The ecology of a freshwater crustacean: Lepidurus arcticus (Brachiopoda; Notostraca) in a High Arctic region

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THE ECOLOGY OF A FRESHWATER CRUSTACEAN: *LEPIDURUS ARCTICUS* (BRANCHIOPODA; NOTOSTRACA) IN A HIGH ARCTIC REGION

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Tiivistelmä – Referat – Abstract

Lepidurus arcticus (Pallas, 1793) is a keystone species in High Arctic ponds, which are exposed to a wide range of environmental stressors. This thesis provides information on the ecology of this little studied species by paying particular focus on the sensitivity of *L. arcticus* to acidification and climate change. Respiration, reproduction, olfaction, morphology, salinity and pH tolerance of the species were studied in the laboratory and several environmental parameters were measured in its natural habitats in Arctic ponds.

Current global circulation models predict 2–2.4 °C increase in summer temperatures on Spitsbergen, Svalbard, Norway. The *L. arcticus* respiration activity was tested at different temperatures (3.5, 10, 16.5, 20, 25 and 30 °C). The results show that *L. arcticus* is clearly adapted to live in cold water and have a temperature optimum at +10 °C. This species should be considered as stenothermal, because it seems to be able to live only within a narrow temperature range.

L. arcticus populations seem to have the capacity to respond to the ongoing climate change on Spitsbergen. Changes can be seen in the species' reproductive capacity and in the individuals' body size when comparing results with previous studies on Spitsbergen and in other Arctic areas. Effective reproduction capacity was a unique feature of the *L. arcticus* populations on Spitsbergen. *L. arcticus* females reached sexual maturity at a smaller body size and sexual dimorphism appeared in smaller animals on Spitsbergen than anywhere else in the subarctic or Arctic regions. *L. arcticus* females were able to carry more eggs (up to 12 eggs per female) than has been observed in previous studies. Another interesting feature of *L. arcticus* on Spitsbergen was their potential to grow large, up to 39.4 mm in total length. Also cannibalistic behaviour seemed to be common on Spitsbergen *L. arcticus* populations. The existence of different colour morphs and the population-level differences in morphology of *L. arcticus* were unknown, but fascinating characteristic of this species. Spitsbergen populations consisted of two major (i.e. monochrome and marbled) and several combined colour morphs. Third interesting finding was a new disease for science which activated when the water temperature rose. I named this disease to Red Carapace Disease (RCD).

This High Arctic crustacean lives in ponds between the Arctic Ocean and glaciers, where the marine environment has a strong impact on the terrestrial and freshwater ecosystems. The tolerance of *L. arcticius* to increased water salinity was determined by a LC_{50} -test. No mortality occurred during the 23 day exposure at low 1–2 ‰ water salinity. A slight increase in water salinity (to 1 ‰) speeded up the *L. arcticus* shell replacement. The observations from natural populations supported the hypothesis that the size of the animals increases considerably in low 1.5 ‰ salt concentrations. Thus, a small increase in water salinity seems to have a positive impact on the growth of this short-lived species.

Acidification has been a big problem for many crustaceans, invertebrates and fishes for several decades. *L. arcrcius* does not make an exception. Strong acid stress in pH 4 caused a high mortality of mature *L. arcticus* females. The critical lower limit of pH was 6.1 for the survival of this acid sensitive species. Thus, *L. arcticus* populations are probably in danger of extinction due to acidification of three ponds on Spitsbergen. A slight drop (0.1–1.0) in pH values can wipe out these *L. arcticus* populations. The survival of *L. arcticus* was strongly related to: (1) the water pH, (2) total organic carbon (TOC) and pH interaction, (3) the water temperature and (4) the water salinity. Water pH and TOC values should be monitored in these ponds and the input of acidifying substances in ponds should be prevented.

Avainsanat – Nyckelord – Keywords Acidification, bird predation, cannibalism, climate change, colouring, conservation, *Daphnia pulex*, dispersal, , High Arctic ponds, LC_{50}, living fossil, morphology, moult, parasite, olfaction, pH, Q_{10}, Red Carapace Disease, reproduction, respiration, salinity, sensitivity to environmental stressors, Svalbard, temperature, temporary ponds, water chemistry.

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Tiivistelmä – Referat – Abstract

Lepidurus arcticus (Pallas, 1793) on avainlaji arktisissa lammissa, joissa se on altistunut useille ympäristön stressitekijöille. Tutkielmassa selvitetään tämän vähän tutkitun lajin ekologiaa keskittyen lajin herkkyyteen happamoitumiselle ja ilmastonmuutokselle. Lajin hengitysaktiivisuutta, lisääntymistä, hajuaistia, morfologiaa sekä suolan ja pH:n sietoa tutkitiin laboratoriossa ja useita ympäristömuuttujia mitattiin arktisista lammista.

Maailmanlaajuinen ilmastomalli ennustaa 2–2,4 °C nousua kesälämpötiloihin Huippuvuorilla Norjassa. *L. arcticus* lajin hengitysaktiivisuutta mitattiin eri lämpötiloissa (3,5; 10; 16,5; 20; 25 ja 30 °C). Tulokset osoittivat, että *L. arcticus* on selvästi sopeutunut elämään kylmissä vesissä ja sen lämpötila optimi on 10 °C. *L. arcticus* lajia tulisi pitää stenotermisenä lajina, koska se näyttää sietävän vain vähäistä lämpötilan vaihtelua.

