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Scavenging amphipods in the high Arctic

Studies of benthic and sympagic amphipods in the genera
Onisimus and *Anonyx*



Henrik Nygård

A dissertation for the degree of
Philosophiae Doctor

May 2011



Scavenging amphipods in the high Arctic

Studies of benthic and sympagic amphipods in the genera
Onisimus and *Anonyx*

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May 2011

SUMMARY

The main objective of this study was to increase our knowledge about the ecology of scavenging amphipods, particularly amphipods within the genera *Onisimus* and *Anonyx*. Specifically, the emphasis was to increase the knowledge of ice-associated (sympagic) *Onisimus*-species, but as these species are rather inaccessible, an approach using benthic congeners as proxies was chosen. By studying the shallow-water scavenging amphipods, a high temporal resolution in sampling could be achieved, resulting in detailed descriptions of life cycles and reproduction parameters of *Onisimus caricus* and *O. litoralis*. As seasonal studies on the amphipod scavenging guilds in the Arctic are rare, this study also includes a description of the seasonal variations in the amphipod scavenging guild in two fjords in Svalbard, Norway. Because *Anonyx*-species (together with the *Onisimus*-species) are conspicuous in shallow-water areas in arctic fjords and also sporadically recorded in sea ice, *Anonyx nugax* was also included in the study. By extrapolating the results from the life history-studies on *O. caricus* and *O. litoralis* to the sympagic congeners, new ideas and hypotheses for future studies were obtained.

The results indicate that although the length of the life cycle differed remarkably between *O. caricus* and *O. litoralis*, both species are semelparous and incubating eggs during winter. The brood release in *O. litoralis* coincided with the phytoplankton spring bloom, while *O. caricus* released its brood in summer when the peak in settling organic material occurred. *Onisimus litoralis* was, based on its energy budget, classified as an income breeder, where concurrent feeding was invested in egg production. Year-round feeding is expected, as length growth was continuous and no build up of energy reserves before the winter was observed.

The amphipod scavenging guild differed between the fjords with a dominance of *O. caricus* in the ice-free Adventfjorden and a dominance of *Anonyx*-species in the seasonally ice-covered Rijpfjorden. The climatologic differences between the fjords were distinct, with the presence of sympagic amphipods in Rijpfjorden. A decrease in the baited trap catch sizes was observed in summer, indicating that the amphipods were differently attracted to bait depending upon season. This pattern was shifted with approximately two months in Rijpfjorden, likely because of the climatologically delayed production regime, and was probably caused by ontogenic processes, a change in feeding behavior and/or avoidance of predation. Fatty acid composition and

stable isotope data indicated different feeding preferences among the scavenging amphipods. *Onisimus litoralis* and *O. glacialis* were suggested to mainly be herbivorous-omnivorous, *O. caricus* was mostly carnivorous/scavenging, while *O. nanseni* was mainly predating on *Calanus* spp. *Anonyx nugax* was suggested to be a carnivore predating on *Calanus* spp. as well as feeding on detritus.

The sea ice can serve as a temporal habitat for benthic crustaceans. The decapod *Eualus gaimardii gibba* was found to utilize the sympagic habitat as a temporal feeding ground. However, its low tolerance to salinity changes, restrict its utilization of the sea ice habitat to periods when the salinity is stable. *Anonyx nugax* was also observed in the sea ice environment, periodically in high numbers. Compared to *A. nugax* collected from the bottom, the individuals collected below ice had low lipid content, and were especially depleted in triacylglycerols, indicating a poor nutritional status. This could indicate that also they migrated to the ice in search for food.

Extrapolating the knowledge gained on benthic *Onisimus*-species to sympagic congeners showed that *O. nanseni* likely follows a similar life strategy as *O. litoralis*, being an income breeder. Additionally, the extended parental care by investing in a “start pack” of energy to the offspring is likely similar in these two species. Further, it could be hypothesized that *O. nanseni* and *O. glacialis* need a higher reproductive output in order to compensate for the high variation in the extent and loss of their sea ice habitat. However, further studies are needed to confirm this. A first step would be to obtain good winter samples, containing ovigerous females of *O. nanseni* and *O. glacialis*, that could give information on reproduction parameters and thus illuminate their life strategies and adaptations towards the sea ice habitat.

Contents

List of papers	2
1. INTRODUCTION	3
1.1. Scavenging amphipods	4
1.2. <i>Onisimus</i> and <i>Anonyx</i>	4
1.3. Sea ice fauna	5
2. OBJECTIVES	7
2.1. Overview of themes and research questions	8
3. MAIN RESULTS AND DISCUSSION	10
3.1. Life histories of <i>Onisimus</i> -species	10
3.2. Environmental conditions in Adventfjorden	11
3.3. Seasonal energy allocation in <i>O. littoralis</i>	12
3.4. Seasonality in the shallow-water amphipod scavenging guild	13
3.5. The role of sea ice for benthic species	14
3.6. Extrapolation of results to sympagic species	15
4. CONCLUDING REMARKS	20
ACKNOWLEDGEMENTS	21
REFERENCES	22
Papers	I-V

List of papers

Paper I

Henrik Nygård, Mikko Vihtakari and Jørgen Berge

Life history of *Onisimus caricus* (Amphipoda: Lysianassoidea) in a high Arctic fjord. Aquatic Biology 5:63-74, 2009

Paper II

Henrik Nygård, Jago Wallenschus, Lionel Camus, Øystein Varpe and Jørgen Berge

Annual routines and life history of the amphipod *Onisimus litoralis*: seasonal growth, body composition and energy budget. Marine Ecology Progress Series 417:115-126, 2010

Paper III

Marek Zajaczkowski, Henrik Nygård, Else Nøst Hegseth and Jørgen Berge

Vertical flux of particulate matter in an Arctic fjord: the case of lack of the sea-ice cover in Adventfjorden 2006-2007. Polar Biology 33:223-239, 2010

Paper IV

Henrik Nygård, Jørgen Berge, Janne E. Søreide, Mikko Vihtakari and Stig Falk-Petersen

The amphipod scavenging guild in two Arctic fjords: seasonal variations, abundance and trophic interactions. Manuscript

Paper V

Henrik Nygård, Jørgen Berge, Bjørn Gulliksen and Lionel Camus

The occurrence of *Eualus gaimardii gibba* Krøyer 1841 (Crustacea, Decapoda) in the sympagic habitat: an example of benthos-sympagic coupling. Polar Biology 30:1351-1354, 2007

The papers are re-printed with kind permission from Inter-Research (Papers I and II) and from Springer Science + Business Media (Papers III and V).

