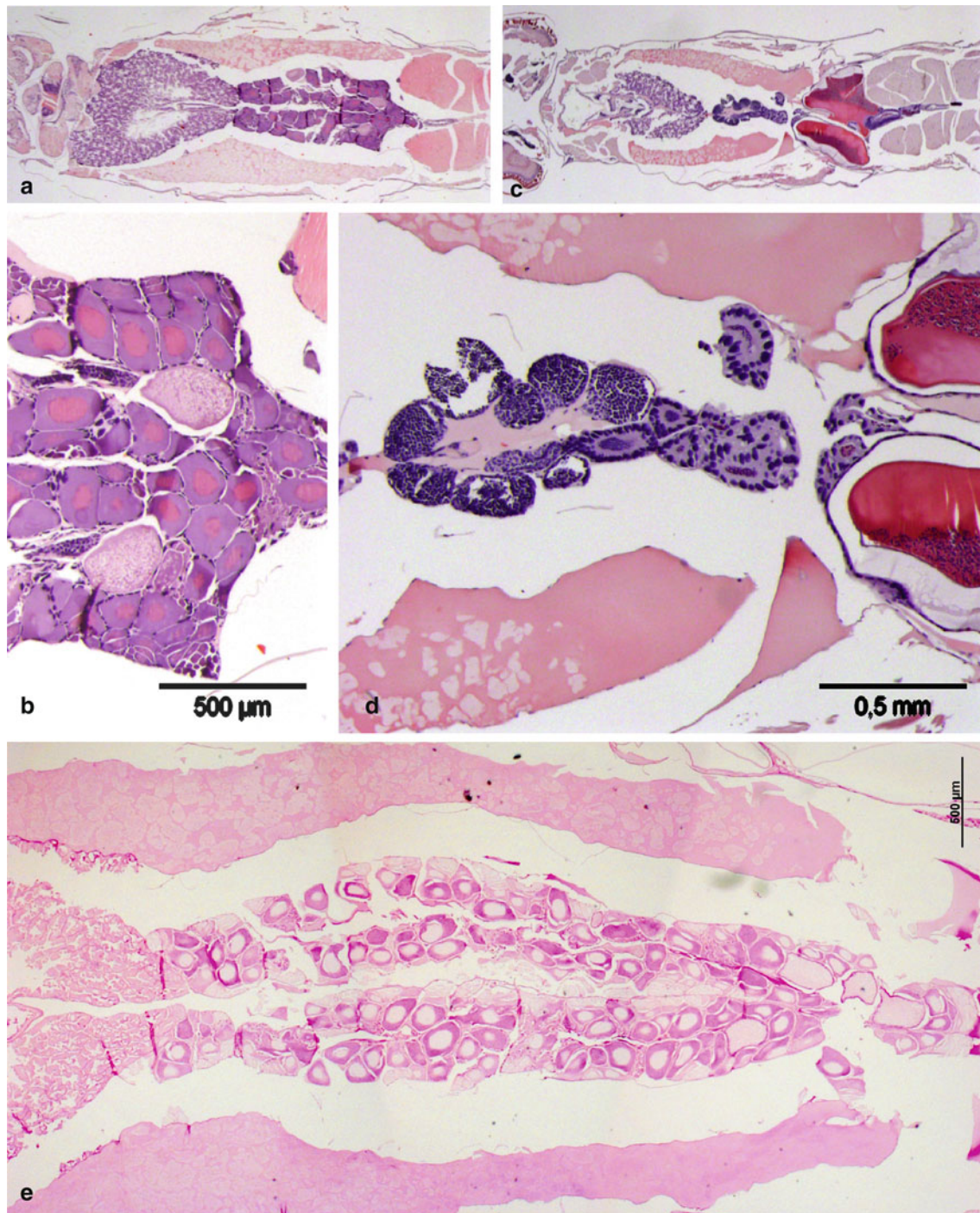


◀ **Fig. 3** *Thysanoessa raschii*, development of fertile eggs after spawning. Same magnification **a** Cleavage 1 and 2; polar body visible in *left* egg; approximately 10 min after spawning, **b** early blastula with blastoporus marked by natural colour, **c** late blastula, **d** gastrulation; 9–12 h after spawning, **e** hatching nauplius, **f** 1st nauplius, **g** 2nd nauplius