L. arcticus populaatioilla vaikutti olevan kyky reagoida meneillään olevaan ilmastonmuutokseen Huippuvuorilla. Ilmastonmuutoksen aiheuttamia muutoksia voidaan nähdä lajin lisääntymistehokkuudessa ja yksilöiden koossa, kun tuloksia on vertailtu aikaisemmin Huippuvuorilla ja muilla arktisilla ja subarktisilla alueilla tehtyihin tutkimuksiin. Tehokas lisääntyminen oli ainutlaatuinen piirre Huippuvuorten *L. arcticus* populaatioissa. Naaraat saavuttivat sukukypsyyden pienemmässä koossa ja pystyivät kantamaan enemmän munia (jopa 12 kappaletta) Huippuvuorilla kuin mitä on havaittu minkään muun alueen *L. arcticus* populaatioissa. Toinen mielenkiintoinen piirre Huippuvuorten *L. arcticus* yksilöissä oli niiden kyky kasvaa kookkaaksi (jopa 39,4 mm) ja kolmanneksi populaatioissa esiintynyt kannibalismi. Eri värimuotojen olemassaolosta tai populaatioiden välisistä morfologisista eroista ei tiedetty aikaisemmin mitään. Huippuvuorten populaatioista löytyi kaksi päävärityyppiä (yksivärinen ja marmorikuvioinen) sekä useita värityyppien yhdistelmiä. Kolmas mielenkiintoinen löytö oli tieteelle uusi sairaus, joka aktivoitui lämpötilan noustessa. Nimesin sairauden punaisen selkäkilven sairaudeksi (Red Carapace Disease, RCD).

Tämä arktisten alueiden äyriäinen elää lammissa Jäämeren ja jäätiköiden välissä, missä merellisellä ympäristöllä on voimakas vaikutus maa- ja vesiekosysteemeihin. *L. arcticus* lajin suolaisuudensietoa määritettiin LC_{50} -kokeella. Kuolleisuutta ei havaittu matalissa 1–2 ‰ suolapitoisuuksissa 23 päivän kokeessa. Pieni nousu veden suolapitoisuudessa (1 ‰) nopeutti *L. arcticus* yksilöiden kuorenvaihtoa. Havainnot luonnon populaatioista tukivat hypoteesia, että eläinten koko kasvaa huomattavasti matalassa 1,5 ‰:n suolapitoisuudessa. Näin ollen vähäisellä veden suolapitoisuudella näyttäisi olevan positiivinen vaikutus tämän lyhytikäisen lajin kasvuun.

Happamoitumien on ollut suuri ongelma monille äyriäisille, hyönteisille sekä kaloille jo useita vuosikymmeniä. Voimakas happamoitumisen aiheuttama stressi (pH 4) aiheutti korkeaa kuolleisuutta sukukypsissä *L. arcticus* naaraissa. Tämän happamoitumiselle herkän lajin kriittinen pH:n raja arvo oli 6,1. Tästä syystä *L. arcticus* populaatiot ovat vaarassa tuhoutua kolmesta tutkimuslammesta happamoitumisen vuoksi. Pieni lasku (0,1–1,0) pH:ssa voi hävittää nämä *L. arcticus* populaatiot. *L. arcticus* lajin selviytyminen oli voimakkaasti yhteydessä: (1) veden pH-arvoon, (2) orgaanisen hiilen kokonaismäärän (TOC) ja pH:n yhteisvaikutukseen, (3) veden lämpötilaan sekä (4) veden suolapitoisuuteen. Veden pH ja TOC arvoja tulisi tarkkailla näissä lammissa ja happamoittavien aineiden pääsy lampiin tulisi estää.

Avainsanat – Nyckelord – Keywords Arktiset lammet, *Daphnia pulex*, elävä fossiili, hajuaisti, happamoituminen, hengitys, herkkyys ympäristön stressitekijöille, Huippuvuoret, ilmaston muutos, kannibalismi, kuorenvaihto, LC_{50}, leviäminen, lintusaalistus, lisääntyminen, loinen, lämpötila, morfologia, pH, punaisen selkäkilven sairaus, Q_{10}, suolaisuus, tilapäiset lammet, vesikemia, ympäristönsuojelu, väri.

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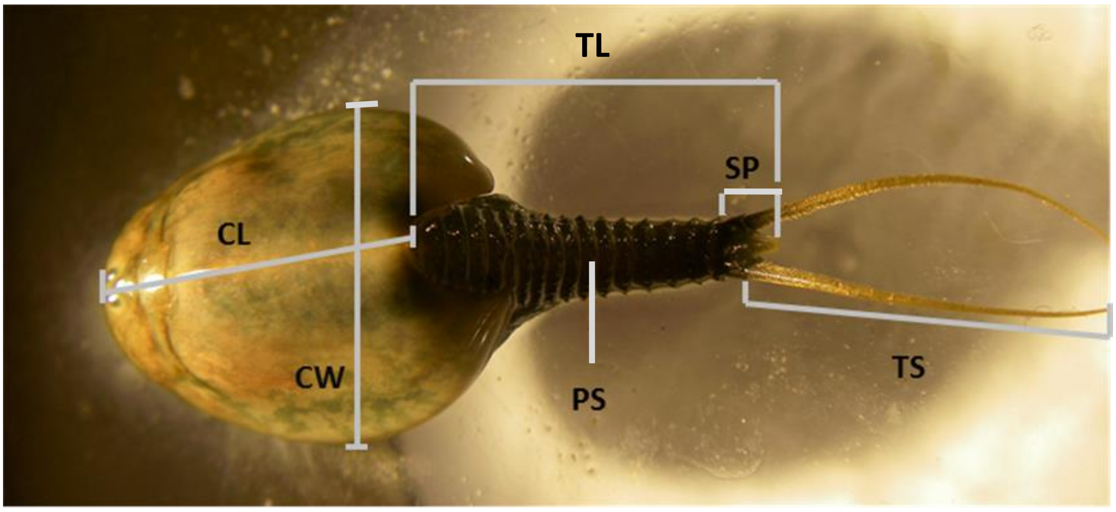
Abbreviations

