Master of Science Thesis

Life history of an Arctic crustacean *Onisimus caricus* (Amphipoda: Lysianassidae) as deduced from baited trap samples taken from Adventfjorden, Svalbard

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ABSTRACT

Life history of the amphipod *Onisimus caricus* (Hansen, 1887) was examined in Adventfjorden, Svalbard from samples collected with baited traps. Sampling was carried out in shallow water over the course of 10 months between September 2006 and August 2007. The life cycle of the species was estimated from gender-specific size-frequency distributions with the help of kernel density estimates and mixture distribution analysis. Reproductive parameters of the population were estimated and compared to those of other amphipod species. The life cycle of the species was suggested and the growth rates were modeled based on the life cycle. The modeled growth was compared to the growth of other *Onisimus* species. The potential sampling biases, such as the attraction of *O. caricus* to the bait, were discussed. The life span of the species was suggested to be as long as 5 years, which is longer than the previous estimate of 3 years. The mating time of the species was found to occur in the mid-winter and the hatching of juveniles from late June to mid-August. The hatching time of the juveniles coincides with the peak in zooplankton mortality. Even though the life cycle estimate in this study is based on strong evidence and a large sample (6832 specimens from 10 months throughout a year), there is room for criticism. Other possible life cycles were discussed. In any case, it is probable that the life history of the species is semelparous (one brood during life time) and perennial (life span more than two years), with a possibility of iteroparism (two broods during life time). A hypothesis that sexual maturity is dependent on a certain number of molts rather than body size would explain the high variation in the size of egg-bearing females observed. This would support a semelparine *O. caricus* population, where the reproductive success of females would be determined by the growth rate. Remarkably large egg size, long life span, slow growth and potential semelparity suggest that *O. caricus* can be classified as an A-selected species, which is defined as a selection for predictably unfavorable habitats

HUIPPUVUORTEN YLIOPISTOKESKUS, Arktisen biologian osasto

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos
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TIIVISTELMÄ

Onisimus caricus (Hansen, 1887) katkan elinkiertoa Huippuvuorten Adventvuonosta tutkittiin mertanäytteenotoilla. Näytteenotto suoritettiin ympärivuotisesti kymmenenä kuukautena syyskuusta 2006 elokuuhun 2007 suhteellisen matalassa vedessä. Lajin elinkierto arvioitiin perustuen sukupuolispesifiseen pituus-frekvenssi jakaumaan, jota tarkasteltiin sekajakauma-analyysillä sekä kernel-tiheysestimaateilla. Lisääntymisparametrit arvioitiin ja niitä verrattiin muihin katkalajeihin. Kasvu arvioitiin ja mallinnettiin sijoittamalla sekajakauma-analyysin antamat kohorttien keskiarvot ajallisesti arvioituun elinkiertoon. Saatua kasvukäyrää verrattiin toisiin *Onisimus* -suvun katkoihin. Lajin elinkierto hahmotettiin kokonaisuudessaan ja elinkierron kannalta tärkeimpien vaiheiden ajoittumista lyhyeen, mutta tuottoisaan arktiseen kesään pohdittiin. *O. caricus* katkan elinkaareksi saatiin viisi vuotta, mikä on yllättävän pitkä aika verrattuna aiemman tutkimuksen perusteella arvioituun kolmeen vuoteen. Lajin paritteluaika sijoittui keskitalveen. Naaraat kantoivat munia keskikesään, jonka jälkeen munat kuoriutuivat heinä-elokuussa. Kuoriutumisaika ajoittui samaan ajankohtaan kuin oletettu huippu eläinplanktonin kuolleisuudessa. Vaikka arvioitu elinkierto perustuu vahvoihin todisteisiin ja suureen näytekokoon, tuloksiin liittyy epävarmuutta. Kritiikin lähteitä pohdittiin ja vaihtoehtoisia ratkaisuja elinkierroksi punnittiin. Vaikka muita vaihtoehtoja elinkierroksi saattaa olla, on todennäköistä, että laji on elinkiertopiirteiltään semelparinen (yksi poikue elinaikana) ja monivuotinen. Mahdollisuutta iteroparian (kaksi poikuetta elinaikana) ei voitu sulkea pois. Tällöin naaraat tuottaisivat yhden poikueen neljäntenä keväänään ja toisen viidentenä. Kirjallisuudessa esitetty hypoteesi, että sukukypsyys saavutettaisiin tietyn kuorenvaihtomäärän jälkeen, tukisi havaittua munia kantavien naaraiden suurta kokovaihtelua. Huomattavan suuri munien koko, pitkä elinkaari, hidas kasvu ja mahdollinen semelparisuus kaikki tukevat lajin luokittelemista elinkiertopiirteiltään A-kategoriaan, joka on perinteisemmän K-kategorian vastine äärimmäisiin olosuhteisiin.

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1. INTRODUCTION AND BACKGROUND

1.1. Order Amphipoda

The Amphipoda is an order of crustaceans that includes approximately 9 300 described species (Vader 2005, updated by Vader pers. comm.). It is one of the most diverse orders among crustaceans. Vader (2005) conjectured that the total number of amphipod species in the world may be as high as 30 000 to 40 000. As well as being a diverse order, Amphipoda is also a widespread group. The vast majority of amphipod species live in the oceans in all latitudes from the polar oceans to the equator spanning all possible depth zones. There are also some terrestrial amphipods, which only live in moist places, for example on beaches or under leaf litter in forests (Schram 1986). In addition, amphipods are found in fresh water bodies. For example, 366 amphipod species, little more than 20 % of the total number of the fresh water amphipod species found from the world, has been described from Lake Baikal, Southern Siberia (Vader 2005).

According to traditional amphipod classification (Lincoln 1979, Barnard & Karaman 1991) order Amphipoda is divided into four suborders: (1) Gammaridea are primarily benthic amphipods, with perhaps 20 % pelagic species. Being the most abundant suborder in the Arctic regions, Gammaridea encompass approximately of 85 % of all described species globally; (2) Hyperiidea are found only in pelagic environment and belong to the Arctic fauna; (3) Caprellidea consists of skeleton shrimps, which are typically associated with kelp forests, but there are also some ectoparasites of marine cetaceans belonging to the group; and finally (4) Ingolfeillidia. However, this conventional amphipod classification has been widely debated (cf e.g. Barnard & Karaman 1991, Berge et al. 2001, Englisch 2001, Myers & Lowry 2003, Vader 2005). This study focuses on Gammaridean amphipods, more exactly the amphipod *Onisimus caricus*, which belongs to the superfamily Lysianassoidea. The superfamily dominates the necrophagous fauna in shallow coastal areas and fjords of the Arctic (Thurston 1979, Oliver & Slattery 1985, Presler 1986, Sainte-Marie 1986a, Slattery & Oliver 1986, Kaufmann 1992, Sainte-Marie 1991, Legeżyńska et al. 2000, Legeżyńska 2001).

Gammarideans are flattened from side to side, but more accurately, they are defined by the presence of three pairs of uropods (tail-limbs) and usually by having the first two pairs of legs, called gnathopods, modified to help in grasping food (Figure 1). Amphipods, like tanaids and isopods, lack a carapace covering the thorax, but they have seven thoracic and six abdominal plated segments, which support and provide shelter for the gills and other soft parts of the animal. The arrangement of the gills and outer plates in the thorax, called coxae, provide shelter for the eggs, which are carried externally by the female. The head carries two pairs of antennae, the stalkless eyes, and the mouthparts (Schram 1986, Barnard & Karaman 1991). The name “amphipod” comes, from having seven pairs of walking legs of which the first four reach backwards and the fifth to seventh reach forwards (Berge pers. comm.). The abdomen is divided into two parts: three segments with brush-like limbs, called pleopods, and three with short immobile rod-like uropods.

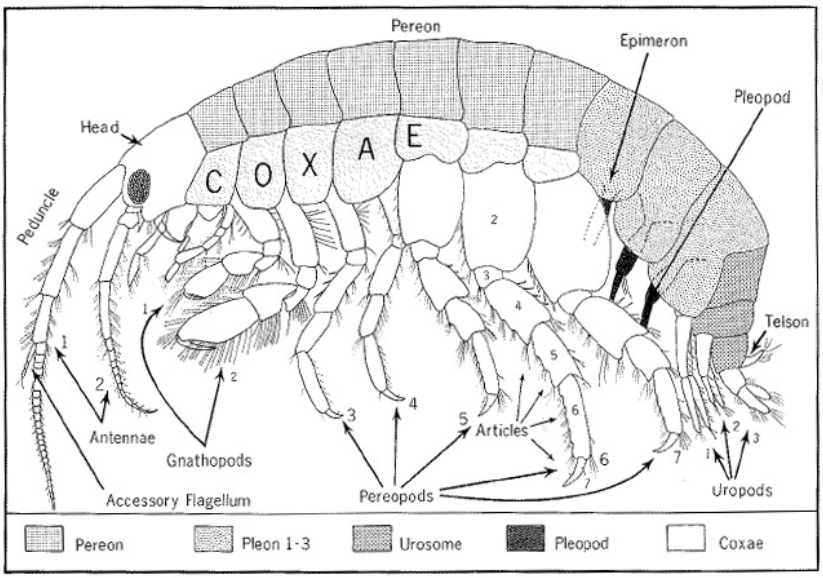

Figure 1. General external structure of a gammaridean amphipod (Barnard & Karaman 1991).

Despite of their relatively clumsy appearance, certain amphipods are surprisingly good swimmers. For swimming at steady speed, amphipods use mainly pleopods. In addition, they can use their tail for fast sudden movement in order to escape predators. Most benthic amphipods use their five last thoracic legs for walking along the substrate (Schram 1986, Barnard & Karaman 1991). The size of amphipods varies amongst and within the species. Typical body length for an adult amphipod is from a few millimeters to a few centimeters, depending on the species, but amphipods as long as 23 cm have been recorded (Barnard & Ingram 1986, Barnard & Karaman 1991).

The life cycle of gammaridean amphipods typically consists of five different periods (Figure 2). Since the sexes of amphipods are separate, eggs develop in the brood pouch of the females. Moreover, the number of eggs in a clutch varies highly among species (Steele & Steele 1975a, Barnard & Karaman 1991). The length of the hatching period depends on the water temperature and the egg size, and varies at least from two days to half a year (Sainte-Marie 1991). Unlike most crustaceans, the amphipods lack a free-living larval stage and juveniles look very much like the adults. Furthermore, it is common amongst most of the gammaridean species that females provide shelter for their offspring in the brood pouch for a couple of weeks after hatching. Once the juveniles are big enough to start living on their own, they are released.

The growth of amphipods is connected to the change of the rigid exoskeleton. After a varying time period and a certain number of molts (Sexton 1924), juveniles achieve characteristics typical to their sex. The males are characterized by the presence of genital papillae (penis) and often by enlarged eyes and gnathopods (Skadsheim 1982, Barnard & Karaman 1991). The males of Lysiannasidae have usually longer second antennae than females, because of their habit to swarm and actively find females by smell (Conlan 2004). The females in turn are characterized by the presence of oostegites (brood plates) (Barnard & Karaman 1991). Development of sexual characteristics requires time and probably a certain number of molts, before specimens mature and are ready to mate (Hammersmith & Coyle 1991).

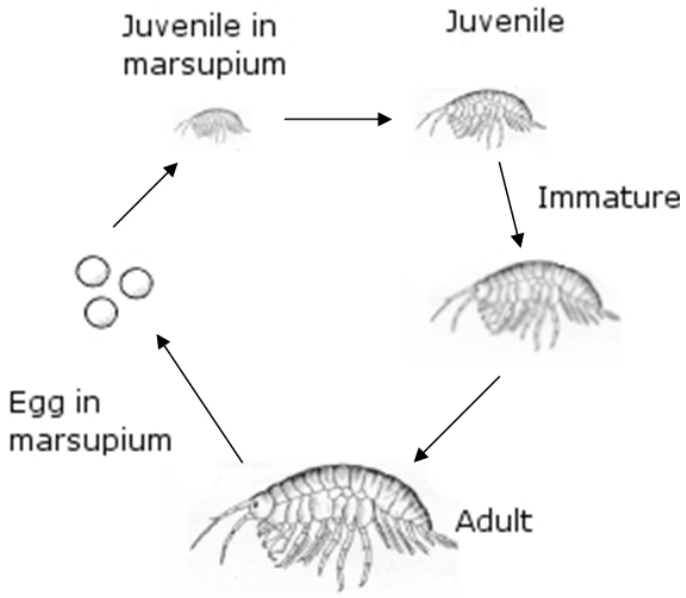

Figure 2. General life cycle of a gammaridean amphipod (modified from Birmingham et al. 2005)

In the Arctic regions amphipods are commonly the only significant crustaceans in biomass from shallow water and tidal flats, where some of the bird species, such as waders (Węsławski et al. 2000) and arctic tern (*Sterna paradisea*) (Kovacs 2006), are feeding. This is one reason why amphipods are considered as a key element in the Arctic food webs (Węsławski et al. 2000). In addition to birds, amphipods are an important food source for other invertebrates and vertebrates including polar cod (*Boreogadus saida*) (Arndt et al. *in prep*), young white whale (*Delphinapterus leucas*) (Heide-Jørgensen & Teilmann 1994) and ringed seal pups (*Pusa hispida*) (Hobson & Welch 1992, Kovacs 2006). Most of the lysianassid species are necrophagous or detrivorous. In addition to detritus, amphipods recycle pollutants deposited in the seafloor causing the accumulation of pollutants in the food chain (Svendsen et al. 2007). Some sympagic (sea ice-associated) amphipod species play an important role in the ice communities by feeding on algae during the ice algal bloom, even though they are not as important as Calanoids (Copepoda) in linking the primary producers to the higher trophic levels (Arndt & Swadling 2006, Arndt et al. *in press*).

1.2. Life histories of gammaridean amphipods

Knowledge of life history characteristics of single species is important for understanding both the population biology of the species and the ecology of communities. Furthermore, life history features, which are affected by environmental conditions, may result in very different life cycles, size and age class structures and secondary productivity between populations of the same or related species over their distributional ranges (Hammersmith & Coyle 1991). When enough research has been conducted on the ecology of communities, the knowledge can be used to deduce interactions between communities in the ecosystem. Such knowledge of ecosystems can lead to a better understanding of diverse life in the oceans. Understanding this diversity could potentially lead to an increased human awareness towards life in the oceans,

which in turn could raise awareness of the importance of conserving the unique ocean ecosystems world wide.

There are a relatively large number of high-quality publications dealing with life history features of the Arctic and the deep-sea gammaridean amphipods (e.g. Wildish 1982, Sainte-Marie 1991, Hammersmith & Coyle 1991, Węsławski et al. 2000, Węsławski & Legeżyńska 2002, Arndt & Beuchel 2005). Generally shallow cold-water gammaridean, especially lysianassid, the amphipod assemblages remind those in the deep-sea, but while the deep-sea communities have some extremely large members, amphipod assemblages in the shallow cold-water seem to lack those large species (Sainte-Marie 1991).

According to the traditional idea of two types of life history selection operating in contrasting environments unpredictable habitats would favor species with short life cycle, high fecundity and good colonizing abilities (MacArthur & Wilson 1967). Species with these life history traits are commonly referred as r-selected. In contrast, species associated with K-selection, having longer life cycle, lower fecundity, and in general, being better competitors for resources, would be more competitive in crowded predictable favorable habitats. Greenslade (1983) updated this habitat templet with predictably unfavorable habitats, such as those in the Polar regions. He suggested adversity selection, abbreviated as A-selection, for these habitats. Before this suggestion, it was concluded that K breeding strategy appeared to be universal in both Arctic and Antarctic benthic crustaceans and fishes (Thorson 1950, Clarke 1980). Predicted life history traits for A-selection are great longevity, slow growth, late maturity and low fecundity. After Greenslade (1983) it has been considered that arctic crustacean fall rather to A-selection category as in general high-latitude (cold water) gammaridean amphipods are characterized by one brood per year (univoltinism), large body size, delayed maturity, long life cycle, large embryos and few broods in life time (Sainte-Marie 1991, Węsławski & Legeżyńska 2002).

In order to succeed in breeding, it is important to synchronize the release of the brood with optimal conditions especially in the Polar regions (e.g. Thorson 1950). Most of the publications on the biology of sub-polar and polar marine invertebrates report strong seasonally correlated breeding as a general pattern (Dunbar 1957, Kuznetsov 1964 after Węsławski & Legeżyńska 2002, Steele 1967, Steele 1972, Steele & Steele 1972, Thurston 1972, Steele & Steele 1975, Clarke 1979). Further, studies have shown that the polar amphipods tend to have only one distinctive reproductive period per year and thus the cohorts in the length–frequency distribution are often considered as age-classes in life history studies of the Arctic amphipods (e.g. Steele & Steele 1975, Boudrias & Carey 1988, Sainte-Marie 1991, Poltermann 2000, Węsławski et al. 2000, Beuchel & Lønne 2002, Węsławski & Legeżyńska 2002, Arndt & Beuchel 2005).

Typically the Arctic amphipods breed only once during their life time (Dunbar 1957, Kuznetsov 1964 after Węsławski & Legeżyńska 2002, Steele & Steele 1975, Tzvetkova 1977, Kosztneyn et al. 1995), but two or even more broods are not rare in some superfamilies (Hammersmith & Coyle 1991). In a study of life cycles of some Arctic amphipod species Węsławski & Legeżyńska (2002) found that almost all species incubated eggs during the polar night and released their offspring in early April. However, there were also exceptions, since some species were reported to incubate during the summer. It has been noticed, that even though breeding is highly synchronous within a population of particular amphipod species, time of the breeding may vary among species and populations (Sainte-Marie et al. 1990,

Sainte-Marie 1991, Węsławski & Legeżyńska 2002). Breeding of most of the species studied by Węsławski & Legeżyńska (2002) was synchronized with development of algal bloom, which in turn is controlled by solar cycle (Wiktor 1999). A summary of life cycles of a few amphipod species occurring on Svalbard is shown in Figure 3 (Węsławski & Legeżyńska 2002). The summary shows high variation in longevity of the life cycles with small species having one year life span, typical to temperate areas (Sainte-Marie 1991), and the largest with over four years life expectancy (Węsławski & Legeżyńska 2002).

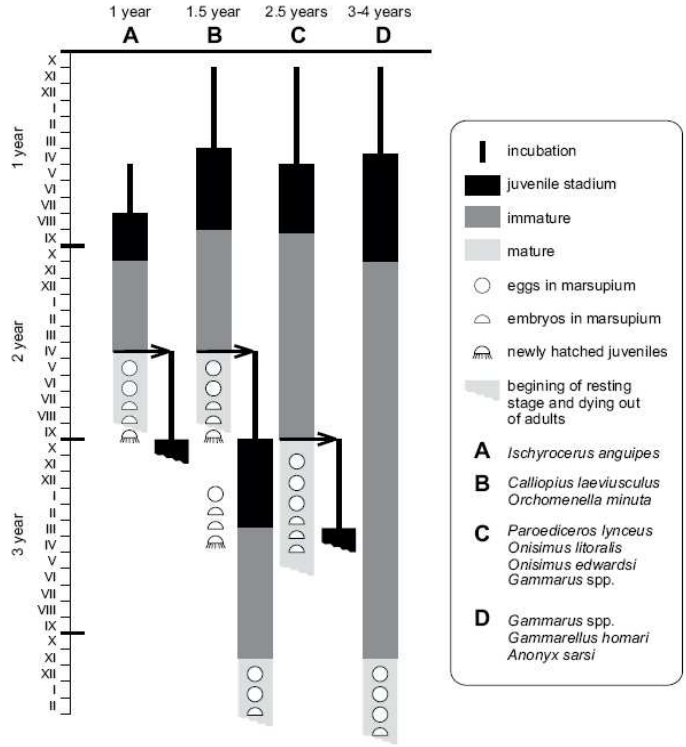

Figure 3. Life history diagram of a few amphipod species occurring on Svalbard (Węsławski & Legeżyńska 2002).