1. INTRODUCTION

In this thesis, I present results from my studies on arctic scavenging amphipods. The main goal was ultimately to increase our knowledge on ice-associated (sympagic) amphipods, by using closely related benthic species as proxies. The thesis is thus based upon the ecological and evolutionary close links between scavenging benthic and sympagic amphipods. It consists mainly of seasonal studies of benthic amphipods from two fjords in Svalbard, Norway, namely Adventfjorden (as part of the Isfjorden-system) and Rijpfjorden (Fig. 1). I will present the results from the studies on shallow-water scavenging amphipods in these two fjords and later extrapolate them to sea ice amphipods. Hence, by comparing this knowledge with information found in the literature on sympagic amphipods, the current basis for our understanding of this complex sympagic system, that is under a strong decline following the current warming of the Arctic, is increased.

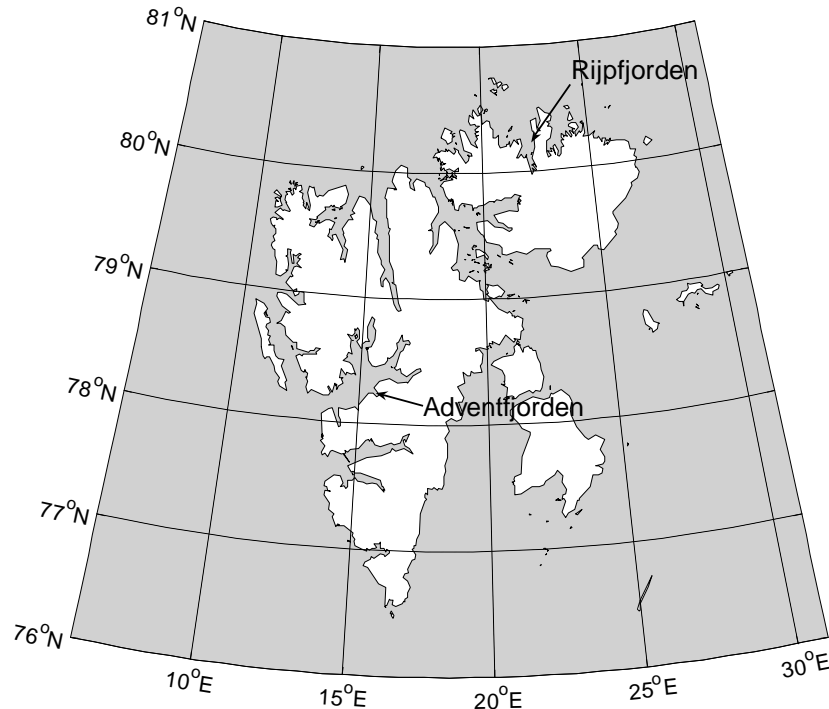


Figure 1. Map showing the archipelago of Svalbard, Norway, with the study locations Adventfjorden and Rijpfjorden indicated.

1.1. Scavenging amphipods

Scavenging animals feed on dead organisms and play a key role in circulating and dispersing organic material from food falls (Britton & Morton 1994). As carrion is a scarce food source in comparison to the vast area of the oceans, few marine species are adapted for obligate scavenging (Britton & Morton 1994, Dauby et al 2001, De Broyer et al. 2004), and most necrophagous species are therefore facultative scavengers with an omnivorous diet (Sainte-Marie 1984, Slattery & Oliver 1986, Sainte-Marie et al. 1989, Legeżyńska 2001, 2008). Although scavengers are found in many phyla, lysianassoid amphipods and nassariid gastropods are groups that most closely approximate the concept of marine scavengers (Britton & Morton 1994). Lysianassoid amphipods are a species rich group and appear to be especially important scavengers in continental shelf polar waters, as well as in the deep-sea (Vader & Romppainen 1985, Legeżyńska et al 2000, De Broyer et al. 2004, Premke et al. 2006). While many of the deep-water species show special adaptations towards scavenging (Dahl 1979, De Broyer et al. 2004), shallow-water lysianassoid amphipods seem less specialized and are likely to have broader diets (Sainte-Marie 1984, Slattery & Oliver 1986).

Due to their feeding behavior and attraction to bait, scavenging amphipods can be collected in large numbers by using baited traps (e.g. Busdosh et al. 1982, Vader & Romppainen 1985, Sainte-Marie 1986). In the Arctic, lysianassoid amphipods have been studied by means of baited traps or baited camera setups both in the deep sea and in shallow coastal areas (e.g. Węsławski et al. 1991, Hargrave et al. 1995, Legeżyńska et al 2000, Premke et al. 2006). Thus, there is information available on species distributions, feeding behavior and life history traits of scavenging amphipods in the Arctic (Węsławski et al. 1991, Legeżyńska et al 2000, Legeżyńska 2001, Węsławski & Legeżyńska 2002, Legeżyńska 2008). However, few studies have had a year-round sampling approach and thus, good information on seasonality in the scavenging guild was lacking.