UNIS	The University Centre in Svalbard
IPCC	Intergovernmental Panel on Climate Change
ACIA	Arctic Climate Impact Assessment
CDOM	Coloured dissolved organic matter
DOC	Dissolved organic carbon
TOC	Total organic carbon
${}^{tot}N$	Total nitrogen
${}^{tot}P$	Total phosphorus
TN:TP	Total nitrogen/phosphorus ratio
OM	Sediment organic matter
Chl-a	Chlorophyll-a
UV	Ultraviolet radiation
UVB	Ultraviolet B, 315–280 nm
pH	Measure of acidity
O_2	Oxygen
CO_2	Carbon dioxide
HCL	Hydrochloric acid
NaOH	Sodium hydroxide
LC_{50}	Median lethal dose
MetNet	Net which protects *L. arcticus* from mixer
RCD	Red carapace disease

L. arcticus morphological parameters

CL	Length of carapace
CW	Width of carapace
TL	Length of telson
TS	Length of telson setae
SP	Length of supra anal plate
PS	Number of posterior segments not covered by the carapace



CONTENTS

1. Introduction

The tadpole shrimp *Lepidurus arcticus* (Branchiopoda, Nostostraca) lives in freshwater lakes and temporary ponds in the Arctic region, where it has a circumpolar distribution (Arnold 1966). *L. arcticus* has been found all over the Arctic region including northern Norway, Finland, Iceland, Greenland, Russia and Canada (Fox 1949, Koli 1955, Arnold 1966, Bushnell & Byron 1979, Einarsson 1979, Vekhoff 1997, Bennike & Hedenäs 1995, Jeppesen et al. 2001, Hessen et al. 2004, Mantovani et al. 2004, Rautio et al. 2009 and Wojtasik & Brylka-Wolk 2010). It has also been observed outside the Arctic region in the South Norwegian Mountains (Fjellheim et al. 2001, Sars 1896) and Kuril Islands in the North Asia (Sayenko & Minakawa 1999). *L. arcticus* is the only notostracan species found in permanent and temporary ponds in Svalbard. The lack of morphological changes since the past 250 million years has lead to the description of Notostraca species as living fossils (Korhola & Rautio 2001). *L. arcticus* can be considered as a relict species over its southern range of distribution, where it is commonly threatened due to extensive stocking and immigration of fish, acidification and global warming (Hessen et al. 2004). *L. arcticus* is also an important food item for birds such as arctic terns (*Sterna paradisaea*) and purple sandpiper (*Calidris maritime*) (Summerhayes & Elton 1923, Montague 1925), and also for fish such as brown trout (*Salmo trutta*) (Sømme 1934, Borgstrøm et al. 1985), Arctic charr (*Salvelinus alpinus*) (Jeppesen et al. 2001) and minnow (*Phoxinus phoxinus*) (Borgstrøm et al. 1985).

Information on the biology of *Lepidurus* sp. is in general limited and incomplete. In particular little is known about the *L. arcticus* populations on Spitsbergen, Svalbard in the European High Arctic. Only a few studies of seasonal occurrence of *L. arcticus* have been conducted in lakes and ponds in Greenland (Poulsen 1940a, b, Arnold 1966), in Norway (Sømme 1934), *Lepidurus lemmoni* in a large alkali lake in California (Lynch 1966) and *Lepidurus packardi* in temporary ponds in northern California, U.S.A (Ahl 1991).

The polar region is a unique environment characterized by an annual freeze- thaw cycle coinciding with a cycle of constant winter darkness and summer daylight. High-latitude biota and environments have been considered relatively stable compared with those of more temperate regions, where human civilization has a greater impact. However, Arctic regions have been warming since the mid-1800s (Overpeck et al. 1997) and the warming has significantly accelerated during the recent decades (Overpeck et al. 1997, Serreze et al. 2000, ACIA 2004) and is expected to continue throughout this century (Overpeck et al. 1997, IPCC 2001). Although the Arctic is one of the least disturbed regions on Earth, it may also be one of the most susceptible to both natural and human-induced climate change. Overpeck et al. (1997) conclude that Arctic temperatures are in the 20th century the highest in the past 400 years. The mean air temperature on Spitsbergen during the summer months (June–August) was 1.4–6.5 °C between 1961–1990 (Norwegian Meteorological Institute 2011). The summer temperature of surface waters and air has increased by approximately 2 °C since 1962 in the High Arctic Lake Kongressvatn on Spitsbergen (Holm et al. 2011). Current global circulation models predict 2–2.4 ºC increase in summer temperatures on Spitsbergen (IPCC 2007). Water temperature may rise above 19 °C in some shallow ponds. This will create a great danger for *L. arcticus,* because it requires cold 3–19 °C (Arnold 1966) and clean water (Fjellheim et al. 2001). Hence, *L. arcticus* may potentially act as an indicator species to environmental change in the Arctic freshwaters.

L. arcticus has a pelagic life style until it reaches the 5th instar when it becomes benthic and starts preying primarily on other invertebrates (Arnold 1966, Miller 1980). Stomach content analyses suggest that *L. arcticus* can also feed on detritus, bacteria and different kinds of plants and algae including moss leaves, lichens, diatoms, green algae and other larger algae (Sømme 1934, Einarsson 1979). *L. arcticus* can feed effectively on zooplankton including both cladoceran (e.g. *Alona rectangulata*, *Acroperus harpae* and *Daphnia pulex*; Einarsson 1979, Christoffersen 2001) and copepod species (e.g. *Cyclops* and *Heterocope*; Sars 1896). The large (>12.5 mm) *L. arcticus* can consume even up to 18 *Daphnia* individuals per hour (Christoffersen 2001). A close relative species of *L. arcticus*, *Triops longicaudataus* (Notostraca), has even been proposed as a biological control agent of mosquitoes (Tietze & Mulla 1991). *L. arcticus* has also been observed to feed on mosquitoes (Johansen 1922, Einarsson 1979) and carcases of other *L. arcticus* in laboratory experiments (Johansen 1911, Arnold 1966). *L. arcticus* can also consume fish eggs (Sars 1896) demonstrating an interesting predator–prey relationship between this crustacean and various northern fish species. Various, but limited, food resources are available for *L. arcticus* at different times of open-water period in the severe High Arctic conditions. Food intake studies indicate that the *L. arcticus* should non-selectively feed as various food items as possible (Sømme 1934, Einarsson 1979).