Amphipod species on Svalbard show great variation in number (4-500) and size (Ø: 0.23-1.6 mm) of eggs laid per female, even though all of the benthic species investigated from Svalbard seem to be K, or rather, A strategists (Węsławski & Legeżyńska 2002). The size of egg affects the incubation time. Steele & Steele (1975a) estimated that a gammaridean egg, with a diameter of 1 mm, needs 120 days for incubation in a cold temperate sea. The mean incubation time estimated by Węsławski and Legeżyńska (2002) for amphipods occurring on Svalbard, was approximately 150 days. Females of amphipods observed in the Svalbard area belonged to the largest specimens known in their species (Węsławski & Legeżyńska 2002).

1.3. The study species, *Onisimus caricus*

The amphipods belonging to genus *Onisimus* have been reported to be opportunistic scavengers and predators (Murdoch 1885, Dahl 1953, Busdosh et al. 1982, Vader & Romppainen 1985, Sainte-Marie 1986a). Some species such as *O. litoralis* (Krøyer, 1845) and *O. glacialis* (GO Sars, 1900) are generally deposit-feeders or herbivores, while *O. caricus* is a

well-know scavenger and an opportunistic predator (Vader et al. 2005, Legeżyńska 2008), even though opportunistic scavenging behavior has been recorded as well from species which have thought to be herbivores. The type material of the species was collected “from dead dogs” during the *Dymphna* expedition to the Kara Sea (Hansen 1887). Later the species has been commonly caught by baited traps (Legeżyńska et al. 2000).

Onisimus is a widely distributed genus, which dominates shallow water scavenging fauna in the Arctic together with another lysianassid genus *Anonyx*. *Onisimus* species have been recorded mainly from shelf seas of the Arctic, the boreal North Atlantic and the Pacific, but also from the Caspian Sea (Lowry & Stoddart 1993). A few *Onisimus* species have been adapted to use the sea-ice as an “upside-down benthic habitat” (Mohr & Tibbs 1963) and their distribution follows mainly the extent of the sea-ice (Vader et al. 2005). *Onisimus caricus* has a circum-arctic distribution. It has been recorded from around Svalbard and Franz Joseph Land in the Barents Sea region and Ellesmere Island in the Canadian Arctic (Legeżyńska et al. 2000, Vader et al. 2005). There are also records from the Siberian Arctic: the species is found from the Kara Sea (Hansen 1887), the Laptev Sea (Gurjanova 1985, Golikov 1990, both after Vader et al. 2005) and the East Siberian Sea (Gurjanova 1985, after Vader et al. 2005). Some single records have been made from the Beaufort Sea north of Alaska and as far south as from the Norwegian Sea (Gurjanova 1985, after Vader et al. 2005). The species has been found mainly from shallow waters of the glacial bays, but it has also been collected from the depths down to 200 meters (Węsławski 1991, Zajączkowski & Legeżyńska 2001).

The wide distribution of the genus *Onisimus* amphipods and their dominance in the scavenging fauna in shallow waters of the Arctic has been thought to be partly because of their diet plasticity and brackish water tolerance (Arndt et al. 2001). The diet of *O. caricus* has been conjectured to vary during a year (Zajączkowski & Legeżyńska 2001). Zajączkowski & Legeżyńska (2001) narrated that during the main melting season *O. caricus* was very likely the most important species making use of the sinking dead zooplankton. Gut content analysis in Legeżyńska (2008) confirmed this observation. Pelagic crustacean occupied 78 % of the gut content of 50 examined specimens. Marine zooplankton species are sensitive to brackish water and have been reported to have high local mortality in glacial bays during the melting season, when the surface layer has low salinity (Węsławski & Legeżyńska 1998, Zajączkowski & Legeżyńska 2001, Eiane & Daase 2002). Zajączkowski & Legeżyńska (2001) conjectured that before and after the melting season large and highly motile *O. caricus* probably feeds on more dispersed carrions.

O. caricus is amongst the largest species within the genus (Lowry & Stoddart 1993, Vader et al. 2005). Węsławski & Legeżyńska (2002) suggested a three years maximum life span for the species. However, the proposed life span is slightly dubious, because it was based only on 84 specimens from July. The researchers also found that *O. caricus* females have a low number of large eggs, supporting A-selection for the species.

1.4. Baited traps as sampling method

Quantitative methods should be used, when studying population dynamics and life cycles, (Gotelli 1998). There is almost an unlimited variety of sampling methods developed for marine benthos, but some methods are better than others for a particular study (Eleftheriou & Mclntyre 2005). When choosing the method, the aims of the study and resources should be

considered. However, qualitative methods developed for highly motile hyper-benthic organisms in shallow water are few.

Baited traps are cylindrical plastic tubes closed with a net on one end and with a funnel, which functions as an entrance, on the other. A bait is placed inside of the trap to attract animals. The traps are frequently used to study scavenging fauna (Busdosh et al. 1982, Sainte-Marie 1986, Legeżyńska et al. 2000, Arndt 2004, Arndt & Beuchel 2005), partly because they are cheap and easy to use, and partly because they are effective for motile scavenging species (Legeżyńska et al 2000, Eleftheriou & Moore 2005). Maybe because baited traps are not a quantitative sampling method, they have not been used in life history studies before, as far as known. The fact that the traps have not been used in such studies does not necessarily mean that using them is not feasible, if potential biases connected to the sampling method are taken into account.

1.5. Definition of life history terms used in the study

Terms used in amphipod life history studies in the literature are quite confusing and the meaning of a term may vary from a publication to a publication. In this study terms are tried to use consistently, but in order to avoid confusion definition is needed for some terms. In this study *life history* means attributes of the population, which lead to reproduction; for example *life cycle, life span* and different reproduction parameters, such as average number of eggs, mating, spawning time etc. are understood as part of life history. The word *life cycle* is used to mean a theoretical life connected to reproduction and sexual stages of an average animal from the population starting from an egg continuing until death. Word *life span* is a synonym for a term *maximum life span* or *longevity* meaning theoretical maximum for an average animal in the population including time after reproduction. Especially the meaning of life span differs in the literature. Some literature counts life span from an egg to mating. In this study life span was understood as maximum age of an animal. This gives half year longer values than some literature (for example Węsławski & Legeżyńska 2002).

1.6. Aims and hypothesis of the study

Even thought relatively much is known about the feeding behavior and diet of *O. caricus* (Legeżyńska et al. 2000, Legeżyńska 2001, Zajączkowski & Legeżyńska 2001, Legeżyńska 2008), life history traits of the species is composed only of a few words and is based on one sample consisting of 86 individuals (Węsławski & Legeżyńska 2002). Since life cycle is known and it might vary depending on locality (Hammersmith & Coyle 2001), *O. caricus* is an excellent easily caught species to introduce new aspects, such as baited traps and different statistical methods, to a life history study. Moreover, the observed life history characteristics can be compared with those of the well-known *Onisimus* species, such as *O. litoralis, O. nanseni* and *O. glacialis*.

The main aim of this study was to shed light on the remaining obscurities in the life history traits of *O. caricus*, to describe them in more detail, and to investigate if such a study is feasible to carry out using baited traps as a sampling method. On the basis of the environmental characters and the previous knowledge (Węsławski and Legeżyńska 2002) on the life history traits of *Onisimus caricus* and related species, a perennial (more than two years) semelparous life history with A-reproductive strategy for *Onisimus caricus* was hypothesized. The secondary aim of this project was to test this hypothesis.

2. MATERIALS AND METHODS

2.1. Description of the study area

Samples were collected in Adventfjorden, Svalbard at 78°15' N, 15° 35' E from 29 September 2006 to 15 August 2007 (Figure 4). The climate of the region is strongly affected by the warm West Spitsbergen Current, which makes oceanographic conditions in the open fjords on the west coast of Spitsbergen rather sub-arctic considering the high latitude (Meincke et al 1997, Pfirman et al 1994, Hop et al. 2002, Lydersen et al. 2004). Isfjorden is an open fjord, which enables the entrance of warm and saline Atlantic Water masses from the continental slope to the fjord system. Atlantic influence can be seen in the water properties of open side fjord as far in Isfjorden as Adventfjorden (Berge et al. 2005, UNIS course reports 1996-2007) On land, the warmest month in the region is July, with monthly mean air temperatures varying from 5 to 6 °C and the lowest temperatures are recorded from January to March (monthly mean air temperature -15 °C) (Hisdal 1985).

Figure 4. Overview map of the study location (Map: Norwegian Polar Institute 2000).

Longyearbyen, the largest settlement on Svalbard, is located on the shore of Adventfjorden. The fjord is one of the southern arms of Isfjorden, the largest fjord system of west Spitsbergen. Adventfjorden is 8 km long and 5.4 km wide, and without a threshold at the opening. Bottom depth close to the mouth of the fjord exceeds 100 meters. The depth gradually declines towards the innermost part of the fjord with an inclination varying from 1° to 3°. The central part of the fjord has a depth close to 70 meters and banks leading down are relatively steep (Zajączkowski & Włodarska-Kowalczuk 2007). The shores of the fjord are

exposed, and the bottom type is gravely mud, changing to finer sediments towards the middle parts of the fjord or the deltas of the two rivers entering the fjord.

The innermost part of Adventfjorden is a tidal flat, where the relatively small glacier-fed rivers Adventelva and Longyearelva run. Steep environmental gradients in the water masses caused by freshwater input from glaciers during melt season, are reported to cause high zooplankton mortality (Węsławski & Legeżyńska 1998, Zajączkowski & Legeżyńska 2001, Hop et al. 2002, Eiane & Daase 2002). Węsławski et al. (1999) estimated that during the 4 month-long melt season, the river Adventelva transports water with an average rate of 3.6 m^3s^{-1} and the mean concentration of suspended solids of 309 ± 177 mg l^{-1}. Even though the river Longyearelva flows at a lower rate on average (2.04 m^3s^{-1}), the mean concentration of suspended solids during summer is usually higher (471 ± 221 mg l^{-1}). During the winter, the rivers are frozen and the supply of terrigenous material into the fjord ceases, but the sewer of Longyearbyen runs to Adventfjorden, without nutrient processing, and causes a constant flux of nutrients to the fjord, even during the coldest period (Velvin et al. 2006). In addition, the condensation system of the Longyearbyen coal power station causes artificial warm water input into the fjord (Velvin et al. 2006).

Tidal flat and particle flux properties of Adventfjorden are described in Zajączkowski & Włodarska-Kowalczuk (2007). The tidal flat is 0.9 km wide during low tide, and the bottom inclination does not exceed 0.1^o. The prodelta slope reaches an inclination of $15\text{-}19^o$ and terminates at a depth of 30 m. A surface current of approximately 1.5 m thick brackish water layer extends in summer at least 0.8 km from the river mouths. The highest concentration and flux of suspended solids is reported to exist at the edge of the tidal flat and over the upper slope of the delta. Both the concentration and the solid particle flux decrease with increasing distance from the river mouths. Suspended material causes murky surface layer, which blocks visibility to the water masses below (Zajączkowski & Włodarska-Kowalczuk 2007). Sedimentation is tidally controlled. Sediments are deposited during floods and resuspended and redeposited during ebbs. The prodelta slope is eroded by occasional events such as intense storms or ice scouring (Zajączkowski & Włodarska-Kowalczuk 2007).

During the sampling winter 2006-2007 Adventfjorden remained open. At it's coldest (-1.2 C^o) water was in April and warmest (7.3 C^o) in August. Salinity was highest in March (35.5 psu) and lowest in August when surface salinity was 10.3 psu (Figure 5). Both, salinity and temperature changed fast between in the time interval from 22 of May to 26 of July.

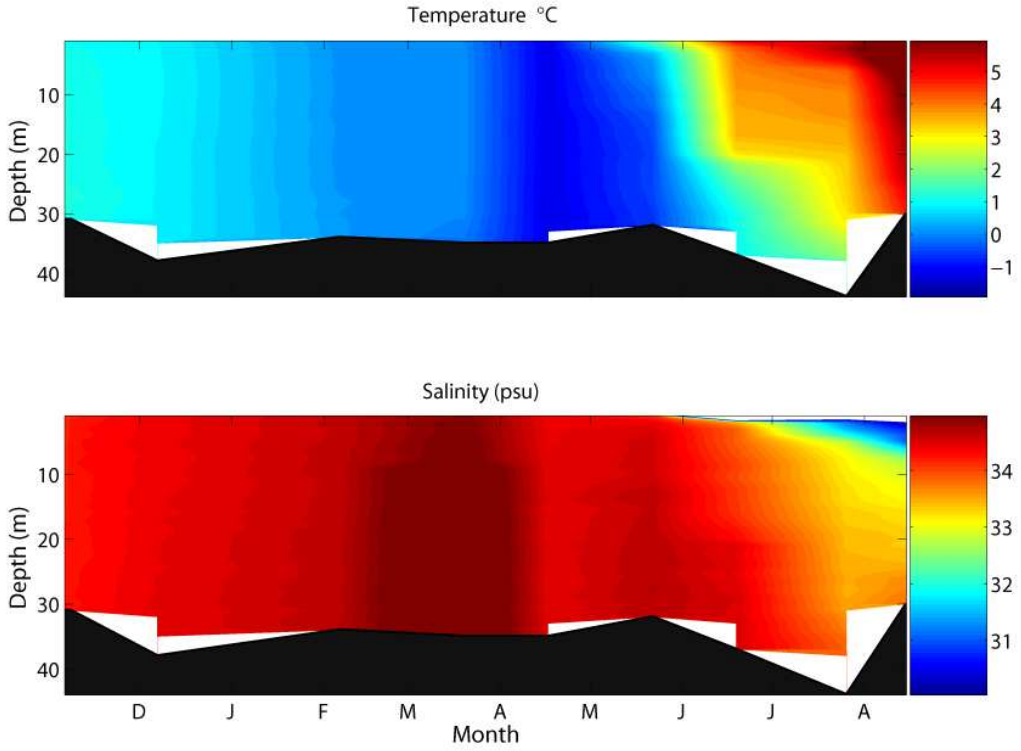

Figure 5. Temporal bathymetric variation of salinity and temperature at the CTD station (marked as CTD in Figure 8) during the study period. Letters on x-axis are months from 8.11.2006 to 15.8.2007.

2.2. Sampling

The amphipod sampling was carried out by baited traps, which are cylindrical plastic tubes closed with a net on one end, and with a funnel, functioning as an entrance, on the other (Figure 6) (*e.g.* Busdosh et al. 1982, Sainte-Marie 1986, Slattery & Oliver 1986, Sainte-Marie et al. 1989). Five baited traps were attached to a rope at varying distances from 15 to 50 meters to form a transect (Figure 7). At each sampling occasion this set of traps was deployed on the bottom for approximately 24 hours at few sites in Adventfjorden (Figure 8, Table 1). A piece of chicken with average weight of approximately 30 grams was used as bait in each trap.

The three main sampling transects were located close to the innermost part of the fjord few hundred meters from the tidal flat. Transect 1 was located near the estuary of the river Longyearelva and had slightly finer bottom sediment than the other localities. One end of the transect was placed to a depth of 1-3 meters and the other end was typically at a depth close to 30 meters. Transect 2 was placed in a slightly more exposed locality. The bottom type was muddy gravel and depth, where the transect was lying, varied from two to 34 meters. The deeper end of Transect 3 was located close to the outlet of the sewer of Longyearbyen. The bottom type was fine mud mixed with gravel. The shallower end was located at 1 meter depth.

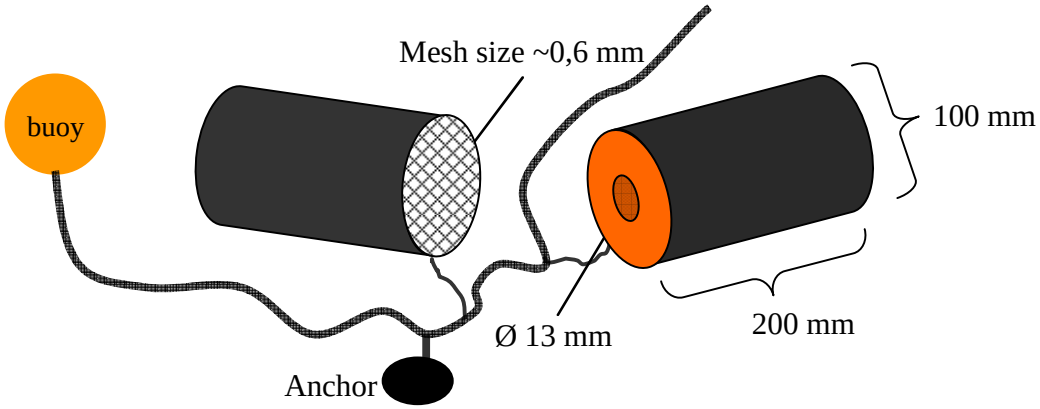

Figure 6. General sketch of baited traps used in the study.

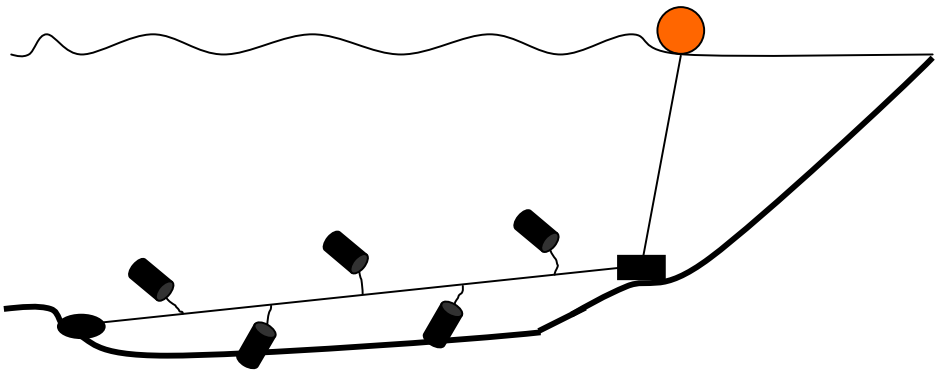

Figure 7. Transect design for the trap-sampling.

Sampling was done monthly from September in 2006 to August in 2007, excluding January and July (Table 1). Bottom depth of each spot, where a trap was dropped in the water, was recorded. The three main transects were used each month, except in September, when sampling places were tested with a trial sampling.

CTD (conductivity-temperature-depth measuring instrument) cast from a permanent station, marked with a buoy, was taken during each sampling after 7.11.2006. The used instrument was STD/CTD model SD 204 produced by SAIV A/S equipped with a chlorophyll fluorometer and a turbidity sensor both produced by Seapoint Sensors Inc. Suspended organic matter and chlorophyll concentration data used in the study were got from measurements done from sediment traps by Zajączkowski (unpubl). Suspension was extracted with a 20µm filter. Turbidity, measured with the CTD, was recorded as average of the highest sensible values at the surface. Light intensity data were measured as light intensity in air from Ny-Ålesund (79^{o} N) (Berge et al. unpubl).