1.2. *Onisimus* and *Anonyx*

The genus *Onisimus* includes about 25 species (Vader et al. 2005) with a circum-arctic distribution in both arctic and subarctic shallow-water environments (Holmquist 1965), but has also been found in deeper water down to 700 m (Lowry & Stoddart 1993). Most *Onisimus* species are benthic, but *O. nanseni* and *O. glacialis* live in

close association with sea ice (Arndt & Swadling 2006) whereas *O. litoralis* is commonly regarded as a benthosympagic species (Carey & Boudrias 1987, Gradinger & Bluhm 2010). In this study, however, I will refer to *O. litoralis* as a benthic species since sea ice was not present in Adventfjorden during my study and hence, all of my data is from a benthic population. Belonging to the family Lysianassidae, many of these typical cold-water species are known for their scavenging behavior and attraction to baited traps (Vader & Romppainen 1985, Legeżyńska et al. 2000). Based on morphological characters, a close taxonomic relationship has been shown between *O. nanseni*, *O. glacialis* and *O. litoralis* (Holmquist 1965, Vader et al. 2005). Thus, it seems realistic to assume similarities also in their life histories.

The genus *Anonyx* is in many ways (ecology, distribution) very similar to *Onisimus*. It consists of cold-water species with a circum-arctic distribution (Steele & Brunel 1968). Many species are scavengers and together with *Onisimus*, *Anonyx* dominates the shallow-water amphipod scavenging guild in the Arctic (Legeżyńska et al 2000). Two species of *Anonyx*, *A. nugax* and *A. sarsi*, are occasionally found in connection to sea ice in shelf areas (Melnikov & Kulikov 1980, Werner et al. 2004, Paper IV) and juvenile *A. sarsi* has additionally been observed in sea ice off-shelf north of Svalbard (J. Berge pers. comm.). The finding of *A. sarsi* in the ice north of Svalbard is interesting, since back-trajectories of the ice drift showed that the ice had been drifting over deep water for a period longer than the age of the specimens and may suggest that this species can either reproduce in or colonize, from relatively great depths, the sea ice habitat (J. Berge pers. comm.).

1.3. Sea ice fauna

The arctic sea ice hosts a variety of organisms, ranging in size from bacteria and viruses to protists, and further to meio- and macrofauna (Deming 2010, Arrigo et al. 2010, Caron & Gast 2010, Bluhm et al. 2010). Of the latter, crustaceans, together with polar cod (*Boreogadus saida*), are the most common, with amphipods being the most conspicuous group (Gulliksen & Lønne 1989, Gradinger & Bluhm 2004, Arndt & Swadling 2006). Organisms living in or in close connection with the sea ice are usually referred to as sympagic (Carey 1985, Gulliksen & Lønne 1991), and are further divided into groups of ‘autochthonous’ and ‘allochthonous’ species (Melnikov & Kulikov 1980, Gulliksen & Lønne 1989). Representatives of the former group are believed to be restricted to the Arctic, whereas the latter is known from both the

Arctic and the Antarctic (Gulliksen & Lønne 1991). The autochthonous species are by definition dependent upon sea ice during all stages of their life. Sympagic amphipod species that have been regarded as autochthonous are *Gammarus wilkitzkii*, *Apherusa glacialis* and *Pleusymtes karsteni* (Arndt & Swadling 2006, Macnaughton et al. 2007), while the status of the also regularly found *Onisimus nanseni* and *O. glacialis* is more uncertain (Arndt & Beuchel 2006) although many authors treat them as autochthonous (e.g. Lønne & Gulliksen 1991b, Hop et al. 2000). Other examples of autochthonous species are the harpacticoid copepod *Tisbe furcata* and the cyclopoid copepod *Cyclopina* sp. (Arndt & Swadling 2006). Allochthonous species, on the other hand, spend only part of their life in the sea ice, using it as shelter, foraging ground and/or nursing area (Carey & Boudrias 1987, Boudrias & Carey 1988, Werner et al. 2004). Examples of arctic species in this group include common and widespread amphipods like *O. littoralis*, *Anonyx sarsi*, *Eusirus holmii*, *Ischyrocerus anguipes* and *Weyprechtia pinguis* (Carey 1985, Carey & Boudrias 1987, Siferd et al 1997, Werner et al. 2004, Macnaughton et al. 2007, Paper V), decapods like *Eualus gaimardii* (Melnikov & Kulikov 1980, Paper V) and the polar cod (Lønne & Gulliksen 1989). The allochthonous species have either a benthic or pelagic origin; those with a benthic origin probably being restricted to relatively shallow coastal and shelf areas, while the ones with pelagic origin can occur in the ice even in the deep Arctic Ocean (Carey 1985, Melnikov 1997, Siferd et al 1997).

The sea ice plays a significant role in the arctic marine ecosystem. The extent of the arctic sea ice varies between 4.3 (September) and 15.7 (February-March) million km² (Comiso 2010) and ice algae may contribute up to 57 % of the total primary production in the Arctic Ocean (Gosselin et al. 1997). Key species such as the calanoid copepods *Calanus glacialis* and *C. hyperboreus* are highly dependant on the ice algae bloom (Falk-Petersen et al. 2009, Søreide et al. 2010). The sympagic amphipods are as well key actors in transferring the energy from the primary production to vertebrates like polar cod, little auk (*Alle alle*), black guillemot (*Cepphus grylle*), Brünnich's guillemot (*Uria lomvia*) and ringed seal (*Pusa hispida*) (Bradstreet & Cross 1980, Lønne & Gulliksen 1989, Węśławski et al. 1994). Several studies have documented distribution and abundances (Gulliksen 1984, Lønne & Gulliksen 1991a, 1991b, Carey 1992, Siferd et al. 1997, Poltermann 1998, Gradinger et al. 1999, Hop et al. 2000, Werner & Gradinger 2002, Hop & Pavlova 2008), physiological adaptations (Aarset & Aunaas 1987a, 1987b, 1990a, 1990b, 1990c,