Animals have receptors to sense the world around them. In some crustaceans, olfaction senses may be more important in terms of survival. Invertebrates have a good sense of smell (Nuorteva 1963) and this sense helps many species to find their food or mating partner. It has been known for a long time that invertebrates have a sense of smell, but due to experimental difficulties, this sense has been poorly studied. However, olfaction abilities of Colorado beetle (*Leptinotarsa decemlineata*) have been studied extensively. De Wilde et al. (1969) and Visser & Nielsen (1977) reported attraction of Colorado beetles by volatiles of potato plant *(Solanum tuberosum).* Only a few studies have investigated the olfactory ability of crustacean species. It is known that olfaction is located in specialized sensory cells, for example in the antennae of invertebrates. *L. arcticus* does not make an exception to this. The end of first pair of antennae has numerous small olfactory papillae (Sars 1896). For aquatic organisms (e.g. crustaceans and fish) the water-soluble chemicals are present in the surrounding water. Because smell is evidently an important sense for various aquatic organisms (Dittman & Quinn 1996, Barbin 1998, Raethke et al. 2004), *L. arcticus* may also use it to locate food as well as predators and mating partners in the relatively unproductive Arctic ponds.

Bait traps attract predatory aquatic insects such as larval and adult stages of water beetles (e.g. *Dytiscus marginalis*) and adult water scorpions (e.g. *Nepa cinerea*). *L. arcticus* can also be captured using traps with dead fly as bait (Olga Makarova personal communication 2011). Thus, olfaction may also be a critical factor for the *L. arcticus* survival and reproduction success of *L. arcticus* in the oligotrophic High Arctic ponds. Therefore, it is important to study whether *L. arcticus* can use olfaction. The olfaction can play an important ecological role in the *L. arcticus* population dynamics, if this sense helps the animal to find food such as injured conspecifics.

L. arcticus lives in ponds and lakes located close to the sea on Spitsbergen. As a consequence, some lakes and ponds are slightly saline, especially when they are located near the sea level and have a connection to the sea like in lake Kongressvatn located southeast of Kapp Linné (Holm et al. 2011). On Spitsbergen many lakes and ponds inhabited by *L. arcticus* are located near (50–4200 m) to the Arctic Ocean. Hence, it is possible that the salt concentration in these ponds can be altered due to sea spray. Paleolimnological studies have shown that *L. arcticus* have occurred in ponds located on former sea beds (Bennike & Hedenäs 1995). The sediment in former sea beds may contain salt and thus make the water saline. In such habitats *L. arcticus* have probably had to adapt to increased water salinity. Lakes and ponds in the Arctic regions also experience considerable evaporative water loss, sometimes resulting in the formation of athalassic (i.e. not of marine origin) saline systems (Prowse et al. 2006). Paleolimnological data indicates increased water salinity due to a recent shift to drier conditions or increased evaporation in a small athalassic lake located in the subarctic Yukon Territory, Canada (Pienitz et al. 1992). Like in other Arctic areas, precipitation on Spitsbergen is low (often less than 350 mm annually) and the permafrost seals the subsoil. The snow- and ice-melt provide a flush of water and nutrients to rivers from late June to early August, whereas melting of glaciers accounts for most of the water run-off in August and September (Svenning & Gullestad 2002). However, some ponds can dry out during the short Arctic summer and before the ponds dry completely the salinity concentration can rise remarkably. Therefore, it is important to study the tolerance of *L. arcticus* to potential changes in water salinity induced by global warming.

A characteristic of oligotrophic lakes on Spitsbergen is their high transparency (Hessen 1996). The colouration of aquatic animals may have major biological relevance in these transparent waters, because these animals are clearly visible to their aquatic and terrestrial predators. Cryptic colouration or camouflage is an adaptation that decreases the predation risk of an animal (Edmunds 1974, Merilaita 2003). Colour can also protect the animal against UV radiation, heat and cold. Camouflage can also be important for predators because the predator can hide both their own predators and preys. For example, the females of crab-spider (*Thomisidae*) can change their body colour to match with the flowers they sit on while hunting (Oxford and Gillespie 1998). Crustaceans have also been shown to be able to form different, seasonally-varying colour morphs (Bishop 1969, Heath 1974). Some colour morphs imitate natural microhabitat mosaic more than the others (Salemaa 1978). An interesting example of crustaceans' capability to camouflage is the numerous colour morphs of a marine isopod (*Idotea baltica*) in the highly varying microhabitats of Baltic Sea (Salemaa 1978). Unlike morphological variables such as carapace length or width, colour is not an inherent property of the object, but in contrast a product of the brain of the animal perceiving the object (Thompson et al. 1992). For example, birds and fish (Jacobs 1992) and even some crustaceans (Cronin and Marshall 1989) can see ultraviolet wavelengths of light. In the constant daylight of the Arctic summer, both cryptic coloration and camouflage and even mimesis might be functionally important features for crustaceans. However, little is known about the cryptic colouration of *L. arcticus* in the Arctic areas.

Living Notostraca are often brightly coloured due to two main pigments in the body and the brown colour of the exoskeleton (Longhurst 1955). The internal pigments are haemoglobin (Régnard and Blanchard 1883) and a dark blue-green pigment which occur in many parts of the body (Longhurst 1955). The blood of crustacean species contains low amount of viscous, copper-based respiratory pigment called hemocyanin, which is dissolved in the haemolymph (Thorp & Covich 2001). More recently Rautio et al. (2009) showed that *L. arcticus* usually have five major carotenoid pigments: fucoxanthin, zeaxanthin, canthaxanthin, astaxanthin and cyanobacterial pigment echinenone, which was the primary *L. arcticus* carotenoid pigment. Differences in colouration are likely to be dependent on variations in the physical environment, *L. arcticus* genotype and the differences in *L. arcticus* diets. Nonetheless, the underlying controls on the colouration, growth rate and size of *L. arcticus* remained unclear.