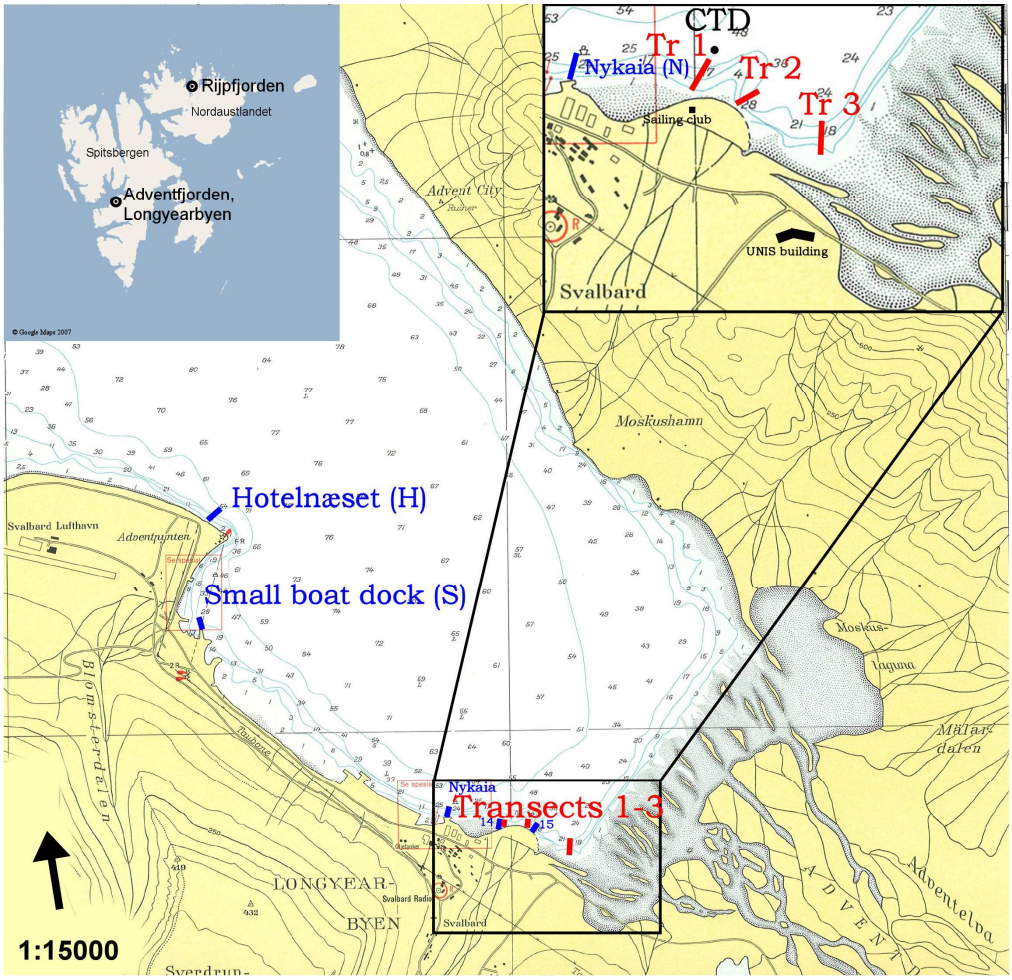

Figure 8. The sampling sites of the study. The main sampling sites are marked with red and those marked with blue were sampled only once. Full name and exact location of the sites are presented in Table 1. Detailed map: Statens kartverk (1959). Overview map: Google Maps (2007).

Table 1. Details of the trap-sampling. In October and November a double set of traps was used. Abbreviations refer to Figure 8.

Adventfjorden

Date	n of traps	Depth range (m)	Sites
29.9.06	25		H,S,N,1,2
19.10.06	30	2-18	1,2,3
7.11.06	30	2-24	1,2,3
7.12.06	15	2-31	1,2,3
8.2.07	15	1-34	1,2,3
21.3.07	15		1,2,3
19.4.07	15	2-33	1,2,3
23.5.07	15	1-28	1,2,3
20.6.07	15	1-33	1,2,3
15.8.07	15		1,2,3

Abbreviations

	Name	Coordinates
H	Hotellnæset	78°14.832' N 15°32.477' E
S	Small boat harbour	78°14.362' N 15°32.283' E
N	Nykaia	78°13.505' N 15°37.307' E
1	Close to the Sailing club	78°13.688' N 15°38.820' E
2	Close to the Polish hut	78°13.621' N 15°39.227' E
3	Close to the sewer outlet	78°13.574' N 15°39.711' E

2.3. Laboratory procedures

Samples were washed in sea water and preserved in 70 % ethanol, or 4 % borax buffered formaldehyde-in-sea-water solution in cases where lab work was known to be delayed, and were studied in the lab from a week to a year after sampling. The fixation of amphipods may have different shrink-effect between different solutions (ethanol and formaldehyde), but the effect on hard and robust lysianassid amphipods can be expected to be insignificant compared to other biases (Vader, personal communication). Captured amphipods were determined to species with help of dissecting microscope (Leica MS5 and Leica MZ16). Identification of *Onisimus* species followed Vader et al. (2005) and Johnsen (unpubl.). For final confirmation of the species, detailed drawings in Vader et al. (2005) of *Onisimus caricus* type specimens were studied and compared to specimens present in the samples.

After sorting to species, subsamples of approximately 100 *O. caricus* were randomly picked out from each sample by mixing the sample bottle and using a spoon to grab a random amount of amphipods. Since no abundance estimates of the population were done the method was considered to be sufficient randomization. If only one trap was full and others almost empty, no subsamples were taken, in order to get enough individuals for the length-frequency analyses. From these subsamples, each individual was assigned into one of five different categories according to the maturity and sex: mature female, mature male, immature female, immature male and juvenile. Sex determination was based on the method described in Boudrias & Carey (1988). Sex of an amphipod was recognized mainly by the presence of genital papillae in males and of oostegites (brood plates) in females. When neither of these characters was observable, individuals could not be sexed and were classified as juveniles. Maturity of females was determined from the shape and length of oostegites, where long oostegites with long setae in the tip confirmed maturity. Oostegites were observed on the detached fourth pereopod, on which they are easily found, if present (personal observation).

Maturity of *Onisimus caricus* males was not possible to define certainly from the length of second antennae, because elongation is not as obvious as with some other lysianassid species. Nevertheless, males with significantly longer second antennae were designated as “mature” (or Mm) to make grouping of the males possible in the later analyses. Individuals with shorter second antennae were classified as “immature” (or Mim).

During the end of the study period, a small subsample of females was randomly picked out from the samples and the length of oostegites was examined to give additional data for the life cycle and growth estimation. Females with different development of oostegites were grouped into six categories: 1) Mature, long oostegites with long setae on the tip (Fm); 2) almost mature, long fully developed oostegites with short setae on the tip (Ffll); 3) long oostegites, almost as long as in adult and without setae (Flng); 4) intermediate sized oostegites without setae (Fint); 5) short, but notable oostegites without setae (Fsm) and 6) tiny newly developed oostegites, small node, difficult to notice (Ftny).

After sex determination, the length of the first pereonal segment (Ls), which was used as a proxy for length of an amphipod, was measured. The method was adopted from literature (Skadsheim 1982, Beuchel 2000, Beuchel & Lønne 2002, Arndt & Beuchel 2005) (Figure 9), where Ls is considered to be a more reliable and faster method to estimate the length of an amphipod than total length (Lt), measured from tip of the rostrum to the tip of telson, because the curvature of the body affects the result. Skadsheim (1982) estimated that measuring an

amphipod in a curved shape can result up to a 30 % overestimation of the length compared to a stretched shape. Since calibrated magnification of the microscopes used in the study had magnification of 17X, the length of the first pereonal segment was measured to the nearest 0.06 mm.

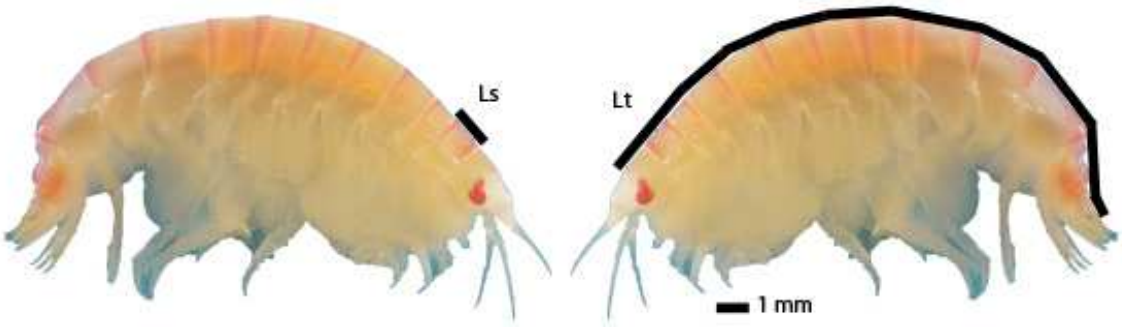

Figure 9. Studied species *Onisimus* caricus. Dark lines illustrate the measured length of first pereonal segment (Ls) and total body length (Lt).

In order to compare results with previous studies, which refer to Lt rather than Ls, high resolution photographs of 100 individuals of *Onisimus caricus* were taken from the October 2006 sample, and used to create an equation to convert Ls to Lt. The procedure was repeated with 27 individuals from the April 2007 sample to confirm the validity of the equation.

The shortest and longest diameter of every egg available was measured with 32X magnification to the nearest 0.03 mm. The development stage of each egg was classified to 6 categories: A) All or most of the eggs look like an amphipod with visible pereopods and tail, some yolk is still covering juveniles; B) outer membrane is lacking, yolk has the shape of an amphipod and some of the eggs have a visible tail or pereopods; C) outer membrane is lacking, yolk has the shape of an amphipod, but no pereopods or tail is visible; D) eggs are round, but outer membrane is broken; E) eggs are round, but outer membrane is distinct; F) eggs are round and shiny, outer membrane is close to the yolk.

2.4. Data handling

Microsoft Excel 2003 was used as a tool to input and arrange the data. R-statistics environment (Venables et al. 2002) was used to handle all statistics in the thesis. Image manipulation was done with the GNU Image Manipulation Program, GIMP 2.2 (Kimball et al. 2007), and the image analysis program ImageJ 1.38x (Rasband 2007). The thesis was written with Microsoft Word 2003. Salinity, temperature and turbidity plots were created with MatLab 7.0 contour -function by Malin Daase.

Ls and Lt were measured following Arndt and Beuchel 2005 (Figure 9), from the high resolution photographs of *Onisimus caricus.* To standardize the curvature of the body, the amphipod was pushed to the maximum curvature before being photographed, the allometric relationship between Ls and Lt was plotted (Figure 10) and a linear least square regression analysis was run with R-statistics (Venables et al. 2002). The resulting linear regression model (ANOVA: $F=3226$, $df=127$, $p<0.0001$) was:

$$Lt = 17.3348 * Ls - 0.5443 \qquad \text{(Equation 1)}$$

The coefficient of determination for the regression was 96.2 % and residuals followed the normal distribution. A single Lt value could be predicted within ±1.29 mm with the regression in 95 % certainty. Much of the uncertainty stems from measurement error. Since the precision of the Ls measurement was 0.06 mm, Lt was theoretically possible to estimate at the accuracy of 1 mm (± 0.5 mm) (i.e. 17.3348 * 0.06 – 0.5443). Precision of Lt measurement was not estimated.

The modeled length for the largest mature female was slightly greater (4 mm or 18 %) than for the largest total length reported in the literature (Węsławski & Legeżyńska 2002, Vader et al. 2004), but the sample size in this study was much larger than in the other studies. The difference may be caused by a difference in measuring technique, since the curvature of the body is known to affect the total length measurement.

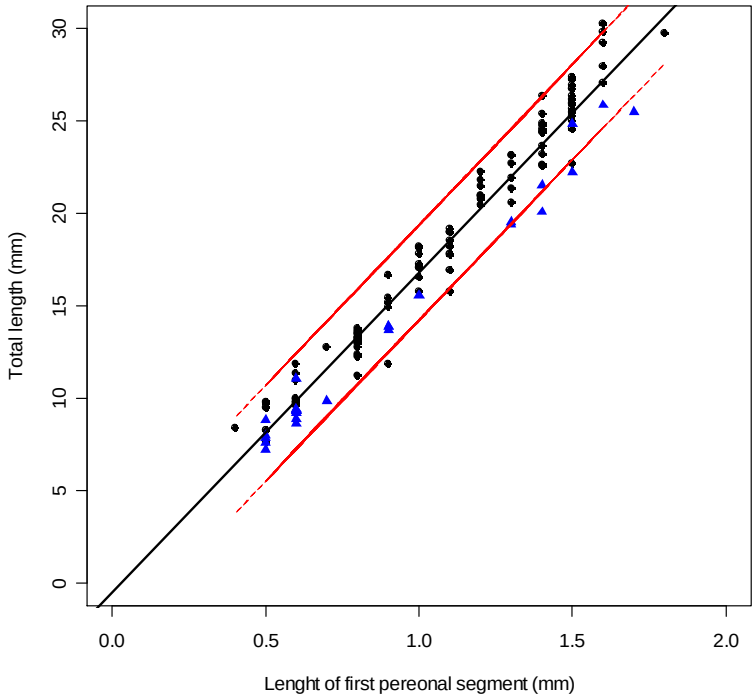

Figure 10. The relationship between length of first pereonal segment (Ls) and total length of *Onisimus caricus*. Black dots represent observations from measurement 1, blue triangles observations from measurement 2, solid black line is the regression line (Lt=17.3348*Ls-0.5443, R^2=0.96, ANOVA: F=3226, d.f. 127, p<0.0001), and red lines are 95 % confidence limits of the prediction.

Measurements from October 2006 and April 2007 samples gave different slopes and intercepts for the regression, and the residuals of the measurements compared to the regression model presented in Figure 10 differed significantly from each other (1-ANOVA: F=18.8, df=155, p<0.001). Since it was not known which measurement was more reliable, the measurements were combined and the difference was assumed to be caused by problems in standardizing the curvature of the body when taking photographs. Lengths of *Onisimus caricus* are given in form [Ls]/[Lt] mm in the later text, where [Ls] gives length of first pereonal segment and [Lt] total length of an animal calculated with the Equation 1.

Measured individuals were grouped into size classes on Ls-values with intervals of 0.1 mm and plotted as histograms to visualize length-frequency distribution of each sampling occasion (month). Kernel density estimate (density –function in R statistics) was used as a reference for trustworthy length-frequency distribution of observations, in deriving gender-specific size cohorts and in interpretation of the life cycle. Histograms were visually compared to kernel density estimate calculated for the same data of observations.

Histograms were used when deriving mean values and standard deviations of the gender-specific size cohorts with the help of the mixture distribution analysis (MacDonald & Pitcher 1979, Macdonald & Green 1988) using the "mixdist" –package (MacDonald & Du 2004) as part of R-statistics environment. Mixture distribution analysis was originally developed for computationally visualizing age-groups in fisheries and to reduce laboratory time in the aging large samples of fish (Macdonald & Pitcher 1979), but it has been used in amphipod studies to separate means and standard deviations from visible size cohorts (Beuchel & Lønne 2002, Arndt & Beuchel 2005).

Analyzing mixture distributions is a relatively complicated process. However, analyses were made after an excellent step-by-step guide for the program provided by Du (2002). The program was run in an interactive mode by stepwise optimization of the relative abundance (proportions: π), means (Ls: μ) and standard deviations (Ls: σ) of cohorts.

In order to help the program to estimate the parameters, the program was run with 10 expectation-maximization (EM) -steps (explained in detail in Dempster et al. 1977) and with either of two different constraints for standard deviation. The best fitting set of constraints was chosen visually by comparing the model to kernel density estimate. Generally, variances were run with a constraint assuming variances to be equal (SEQ), but in some cases, when a sharp peak of small individuals occurred in the data, the equal coefficient of variation (CCV) was used for each cohort. In most cases the best fitting distributions were normal, but in the cases of sharp peak of juveniles, log-normal distribution was chosen. Because using baited traps is not a quantitative method, the abundance of cohorts was ignored.

In addition to graphical output, the program gave goodness-of-fit (χ^2) and significance value (p) for each analyze. The value is calculated with Chi-square test and it indicates how well the mixture distribution model fits the histogram of observations overall (Macdonald & Green 1988). However, the Chi-square values given by the program were generally very high, indicating poor fit of the models, even though visually scrutinized models fitted the kernel distribution almost perfectly. This was thought to be due to few reasons. In some cases histograms did not fit to the kernel distribution very well. It was difficult to determine interval for the data, which would have created smooth normally distributed histograms. When the interval was lowered, there were many groups with less than five observations each. Sometimes, even though longer interval was used, it was impossible to model mixed distributions without some groups fewer than 5 observations in between of the cohorts. It was concluded that higher subsample size should have been chosen in order to obtain better goodness-of-fit.

Since estimating life history parameters is always more or less surmising, the aim was not to proof the assumptions of the life history statistically. Thus visual fit to the kernel density estimates of the models were used rather than single p-values. However, even though models did have poor goodness-of-fit values to histograms, visual examination proved that

models fitted quite well to the kernel density estimates (Appendixes 1-3). After all, mixture distribution analysis was used only to estimate mean values of cohorts to obtain data for growth curve estimation. More trustworthy kernel density estimate was used in interpretation of cohorts and the life cycle.

In order to estimate amount of observations in a cohort, theoretical upper limits were given for cohorts by visual estimation from size-frequency. Limits for cohorts were calculated from cumulative distribution functions in a way that 99 % of the area of the model was inside the limits. Theoretical limits for the cohorts were used to obtain the amount of observations in each size cohort. Monte Carlo simulation, with corresponding n for each cohort, was used to produce the theoretical lengths for cohorts. The method gave slightly (0.03/0.11-0.08/0.95 mm) different mean values for the cohorts than the mean values calculated straight from observed lengths of the cohorts, but allowed overlap of the cohorts and thus made it possible to compare length differences between cohorts with Welch two sample t-tests and ANOVAs. In addition to kernel densities and mixture distribution analysis, additional information from the length of brood plates of immature females was brought for help to estimate the growth of females.

For comparison of reproductive parameters of *Onisimus caricus* with literature, the sex ratio was calculated for all males and females (males : females), including immature specimens. Reproductive cost (RR%) was calculated after Wildish 1982 as percentage of brood volume to female volume. The volume of each egg-bearing female was estimated with equation:

$$V_{female} = \pi d^2 * Lt \qquad \text{(Equation 2)}$$

Where d is the height of the fourth pereon segment and Lt total length. The volume of each egg was estimated with equation:

$$V_{egg} = 4/3\ \pi r^3 \qquad \text{(Equation 3)}$$

Where r is mean of the shortest and longest radius of the egg.

Finally, the growth of *Onisimus caricus* was modeled from mean lengths of cohorts derived with the mixture distribution analysis. Polynomial growth function was used:

$$Lt=a*t^2 + b*t^2 + c*t + d \qquad \text{(Equation 4)}$$

Where Lt is total length of an animal at age of t (with 1/12 interval) and a, b, c and d are constants used to fit the model.

Furthermore, the Gompertz growth function (GGF) was fitted, because it has been used in growth modeling in earlier studies (Beuchel & Lønne 2002, Arndt & Beuchel 2005) and allowed comparison between parameters of the model. The equation of the GGF is:

$$Lt = Lt_{lim} * e^{-k(t-t¤)} \qquad \text{(Equation 5)}$$

where Lt is the total length of the animal at age t years, Lt_{lim} asymptotic final length of *Onisimus caricus*, k the growth constant, t¤ age of the growth inflexion and t age in years.

3. RESULTS

3.1. Catch

In total 17005 specimens of *Onisimus caricus* were caught during the study period with baited traps. The monthly catch (Table 4) with a temporal variation of environmental variables, including light intensity, turbidity, chlorophyll concentration and suspension of organic matter, are presented in Figure 11. A double set of traps was used in October and November to assure a working trap on each locality along a transect. Because of the large number of amphipods in the catch, single traps at each locality were used thereafter. Therefore, the catches of October and November were divided in two to make them comparable with other months. The light intensity data were considered to correlate with the light conditions in Adventfjorden, even though the data were obtained from one degree of latitude to the north off the study area.