Aarset 1991, Kiko et al 2009, Fuhrmann et al. 2010), diets (Werner 1997, Poltermann 2001, Scott et al. 2001, Werner et al. 2002, Arndt et al. 2005a, Arndt & Swadling 2006, Søreide et al. 2006), life history traits (Poltermann 2000, Poltermann et al. 2000, Beuchel & Lønne 2002, Arndt & Beuchel 2006, Arndt & Swadling 2006), pollution effects (Borgå et al. 2002a, 2002b, Haukås et al. 2007, Camus & Olsen 2008, Olsen et al. 2008, Hatlen et al. 2009) and fate (Werner et al. 1999, Arndt & Pavlova 2005, Arndt et al. 2005, Gradinger et al. 2010) of the sympagic amphipods, but due to logistical constraints with studying this remote group the understanding of their ecology is still incomplete. Especially, observations from winter are scarce, as most samples have been collected during the light half of the year. Since most arctic amphipods mate in autumn and carry the brood through the winter to release it in spring (Węśławski & Legeżyńska 2002), especially information about the reproduction is limited. For *Gammarus wilkitzkii* and *Apherusa glacialis* observations from winter give some indications of their reproduction (Melnikov 1997). Poltermann et al. (2000) reared *G. wilkitzkii* in aquaria and studied its reproduction parameters under laboratory conditions in addition to field observations in summer, where also *A. glacialis* was studied. When it comes to the two sympagic *Onisimus*-species, however, very little is known about their reproduction as records of gravid females are rare (Arndt & Beuchel 2006).

2. OBJECTIVES

The aim of this work was to increase the knowledge about the ecology and reproduction parameters of the sympagic *Onisimus*-species. The main rationale was to study easier the accessible *Onisimus*-species, such as *O. littoralis* and *O. caricus* and relate the findings to the closely related *O. nanseni* and *O. glacialis* (Vader et al. 2005). By studying *O. littoralis* and *O. caricus* a high temporal resolution in sampling could be achieved, including the polar night, and thus also detailed information on their life cycles and reproduction parameters. By understanding the life strategies of the benthic *Onisimus*-species, parallels to the sympagic congeners are drawn, and life history aspects of the sympagic species discussed.

Additionally, as some *Anonyx*-species have shown to potentially be important in the sympagic environment, and often co-occurring with benthic *Onisimus*-species

in the shallow-water amphipod scavenging guild (Legeżyńska et al. 2000), feeding patterns and temporal distribution of *A. nugax* and its occurrence in the sympagic habitat were also included in this study.

2.1. Overview of themes and research questions

The main results of this thesis are divided in the following themes, followed by respective research questions:

Life histories of *Onisimus*-species (Paper I, II)

- Life history traits of species set the base for understanding the biology of populations and ecology of communities. By following *O. caricus* and *O. litoralis* (almost) monthly throughout a full year, life histories of these species were studied. Here, life history traits will be presented and later used as a starting point for comparing these benthic species to the sympagic *Onisimus*-species.

Specific research questions:

- How long are the life cycles of *O. caricus* and *O. litoralis*, respectively?
- How do these species time their life cycles?

Environmental conditions in Adventfjorden (Paper III)

- In order to understand the timing of the life history events in organisms, the environmental conditions they encounter must be known. Here, both abiotic (temperature, salinity, sedimentation rates) and biotic (primary and secondary production) factors in the environment hosting *O. litoralis* and *O. caricus* are presented and used as background for understanding their life strategies.

Specific research questions:

- When is the peak in primary production?
- When is the highest input of organic material to the bottom?

Seasonal energy allocation in *O. litoralis* (Paper II)

- The allocation of energy to growth, maintenance, reproduction or stores form the base of a species' life strategy. Here, the energy content and composition

as well as metabolism of *O. littoralis* is studied in two cohorts over a year (thus covering its life span) and related to growth and reproduction.

Specific research questions:

- Is *O. littoralis* building up energy reserves for overwintering?
- Can *O. littoralis* be categorized to either an income or a capital breeder?

Seasonality in the shallow-water amphipod scavenging guild (Paper IV)

- Baited trap sampling is at best a semi-quantitative method, with many constrictions. It is a passive sampling method and many factors affect the animals' attraction to bait. Here, I present and discuss the seasonal variation in baited trap samples in two arctic fjords with differing climatic conditions; the ice-free Adventfjorden and the seasonally ice-covered Rjippfjorden. Additionally, the feeding behavior among *Onisimus glacialis*, *O. nansenii*, *O. littoralis*, *O. caricus* and *Anonyx nugax* are studied by fatty acid composition analyses, as well as stable isotope analyses for the latter four species.

Specific research questions:

- Are there differences in the amphipod scavenging guilds between the fjords?
- How is the environmental seasonality affecting the attraction of amphipods to bait?
- Is it possible to observe any differences in the diets among the scavenging amphipods?

The role of sea ice for benthic species (Paper IV, V)

- Benthic species have regularly been recorded in the sympagic habitat. Explanations for this benthosympagic coupling have been presented for several species, e.g. *O. littoralis* (Carey & Boudrias 1987) and *Anonyx sarsi* (Werner et al. 2004). Here, I present findings of the decapod *Eualus gaimardii gibba* and the amphipod *A. nugax* in the sympagic habitat.

Specific research questions:

- What is the role of sea ice for the benthic species *Eualus gaimardii gibba* and *Anonyx nugax*?

Extrapolation of results to sympagic species

- In this part I will use the knowledge gained in the studies on benthic *Onisimus*-species and extrapolate it to the sympagic congeners. Based on what we know about the sympagic species, I will discuss what can be assumed based on the benthic species, and what remains uncertain about their life histories. As a result of this, I suggest ideas for future studies.

Specific research questions:

- How can the knowledge on the benthic *Onisimus*-species be extrapolated to the sympagic congeners?
- Can we increase our understanding of the life strategies of the sympagic species, and identify gaps in our knowledge by using benthic species as proxies?