Little is known about the responses of Notostraca species to the highly fluctuating conditions in Arctic freshwater ecosystems. This study describes the ecology of *L. arcticus* in permanent and temporary ponds on Spitsbergen. The material was collected from 23 ponds all over the Spitsbergen in summer 2010. This study aims to review the existent literature on the ecology of *L. arcticus* and other Notostraca species as well as to collect physical, chemical and biological data from several ponds on Spitsbergen inhabited by *L. arcticus.* The main objective was to provide information on the distribution and ecology of *L. arcticus* in the High Arctic region of Spitsbergen. The second purpose was to study the morphology of *L. arcticus* and to compare the results with previous observations from other Arctic regions. Finally the study focused on four main study hypotheses:

1.) Acidification and increased water salinity and temperature induced by global warming can lead to higher mortality and potential extinction of *L. arcticus* in Arctic ponds.
2.) *L. arcticus* can be used as an indicator species of environmental change in Arctic regions.
3.) *L. arcticus* is cannibal and can use chemical cues to localize injured conspecifics.
4.) Camouflage is an important characteristic for *L. arcticus* and this crustacean´s colouration varies within and between Arctic ponds.

2. Material and methods

2.1. Study area

This study was conducted on the western and northern parts of Spitsbergen, Svalbard, Norway (78°–79° N, 11°–16° W) (Figure 1). Western coast of Spitsbergen is a mountainous area, whereas the other areas are mostly flat plateau land or raised beach. The annual precipitation is very low and mostly accumulates as snow during the winter. The climate of Spitsbergen can be characterized as an "Arctic semi-desert" with short cool summers, long winters and an annual precipitation of only 200–300 mm (Van Geest et al. 2007). Most ponds are situated on lowland areas close to the Arctic Ocean. Spitsbergen is also characterized by extreme seasonal changes in light conditions, varying from the constant daylight in summer to the complete darkness in winter (polar night lasting from 26th October to 15th February). There is no diurnal photoperiod gradient in the lakes during the ice-free season because Spitsbergen is located at such high latitude. The coastal regions of Arctic are often foggy and thus much less favourable areas for plants than the clearer and sunnier interiors of the fjords (Summerhayes & Elton 1923).

The climate on Spitsbergen is relatively mild for a region at such high latitude due to the Gulf Stream drift approaching the west coast. However, the air temperature may be below the freezing point even in summer. The climate in Arctic regions has warmed since the late 1800s and the global warming is likely to continue in the future. On Spitsbergen the mean annual temperature in 1872–1922 was -8.0 °C, while the mean temperature in July was 4.6 °C (Summerhayes & Elton 1923). In 1961–1990 the mean annual temperature on Spitsbergen had risen to -6.1 °C (Norwegian Meteorological Institute 2011) and in 1981–2010 the mean temperature was -4.6 °C (Førland et al. 2011). During the last two decades, the annual temperature has increased by 1.0–1.2 °C per decade and the winter