Environmental conditions affected the sampling. In December strong wave action after a storm caused a failure of three traps. Number of amphipods caught in April would have been low, like in May unless one trap would not have contained almost all of the amphipods sampled (960). Drifting sea ice moved one transect off the target and might have affected the catch. In August, harsh ocean conditions caused one of the transects to get filled with mud and the catch of the transect was consequently relatively small. Moreover, in September only two transects which were deployed to regular sampling localities collected *O. caricus*.

The total catch of *O. caricus* was high during the polar night and started to decline before light came back in February (Figure 11). The minimum catch occurred in May with 77 specimens and in June the catch of *O .caricus* climbed up to 2469 specimens. The catch of the species declined to 496 specimens in August.

Surface water turbidity started to peak up in May, when the maximum turbidity was nine FTU (Figure 11, Figure 12). The depth of the layer with turbidity more than two FTU was approximately one meter. In June maximum turbidity was higher, 23 FTU and layer with turbidity more than two FTU reached to the depth of 16 meters. Turbidity decreased to July's measurement, when the maximum turbidity of the surface layer was 9 FTU and depth of the layer with turbidity more than two FTU reached only to five meters, even though turbidity was again higher in the water column at greater depth. In August turbidity was highest during the measurement series. Maximum turbidity peaked up to 133 FTU and lowest turbidity, 5 FTU, of the whole water column was measured close to the bottom.

The chlorophyll concentration of the material collected by the sediment traps at five meters depth was consistently below 1 mg l^{-1}, except for April with a concentration of 21.0 mg l^{-1} (Zajączkowski, unpubl.) (Figure 11). A similar trend was observed in the concentration of sedimenting organic suspension (>20µm) (Zajączkowski, unpubl.). The concentration of suspension varied between 0.08 and 0.17 mg l^{-1} during the winter, but peaked up in April with almost 30 fold increase (3.7 mg l^{-1}) compared to the preceding month. The concentration of suspension was relatively high, 1.26 mg l^{-1}, also in May but settled down to the winter level in June and August. According to these results, the algal bloom occurred somewhere between late March and late April in Adventfjorden.

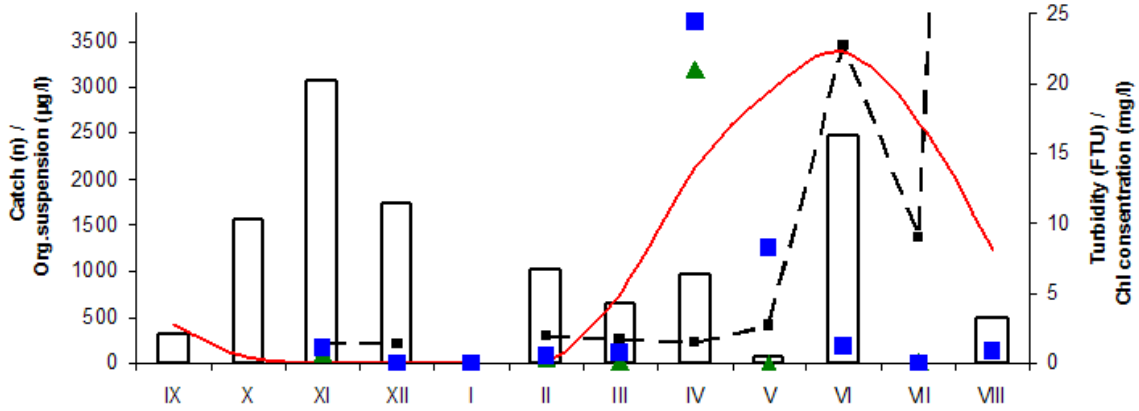

Figure 11. Number of *O. caricus* caught monthly (bars) together with seasonal variation of relative light intensity in air in Ny-Ålesund, Svalbard (Berge et al. unpubl.) (red solid line), turbidity (black dashed line), Chl concentration (green triangles) and suspension of organic matter (>20µm) in Adventfjorden (Zajączkowski unpubl) (blue squares). Roman numbers indicate sampling months from September 2006 to August 2007.

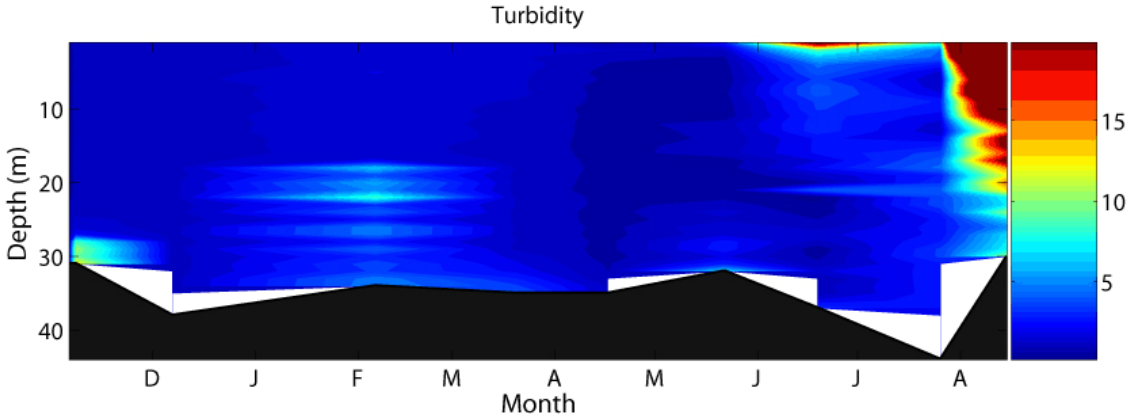

Figure 12. Temporal bathymetric variation of turbidity at the CTD station (marked as CTD in Figure 8). Letters on x-axis are months from 8.11.2006 to 15.8.2007

3.2. Size and gender structure of *O. caricus* in the samples

3.2.1. Cohort classification

The catch varied between months, but certain cohorts were present throughout the study (Figure 13). Variation in size frequency distribution was derived to size cohorts with the help of mixture distribution models, which were visually fitted to kernel distributions (Appendixes 1-3). It is important to notice that sample sizes referred in this chapter are from randomized subsamples. Total sample sizes are listed in Table 4.

Length-frequency distribution of juveniles tended to be positively skewed (Figure 13, Appendix 1). Only in March, June and August the distribution was bimodal. In other samples the tail of the distribution had approximately the same mean value than second peaks in the bimodal distributions. The first peak of the juvenile length-frequency distribution was referred

as the first cohort of juveniles (J1). The second cohort of juveniles (J2) was modeled to the second peak or tail of the juvenile distribution.

J1 had mean length of 0.50(Ls)/8(Lt) mm with a standard deviation of 0.07/0.7 mm (Appendix 1, Table 2). The smallest observation of the cohort was smallest juvenile measured during the study with length of 0.29/5 mm. Ninety-nine percent of values in the modeled cohort were between 0.32/5 and 0.68/13 mm. The theoretical upper limit of the cohort was set at 0.65/11 mm. The second cohort of juveniles (J2) had a mean value of 0.76/13 mm and a standard deviation of 0.10/1.2 mm. The theoretical size of the cohort varied between 0.65/11 and 1.00/17 mm and 99 % of values in the modeled cohort were between 0.50/8 and 1.02/17 mm. All amphipods which were identified as juveniles, and were bigger than the upper limit of J2, were placed in the third cohort of juveniles (J3). Mean value of J3 was 1.1/19 mm and standard deviation was 0.1/1.2 mm. Ninety-nine percent of the values in the modeled cohort varied between 0.84/14 and 1.36/22 mm. J3 was not separated from monthly samples, but was used only in Figure 14 to help the interpretation of the life cycle (see chapter 4.4)

Females were classified into three cohorts: two cohorts of immature females and one cohort of mature females overlapping with the second cohort of immature specimens (Appendix 2, Table 2). The distribution of immature females was negatively skewed. The same principle, than with juveniles, was used when estimating immature female cohorts. This time the first cohort of immature females (F1) was formed of the tail of the distribution. F1 had lower length limit of 0.88/15 mm, a mean of 1.15/19 mm and an upper limit of 1.30/22 mm. The upper length limit was derived from the size where the growth rate of females was observed to flatten down (Figure 14). The second cohort of females (F2) had a lower length limit of 1.31/22 mm and a mean of 1.42/24 mm. The upper limit was the length of the largest immature female (1.68/29 mm) found during the study. Standard deviation for both cohorts was 0.10/1.2 mm. Last cohort of females consisted of mature specimens (Fm). Lower and upper limits were the lengths of smallest (1.29/22 mm) and largest (1.77/30 mm) mature females captured. The mean length of the cohort was 1.53/26 mm.

Males had mostly two, but in some cases one, size cohorts (Appendix 3, Table 2). However, the classification of males was based mainly on the length of the second antennae. Generally immature males had unimodal length-frequency distribution, but from April's and June's sample bimodal distribution was estimated. The lower length limit of the immature males (Mim) was the smallest male (0.76/13 mm) identified in the study. They had a mean length of 1.20/20 mm and theoretical upper limit of 1.53/26 mm. Mature males had always unimodal distribution. The theoretical lower length limit of the mature males was 0.82/14 mm and mean 1.37/23 mm. The upper length limit of the cohort was the length of the largest male (1.71/29 mm) caught in the study.

3.2.2. Changes in the cohort characteristics during the year

3.2.2.1. First cohort of juveniles (J1)

The first cohort of juveniles (J1) was present in the size-frequency data every month. The mean values and standard deviations of the cohorts varied slightly between months (Table 2, Appendix 1). Sharp peaks (σ: 0.05/0.3-0.07/0.7 mm) with small mean values (μ: ~0.45/ 7 mm) occurred in February, May, June and August. Slightly greater values (μ: ~0.53/8.6 mm) with the same standard deviation (σ: ~0.07/0.7 mm) were calculated from October's,

November's and December's samples. Large size (μ: ~0.65/11 mm) with wide distribution (σ: ~0.15/2.1 mm) was modeled in September and April, when it was not possible to separate J2 from the distribution. In March the distribution relatively similar to April, but two peaks were assumed.

Despite a small sample size, there was a distinctive peak of small juveniles from 0.35/6 to 0.50/8 mm in the sample of May (Figure 13). Difference between the smallest juveniles recorded among months was only one measuring unit (0.06 mm) varying from 0.29/5 to 0.35/6 mm.

In total 4112 juveniles were identified during the course of the study. It was possible to estimate the number of juveniles belonging to each cohort using theoretical limits. In total, J1 consisted of approximately 2550 individuals, while 1330 and 230 individuals were classified to J2 and J3, respectively. The relative frequency of J1 was approximately from one to six times as high as that of J2, depending on the month (Appendix 1, Figure 13). Even so, J2 had higher standard deviations and thus J1 was generally one to three times more abundant than J2. An exception was March, when J2 was slightly more abundant than J1.

3.2.2.2. Second cohort of juveniles (J2)

A clear second cohort of juveniles (J2) was found in June and August. Generally hypothetical cohort was difficult to separate from J1. It rather seemed that J2 was a tail for J1. Furthermore, in May, there were some bigger juveniles, but the amount of the observations was not high enough to do reliable estimates of the mean value of the potential second cohort.

In October, November, December and February the mean length and standard deviation of the individuals in the cohort were close to 0.9/16 mm and 0.14/1.9 mm, respectively. In March, the individuals of the cohort were smaller, with a mean length of 0.76/13 mm. June and August were again similar to each other and had slightly higher mean values (μ: 0.80/13 and 0.79/13 mm) than March, but lower than during the autumn and winter. Standard deviations of J2 were almost twice as high as those of J1 and stayed quite stable (σ: 0.11/1.4-0.13/1.7 mm) during the spring and summer.

3.2.2.3. Third cohort of juveniles (J3)

Individuals classified to J3 were thought to represent transition to males and females. The size of cohort overlapped with first immature cohorts and some of the observations in the cohort were thought to be due to identification error. The fact that most of the big juveniles were identified from the samples (September, October, November, December and May) which were examined in the early period of the study or by other students supports this assumption. However, it is relatively safe to suppose that mistakes with identification were minimal, when experience increased towards the end period of the study period (February, March, April, June and August).

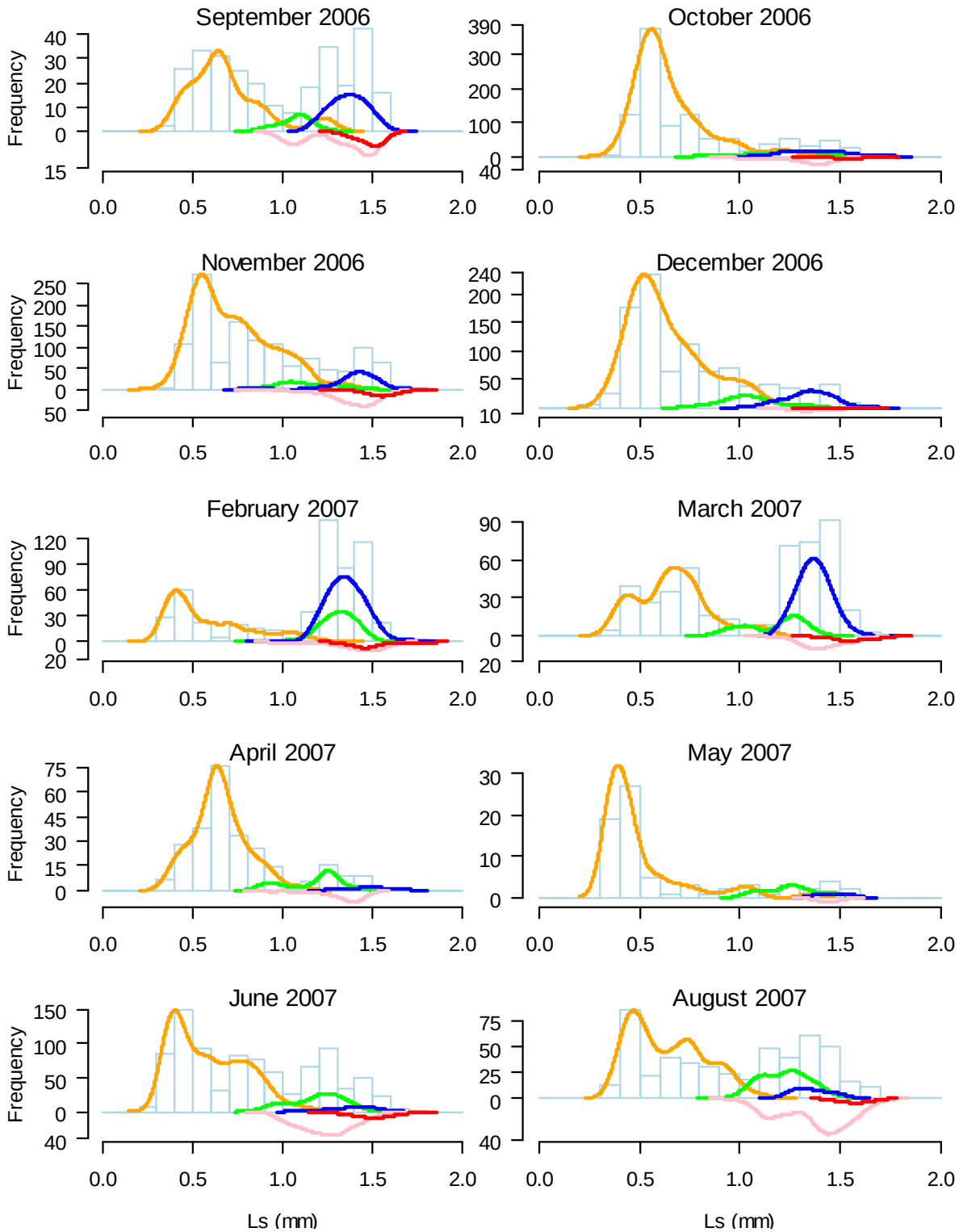

Figure 13. Length-frequency histogram and gender structure of the *O. caricus* catch. The lengths of first pereonal segment (mm) are grouped on the x-axis with an interval of 0.1 m. The value shown on the axis is the lower limit of the group. Histograms show distribution of the whole sample. Lines show kernel distributions of genders. Orange colour refers to juveniles, green to immature males, dark blue to mature males, pink to immature females and red to mature females.

Table 2. Characteristic values of the cohorts. Columns from the left: sampling month, subsample size, gender and mean (μ), standard error of mean (s.e.) and standard deviation (σ) of each cohort, distribution and constraint for standard deviation used in the modelling (simple mean = no MIX used), goodness-of-fit (χ^2), significance level and degrees of freedom for the model, and finally on the right end, minimum and maximum length of *O. caricus* belonging to the particular group. Uncertain estimates are indicated by a star (*). Cohorts (cohort no) are numbered with a running number starting from the lowest Ls value towards the highest. All lengths are reported in millimetre length of first pereonal segment.