3. MAIN RESULTS AND DISCUSSION

3.1. Life histories of *Onisimus*-species

The life histories of *O. caricus* (Paper I) and *O. litoralis* (Paper II) were studied in detail by monthly sampling in Adventfjorden for a full year. *Onisimus caricus* had a 5-year life cycle with females carrying eggs from February to June (Fig 6. in Paper I). The brood release most likely took place in July. They lived as juveniles their two first years and started developing sexual characters in their third year. Males started maturing already in their fourth year, possibly mating already then, while females matured in their fifth year. Thus, males may potentially be iteroparous, whereas females seemed to follow a strict semelparous strategy. The brood size in *O. caricus* varied from 7 to 17, consisting of large eggs (1.68 ± 0.11 (SD) mm in diameter).

Onisimus litoralis had a clear 2-year semelparous life cycle in Adventfjorden (Fig. 1 in Paper II), similar to what has been reported elsewhere (Boudrias & Carey 1988, Sainte-Marie et al. 1990, Węśławski et al. 2000). Mating and egg production took place in November and the females were carrying the brood until April-May. The first year they lived as juveniles and started developing sexual characters during their second spring and matured in the autumn prior to the mating season. In *O.*

litoralis, the average brood size was 42 ± 15 (SD) and the egg diameter was 1.15 ± 0.26 (SD) mm.

Life histories of polar marine organisms are affected by the seasonality of the environment (Arndt & Swadling 2006, Peck et al. 2006). The pronounced seasonality in primary production governs the life cycles of the consumers, favoring a single brood per year timed to the productive period (Węśławski & Legeżyńska 2002). In *O. litoralis*, the brood release is timed to the spring algal bloom, whereas *O. caricus* has timed its brood release to the summer when the input of organic material to the benthos is highest (Paper I, II, IV). Thus, the juveniles of both species are released when conditions are favorable and food is abundant.

3.2. Environmental conditions in Adventfjorden

From November 2006 to October 2007 environmental conditions in Adventfjorden were measured regularly (Paper III). Suspended minerals, organic matter, particulate and dissolved organic carbon, chlorophyll *a* and their vertical fluxes were, in addition to temperature and salinity, measured. The species composition of phytoplankton and abundance of zooplankton was also investigated.

Adventfjorden remained ice-free through the winter 2006-2007 and the lowest temperature was recorded in April (-1.2 °C). The water column was well mixed from November to April, but from May the surface water started warming and reached a maximum temperature of 7.4 °C in August. The influence of freshwater input to the fjord was significant during the summer months. The salinity, from being >34 PSU in the whole water column from November to May, dropped in the surface layer to <5 PSU in July and the influence of freshwater was observed down to 30 m during the summer months. In October, the water had cooled and the input of freshwater to the fjord was terminated, and a homogeneous water mass occurred again.

During winter, the organic matter in suspension and settling to the bottom was low. In April, the spring bloom of phytoplankton increased the amount of organic carbon in the water, but the vertical flux of organic carbon to the bottom remained low. In summer, a significant delivery of turbid melt-water to the fjord increased the amount of suspended matter in Adventfjorden. The sedimentation rates were highest in July and August for both organic and inorganic matter.

The ice-free conditions in Adventfjorden favored an early spring bloom of phytoplankton. However, the flux of organic carbon to the bottom after the spring

bloom was low, probably due to intense grazing by zooplankton, especially Cirripedia nauplii. The main flux of organic material to the benthos occurred in late summer, likely as a result of flocculation with inorganic particles.

3.3. Seasonal energy allocation in *O. littoralis*

Onisimus littoralis is living in a highly seasonal environment and its life history is closely connected to the annual cycle. In order to investigate how energy is allocated to its activities, the energy constituents and metabolism of *O. littoralis* was studied by analyzing total lipid, total protein and total carbohydrate content as well as the activity of the electron transport system (ETS) throughout its life span (Paper II). The results showed that newly released juveniles had high lipid content, but after the first months the lipid content decreased and was thereafter relatively stable. The protein content increased during the summer in both cohorts to be at its highest level in autumn, before it decreased in late-autumn and winter. The carbohydrate content was low with an increase in the spring months (Fig. 4 in Paper II). By converting the body constituents into energy equivalents, the total energy content of *O. littoralis* could be calculated. As lipids contain most of the energy in *O. littoralis*, newly released juveniles had the highest energy content. After the first summer the energy content was quite stable through the winter and increased again during the next summer (Fig. 5 in Paper II). By measuring the ETS-activity and converting it into oxygen consumption, the energy need for metabolism could be estimated. The energy consumption was highest among the newly released juveniles and showed a seasonal pattern with increased metabolic activity during the summer (Fig. 5 in Paper II). Temperature-dependent metabolism and an increased need for energy demanding osmoregulation due to freshwater input to the fjord are probable explanations for the increased energy demand during summer (Percy 1975, Aarset & Aunaas 1990a, 1990b, Shea & Percy 1990).

The pattern in length growth in *O. littoralis* demonstrated year-round growth, with an increased growth rate during summer for both cohorts (Fig. 1 in Paper II). No build up of lipid reserves was seen and the relatively stable lipid content through the winter showed that *O. littoralis* feed year-round to compensate for growth metabolic costs. Additionally, it showed that *O. littoralis* relied on concurrent feeding for egg production, indicating that it can be categorized as an income breeder (Jönsson 1997, Varpe et al. 2009). The importance of the spring bloom of ice algae and

phytoplankton has been shown for *O. littoralis* (Carey & Boudrias 1987, Gradinger & Bluhm 2010) and especially for the young life stages (Boudrias & Carey 1988). The high lipid content, and thus also energy content, of newly released juveniles indicated that they received a start pack of energy from their mothers. This start package was consumed during the first months and might be an adaptation to buffer for environmental unpredictability. For example a warmer climate, with a reduced ice cover and an earlier onset of the phytoplankton spring bloom (Paper III), could induce a mismatch between the brood release and the spring bloom. Hence, the start pack of energy to the juveniles adds flexibility to the life strategy of *O. littoralis*.