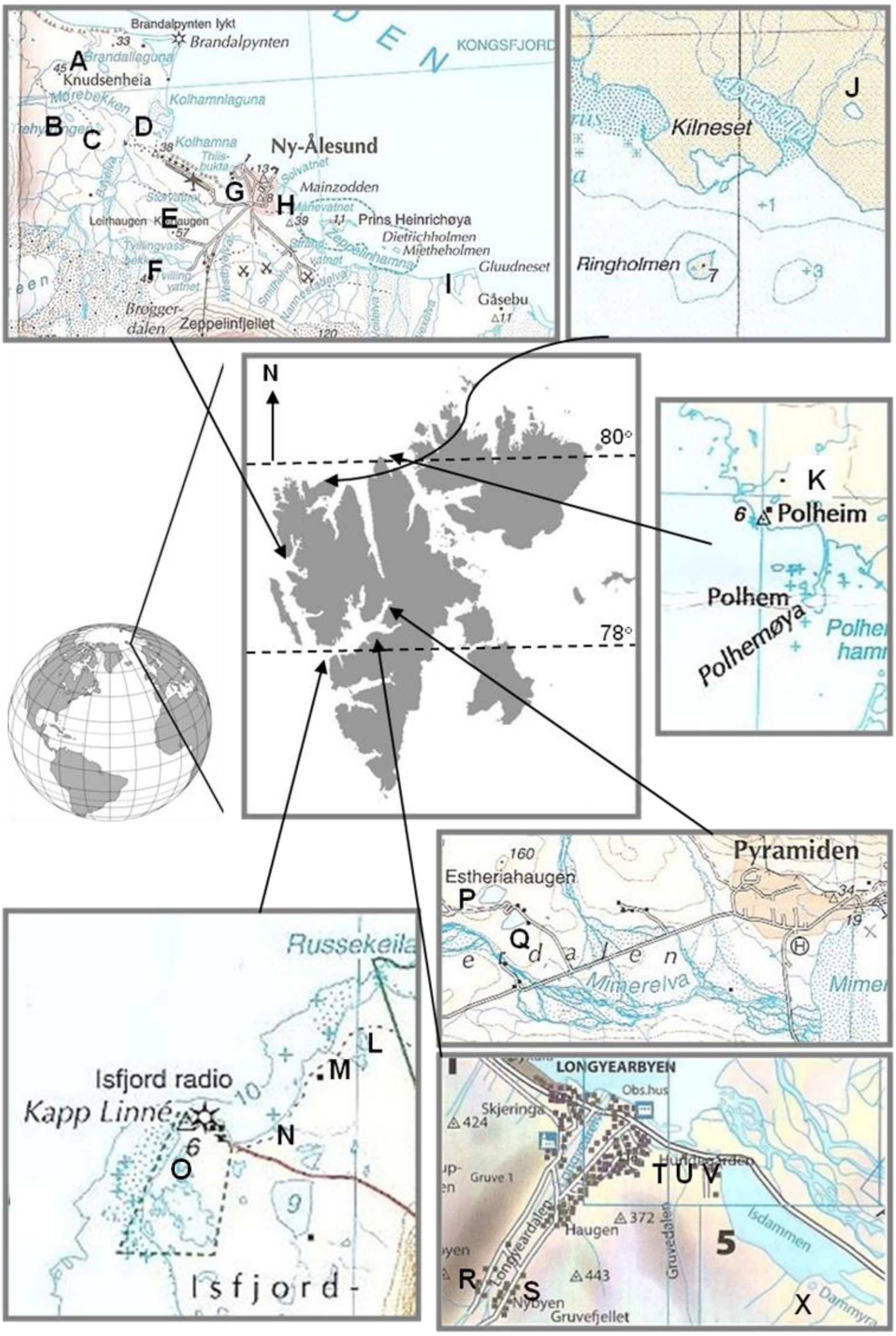


Figure 1. Ponds on the Spitsbergen Arctic Archipelago, Norway. Location map and detail maps of Ny-Ålesund, Reinsdyrflya; Kilneset, Mosselhavøya; Polheim, Kapp Linné, Pyramiden and Longyearbyen areas. The letters on the map represent the locations of ponds. A=Brandallaguna, B=Trehyrdingen 2, C=Trehyrdingen 1, D=Kolhamna, E=Storvatnet, F=Tvillingvatnet, G=Goose pond, H=Solvatnet, I=Gluudneset, J=Kilneset, K=Polheim, L=Pond 2, M=Pond 1, N=Pond 3, O=Pond 4, P=Pond 5, Q=Pond 6, R=Longyearbyen, S=Nybyen, T=Adventdalen first pond, U=Adventdalen second pond, V=Adventdalen third pond and X=Dammyra. Note that the scale differs between the maps.

temperature has increased by 2–3 °C per decade on the Spitsbergen region (Førland et al. 2011).

The mean temperature in July is not the same in all areas on Spitsbergen, being 6.5 °C in Longyearbyen, 4.9 °C in Ny-Ålesund and 4.8 °C in Kapp Linné in 1961–1990 (Norwegian Meteorological Institute 2011). In July 2010 the air temperatures were 0.1–0.9 °C above the mean on Spitsbergen (Table 1). Longyearbyen is situated further up the fjord than Kapp Linné and consequently has a more continental climate. The Kapp Linné region is often foggy, because the coast is exposed to the open ocean without any protection. Also the annual precipitation on Spitsbergen shows remarkable spatial variation and a gradual decrease eastwards towards the interior of the island, being 480 mm in Kapp Linné, 385 mm in Ny-Ålesund and 210 mm in Longyearbyen (Norwegian Meteorological Institute 2011).

Table 1. Mean summer temperature (Temp., °C) and precipitation (Prec., mm) on Spitsbergen in 2010 (Norwegian Meteorological Institute 2011). Precipitation is the sum of the mean precipitation during the summer months (June–August).

Place	Temp., °C in June	Temp., °C in July	Temp., °C in August	Temp., °C in September	Prec., (mm)
Svalbard Airport, Longyearbyen	3.5	6.6	4.8	2.0	37.9
Ny-Ålesund	2.8	5.7	3.4	1.2	40.3

The study was conducted in 23 shallow (<3 m) ponds situated at low altitudes (<100 m a.s.l.) in five different areas around the Spitsbergen (Figure 1). *L. arcticus* was present in 20 ponds. Ponds without *L. arcticus* population were located in Ny-Ålesund (Gluudneset and Geese pond) and in Pyramiden (pond 5). In this High Arctic tundra region, all trees are small (<1 m high) (Väre and Partanen 2009) and thus do not prevent the prevailing winds around the ponds. All the study ponds most likely freeze solid during the winters and thus are fishless.

The pond shores are dominated by mosses and stones and some areas are exposed to strong wave action from the prevailing winds. Water mosses colonize only relatively small areas of the ponds because of the frequent periodicity of high turbidity. Water mosses (Bryophyta) are important habitats providing a physical refuge for *L. arcticus* against predators and UV-radiation. The sediment in the ponds consists of mud, clay, stones, gravel and even coal (Appendix 3). All ponds, except in Reinsdyrflya (Kilneset), were clear and the bottom was easily seen from the water surface. The water in Kilneset was turbid due to suspended clay. Only two ponds (Kolhamna and Adventdalen first pond) were temporary annual pools that dried completely during the summer. Other study ponds were permanent ponds. All the study ponds were situated relatively near the sea (0.05–4.2 km) and a glacier (0.7–12.2 km).

Ponds and wetlands on Spitsbergen provide important habitats to a wide variety of waterfowl and other bird species as well as to some mammals. Typical bird species living near the Spitsbergen ponds include barnacle goose (*Branta leucopsis*), arctic tern (*S. paradisaea*), purple sandpiper (*C. maritima*), dunlin (*Calidris alpina*), grey phalarope (*Phalaropes fulicarius*), common eider (*Somateria mollissima*), red-throated driver (*Gavia stellata*), black-legged kittiwake (*Rissa tridactyla*), glaucous gull (*Larus hyperboreus*), ivory gull (*Pagophila eburnea*), arctic skua (*Stercocarius parasiticus*), northern fulmar (*Fulmarus glacialis*), long-tailed duck (*Clangula hyemalis*), black guillemot (*Cepphus grylle*) and snow bunting (*Plectrophenax nivalis*). Typical mammals on Spitsbergen are Svalbard reindeer (*Rangifer tarandus platyrhynchus*), arctic fox (*Alopex lagopus*) and polar bear (*Ursus maritimus*) (Appendices 1). Some species are rare worldwide such as the ivory gull and grey phalarope. Polar bear is classified as a vulnerable species. Wetlands, deltas and ponds in the coastal and inland regions are common feeding and breeding grounds for many waterfowl species during the spring and summer months (Prowse et al. 2006).