		cohort no	1.			2.								
Month	n	gender	μ	s.e.	σ	μ	s.e.	σ	method	χ^2	p	d.f.	min	max
IX	154	juveniles	0.64	0.01	0.14	1.18	0.05	0.14	norm, SEQ	29.6	0.0000	6	0.35	1.29*
	16	M im	1.08	0.02	0.10				norm, SEQ	2.2	0.3391	2	0.88	1.24*
	77	M m	1.36	0.01	0.11				norm, SEQ	11.8	0.0028	2	1.18*	1.59
	28	F im	1.06	0.07	0.09	1.44	0.02	0.09	norm, SEQ	2.7	0.4955	5	1.00*	1.53
	11	F m	1.48	0.02	0.06				simple mean				1.35	1.53
X	838	juveniles	0.56	0.01	0.08	0.89	0.02	0.14	norm, CCV	219.7	0.0000	6	0.35	1.35*
	53	M im	1.23	0.02	0.15				norm, SEQ	3.1	0.6897	5	0.82	1.53*
	46	M m	1.37	0.02	0.15				norm, SEQ	11.2	0.0241	4	1.12*	1.71
	65	F im	1.12	0.03	0.08	1.40	0.02	0.08	norm, SEQ	8.3	0.0039	5	1.00*	1.59
	18	F m	1.54	0.01	0.06				simple mean				1.41	1.65
XI	909	juveniles	0.55	0.01	0.10	0.90	0.01	0.16	norm, CCV	191.0	0.0000	8	0.29	1.41*
	78	M im	1.11	0.02	0.16				norm, SEQ	5.7	0.2229	4	0.88	1.47*
	79	M m	1.41	0.01	0.13				norm, SEQ	47.4	0.0000	6	0.82*	1.65
	102	F im	1.11	0.06	0.10	1.42	0.02	0.10	norm, SEQ	12.9	0.0120	4	0.88*	1.65
	56	F m	1.55	0.01	0.08				simple mean				1.35	1.71
XII	767	juveniles	0.51	0.00	0.08	0.84	0.01	0.13	norm, CCV	57.7	0.0000	7	0.29	1.35*
	63	M im	1.04	0.02	0.15				norm, SEQ	6.9	0.1419	4	0.76	1.35*
	93	M m	1.33	0.01	0.12				norm, SEQ	11.6	0.0209	4	1.06*	1.65
	23	F im	1.36	0.02	0.12				norm, SEQ	2.1	0.1519	1	1.24*	1.53
	7	F m	1.50	0.03	0.07				simple mean				1.41	1.59
II	173	juveniles	0.44	0.01	0.07	0.87	0.02	0.14	norm, CCV	14.3	0.0459	7	0.29	1.29*
	153	M im	1.30	0.01	0.13				norm, SEQ	26.0	0.0000	4	0.88	1.47*
	220	M m	1.35	0.01	0.12				norm, SEQ	43.1	0.0000	6	0.94*	1.71
	27	F im	1.19	0.04	0.07	1.48	0.02	0.07	norm, SEQ	0.7	0.4138	5	1.00*	1.59
	11	F m	1.50	0.04	0.12				simple mean				1.35	1.77
III	191	juveniles	0.49	0.02	0.09	0.76	0.02	0.13	lnorm, CCV	26.2	0.0000	4	0.35	1.18*
	33	M im	0.99	0.02	0.06	1.26	0.01	0.06	lnorm, SEQ	5.8	0.1233	3	0.88	1.41*
	193	M m	1.37	0.01	0.09				norm, SEQ	14.1	0.0009	2	1.24*	1.65
	40	F im	1.42	0.02	0.11				norm, SEQ	0.4	0.8028	2	1.18*	1.59
	8	F m	1.59	0.02	0.07				simple mean				1.53	1.71
IV	217	juveniles	0.65	0.01	0.15				norm, SEQ	18.3	0.0191	8	0.35	1.12*
	23	M im	0.93	0.03	0.06	1.26	0.02	0.06	norm, SEQ	5.7	0.1245	3	0.88	1.41*
	6	M m	1.45	0.06	0.15				lnorm, SEQ	0.2	0.8895	2	1.29*	1.65
	18	F im	1.04	0.07	0.08	1.37	0.03	0.08	norm, SEQ	0.2	0.6374	1	0.94*	1.44
	0	F m												
V	62	juveniles	0.42	0.01	0.07	1.02	0.06	0.18	norm, CCV	21.4	0.0109	9	0.35	1.53*
	7	M im	1.25	0.05	0.14				simple mean				1.06	1.47*
	2	M m	1.47	0.06	0.08				simple mean				1.41*	1.53
	2	F im	1.44	0.03	0.03				simple mean				1.41*	1.47
	0	F m												
VI	553	juveniles	0.45	0.01	0.07	0.79	0.01	0.13	norm, CCV	29.7	0.0001	7	0.29	1.18*
	144	M im	0.97	0.02	0.09	1.25	0.01	0.09	norm, SEQ	15.9	0.0032	4	0.88	1.47*
	29	M m	1.40	0.02	0.12				norm, SEQ	8.5	0.0141	2	1.12*	1.53
	111	F im	1.23	0.01	0.15				norm, SEQ	13.5	0.0090	4	0.94*	1.53
	41	F m	1.50	0.02	0.11				simple mean				1.29	1.71
VIII	249	juveniles	0.45	0.01	0.07	0.78	0.01	0.11	norm, CCV	33.2	0.0000	5	0.35	1.13*
	97	M im	1.23	0.01	0.12				norm, SEQ	7.1	0.0701	3	0.94	1.50*
	31	M m	1.36	0.01	0.11				simple mean				1.25*	1.50
	105	F im	1.18	0.02	0.09	1.46	0.01	0.09	norm, SEQ	9.5	0.0086	2	1.00*	1.69
	10	F m	1.57	0.02	0.06				simple mean				1.50	1.63

3.2.2.4. First cohort of immature females (F1)

A quite clear peak for the first cohort of immature females was separated from the length-frequency distribution of immature females only in September, October and August (Appendix 2). The cohort was not visible in December, March and June. Furthermore, the F1 was weak in November and April and seemed to be more like a tail for F2 distribution. Again, in May the small number of observations prevented separating the cohorts in the distribution. The mean value of the cohort was quite stable (μ: 1.11/19-1.18/20 mm) in November, February and August with standard deviations varying from 0.07/0.7 mm to 0.09/1.0 mm.

The smallest immature female was recorded in November with a length of 0.88/15 mm. Small individuals (0.94/16-1.00/17 mm) were recorded as well in September, October, February, June and August. In December, March and May the size of the smallest immature female was slightly bigger (1.18/20-1.41/24 mm) than the other months. In total 521 immature females were caught. F2 was two to four times more abundant than F1.

3.2.2.5. Second cohort of immature females (F2)

The second cohort of immature females was recorded every month during the study (Appendix 2). Higher mean lengths (μ: 1.42/24-1.46/25 mm) were observed in September, November, February, March and August, while lengths from October, December and April were lower (μ: 1.35/23-1.38/23 mm). Standard deviation of the cohort was quite stable, varying between 0.07/0.7 and 0.10/1.2 mm.

The largest immature female was recorded from August sample and had length of 1.69/29 mm. The second largest immature female in the sample was recorded from November, with a length of 1.65/28 mm. The value was lower during the winter and higher during the summer and autumn.

3.2.2.6. Mature females (Fm)

Mature females were captured throughout the year, except in April and May (Appendix 2). In total 162 mature females were caught. The females were most numerous in November's (56) and June's (41) samples. The mean size of adult females was highest in March (μ: 1.59/27 mm) and lowest in September (μ: 1.48/25 mm). The largest females were captured in February (μ: 1.77/ 30), followed by March and June with the length of 1.71/29 mm. Standard deviations of the cohort varied between 0.05/0.3 and 0.11/1.4 mm.

3.2.2.7. Immature males (Mim)

In total 667 immature males were identified. Most of them were caught in February (153), followed by June (144) and August (97). In September the number of immature males caught was only 16, which is few compared to the amount of mature males (77).

Immature males were present each month in the samples (Appendix 3). Generally the size-frequency distribution was unimodal. Exceptions were March, April and June, when two cohorts seemed to occur in the distribution, even though sample size was low in March (33) and April (23). The first cohorts in the bimodal distributions (μ: 0.93/16-0.99/17 mm) had slightly lower mean length than the unimodal distributions September and December, which had lower mean value (μ: 0.93/16-0.99/17 mm) compared to the other unimodal distributions. The second cohorts of the bimodal distributions were comparable in mean length with the

unimodal distributions, with a higher mean value, in October, February and August (μ: 1.22/21-1.30/22 mm). November had a mean value between low and higher values (μ: 1.13/19 mm). Low number of observation (7) prevented cohort examination in May.

Standard deviations of the unimodal distributions were comparable to those of J2, with values close to 0.14/1.9 mm. In February and August the cohorts were slightly sharper (σ: 0.11/1.4-0.12/1.5 mm). Furthermore, in September the cohort was relatively sharp (σ: 0.09/1.0 mm), but number of observations was low (16). In the case of bimodal distributions, the standard deviations of the peaks were low (σ: 0.06/0.5-0.09/1.0 mm).

The smallest immature males captured were from December and had lengths of 0.76/13 mm. In October the smallest immature males were 0.82/14 mm and in September, November, February, March, April and June, 0.88/15 mm. In August the length of the smallest immature males was slightly higher (0.94/16 mm), even though the number of observations was relatively large (97).

3.2.2.8. Mature males (Mm)

Mature males were present in the samples every month (Appendix 3). In October, April, June and August the distribution was flat, *i.e.* standard deviation of the cohorts was markedly large. However, the sample size was quite low in April (5) and August (31), but relatively high in October (46) and June (144). During most of the study the mean lengths of unimodal distributions were stable (μ: 1.34/23-1.37/23 mm) and standard deviations varied between 0.08/0.8 mm and 0.13/1.7 mm. In February immature and mature male cohorts were almost identical with mean length of ~1.3/22 mm

Males classified as “mature” were generally more abundant, with 776 specimens, than immature males or females. The largest number of males with long second antennae were captured in February (220), followed by March (193) and December (93). In May only two mature males were identified. The smaller one had a length of 1.29/22 and the bigger one 1.65/28. The biggest mature males were captured in February and October, and they had a length of 1.71/29 mm. Slightly smaller mature males (1.65/28 mm) were captured in November, December, March and April. During summer and early autumn, the size of the biggest mature males was smaller.

3.2.3. Length differences among cohorts

Length differences were tested based on the Monte Carlo simulated values from modeled cohorts. The first (J1) and the second (J2) cohort of juveniles were significantly different in length (Table 3). The difference between mean values was 0.32/5 mm. Furthermore, J2 differed significantly from the third cohort of juveniles (J3) with 0.41/7 mm in mean. The third cohort of juveniles did not differ significantly from immature females with “tiny” nor did it differ from first cohort of females. The smallest specimen from J3 was bigger than the smallest immature female with “tiny” oostegites, which had a length of 0.94(Ls)/16(Lt) mm. Mean length difference between J2 and Ftny was 0.35/6 mm.

There was a significant difference in length between the first cohort of females (F1) and second cohort of females (F2). The difference in mean length was 0.31/5 mm. Adult females had two measuring units (0.14/2 mm) higher mean length than F2. However, due to high

sample, size the cohorts differed significantly from each other. F2 did not differ significantly from immature females with intermediate sized oostegites.

Immature females classified to different oostegite development stages showed high variation in size within a group, but if put in order by mean size, the length followed the length classification of oostegites (Figure 14). Differences in mean length were not significant after "intermediate" sized oostegites were reached. The smallest and largest female with "small" brood plates (0.94/16 and 1.31/22 mm) had the same size as the smallest and largest female with "tiny" oostegites. However the difference in mean length between these two groups (0.13/2 mm) was significant. The largest specimen from both groups was slightly bigger than the smallest adult female (1.29/22 mm) found during the study. Furthermore, the smallest female with "intermediate" oostegites (1.25/21 mm) was only one measuring unit smaller than the smallest adult female. The biggest female from the "intermediate" group had a length of 1.56/27 mm. The four females with "long" oostegites varied between 1.37/23 mm and 1.56/27 mm in length. Largest specimen found during the study was an adult female with a length of 1.76/30 mm.

The immature females with "small" oostegites differed from specimens with "intermediate" sized brood plates with 0.21/3 mm. On the other hand, the females with "intermediate" oostegites did not differ from the females with "long" oostegites nor did the "long" oostegited specimens from the adults. This was caused by a low number of observations in the group "Flng". However, the mean length difference was only slightly more than one measuring unit (0.08/1 mm). Immature females with intermediate sized oostegites differed from adults significantly by 0.14/2 mm. Adult females were the biggest group in mean length.

Males had a high size variation within the groups. Immature males differed significantly from all groups of juveniles in length (1-ANOVA and paired t-tests); even though the mean length difference from J3 was only 0.09/1 mm. Mature males differed 0.19/3 mm from immature males in mean length. If the first cohort of immature males was excluded from Mm, the difference was only slightly higher (0.23/3 mm). However, in this case, the outliers seen in Figure 14 figure were absent.

Table 3. Test statistics among cohorts.

Test between		difference (Ls)	difference (Lt)	test	t / F	df	p
J1	J2	0.25	4	t-test	83.2	2127.9	0.000
J2	J3	0.38	6	t-test	52.9	321.5	0.000
J2	Ftny	0.37	6	t-test	22.7	39.1	0.000
J3	Ftny			t-test	0.1	49.9	0.890
J3	F1			t-test	1.1	435.0	0.265
F1	F2	0.28	5	t-test	32.8	429.1	0.000
F1	Ftny			t-test	0.7	50.5	0.464
F2	Ftny	-0.30	-5	t-test	17.2	45.3	0.000
F2	Fint			t-test	1.0	136.5	0.299
F2	Fm	0.14	2	t-test	12.0	336.1	0.000
Ftny	Fsml	0.13	2	t-test	4.2	49.6	0.000
Fsml	Fint	0.21	3	t-test	8.9	31.4	0.000
Fint	Flng			t-test	1.2	3.3	0.290
Fint	Fm	0.14	2	t-test	10.0	168.5	0.000
Flng	Fm			t-test	1.5	3.1	0.220
J1,J2,J3	Mim			1-ANOVA	11161.2	3, 4775	0.000
Mim	Mm	0.19	3	t-test	23.6	1169.6	0.000

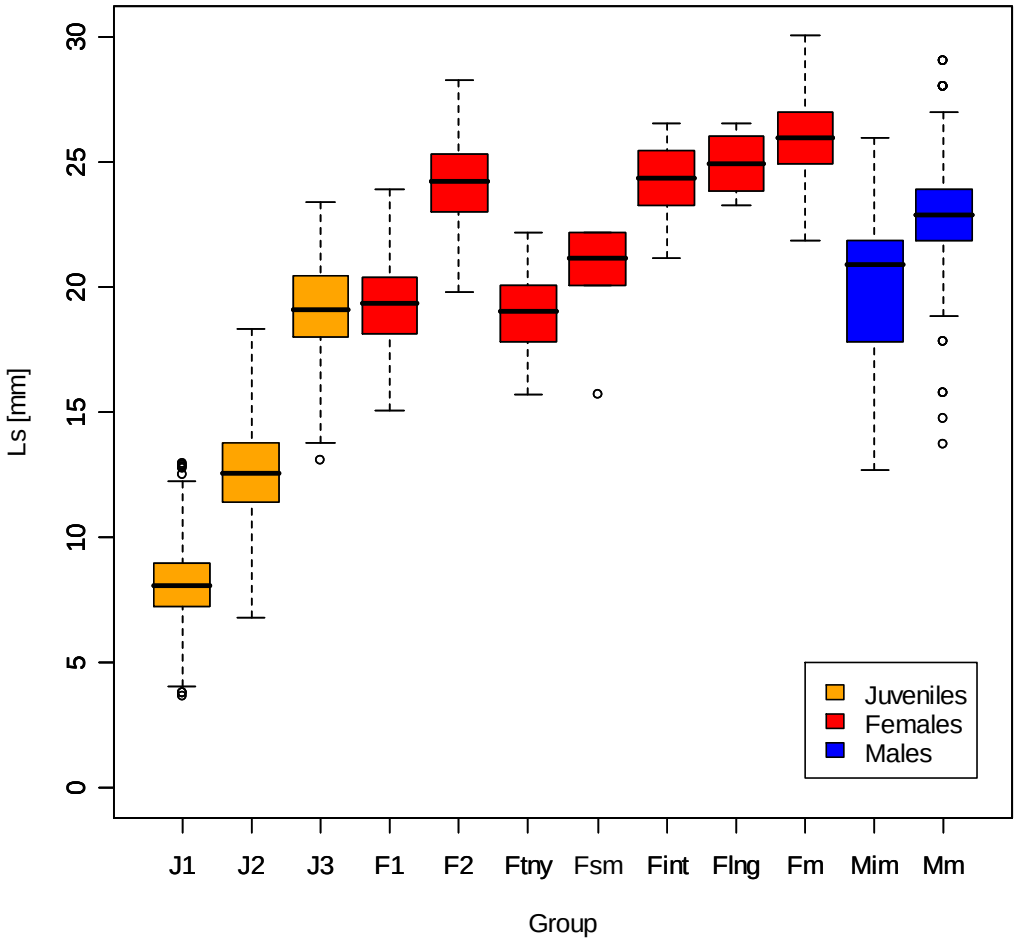

Figure 14. Median, quartile, 95 % of observations and outliers of total length for *Onisimus caricus*. Values for juvenile (orange colour) and immature female cohorts, F1 and F2, are drawn with Monte Carlo simulation from the models derived with mixture distribution analysis. Females with letter abbreviations are related to the development of oostegites. Males were grouped after the length of second antennae. Number of observations for different groups were: J1 = 2554 (1st juvenile cohort), J2 = 1331 (2nd juvenile cohort), J3 = 236 (3rd juvenile cohort), Ftny = 38 (with "tiny" oostegites), Fsml = 22 (with "small" oostegites), Fint = 77 (with "intermediate" oostegites), Flng = 4 (with "long" oostegites), Fm = 162 (mature female), F1=204 (1st immature female cohort), F2=314 (2nd immature female cohort), Mim = 667 ("immature" males) and Mm = 776 ("mature" males).

3.4. Reproduction

Average sex ratio (all males : all females) was 2.1 (Table 4). The sex ratio was higher during time interval from December to March thus indicating an increased proportion of males in the catch for this period. The ratio was high also in May, but that was probably due to the small sample size. Furthermore, in September sex ratio was slightly higher (2.4) than during rest of the year. Exclusion of the period with raised sex ratio from December to March would decrease the ratio to 1.2.

Table 4. Sample size, sex ratio (males/females) and reproduction parameters of the studied *Onisimus caricus* population for each month separately and for all months together. Lengths are given both in total length (Lt) and first pereonal segment length (Ls).

Month		total catch	sample size	sex ratio	female maturity	egg bearing females	mean lenght of egg bearing F	max-min lenght of egg bearing F	mean number of eggs / fem	min-max number of egg / fem	mean diameter of eggs	Egg devel. stage
		n	n	M:F	%	n	mm ± sd	mm ± sd	n ± sd	n	mm	
IX		325	284	2.4	28							
X		3131	1020	1.2	29							
XI		6139	1224	1.1	36							
XII		1721	953	5.2	23							
II	Lt	1035	584	9.8	29	3	26.2 ± 1.3	25-28	7.0 ± 0.0	(3)-7	1.75 ± 0.11	F
	Ls						1.56 ± 0.07	1.50-1.63				
III	Lt	638	466	4.6	16	3	25.8 ± 0.6	25-27	8.5 ± 4.0	(3)-12	1.65 ± 0.09	F
	Ls						1.52 ± 0.04	1.50-1.56				
IV		974	265	1.6	0							
V		77	73	4.5	0							
VI		2469	878	1.4	24	27	25.1 ± 1.9	22-29	15.5 ± 2.7	(10)14-17	1.67 ± 0.11	D-A
							1.48 ± 0.11	1.29-1.71				
VIII		496	494	1.1	9							
All	Lt	17005	6241	2.1	16	33	25.2 ± 1.7	22-29	11.4 ± 4.4	(3)5-17	1.68 ± 0.11	F-A
	Ls						1.49 ± 0.10	1.29-1.71				

Average female maturity percent was 16. The value was higher during the autumn and early spring and decreased by late winter. No mature females were found from the samples in April and May. 24 % of females were mature in June and only 9 % in August.

Most of the egg bearing females were found from the samples taken in June, whereas a few specimens were caught in February and March. Mean length of the egg bearing females was 1.49(Ls)/25(Lt) mm and standard deviation 0.10/1.7 mm. The smallest gravid female captured had a length of 1.29/22 mm and the largest one 1.71/29 mm.

Mean number of eggs per female was 11 with a standard deviation of 4. All females with only 3 eggs (n = x) were supposed to have lost eggs during the sampling and preservation and they were left out from the average calculation. The smallest and the largest number of eggs thus found from a female was 5 and 17, respectively.

Mean diameter of eggs was 1.68 mm with standard deviation of 0.11 mm. Eggs were significantly bigger in February compared to March and June, but March and June did not differ significantly (1-ANOVA: F=4.88 p=0.01 and TukeyHSD). The difference in the egg diameter was ~0.09 mm, which was three times the accuracy used in egg diameter measurements. Sample size in February and March was only three eggs each. All of the eggs from February and March were classified to development stage F meaning that eggs were undeveloped. In June some of the embryos had pereopods and a tail visible, even though some yolk was still covering them (stage A). Moreover, in the least developed eggs in June outer membrane was distinct or broken (stage D).

There was no significant relationship between number of eggs and size of females (ANOVA: F=2.64 df=85 p=0.11) nor diameter of eggs and female size (ANOVA: F=0.96 df=85 p=0.32). Reproductive cost values calculated were one order of magnitude too low compared to Wildish (1982). Source of the error was not found either from the measurements or the data in the study. To correct the error, calculated values were multiplied by ten assuming that mistake was either in the formula given by Wildish (1982) or somewhere in the study. However, the corrected value varied from 5 to 10 % depending on mean amount of eggs females were estimated to have. Mean reproductive cost for *Onisimus caricus* was 9 %.