conspicuously coloured, in this case a clear light blue, which confirms observations of Dalpadado and Skjoldal (1991) and Dalpadado (2006). In *M. norvegica*, the corresponding colour is ‘blue-grey’ and stands for a batch of eggs immediately pre-spawn, as histological analysis showed (Buchholz et al. 2006). When the mature eggs have left the ovary, the colour disappears as well. The same phenomenon was observed in the *T. raschii*, which immediately after the catch were placed in Kautex-plastic flasks in fresh sea water either separately or in groups. When the specimens were again inspected approximately 2 h later, all had spawned and the blue colour had vanished (Fig. 2). In the following days, krill in the fjord were regularly checked for blue ovaries but only few specimens were spotted. This observation corresponds to similar records on *M. norvegica* in the Danish Kattegat or the Swedish Gullmarsfjord, indicating that a spawning event is an episode in a sequence of releases of a limited number of eggs. The next batch is spawned after final maturation of another group of young oocytes, a process coupled intimately to the moult cycle, lasting in the order of several days (Cuzin-Roudy and Buchholz 1999). Apparently, the observed swarm of *T. raschii* was engaged in such a spawning event. However, the time available at the station did not suffice to observe, if there was a successive spawn. A later stay in August 2011 showed however, that reproductive activity had come to a standstill.

In order to assess the capacity for reproduction, the ovaries of captured krill were examined histologically and compared. Specimens of *T. raschii* from July 2006 showed reproductive activity in both sexes (Fig. 4). It was frequently noted that *T. raschii* had the most developed ovaries of all species found, for example during May–June in the years 2009 and 2010 (figs. not shown). This period corresponds to the spawning event reported here. The second candidate for a closer look into spawning in Kongsfjorden would be *T. inermis*. To date however, we have not observed a fully developed ovary in this species in Kongsfjorden. Although, ovarian activity was conspicuous early in the year, that is before May. That was possibly temporally close to the spring plankton bloom, as was also communicated by P. Dalpadado (pers. comm.) in line with her previous findings of developing ovaries in *T. inermis* in Kongsfjorden as early as February. In the Barents Sea, *T. inermis* as well as *T. longicaudata* spawn in May/June (Dalpadado and Skjoldal 1991) and in April on the





**Fig. 4** *Thysanoessa raschii*, histology: Horizontal sections from front (left) to first pleon segment (right); **a–d** stained with haematoxylin-eosin; **e** stained with PAS (Periodic Acid Schiff's reagent) for glycoproteic material: **a** overview of female; left to right: hepatopancreas (hpp), ovary, pleon muscles; remains of stored lipid are seen lateral to hpp and ovary; **b** detail of ovary: two mature oocytes can be distinguished by their large size and light colour (lipid yolk dissolved), and many young oocytes in various stages of maturation; **c** overview of male; left to right: hpp, testis, red spermatophores,

residual lateral lipid; **d** detail of male gonad: sperm production and pair of spermatophores ready for transfer; **e** detail of female thorax: small cells of oogonia not stained; oocytes with large nuclei in various stages of vitellogenesis, accumulating glycoproteins that are stained through the PAS-reaction. Mature oocytes at the posterior end of the ovary show no nuclei, and glycoproteins are replaced by lipid yolk with some PAS stain remaining at the cell membranes. (compare: Cuzin-Roudy and Amsler 1991)

Norwegian shelf (Dalpadado 2006) is clearly associated with the spring bloom. The *T. raschii* spawning event in Kongsfjorden would be rather late in view of the usual local spring bloom between February and April. There are probably additional food sources of the fjord system, and they may have initiated final maturation of eggs in May. This temporal–trophic relationship will be more closely observed in the coming seasons. Histology on *T. longicaudata* from the Barents Sea (samples supplied by P. Dalpadado) and even *N. megalops* from Kongsfjorden also showed developmental activity, indicating that low temperatures are not insurmountable to at least facilitate maturation of oocytes. There has been some evidence before that changes in the trophic regime exert a stronger influence than temperature variability (Buchholz et al. 2010).

### Conclusions and perspectives

The future occurrence of full reproductive cycles in any of the five krill species in Kongsfjorden will be taken as an indication of a changing environment, in terms of temperature and food web composition. Furthermore, if krill reproduces successfully in the Arctic, biomass will increase additionally to the krill being advected from the south. So far, the first comparisons of krill densities in the Kongsfjorden starting in 2006 (Buchholz et al. 2010) until autumn 2011 (Buchholz unpub.) showed a trend to reach those of boreal and Barents Sea dimensions (Eriksen and Dalpadado 2011). Comparable densities may indicate similar ecological significance of the krill species. However, krill must be seen in the macro-zooplankton context and furthermore in view of the complete ecosystem of the wider area including the Kongsfjorden. The working groups of the section of Functional Ecology at AWI in an international surrounding at the Ny Ålesund Station and elsewhere will contribute to establish conceptual and numerical models to assess the functions of new components in this system. In the frame of our intended long-term study, observation of krill as likely pivotal species may help to identify shifts in trophic pathways in view of a rapidly changing Arctic.

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