The riparian vegetation surrounding the Arctic ponds is often dominated by a high moss cover. Other typical plants include the mountain sorrel (*Oxyria digyna*), purple saxifrage (*Saxifraga oppsitifolia*), tufted saxifrage (*Saxifraga cespitosa*), brook saxifrage (*Saxifraga rivularis*), dooping saxifrage (*Saxifraga cernua*), polar willow (*Salix polaris*), arctic meadow-grass (*Poa arctica*) and hair grasses (*Deschampsia*) (Appendix 2). In many places the vegetation has a mosaic character (Jónsdóttrit 2005). Mosaic vegetation is quite common near to the study ponds, partly because the permafrost can cause structural changes on the surface, the water table is high or even reaches the surface, and there are early traces of surface erosion in the soil. Arctic vegetation is largely controlled by summer temperatures (Rønning 1996). Since the research area was so extensive, the study areas are described as circumpolar Arctic Bioclimate Subzones A–E, with A standing for the coldest and E for the warmest subzones. The Svalbard archipelago encompasses the three coldest zones: A= Arctic polar desert, B= northern Arctic tundra and C= middle Arctic tundra (Jónsdóttir 2005). All study ponds located in the northern Arctic tundra, subzone B. The characteristic species of subzone B are *Salix polaris* and *Saxifraga oppositifolia,* the vegetation cover is >50 % and the soil organic content is 5–25 % in Svalbard (Jónsdóttir 2005). Mean July temperature is 2.5–4 °C and length of the growing season is 1.5–2.5 months in this subzone. As in other biomes, herbivores may affect the tundra ecosystem by grazing, trampling and manuring. Droppings of reindeers and geese can often be found abundantly along the pond shores (Appendices 4–9). Arctic ponds are important resting and drinking areas for many terrestrial animals.

2.2. Site description

2.2.1. Longyearbyen

Longyearbyen (78°13´N, 15°42´E) is the largest settlement and the administrative centre of Svalbard located on the western coast of Spitsbergen, which is the largest island of Svalbard (Figure 1). Longyearbyen is one of the world´s northernmost towns. There are seven coal mines present, but only one is still operating. A total of six ponds were studied in Longyearbyen region: Longyearbyen, Nybyen, Adventdalen first, second and third pond and the slightly saline Dammyra pond (Figure 2). Vegetation types were defined separately for each pond (Appendices 2). Vegetation type was the willow-field horsetail community in Dammyra, Longyearbyen and Nybyen ponds. The Nybyen pond was a permanent water body for whole summer, even though the pond was remarkably small, only 6 m^2 (Figure 2). Adventdalen first pond was a temporary annual pool that dried up during the summer. Adventdalen second pond located near to a dog kennel where human impact was clearly visible and the vegetation covered only 0–5 % of the ground (Figure 2). Poorly developed plant cover is probably due to disturbance by humans and birds, not due to lack of nutrients or extreme climate. Vegetation type was the shore meadow community in Adventdalen third pond and the poorly developed vegetation describes best the surrounding of Adventdalen second pond. The nutrient-rich delta area of Adventdalen is an important nesting place for many bird species such as arctic terns *(S. paradisaea)*, purple sandpiper *(C. maritima)* and common eiders *(S. mollissima)*. In this area dunlin *(C. alpina),* arctic tern and purple sandpiper evidently feed on *L. arcticus*. Goose droppings were common near all the study ponds in Longyearbyen and two pairs of barnacle geese were nesting near the Longyearbyen pond. More detailed descriptions of the ponds can be found in the Appendices 1–9.

2.2.2. Kapp Linné

Kapp Linné (78°04´N, 13°42´E), Basecamp Isfjord Radio, is situated on the outermost part of the Isfjord on the western coast of Spitsbergen (Figure 1). The old radio station was built in 1933 at Kapp Linné and later provided telecommunications between the Norwegian settlements and the mainland of Norway. Since late 1990s, the radio station buildings have been used as a hotel during the tourist season. Kapp Linné is a very important nesting area for birds and has a sanctuary facilitating the breeding of Common eiders and other bird species during the nesting period. There are numerous ponds and the wetlands have thick moss beds that are easily damaged by footsteps. Four ponds (Pond 1, 2, 3 and 4) were studied in Kapp Linné region (Figure 2). Vegetation type was moss tundra community in all study ponds in Kapp Linné. Goose droppings were found in shores of all the studied ponds. Reindeer droppings were found only in the Pond 2 shore.

2.2.3. Pyramiden

Pyramiden (78°39´N, 16°11´E) is an old Russian settlement and a coal mining town but is nowadays uninhabited. It is located in Billefjord on the western coast of Spitsbergen (Figure 1). Materials from coal mining and an evident human impact were clearly visible around the ponds in Pyramiden (Figure 2). The ponds have been used as a source of drinking water and traces of this activity are still visible. Two ponds (Pond 5 and Pond 6) were studied in Pyramiden region. *L. arcticus* occurred only in Pond 5, where only a single specimen was found. Vegetation type was moss tundra community near the ponds in Pyramiden. No other vegetation except moss was found around Pond 6, and a large part of the moss cover was dead (35–95 %). There were plenty of goose droppings along the shores of Pyramiden ponds.

Figure 2. Photographs taken from the study ponds in Longyearbyen, Kapp Linné and Pyramiden. (A) Longyearbyen pond is situated near to two glaciers and thus the water temperature was low early in the field season. (B) Dammyra pond was a bit saline and in this small pond *L. arcticus* were exceptionally large. (C) Small permanent pond in Nybyen in the end of the field season. (D, E) All ponds in Adventdalen were located near to a dog kennel. (F, G, H, I) Kapp Linné ponds were good habitats for *L. arcticus* and surrounded by abundant moss vegetation. (J, K) Human impact was evident in Pyramiden area. Only one *L. arcticus* individual was found from Pond 5 whereas no *L. arcticus* was observed in Pond 6.