4. DISCUSSION

4.1. Methodical constraints

4.1.1. The sampling method

When studying population dynamics and life cycles, quantitative methods should be used (Gotelli 1998). Numerous factors affect the catching efficiency of baited traps. Sainte-Marie (1986b) noted that, for example, bait size is a major factor in effectiveness of a baited trap. Nevertheless, bait size is not the factor that attracts amphipods to the traps, but smell of the bait (Busdosh et al. 1982, Smith & Baldwin 1982, Smith & Baldwin 1984). Thus the handling, the temperature, and the age of the bait are all factors to consider, if baited traps are wanted to be used even as a semi-quantitative method to collect a particular species. The most difficult factors, in order to standardize the catching efficiency of a baited trap, are those one can not see. Busdosh et al. (1982) stated that amphipods swam slowly along the bottom towards the trap. The way how the traps land to the bottom, when dropped from a boat, does affect to the catching efficiency as well as affects the light conditions and the tidal-phase (Sainte-Marie 1986b).

Baited traps do not collect all groups of a particular species of a scavenging amphipod evenly. Smale et al (2007) reported high seasonality in feeding behavior of a necrophagous lysianassid *Cheirmedon femoratus* in shallow benthic habitats in Antarctica. At least three groups of the population of lysianassid scavenging amphipods are suggested to be under- or overrepresented in the traps depending on the time of the year:

1) Egg-bearing females are rare visitors in baited traps (Hessler et al. 1978, Thurston 1979, Slattery & Oliver 1986, Moore 1994, Legeżyńska et al. 2000). Sainte-Marie (1986b) and Sainte-Marie et al. (1989) reported that average meal size decreases with sexual maturity of *Anonyx sarsi* and *Onisimus litoralis* females, which was caused by gut constriction due to the maturation of gonads and brood development (Sainte-Marie et al. 1990). The non-attraction of mature or maturing females to the baited traps has as well been connected with behaviour to avoid predation (Hessler et al. 1978; Sainte-Marie et al. 1990).

2) Newly released juveniles are either unable to swim distances needed to find the traps or have different foraging strategy and diet than the bigger juveniles. Newly released juveniles may also avoid traps because of potential predation caused by aggregation of large scavengers in the traps. This study shows that baited traps started to catch *O. caricus* in the length of 0.29/4.6 mm. Bregazzi (1972) reported 90 percent mortality within the first year after release in *C. femoratus*. In this study, sharp peak of small juveniles did not appear to the length-frequency data suddenly. Instead relatively sharp peak of approximately 0.5/8 mm juveniles was present in the data throughout the year. This might reflect that 0+ juveniles do not go to the traps simultaneously right after release, but the cohort appears in the trap catch later during the course of the year mixed with age group 1+.

3) Mature males are proposed to be more motile during mating season when trying to find females (Conlan 2004). Thus it could be assumed that males would be more frequently observed from the traps during the mating season.

Busdosh et al. (1982) estimated that the bait attracts scavenging amphipods from at least 30 meters distance. Ingram and Hessler (1983) suggested without direct evidence, that

detection of odor might occur over as great distances as 1 to 2 km in the deep-sea. In collision with these estimates is Sainte-Marie's (1986b) direct observation that lysianassid *Anonyx sarsi* detected 100g bait from distances of 5 to 8 meters, while odor plumes arising from 0.5 to 1 kg of bait were detected from few tens of meters distance. However, large lysianassid scavengers, such as *O. caricus*, are highly motile and can cover distances of many kilometers during a day (Sainte-Marie 1986a)

Baited traps alone are a weak method for studies focusing on population dynamics, reproductive life history traits and population density of hyper-benthic amphipods. One way to project changes in the catch of baited traps to population dynamics would be to produce a correction factor for the baited trap catch by comparing with a quantitative method. A conceivable method would be tubes or frames, open at one and covered by fine mesh at another end, used by scuba divers (Everson & White 1969, Bregazzi 1972). Since diving was not an option during the study period, a correction factor was not possible to estimate.

Even though biased, baited traps are easy and inexpensive to use also in a cold and harsh climate. A baited trap is not a quantitative sampling gear, but if used at same locality, it gives an illustration of the fraction of the scavenger population, which is actively trying to find alimentation. The fact that *O. caricus* was clearly the most abundant scavenger in the catch during the whole study period practically closed off competition between scavenger species, which has been suggested to affect to the catch (Sainte-Marie 1986a). Because breeding of benthic lysianassid amphipods in the Polar regions is established to be strongly seasonally timed and synchronized (Dunbar 1957, Kuznetsov 1964 after Welawski & Legeżyńska 2002, Steele 1967, Steele 1972, Steele & Steele 1972, Thurston 1972, Steele & Steele 1975a, Steele & Steele 1975b, Clarke 1979), length frequency and gender structure data of *O. caricus* obtained from the catch of the traps was considered to be reliable enough to estimate life cycle, life span, growth and reproductive parameters of the species after evaluating possible changes in the feeding behavior during the year (see chapter 4.2 below).

However it needs to be assumed that the traps capture the population relatively randomly, meaning that instead of forming false peaks to the length frequency distribution, the bias of traps is rather observed as lower abundance of certain groups compared to the population in the nature.

4.1.2. The timing

When estimating cohorts, life cycle and growth in the study, September must be seen as a continuum for August, even though samples were taken a year earlier. There are inter-annual changes in the timing of the processes in the Arctic marine environments, but it must be assumed that the processes happen in the same order from year to year. Since environmental conditions concerning mean temperatures, ice cover and currents were quite similar in 2006 and 2007 (Norwegian meteorological institute 2007, UNIS environmental data 2007), it is assumed that no major changes in the timing of the processes happened between these years.

4.1.3. Biases in classifying gender of the animals

Classifying males according to the length of second antennae is a subjective estimate and depends on the situation (*i.e.* how long is the average length of antennae in the examined sample) and the person involved. Apparently length of second antennae is a sign of maturity in Lysianassidae (Steele & Brunel 1968, Carey & Boudrias 1988, Lowry & Stoddart 1993, Vader

et al. 2005), but knowing when the maturity is reached is impossible without a physiological examination. Bias caused by this applies especially to smaller specimens classified as “mature”. However, the length of second antennae seems to positively correlate with the length of first pereonal segment of males. Combined with the cohort analysis made in the study, deduction of the presence of the mature males was done by assuming that the largest cohort of “mature” males had achieved maturity in reality.

The same applies for the largest juveniles classified to the cohort J3, which plausibly contains some immature females with small oostegites, but some of the juveniles achieve female characteristics later than the others. Thus it is noted, that J3 does not consist purely of specimens with identification error. Lengths of the smallest females recorded monthly did not differ between the start and late period of the study. However, length of the smallest cohort of immature females (F1) and the largest juveniles may be mixed during the early period of the study, when measuring was made in hurry due to the large sample sizes, and thus may reflect more the experience of the measurer rather than the biological characteristics of the population.

4.1.4. The statistics

Because of the large amount of relatively complex data, quite complicated statistical analyzes were chosen to help in seeing patterns in the population. The used analyzes contain many pitfalls, which, if not considered, may undermine the credibility of the whole study. On the other hand, if used correctly, the statistics used would firstly give an illustrative picture of the population in the subject of the study and secondly give valuable experience, knowledge and an alternative tool for the future research of life history of scavenging amphipods.

As far as known, kernel density estimates and mixture distribution analysis was used for the first time in a life history study, where the data were collected by baited traps. The shortcomings of baited traps are discussed above and in the chapter 4.2. Nevertheless, use of the mixture distribution analysis needs quite deep understanding of statistics and computer modeling in order to be used safely. After all, it might contain too many pitfalls and one should be very careful before evaluating the results. However, the kernel density estimate is very easy to carry out with help of R –statistics environment. If these two methods are combined with reasoning, biological facts can be deducted relatively safely from the length-frequency data.

However, the mixture distribution analysis has shown to be a credible method to separate cohorts from large number of observations, to give single values, which can be used to describe relatively complicated size-frequency distributions and to use mean values and standard deviations in the growth modeling assuming that recruiting to the population happens relatively synchronized (Macdonald & Pitcher 1979, Macdonald & Green 1988, Beuchel 2000, Beuchel & Lønne 2002, Du 2002, Arndt & Beuchel 2005).

4.2. Behavior of *O. caricus* connected to the attraction to the bait

Smale et al. (2007) noticed a reduced amount of lysianassid amphipods attracted to bait during the summer in Antarctica. They explained the change with different habitat selection of the studied species, *Cheirmedon femoratus* (Pfeffer). The species was assumed to move deeper waters during the Antarctic summer. Similar trend can be seen in the catch of *O. caricus* in this study (Figure 11).

It is unlikely that reduced catch reflects the abundance changes in *O. caricus* population widely. More realistic deduction is that the catch of baited traps rather reflects both local changes in the abundance of a highly motile species (Legeżyńska et al. 2001) and changes in the behaviour of the species connected to reproduction, avoiding of predation and abundance of food.

The total catch of *Onisimus caricus* seems to follow loosely light conditions in the water (Figure 11). During polar night the catch was high. The catch reduced during time when light came back and the water was clear. The number of amphipods in the traps increased with the turbidity of the surface layer, which in turn was assumed to correlate negatively with the light intensity in the water column.

Birds, such as arctic terns, black guillemots and waders, are principle predators of shallow water amphipods on Svalbard (Węsławski et al. 2000). A murky surface layer prevents visibility from air under the surface and offers a cover against plunge diving birds, such as terns (Schreiber & Burger 2001). A thin surface layer may offer protection from terns, but pursuit diving sea birds, such as black guillemots, can still dive below the layer (Schreiber & Burger 2001). A thick layer of murky water and low light conditions in the water column could be thought to offer cover from the both types of predators. In May water turbidity was relatively low as was the catch (Figure 11, Figure 12). Increase of turbidity in June could have been one reason for the higher catch. Thus it is suggested that avoiding predation plays a role in the behaviour of *O. caricus* and reflects to the lower number of amphipods in the traps.

The mating period changes the behaviour in Amphipoda (Sainte-Marie 1986a, Legeżyńska et al. 2000, Conlan 2004). Egg-bearing females are reported to be rarely caught from the traps (Legeżyńska et al. 2000). In a review of mating behaviour of Amphipoda, Conlan (2004) concluded that Lysianassoidea males are non-mate-guarders, meaning that instead of carrying their mates until they are ready to moult and be fertilized, they rather swarm pelagically or benthically at the time when females are ready to mate. The mating period was estimated to last from December to March and females were carrying eggs from February to late June-early August (see chapter 4.3). Changes in the behaviour caused by reproduction season may partly explain the larger number of males in the samples in February-March and the smaller number of females in the samples in April-May. In June, it seemed that females, even though egg-bearing were going to the traps.

O. caricus is considered to be an opportunistic scavenger, which changes its diet during the season (Legeżyńska 2001, Vader et al. 2005). The species is reported to take an advantage of summer mortality of zooplankton caused by osmotic shock (Zajączkowski & Legeżyńska 2001, Legeżyńska 2008). If the availability of dead zooplankton is assumed to correlate with the depth of the brackish surface layer, zooplankton mortality would have been highest during August (Figure 5). A high abundance of dead zooplankton could lead to lower motility of the scavenging amphipods and thus partly explain the smaller catch in August and September. During the winter *O. caricus* is probably more motile feeding on larger carrions (Legeżyńska 2000, Zajączkowski & Legeżyńska 2001, Legeżyńska 2008). Motility could be reflected to the larger catch during autumn and early winter months. The genus *Onisimus* is known to be able to utilize ice algae and sinking phytoplankton during the algal bloom (Boudrias & Carey 1988, Arndt et al. 2005, Vader et al. 2005). Gut content analysis for *O. caricus* made by Zajączkowski & Legeżyńska (2001) showed that small fraction of the diet in July consisted of algae. As an opportunistic feeder *O. caricus* could be able to utilize the algal bloom, at least to

some extent and abundance of the sinking algae would, in turn, reflect to the lower catch observed during April and May.

In conclusion it can be suggested that the catch of baited traps reflects the behaviour of scavenging amphipods. Many factors might affect the behaviour, including reproduction, food availability and avoidance of predation. There is a need of investigate these factors to correct the bias caused by the amphipod behaviour when studying population dynamics. If the changes in the behaviour can be considered and if it can be assumed that the traps catch all parts of the population to some extent, baited traps can be used to estimate life cycle, reproduction and growth of local amphipod populations despite of the bias caused by the sampling method.

4.3. Reproduction

Because of the sampling and determination biases, the sex ratio was calculated from all specimens with sexual characters, rather than calculating the ratio only from mature individuals, which is more common way to estimate the sex ratio. However, the ratio was considered to reflect changes in the mature part of the population, which seemed to be true at least when looking at the kernel densities of length-frequency data (Figure 13). The mean sex ratio of *O. caricus* was 2.3 (Table 4), which is quite high if compared to other Arctic amphipods in Węsławski and Legeżyńska (2002). The number of males compared to females started to increase in December and peaked up in February. This probably indicated breeding time, since males are known to find females by actively swimming (Conlan 2004). The presence of the first egg carrying females in February complies with the statement. If the temporal high values were ignored, the sex ratio was close to 1, which probably was closer to the sex ratio in the real population. Reasons for potentially biased sex ratio are discussed in the chapters 4.1 and 4.2.

The first egg bearing females were captured in February (Table 4). All of the eggs from the six egg-bearing females in February and March were undeveloped and probably newly laid. In June, all of the eggs of 27 captured females were well developed having a shape of an amphipod. Some of the embryos had pereopods and a tail visible. In August neither egg bearing females nor females with juveniles was caught. It seems that the hatching of the juveniles was relatively synchronized and it happened sometime from late June to early-August.

According to Steele and Steele (1975a), development of newly laid eggs in temperatures prevailing during the incubating period in Adventfjorden would take approximately 80 days for *Gammarus oceanicus* and *G. marinus*. However, *Onisimus caricus* has twice as big eggs as *G. oceanicus* (Węsławski & Legeżyńska 2002). Steele and Steele (1975a) estimated 300 days egg development time for a species, which has comparable size of eggs with *O. caricus*. This estimation does not comply with the incubation time observed in this study, which was approximately from 4 to 5 months or from 120 to 150 days. However, it seems that the incubation time observed in this study would be close to the average of the two estimates made by Steele & Steele (1975a).

Arndt & Swadling (2006) concluded that the release of brood in polar crustaceans would generally be timed to the most productive time of the year. Phytoplankton is responsible for most of the primary production that takes place in the pelagic ecosystem (von Quillfeldt 1996). In the Arctic marine environment, algal bloom is established to be the most significant

nourishing event which influences the peak of secondary production and animal migrations (Hegseth 1998). In the northern part of the Barents Sea, the annual production of ice algae may represents between 16 and 22 % of the total annual primary production (Hegseth 1998). The timing of the hatching of *O. caricus* suggested in this study seems not to follow the algal bloom. However, Zajączkowski and Legeżyńska (2001) evaluated that the melting of glaciers forms a brackish water layer on the surface of glacial bays, which causes local mortality to freshwater-sensitive zooplankton. They concluded that *O. caricus* is very likely the most important species taking advantage of the sinking dead zooplankton. During this study the brackish water layer was thickest during August, which would fall on the same time when the juveniles were released.

Węsławski and Legeżyńska (2002) measured the egg diameter of *O. caricus* as 1.4 mm. In this study the mean diameter of an egg was 1.7 mm and volume of 2.5 mm^3. The difference might be due to the fact that in this study the diameter was measured including the outer membrane, if it was not totally distinct. However, this does not exclude the fact that among the Amphipoda *O. caricus* has a considerably large egg relative to the size of the animal. In a review of reproduction of gammaridean Amphipoda Wildish (1982) found that the largest amphipod egg belonged to *Stegocephalus inflatus*, which is approximately twice as large as *O. caricus*. The diameter of the egg was 1.75 mm and the volume 2.81 mm^3. Generally *Onisimus* species tend to have large eggs (Węsławski & Legeżyńska 2002), but *O. caricus* seems to take the upper extreme within the genus.

Węsławski and Legeżyńska (2002) found that the mean number of eggs per *O. caricus* female was 12, which accompanies with the mean estimated in this study (11). The maximum number of eggs found from a female in this study was 17, which again is almost the same as (18) reported by Węsławski and Legeżyńska (2002). The minimum number of eggs per female was difficult to estimate, since some eggs were probably lost during the sampling and preservation. Nevertheless it seems reasonable to believe that some of the females might have had as few as five to seven eggs in their brood pouches. Because of the small sample size and the loss of eggs during sampling, relationship between number or size of eggs and female size was not found, although general trend among the Amphipoda is that bigger females tend to have more eggs (Wildish 1982).

The average brood volume of *O. caricus* (30 mm^3) is comparable with those presented in Wildish (1982) for *Gammarus wilkitzkii* (18-51 mm^3). The same applies for reproductive cost, which was estimated to be 5-12 % for *G. wilkitzkii*. In this study *O. caricus* showed reproductive costs between 5-10 %. The value is considerably higher than in the amphipods with southern distribution, but seems to comply with the Arctic amphipods, which usually are K (or A)-selected.

Sainte-Marie (1989) used Half-Range of Mature Female Body Length (HMFBL) ratio to estimate itero- and semelparity of the cold water gammaridean amphipods. He considered that the ratios between 0.0110 and 0.3478 referred to the semelparous (one brood per life time) species and the species with the ratios more than 0.3478 to iteroparity (several broods per life time). HMFBL ratio calculated for *O. caricus* in this study was 0.1536, which refers to semelparity.

It can be concluded, from the reproductive data, that the life history pattern of *O. caricus* refers to an A-selection, as evaluated also in Węsławski & Legeżyńska (2002). The reproductive pattern is most likely semelparous.

4.4. Interpretation of the cohorts

Since the hatching of juveniles seemed to be relatively synchronized, the size cohorts were thought as year classes and it was assumed that the growth rate between the specimens does not alter in the way that the cohorts would have merged during the period when the specimens were juveniles. Because the population was sampled with baited traps, the bias associated with the sampling method included probably underestimation of the abundance of newly hatched juveniles. The presence of strong peak of J1 in May casted a doubt on the hypothesis that hatching occurred between late June and early-August (Figure 13). Interpretation for the mismatch was that most of the juveniles appeared in the traps in May almost one year after the hatching.

In most cases the first and the second cohort of juveniles did not differ from each other very clearly (Figure 13), but it rather seemed that the distribution of juveniles was positively skewed and had an elongated tail, which was seen as J2. In June and August there were two separable juvenile cohorts. Juveniles in the second cohorts had approximately the same mean length as the tail of juvenile distribution in October, November, December and February. Bregazzi (1972) reported a 90 percent mortality between the first two juvenile cohorts in a benthic amphipod *Cheirmedon femoratus* from Antarctica. Distributions from October to December would show a similar trend, if assuming that the traps collected population at a relatively unbiased manner during those months. On the other hand, this would cast a doubt on the interpretation; that the newly hatched juveniles were not visible in the data before spring.

Second cohort of juveniles and some part of immature male and female distributions tended to overlap. Thus it was supposed that J2, F1 and Mim1 represented the same age group, but reflected natural variation within the cohort. The non-significant size difference between F1 and the immature females with “tiny” or “small” oostegites was considered as evidence for that F1 had short oostegites.

Immature female distribution was negatively skewed. Second cohort of females (F2) did not differ significantly in size from immature females with “intermediate” and “long” oostegites: thus it was assumed that the females from F2 had oostegites similar to these groups (Figure 14). The presence of strong F2 throughout the year (Appendix 2), even during the breeding season was considered to refer to a slacken growth rate when specimens started to reach maturity. Further, this was considered to indicate that F2 and Fm belonged to different age groups and that development from F2 to the adults took approximately one year. Reduced differences in the mean lengths between immature females from larger oostegite development groups complied with this hypothesis, if assumed that each group represented a single molting (Hammersmith & Coyle 1991) (Figure 14).