3.4. Seasonality in the shallow-water amphipod scavenging guild

The amphipod scavenging guild was investigated in two fjords (Adventfjorden and Rjippfjorden) with differing climatic conditions, using baited traps (Paper IV). Whereas Adventfjorden is influenced by Atlantic water (Paper III), Rjippfjorden is influenced by cold arctic water and has a seasonal ice cover lasting up to 8 months per year (Berge et al. 2009, Søreide et al. 2010, Wallace et al. 2010). The species composition differed between the fjords. In Adventfjorden *O. caricus* was the dominating species, whereas *Anonyx*-species, especially *A. nugax*, dominated in Rjippfjorden. The influence of sea ice was apparent in Rjippfjorden with the occurrence of many sympagic species. Even though the differing sediment types between the fjords likely affected the species composition, a clear depth zonation was observed in both fjords, similar to the pattern described by Legeżyńska et al (2000).

The baited trap catch sizes were varying through the year in both fjords (Fig. 2 in Paper IV). In Adventfjorden, the highest catches were recorded in November and very low catches were retrieved in April-May during the phytoplankton bloom, especially in traps shallower than 20 m. On the other hand, in Rjippfjorden, most amphipods were caught in February, while few amphipods were caught in June-July when ice algae were settling and at the onset of phytoplankton bloom. The catch sizes do not necessarily reflect differences in amphipod abundance in the fjords, but rather differences in how attracted the amphipods are to bait. Explanations for the varying catch sizes could be a change in feeding behavior, ontogenic processes, or reducing predation pressure by avoiding light.

Changes in feeding behavior influence the attractiveness of bait to the amphipods (Smale et al. 2007). In winter, food resources are presumably scarce,

hence increasing the amphipods' attraction to bait. During spring and summer when primary production peak, followed by increased secondary production, there is an excess of potential food for the amphipods and they become less attracted to bait.

Prior to the mating period males may increase their motility and be more prone to go into traps (Sainte-Marie 1986, Conlan 1991). After the reproduction, brood carrying females may contract their digestive tract in order to maximize the brood volume and hence stop feeding (Sainte-Marie et al. 1990). Consequently, they are not attracted to bait. Additionally, in many species mature males die shortly after reproduction (Sainte-Marie et al. 1990), which could result in smaller catches.

Avoidance of predation might influence the motility and habitat choice of the amphipods. These large sized amphipods are probably conspicuous prey for visual predators in shallow, clear water, like diving seabirds and shore-birds (Węśławski et al. 1994, Byers et al. 2010, Luukkonen 2009). The size of the catches from Adventfjorden decreased, especially in the shallow traps, during spring, when the light increased and water was clear. Interestingly, in June, when the fjord was retrieving turbid melt-water from land, the catches increased again. However, as Rijpfjorden was ice-covered until July predation by birds can not explain the decrease in catches there. Predation by fish and seals, however, remain unknown.

Based on fatty acid composition in *O. glacialis*, *O. nanseni*, *O. littoralis*, *O. caricus* and *A. nugax* three main feeding groups were identified (Fig. 5 in Paper IV): 1) a herbivorous/omnivorous group with *O. glacialis* and *O. littoralis*, 2) a carnivorous/scavenging group with *O. caricus* and 3) a *Calanus* feeding group including primarily *O. nanseni*. *Anonyx nugax* was situated between groups 2 and 3, suggesting that it was a carnivore predating on *Calanus* spp. as well as feeding on detritus. Stable isotope analyses supported these groupings, as *A. nugax* got the highest trophic position (3.3-3.5), followed by *O. caricus* (2.9-3.3) and *O. nanseni* (2.6-2.9). *Onisimus littoralis* had the lowest trophic position, close to herbivores (1.8-2.8).

3.5. The role of sea ice for benthic species

Many of the species found in arctic sea ice originate from the benthos (Arndt & Swadling 2005). Thus, it is not surprising that several benthic species use the sea ice as an alternative habitat. Observations of the decapod *Eualus gaimardii gibba* in close association to the sea ice undersurface led to the study about the role of sea ice for this

species (Paper V). Analysis of gut contents revealed remains of *Gammarus wilkitzkii*, indicating that *E. gaimardii gibba* foraged in the sympagic environment. However, salinity tolerance experiments showed that *E. gaimardii gibba* is stenohaline and thus not physiologically adapted for a year-round life in the sea ice. Also, as this species was observed connected to the sea ice only in relatively shallow (50-100 m) waters, it is likely that sea ice is a temporary feeding ground for it.

In Rijpfjorden 2008, *Anonyx nugax* was the most common amphipod collected in the baited traps placed directly under the sea ice (Paper IV) and it was occurring in these traps even above water depths of 180 m. In total, 908 individuals of *A. nugax* were caught in traps mounted under ice in April 2008 and 227 individuals were sexed. Of these, 158 (70 %) were mature males, 13 (6 %) were immature males, 53 (23 %) were immature females and 3 (1 %) were juveniles. It is not likely that the scent of the bait in the traps attracted them from the bottom, but rather that they already were present in vicinity to the ice as they were collected above deep water (180 m).

In April 2007, when lipid content was analyzed for specimens collected both on the bottom and under the sea ice, individuals caught in the traps mounted directly under the ice had lower lipid content than those at the bottom. The individuals from the ice were especially depleted in triacylglycerols and had a high content of phospholipids (up to 44 % of total lipids), indicating that they were in a poor nutritional status. As most of the collected *A. nugax* were mature males, these could be individuals that after the reproduction in winter were about to die, or actively trying to replenish their energy stores. *Anonyx sarsi* collected below drifting sea ice in the Barents Sea also showed to have low lipid content, indicating that it migrated to the ice in search for food (Werner et al. 2004). Similarly, as with our observations on *A. nugax*, most of the *A. sarsi* collected under ice in the Barents Sea were males (Werner et al. 2004). The fate of the mature males of *A. nugax* occurring in the sea ice (if they die or are able to replenish their energy stores) remains unknown for the time being.