Immature males, unlike females, had a bimodal size-frequency distribution only during and after the algal bloom (Appendix 3). This was considered as a time, when the males started to achieve sexual characterizes. Clearer unimodal distribution, compared to females, was thought to indicate that the males achieved their sexual characters more synchronously.

Immature and mature males were generally overlapping, but the fraction of larger specimens of the combined distribution consisted of males with long second antennae (Appendix 3). The presence of immature males in relatively high numbers during the mating season referred most likely to two age groups: one consisting of immature males and one of mature specimens. Change of an identification error was present in the transition lengths of the male cohorts, but it was considered relatively safe to assume that larger specimens were their own age group.

If assumed that the cohort classified as “mature males” consisted mostly of specimens, which in reality had reached maturity, the males seemed to reach both the sexual characteristics and the maturity smaller in size than the females (Figure 13). However, the largest males seemed to have only slightly smaller size than the largest adult females. This could indicate presence of two strategies within the mature males: one, which would mature one year earlier, but would remain small in size and the other, which would be larger and one year older. Nevertheless, there was no strict evidence for this theory. The variation within cohorts may reflect natural variation in size, not age or the males could live over two mating seasons

4.5. Life cycle and growth

The length frequency data contains a high amount of noise and no certain deduction of the life cycle can be made. Thus estimating the life cycle is not an easy task and a chance for a misinterpretation is present. However, the following theoretical life cycle with five years maximum life span for *Onisimus caricus* females and four to five years maximum life span for males is suggested (Figure 15).

Eggs hatch sometime between late June and early August. Mean size of individuals belonging to juveniles was small in February, March and especially in May (Figure 13, Appendix 1). This could indicate that a small fraction of newly hatched juveniles would start going to the traps during their first winter, and most of the cohort would appear in the size frequency distribution in May, with a mean size of 0.42/7 mm, after the algal bloom and a potential boost in the growth.

After May, the mean size of the J1 cohort consisting of one year old juveniles would grow slowly during the summer and autumn until February, when a fraction of the cohort of juveniles from last summer would decrease the mean value. In middle of their second winter (February-March) a big proportion of the juveniles would have frequent mouldings (many empty *Onisimus caricus* shells were found from the traps during that time). During the winter biggest specimens of one and half years old juveniles would gradually appear in J2. After assumed boost in the growth during and after algal bloom all of the almost two year’s old juveniles would come out as the second peak of juveniles (J2) in June with a size varying from 0.70/12 mm to 1.0/17 mm (Appendix 1). One peak in the size-frequency distribution in April and possibly in March could indicate the supposed gradual shift in the length and a sharp peak of small specimens in May, the appearance of new juveniles (Appendix 1).

In theory the slow growth could be explained by the fact that it would be profitable for a small juvenile to feed on minute carrions, fragments of zooplankton, algae and detritus (Sainte-Marie 1986a, Dauby et al. 2001), which are frequently accessible especially during the summer because of zooplankton mortality caused by turbidity and brackish surface water layer (Zajączkowski & Legeżyńska 2001, Eiane & Daase 2002) and the high biomass due to the

algal bloom (Arnkværn et al. 2005). This kind of strategy reduces the need of motility and usually leads to lower predation risk and, in turn, to slower growth (Jumars & Gallagher 1982, Ingram & Hessler 1983, Sainte-Marie 1986a, Dauby et al. 2001).

4.5.1. Females

A proportion of the biggest individuals of the age group 2+ could have been started to grow oostegites. Their size would vary from 0.9/15 mm to 1.2/20 mm. The big variation in the size is suggested to be arisen from the varying environmental conditions and the strategy in finding food (minute carrions against carcasses) (Sainte-Marie 1986a, Dauby et al. 2001). During late summer and autumn, more juveniles would achieve sexual characteristics. In November juveniles of the cohort would have a length varying from 0.7/12 mm up to 1.2/20 mm and immature females from 0.8/13 mm approximately to 1.3/21 mm.

Length-frequency data shows a high variation in size of the 3+ age group, which is assumed to consist of cohorts J2 and F1. During the spring and maybe after getting a boost in the growth from abundance of zooplankton after the algal bloom and raised zooplankton mortality the age group would gradually appear in F2. This could be indicated by a great variation and overlap of immature female cohorts in June and August. In September the age group 3+ consisting of the cohort F2 would have a mean size of 1.44/24 mm.

Increased proportion of males with long second antennae and eggs found from females indicates that the mating season lasts approximately from December to February. Presence of strong F2 during that time indicates that the immature females from the age group are not ready to breed, even though their size would be close to the adults.

Beuchel & Lønne (2002) found that growth rate of mature females on *Gammarus wilkitzkii* reduced dramatically. They explained this by the fact that egg carrying females do not mould while having brood. Congruent results are reported in Hammersmith and Coyle (1991) for *Ampelisca* species. Similar decrease in the growth rate can be seen in *O. caricus* (Figure 14). It seems that the growth of *O. caricus* females starts to slacken before the mean length reaches 1.5/25 mm, perhaps because the females may start to allocate energy to developing gonads.

During summer and especially autumn now 4+ years old females would begin to reach maturity. Most of the mature females in June and August could be older individuals from age group 5+. However, little less than half of the adult females without eggs (14) in June could indicate either early maturing of a fraction of age group 4+ or unsuccessful breeding of some specimens from the older age group. In October size of adults from supposed age group 4+ varied from 1.4/23 mm to 1.7/29 mm. The biggest mature females may be old reproduced individuals, which are probably dying off. It seems that even though mature females are present, they would not breed before winter, since no egg-bearing females were found other times. Another alternative could be that the number or activity of egg-bearing females was so low that they were not captured.

During their fifth winter, four and half yeas old mature females, with size varying from 1.3/22 mm to 1.75/30 mm, would mate and start to carry eggs in January-February. The absence of mature females in the samples from April and May can be explained by the observation that egg and juvenile bearing females are a rare catch in the baited traps (see chapter 4.1).

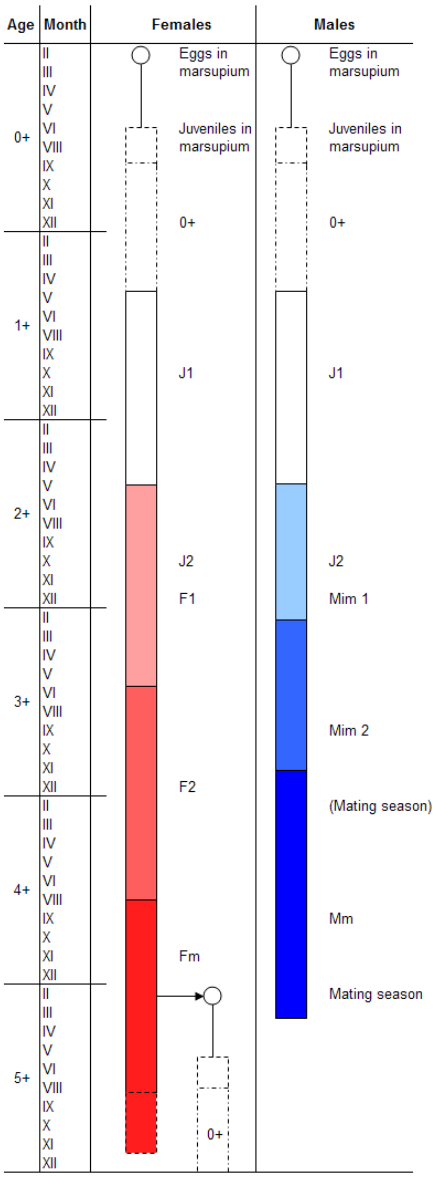

Figure 15. The suggested life cycle for *O. caricus*

The eggs of the females hatch probably in late June-early August. Absence of both eggs and juveniles from female brood pouches in August indicates either short juvenile carrying period or change in the behaviour. It could be that females with juveniles do not go to the traps. The large size of eggs and clear A strategy would suggest longer maternal care.

Wildish (1982) concluded that many cold water gammaridean may have a diapause after the first breeding and they might try breeding again later. The possibility of diapause for the five years old females appears to be low, but it is possible that some of the females mature already during their fourth winter since variation within the cohort was high and the smallest egg-bearing females were only 1.29/22 mm in size. Thus they would have a possibility for another brood. After taking care of their juveniles, five years old females probably die off during the autumn.

4.5.2. Males

It is not possible to make any difference between the life cycle of *O. caricus* males and females during their juvenile stages. There is no evidence to argue that transition from J2 would happen in different manner than in females (Figure 13).

Growth of the males, like it was suggested for females, seems to slow down when reaching maturity. Instead of allocating energy to developing gonads, males have larger gnathopods and are reported to be more active during the time, when they are trying to find a partner (Conlan 2004). The life cycle of the males could be similar to females (Figure 15), but dramatically reduced amount of mature males in the catch after March (Table 2) could refer to faster cessation of males. Thus life span of males would stay slightly shorter than in females. The possibility for maturing already during their fourth winter and thus having an opportunity for two mating periods is more plausible with the males than the females, since quite small males could be classified as "mature". Because of uncertainty in maturity classification, the possibility for four years life cycle in males cannot be excluded.

4.5.3. Suggested life cycle; conclusions and criticism

Węsławski and Legeżyńska (2002) suggested a three years maximum life span for *O. caricus*. They however, had only one sample from July with 84 specimens. Because of the small sample size, they ignored one peak from the length-frequency distribution varying between 10 and 14 (Lt) mm. The peak was comparable to J2 cohort observed in this study. They also assumed that the first cohort of, apparently juveniles, belonged to the age group 0+. First cohort from the study had a median of 6 mm, which was almost the same as the median of cohort J1 (6-8 mm) observed in this study. Precise sampling method for *O. caricus* was not described in Węsławski and Legeżyńska (2002), but personal communication with Legeżyńska confirmed that they also had used baited traps in the sampling. Generally the length-frequency distribution presented in Węsławski and Legeżyńska (2002) was very similar to the distribution from July in this study, even though lengths differed within larger specimens. This can be explained by the different method in the length measurement. Thus shorter life span estimate in the study is suggested to be due to lack of observations throughout year and different interpretation of the results.

Generally in studies on the life cycles of the Arctic amphipods, distinctive peaks in the length-frequency distribution are considered as age groups (Poltermann 2000, Beuchel & Lønne 2001, Węsławski & Legeżyńska 2002, Arndt & Beuchel 2005). In this study the cohorts would have been impossible to see without gender classification, since the kernel distribution of *O. caricus* for all genders combined has two to three peaks. More peaks can be seen from the length-frequency histograms (Figure 13), but some of them are due to measuring intervals used in the study. High mean size of the first peak of juveniles and the occurrence of the peak before the hatching would support the assumption that 0+ age group would be absent in the samples during summer and autumn. Thus there is a strong evidence to argue for a surprisingly long life span for *O. caricus*.

A long life span is not exceptional among the Arctic amphipods. For example Hammersmith and Coyle (1991) reported a five to six years life span for *Ampelisca macrocephala*. Beuchel & Lønne (2001) estimated theoretical life span of *Gammarus wilkitzkii* to be as long as six to seven and half years. Suggested life span for *O. caricus* is two years longer than Arndt & Beuchel (2005) suggested for similar sized ice associated

opportunistic scavenger *O. nanseni* and one year longer than the counterpart for *O. glacialis*, which is thought to be an opportunistic scavenger with more herbivorous diet (Arndt et al. 2005). However, criticism against the suggested life cycle in this study can be directed:

1) The age group 0+ was considered to be unobservable with baited traps. Even though there is evidence to support this hypothesis, it might be that a fraction of the *O. caricus* population releases their juveniles already during the algal bloom, which would comply with theories in the literature (Arndt & Swadling 2006), and J1 would actually consist of the age group 0+. If this would be the case, life span would be one year shorter.

2) The suggested life cycle leans powerfully to the hypothesis of synchronized breeding time generally established in case of Arctic amphipods (Dunbar 1957, Kuznetsov 1964 after Węsławski & Legeżyńska 2002, Steele 1967, Steele 1972, Steele & Steele 1972, Thurston 1972, Steele & Steele 1975, Clarke 1979). However, the presence of mature males and females throughout the year could indicate either that breeding is happening outside of the suggested breeding season or refer to iteroparism in the population. Slightly increased sex ratio and presence of mature females in September could refer to another mating in September. Cohorts in length-frequency distribution could be explained by two juvenile releasing periods: one as suggested earlier in this study and one during the algal bloom. If this would be the case, the life span of *O. caricus* could be as suggested in Węsławski and Legeżyńska (2002).

3) Accelerated growth was observed during and after the algal bloom, but since *O. caricus* is reported to be a species, which utilizes efficiently summer mortality of zooplankton, higher growth rates during summer and early autumn would have been expected. The growth might be so fast that it could mix the cohort structure of the juveniles and lead to a life span significantly shorter than suggested.

On the other hand, the observed hatching time and release of juveniles sometime in August would, indeed, be the best time for juveniles to grow, if utilizing the zooplankton mortality. Even though other possibilities for *Onisimus caricus* life cycle may exists, it is most probable that the life history traits of the species is semelparous (one brood during life time) univoltine (one brood a year) and perennial (life span more than two years) with a possibility of iteroparism (two broods during life time). Large egg size, long life span, relatively slow growth and potential semelparity refer clearly to a K, or rather, A-selected life history pattern, which is common among the Arctic gammaridean amphipods (Sainte-Marie 1991, Węsławski & Legeżyńska 2002), but less common in the species completing their life cycle in the temperate oceans (Sainte-Marie 1991).

4.6. Growth modeling

The growth of *O. caricus* was estimated from the differences in the mean lengths between cohorts, based on the suggested life cycle. The mean lengths were obtained by Mix-analysis. The lengths were plotted against estimated age of the cohort and a simple polynomial growth curve was modeled (Figure 16). To show the fit of the models, the mean lengths of observations from oostegite development groups were plotted with the mean lengths obtained by Mix-analysis. Parameters and R^2 values for functions are listed in Table 5.

In polynomial functions t is time from first June of the life of an animal in months divided by 12. Gompertz growth function fitted for *O. caricus* and mentioned in the table,

overlapped with polynomial growth functions. Estimated growth curves for *Onisimus nanseni* and *O. glacialis* were obtained from Arndt and Beuchel (2005) and fitted with the models for *O. caricus* (Figure 17).

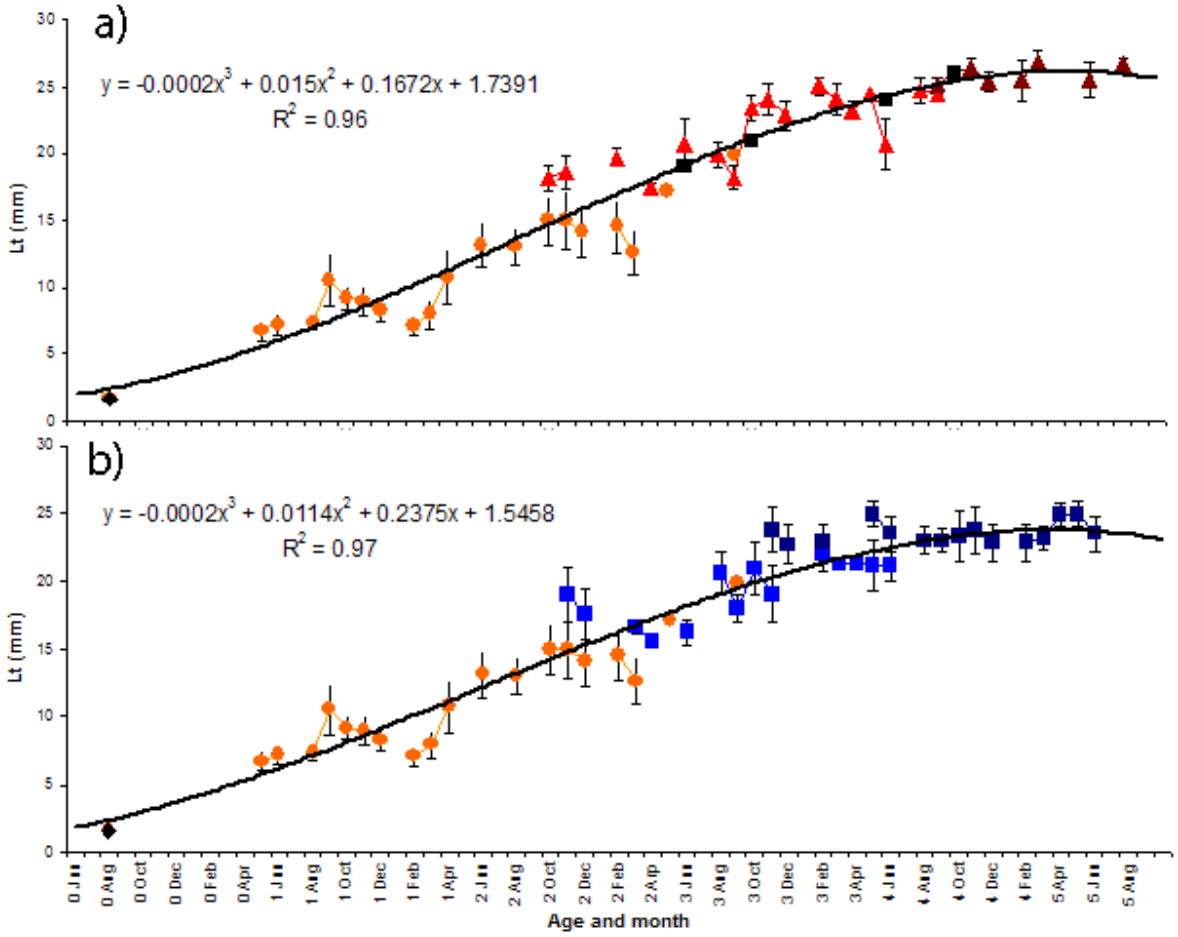

Figure 16. a) the growth of *O. caricus* females. Orange dots represent mean lengths of juveniles, bright red triangles mean lengths of immature females and dark red ones mean lengths of mature females. Black squares shows observed mean lengths of the oostegite development groups. b) the growth of *O .caricus* males. Light blue squares represent mean values of immature males and dark blue ones mean lengths of mature males. A black square with a small value is the mean diameter of eggs. Black lines in both graphs represent the polynomial growth model fitted for a particular gender.

The growth of amphipods is connected to molts, which determines the length increase of the exoskeleton (Hammersmith & Coyle 1991). Furthermore, Hammersmith and Coyle (1991) suggested that sexual maturity is a function of certain number of molts experienced rather than body size. They continued by hypothesizing that the onset of maturity would occur after fixed number of molts. Moreover they found that Sexton (1924) and Shih (1969) approved the hypothesis, because the amphipods they studied had an unchanging number of molts or stages in their life histories.

This hypothesis could explain the high variation in size of maturity observed in this study. Different conditions and success in finding food during the life of females would cause a different growth rate, but molting rate would stay similar regardless of the size. This would

lead to a population with adult females highly varying in size rather than in age. This, in turn, would suggest semelparity (one brood per life time). Further, the size of an adult female is reported to affect amount of eggs produced and, in turn, to reproductive success (Bregazzi 1972). This would lead to a population where reproductive success of females would be determined by success in growth. Perhaps due to low number of egg-bearing females in this study, a relationship between number of eggs and female size could not been found.

Table 5. Growth model parameters for different amphipod species.

Species and gender	Function	L_{slim}	L_{tlim}	k	t_0	R2	Reference
O.caricus F	$y = -0.0002t^2 + 0.0151t^2 + 0.1672t + 1.7391$					0.96	This study
O.caricus M	$y = -0.0002t^2 + 0.0114t^2 + 0.2375t + 1.5458$					0.97	This study
O.caricus	Gompertz	1.71	29.00	0.60	1.60		This study
O.nanseni	Gompertz	1.42		0.92	0.55	0.98	Arndt & Beuchel 2005
O.glacialis F	Gompertz	0.61		1.06	0.72	0.98	Arndt & Beuchel 2005
G.wilkitskii F	Gompertz	2.28	45.30	0.47		1.00	Beuchel & Lønne 2001

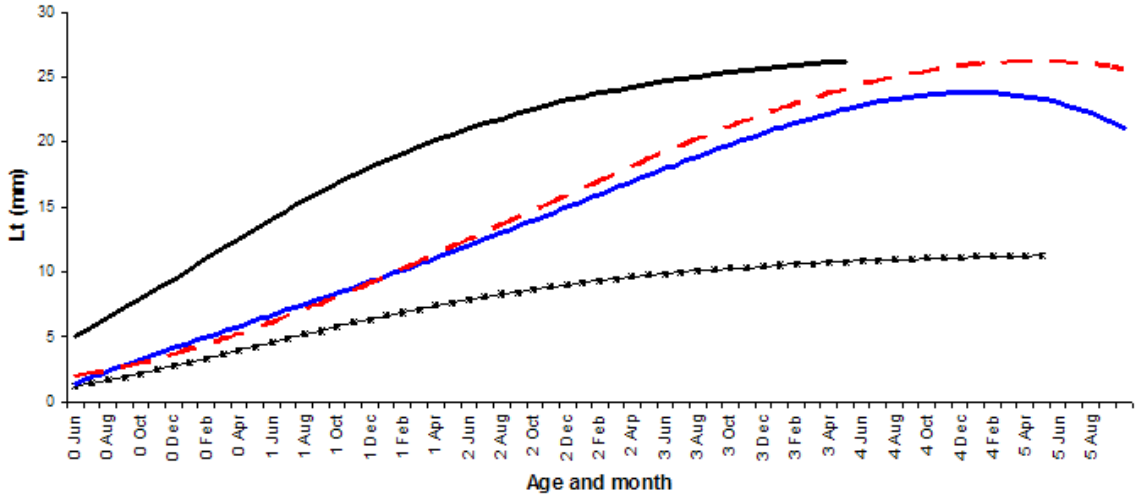

Figure 17. Growth models for different *Onisimus* species. Red dashed and blue solid line represents the polynomial functions for *O .caricus* fitted for females and males respectively. Black line is Gompertz growth model for *O. nanseni* (Arndt & Beuchel 2005) and black line with dots Gompertz growth model for *O. glacialis* (Arndt & Beuchel 2005).

The growth model of *O. caricus* shows an asymptotic growth, which is a common pattern to most vertebrates and some invertebrates (Figure 17) (Hammersmith & Coyle 1991). The growth rate seems to be between *O. nanseni* and *O. glacialis*, when compared to the growth models made by Arndt & Beuchel 2005. Slower rate is due to the longer life span estimated. When one year shorter life span was assumed for *O. caricus* the curve overlapped with *O. nanseni*. This indicates similar growth pattern between these two species, which is not surprising, since both species are opportunistic scavengers from the same genus (Zajączkowski & Legeżyńska 2001, Arndt et al. 2005).

5. CONCLUSIONS

Knowledge of life history characteristics of single species is important for understanding both the population biology of the species and the ecology of communities. Furthermore, life history features, which are affected by environmental conditions, may result in very different life cycles, size and age class structures and secondary productivity between populations of the same or related species over their distributional ranges. When enough research has been conducted on the ecology of communities, the knowledge can be used to deduce interactions between communities in the ecosystem. Such knowledge can lead to a better understanding of the diverse life in the oceans. Understanding this diversity could potentially lead to an increased human awareness towards life in the oceans, which in turn could raise awareness of the importance of the conserving the unique ocean ecosystems world wide.

Highly motile hyper-benthic animals are difficult to sample quantitatively. This study concentrated on the life history of *Onisimus caricus*, introducing a new method of sampling hyper-benthic crustaceans to life history studies. The catch of baited traps used in this study is not quantitative and is influences by the behaviour of scavenging amphipods. Many factors might affect this behaviour, including reproduction, food availability and avoidance of predation. Temporal changes in the behaviour must be considered, but it is assumed that the traps catch all parts of the population to some extent. Baited traps can be used to estimate the life cycle, reproduction and growth of local amphipod populations, because the breeding of benthic lysianassid amphipods in the polar regions is strongly seasonally timed and synchronized.

It was found that the mating of *O. caricus* happens during the mid-winter, probably sometime between December and February. The eggs are carried by females until hatching, which occurs sometime from late June to mid-August. The polar crustaceans have been found to release their brood during the most productive time of the year. However, the timing of the hatching of *O. caricus* juveniles did not follow the algal bloom. Instead the hatch coincided with a potential peak in zooplankton mortality, caused by a brackish water layer during the melting season.

A surprisingly long life span of five years was estimated for *O. caricus*. Newly hatched juveniles are observed in the trap samples almost one year after hatching. Following hatching, juveniles grow for two years before they start to achieve sexual characteristics. Both sexes reach their sexual characteristics slowly during their third year. During the fourth year the growth rate slackens and maturity is reached during the summer and autumn of fifth year. Mating occurs in the mid-winter of the fifth year. Males disappear from the population relatively soon after the mating, but females carry the clutch and die probably during the sixth autumn of their life. There is the potential for breeding during the fourth winter, but this is higher for males than for females.

The high variation in the size of egg-bearing females can be explained by a hypothesis that sexual maturity is a function of certain number of molts experienced rather than body size. This would indicate a semelparine *O. caricus* population where the reproductive success of females would be determined by the success in the growth. The growth pattern of *O. caricus* shows an asymptotic growth. The largest specimen found during the study had a total length close to 30 mm. The growth rate of the species is intermediate between *O. nanseni* and *O. glacialis*, but this is dependent on the length of the proposed life cycle.

The earlier life span estimate for *O. caricus* was three years. The difference between the earlier estimate and the estimate suggested in this study may arise from the small sample size in the earlier study. Even though the life cycle estimate in this study is based on strong evidence and on a large sample (6832 specimens from 10 months throughout a year), it can be criticized. Although other possibilities for *Onisimus caricus* life cycle may exist, it is most probable that the life history of the species is semelparous (one brood during life time), univoltine (one brood a year) and perennial (life span more than two years), with a possibility of iteroparism (two broods during life time). Large egg size, long life span, slow growth and potential semelparity clearly indicates A-selection, which is common among the Arctic gammaridean amphipods in occupying predictably unfavorable habitats, but less common in the species which complete their life cycles in the temperate oceans.

Despite some biases, baited traps seem to be a feasible method to study the life histories of scavenging amphipods if the sample size is high enough and the sampling is done during the most important times of year, including the mating period, the hatching period, the period of accelerated growth and potentially the period when newly hatched juveniles appear in the samples. However, if similar studies of scavenging fauna are continued, additional methods should be introduced. A species-specific correction factor for the trap catch, obtained by methods involving SCUBA diving, would be the next step in such a study. A study concentrating on the biases involved in baited trap sampling is necessary before baited traps can be used to estimate abundances and population dynamics of the scavenging fauna. The life span estimate of this study must be confirmed with additional samples from the sampling locality obtained by SCUBA diving before the results of this study can be published in a scientific journal.

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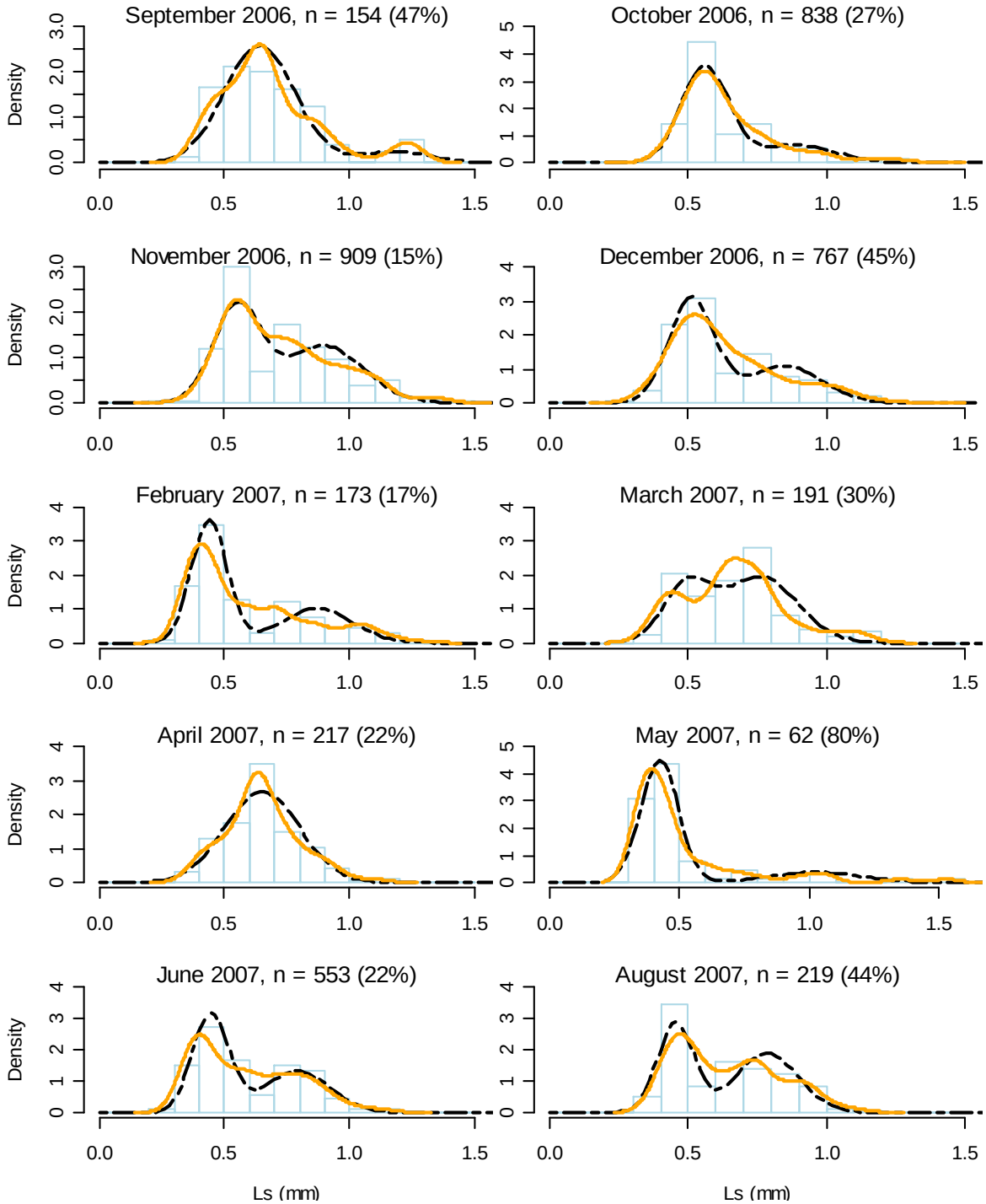
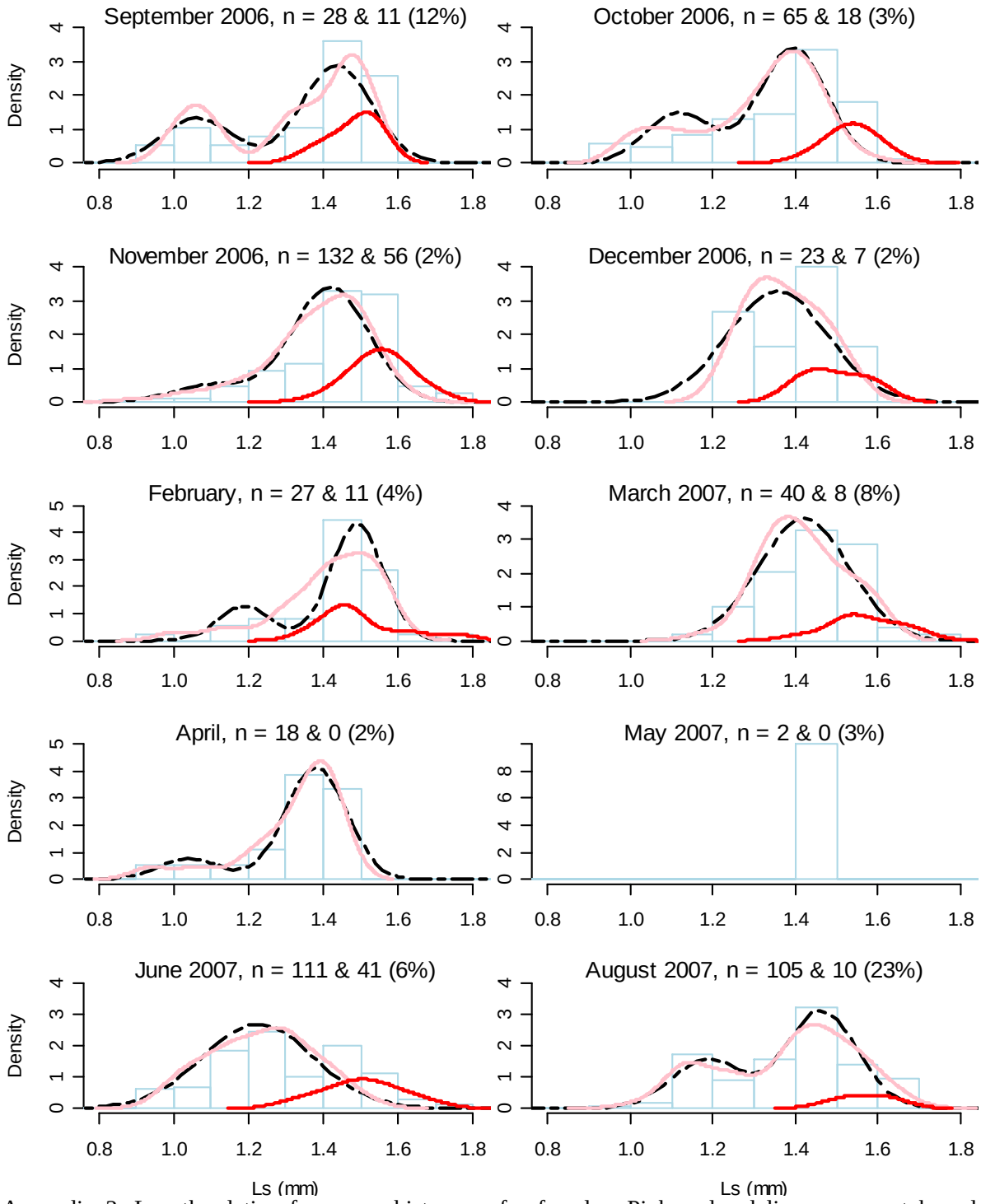
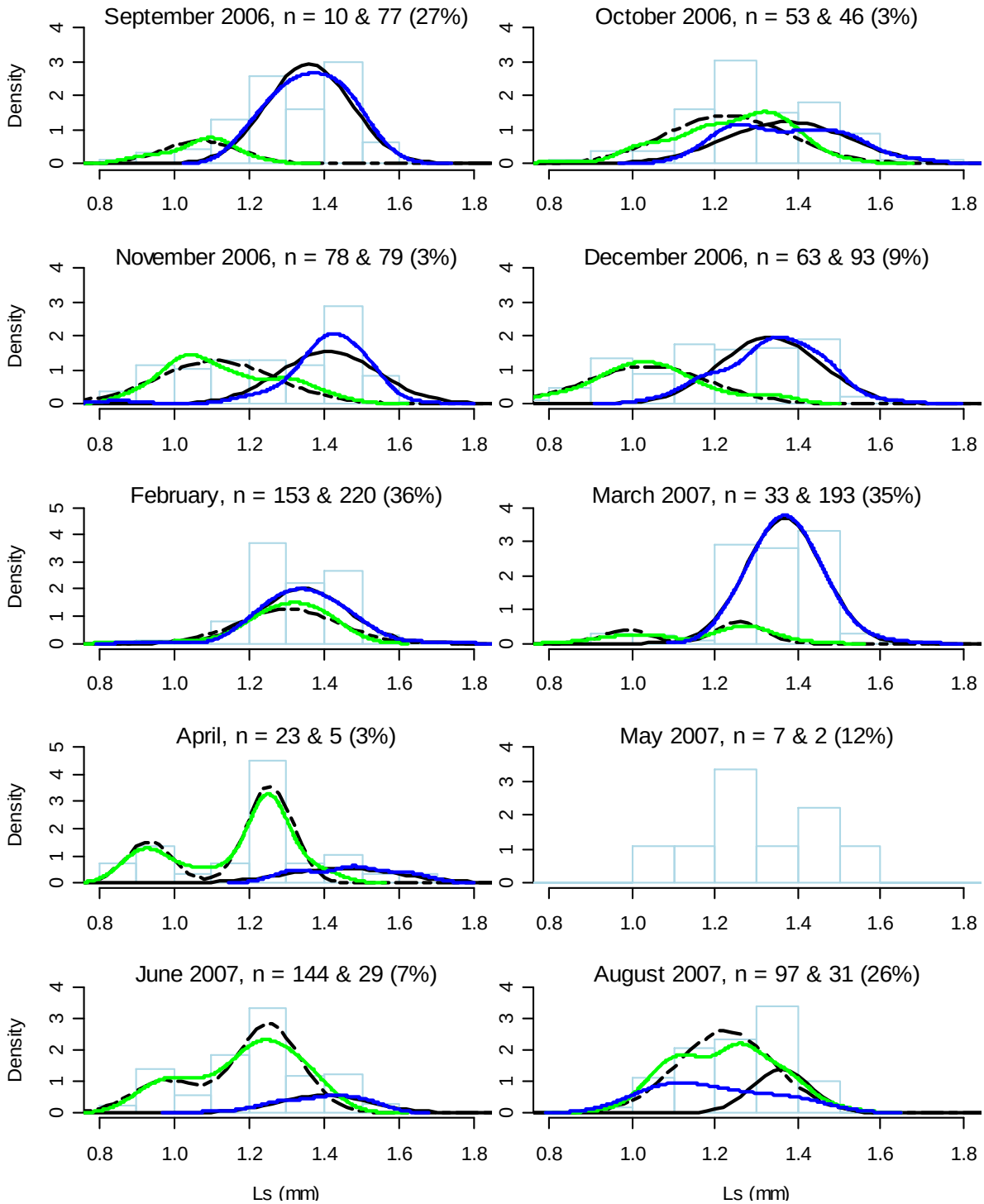
APPENDIXES



Appendix 1. Length-relative frequency histogram for juveniles. Orange line represents kernel density estimate and dashed black line represents the mixture distribution model. Lengths of the first pereonal segment (mm) are on the x-axis with an interval of 0.1 mm (in histogram). Relative frequency is on the y-axis. Randomised subsample size for each month is shown in the title. Value in brackets tells the contribution of the subsample from the total catch.



Appendix 2. Length-relative frequency histogram for females. Pink and red lines represent kernel density estimate for immature and mature females, respectively. Dashed black line represents the mixture distribution model for immature females. Lengths of the first pereonal segment (mm) are on the x-axis with an interval of 0.1 mm (in histogram). Relative frequency is on the y-axis. Randomised subsample size for immature and mature females, respectively, is shown in the title. Value in brackets tells the contribution of the both subsamples combined from the total catch.



Appendix 3. Length-relative frequency histogram for males. Green and blue lines represent kernel density estimate for immature and mature males, respectively. Dashed and solid black lines are the mixture distribution models for immature and mature males. Lengths of the first pereonal segment (mm) are on the x-axis with an interval of 0.1 mm (in histogram). Relative frequency is on the y-axis. Randomised subsample size for immature and mature males, respectively, is shown in the title. Value in brackets tells the contribution of the both subsamples combined from the total catch.