3.6. Extrapolation of results to sympagic species

Even though a substantial amount of information has been collected about *O. nanseni* and *O. glacialis* (Table 1), there are still many open questions when it comes to the ecology of these species and their dependency of sea ice. The fact that the majority of studies only report the “medium” size classes with scarce information about the

Table 1. A compilation of information on *Onisimus nanseni* and *O. glacialis*.

	<i>O. nanseni</i>	<i>O. glacialis</i>	Notes	Reference
Abundance FYI (ind/m ²)	0.0-5.4	0.0-6.2	May-September	Hop & Pavlova 2008
Abundance MYI (ind/m ²)	0.0-10.5	0.0-1.1	May-September	Hop & Pavlova 2008
Abundance MYI (ind/m ²)		0.0-25.7	September	Lønne & Gulliksen 1991b
Abundance landfast ice (ind/m ²)	~10	~10	August	Poltermann 1998
Biomass FYI (g/m ²)	0.00-0.33	0.00-0.09	May-September	Hop & Pavlova 2008
Biomass MYI (g/m ²)	0.00-0.42	0.00-0.04	May-September	Hop & Pavlova 2008
Biomass MYI (g/m ²)		0.00-0.78	September	Lønne & Gulliksen 1991b
Biomass landfast ice (g/m ²)	0.4-0.7	~0.1	August	Poltermann 1998
Life span	2.5 yr	3.5 yr		Arndt & Beuchel 2006
Reproduction mode	iteroparous	iteroparous		Arndt & Beuchel 2006
Brood Size	48-189?	161?		Poltermann 1997
Egg-carrying females	November-May December-February		Oocytes in gonads	Barnard 1959
Newly released juveniles	May November-May December-January			George & Paul 1970
Size at maturity	19.7 mm			Arndt & Beuchel 2006
Growth rate				Barnard 1959
Smallest juveniles	<4 mm <3.6 mm			George & Paul 1970
	8.2 mm			Poltermann 1997
	>25 mm			Arndt & Beuchel 2006
Maximum size	34.1 mm	2.3 mm	Growth curve	Poltermann 1997
	1.1 : 1	4.1 mm	November-May	Arndt & Beuchel 2006
Sex ratio (females:males)	1 : 1.4	14.6 mm	May	Barnard 1959
	1.5 : 1	15.6 mm	August/September	Arndt & Beuchel 2006
		1 : 1.4	May, September	Poltermann 1997
		1.6 : 1	August/September	Arndt & Beuchel 2006
			May	Arndt & Beuchel 2006
			September	Arndt & Beuchel 2006
				Poltermann 1997

smallest life stages and rare reports on mature individuals is noteworthy and has led to questioning their dependency of sea ice to fulfill their life cycle (Arndt & Beuchel 2006). Year-round work done on drifting ice stations (Barnard 1959, George & Paul 1970, Melnikov & Kulikov 1980) report ovigerous females and newly released juveniles of *O. nansenii* caught under the ice from November to May, showing that they may reproduce and rear their young in the sea ice habitat, but compared to the total catches the number of ovigerous females is still low. For example, Barnard (1959) collected in the period November-February 1952-53 in total 17 856 individuals of *O. nansenii* on the T-3 ice station, but only 97 ovigerous females were found (0.5 % of the total catch) and only 81 small juveniles (0.5 % of the total catch). George & Paul (1970) collected 3909 *O. nansenii* in December-February 1969-1970, of which 67 (1.7 %) were ovigerous females and 445 (11.4 %) small juveniles. However, the samples in both studies were collected with baited traps, which could underestimate the abundance of ovigerous females and newly released juveniles (Sainte-Marie et al. 1990, Paper I). In *O. glacialis*, brood release has been observed in February (Griffiths & Dillinger 1981), but as no further information on its reproduction is available the discussion below will be more focused on *O. nansenii*.

Only one study has attempted to estimate the life cycles of *O. nansenii* and *O. glacialis* (Arndt & Beuchel 2006). In this study, a 2.5 year iteroparous life cycle for *O. nansenii* and a 3.5 year iteroparous life cycle for *O. glacialis* were concluded (Arndt & Beuchel 2006). Whereas the modeled life cycle for *O. glacialis* seems reliable and reasonable (although their spring model is based on few observations), the presented life cycle for *O. nansenii* is somewhat doubtful. Their interpretation would mean that the newly released juveniles (<4 mm; Barnard 1959), have more than doubled in length until May, to only grow to a size of 10.3 ± 0.4 (SD) mm or 10.7 ± 0.4 (SD) mm, males and females respectively, until September. As seen for *O. littoralis*, the juveniles grow fast during their first months, but this is during the productive time of the year. Thus, it seems unlikely that the small juveniles of *O. nansenii* would grow that fast during the winter. A possible explanation is that the newly released juveniles were poorly sampled (a few ~4 mm seem to appear on the histogram). Hence, the life cycle of *O. nansenii* could be 3.5 years. In this case, whether the lack of the smallest juveniles was caused by sampling methods or that they were absent from the ice habitat remains unknown. Additionally, as sexual characters were observed only after approximately a year in *O. littoralis*, both growth

and development seem unrealistically fast in the modeled life cycle of *O. nanseni* (Arndt & Beuchel 2006), but additional studies are needed to confirm this.

Observations of ovigerous females and newly released juveniles from November to May suggest that brood release is not strictly synchronized in *O. nanseni*. Assuming similar egg development times as in *O. littoralis* and *O. caricus* (5-6 months), egg production has to take place in June-July for juveniles to be released in December. Accordingly, eggs have to be laid in November-December for juveniles to develop until May. As shown for *O. littoralis* (Paper II), where concurrent feeding was invested into egg production, an income breeding strategy is likely also for *O. nanseni*. This would mean that *O. nanseni*, presumably feeding on *Calanus*, would use the peak in secondary production during spring/summer as energy source for producing eggs. This could add flexibility to its life strategy and might be an adaptation towards the variable conditions in the sympagic habitat, where the onset of primary production, setting the base for secondary production, depend on factors like ice thickness, snow cover and geographic area (Falk-Petersen et al. 2007). Thus, the timing of reproduction would be controlled by the availability of food resources for egg production, and not by timing the reproduction so that the brood release happens during the most favorable conditions for the offspring.

Following the same line of reasoning, it can be hypothesized that the juveniles need a start pack of energy from their mother to survive until the primary production starts when the light returns. Thus, it would have a similar kind of adaptation towards environmental variability as seen in *O. littoralis*. However, more information on the timing of brood release, juvenile feeding strategies and body composition in *O. nanseni* is needed to support this suggestion.

There is no information on brood sizes in *O. nanseni* and *O. glacialis*, but Poltermann (1997) counted oocytes in the gonads and report 87.4 ± 36.4 (SD) (ranging from 48 to 189) and 161 oocytes for *O. nanseni* and *O. glacialis*, respectively. However, the number of oocytes in gonads does not reflect the brood size, since it remains unknown how many of these actually develop into eggs, but it can be used as an indication to estimate the brood size. Thus, the brood sizes in *O. nanseni* and *O. glacialis* could be relatively high, compared to *O. littoralis* (12-61 eggs) and *O. caricus* (7-17 eggs).

The large variations in the extent of the sea ice put an extra challenge to the organisms inhabiting the sympagic habitat. Seen from a perspective of population

dynamics, *O. nansenii* and *O. glacialis* must compensate for a loss connected to part of its habitat drifting out Fram Strait (Hop & Pavlova 2008). Additionally, as the extent of sea ice cover varies remarkable through the year, parts of the population are also lost to the surrounding shelf seas. Thus, it can be hypothesized that the sympagic species need a higher reproductive output than their benthic congeners, and to achieve this, a reduced mortality rate, increased brood sizes or/and finding a refuge during ice free periods could serve as possible solutions. A larger brood size seem possible based on the oocyte-counts (Poltermann 1997), whereas the mortality rates are difficult to estimate based on our present information. As well, the role of shallow benthic habitats as refuges for the sympagic fauna during ice free periods is not well understood and need further investigations. Arndt et al. (2005b) suggested that sympagic species can live in the benthos during ice free periods and recolonize the ice as it re-forms. Gradinger et al. (2010) suggested that ice ridges, which melt slower than level ice, could serve as refuges for sympagic fauna during the melting periods.

The sea ice environment is a complex system, of which our current understanding still is limited. This system is likely to face considerable challenges in a warming Arctic with modeled ice free summers within 50 years (ACIA 2005, Solomon et al. 2007). In order to understand what consequences this will have on the arctic marine ecosystem a continuation of the research in this area is needed. When it comes to sympagic amphipods, the very few observations of ovigerous *O. nansenii* and *O. glacialis* in the ice raise the question if this is only because sampling during winter is scarce combined with use of inappropriate sampling methods, or are they reproducing outside the sympagic habitat? Assuming that brood release take place in winter, egg-carrying females should be present already in autumn when many sampling campaigns have been conducted. Ovigerous females of these species have, however, not been observed elsewhere, neither in the pelagial nor in the benthos. Sampling in winter by using appropriate methods, could unveil their reproduction parameters and thus illuminate their life strategies and adaptations towards the sea ice habitat.

4. CONCLUDING REMARKS

In arctic areas, studies with a high temporal resolution through a full year are scarce. In this study, the shallow-water amphipod scavenging guild was studied in two climatically different arctic fjords, Adventfjorden and Rijpfjorden, with a regular sampling covering all seasons. The high temporal resolution in sampling allowed the life cycles of *O. caricus* and *O. littoralis* to be described in detail and the life history events of these species to be related to the environmental conditions in Adventfjorden. It was shown that the food availability for newly released juveniles controlled the timing of these species' life cycles, and that they preferred different sources of food. In this study, the energy budget of *O. littoralis* was also presented, which increased our understanding of its life strategy. It was categorized as an income breeder that needs to feed year-round to compensate for growth and metabolic activity.

In this study it was also shown that the scavenging amphipods were differently attracted to bait depending on season. Although the species composition of the amphipod scavenging guild differed between the fjords, this pattern was observed both in Adventfjorden and in Rijpfjorden. However, the pattern was shifted with approximately two months in Rijpfjorden, likely because of the climatologically delayed primary production regime. Additionally, the present study found different feeding preferences among the scavenging amphipods; *O. littoralis* and *O. glacialis* were mainly herbivorous-omnivorous, *O. caricus* was mostly carnivorous-scavenging and *O. nansenii* mainly predated on *Calanus* spp. *Anonyx nugax* was shown to be predated on *Calanus* spp. as well as feeding on detritus.

Based on the gained knowledge on *O. littoralis* and *O. caricus*, ideas were transferred to and compared with what we know about the sympagic *Onisimus*-species. Here, it is suggested that *O. nansenii* could be an income breeder, similar to *O. littoralis*. It is also predicted that *O. nansenii* must invest in a start pack for the offspring for them to survive during the first months. In the current study, it is also suggested that *O. nansenii* and *O. glacialis* must have a higher reproductive output than *O. littoralis* and *O. caricus* as the extent of their habitat is highly variable and parts of it are lost every year. However, further studies on this topic are needed, especially more data on the reproductive output of the sympagic fauna, to better understand their life strategies and adaptations towards the sea ice habitat.

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