2.2.4. Kilneset

Kilneset (79°42´N, 13°22´E) is situated in Reinsdyrflya near to the Liefdefjorden on the northern coast of Spitsbergen (Figure 1). The area is part of the Northwest Spitsbergen National Park. Kilneset is in northern Arctic tundra, subzone B, but is located close to polar desert area, the coldest subzone A. One pond was examined in Reinsdyrflya region. Vegetation near to the Kilneset pond was only moss (75–100 % cover) and thus vegetation type was moss tundra community. Reinsdyrflya has a large population of reindeer and common eiders and arctic terns breed on the Reinsdyrflya islands (Stange 2009). Kilneset was the only turbid pond due to clay.

2.2.5. Polheim

Polheim (79°53´N, 16°02´E) is situated in Mosselhalvøya near the Mosselbukta on the northern coast of Spitsbergen (Figure 1). Polheim is historically important site, but only little is known about its nature. The famous polar explorer Adolf Erik Nordenskiöld started his expedition from Polheim in 1872 to the totally unknown interior of Nordaustland. In Mosselhalvøya region, only one pond (Polheim) was examined. The vegetation type was moss tundra community near to the Polheim pond.

2.2.6. Ny-Ålesund

Ny-Ålesund (78°55´N, 11°56´E) is located on the Kongsfjorden on the west coast of Spitsbergen. Ny-Ålesund is an old coal mining town. Since 1964, the place has been developed as an international research village. The local reindeer population had collapsed completely, but 15 reindeer were moved to the region in 1978 and since then the reindeer population has grown (Stange 2009). Nine ponds were studied in the Ny-Ålesund region: “Goose pond”, “Gluudneset”, Tvillingvatnet, Storvatnet, “Kolhamna”, “Trehyrdingen 1”, “Trehyrdingen 2”, “Brandallaguna” and Solvatnet. *L. arcticus* were not found from the Goose pond nor from the slightly saline Gluudneset pond. There were many barnacle geese *(Branta leucopsis)* in Goose pond and Arctic terns in Gluudneset.

Kolhamna was a temporary annual pool that dried up in three weeks during the summer (Figure 3). Cyanobacteria grew near to the Kolhamna pond indicating that the pond had already begun to dry out early in the summer. The bottom of the dried pond was full of footsteps of purple sandpipers. The birds had probably eaten all *L. arcticus* and only *D. pulex* were still alive in the moist sediment in late summer. Ponds in the Trehyrdingen area (Trehyrdingen 1 and 2) looked quite similar, but *L. arcticus* lived in different habitats. In Trehyrdingen 1 *L. arcticus* were found among rocks whereas in Trehyrdingen 2 *L. arcticus* seemed to favour the water mosses and soft sediment.

Tvillingvatnet is a source of drinking water and plumbing repairs were done at the pond shores in summer 2010 (Figure 3). Brandallaguna is located in a very windy area near to sea. In this unusual pond, the sediment released large quantities of methane and *L. arcticus* lived at an unusual depth ≥1.5 m. Solvatnet was a nutrient-rich pond located near to the sea. In this pond *L. arcticus* were large and served as an important food source for arctic terns and purple sandpipers. Purple sandpipers also seemed to eat *D. pulex* during windy days, when these small crustaceans were clustered among the submerged mosses close to the shore. The vegetation type was moss tundra community in Storvatnet, Brandallaguna and Solvatnet ponds.

Figure 3. Photographs taken from the study ponds in northern part of Svalbard and Ny-Ålesund. (L) Mosselhalvøya in Polheim was the northernmost pond in the studied ponds. (M) Reinsdyrflya in Kilneset was the only pond with turbid water. (N, O) No *L. arcticus* were found in Goose pond or in Gluudneset. (P) Ny-Ålesund settlement used the water of Tvillingvatnet for drinking. (Q) Storvatnet was located near the Ny-Ålesund airport. (R, S) Kolhamna temporal pond dried up completely in three weeks. (T, U) Ponds in Trehyrdingen area looked quite similar. (V) Branddallaguna area was very windy and the pond bottom released a lot of methane. (X) Solvatnet was a nutrient-rich pond where *L. arcticus* were exceptionally large.

2.3. Sampling

L. arcticus were sampled from a total of 19 ponds on six locations around the Spitsbergen (Figure 1). Samples were collected between July 6th and September 6th in 2010. The density of *L. arcticus* was determined using traps (see Christoffersen 2001) and a “peltipelle-sampler” which was burrowed approximately 5 cm into the sediment, lift up and the captured animals were counted (Figure 4). Peltipelle-sampler can be used for taking an undisturbed sediment and/or invertebrate sample from a certain area of lake or pond bottom. The sampler has two components: a bottomless bucket and a metal base plate with a handle. This sampler can be used on soft bottoms where it can be carefully set and pushed to a depth of few centimetres. After the base plate is inserted into the slot, an undisturbed sediment sample can be lifted up. Additional samples of *L. arcticus* were collected gently using a hand net and a spoon. A total of 60 individuals were collected from each pond. Half of the animals were preserved in 80 % ethanol and half were frozen. Animals used in laboratory experiments were transported alive to the laboratory in 200 ml bottles, which had a maximum of five individuals per bottle and 150 ml of pond water. 15 extra animals were collected for each laboratory experiment. It should be noted that the water temperature in the bottle should not rise when animals are collected. Human hands can easily raise the temperature of the water, resulting in lower oxygen content and, in the worst case, to the death of animals. The bottles were kept in dark because darkness seemed to reduce the cannibalistic behaviour of *L. arcticus*.

Figure 4. Peltipelle-sampler on the shore of Kapp Linné pond. The sampler is composed of a bottomless bucket and a metal paddle. Photo taken by Anni Pulkkinen.

2.4. Morphological analyses

Morphological analyses were performed on a total of 791 *L. arcticus* sampled from six areas: Longyearbyen (5 ponds), Kapp Linné (4 ponds), Pyramiden (1 pond), Ny-Ålesund (7 ponds), Reinsdyrflya (1 pond) and Mosselhavøya (1 pond). Total of 19 different *L. arcticus* populations were included in these analyses. Individuals from Adventdalen first pond were not included to this data because the pond is connected to the near Adventdalen second pond by a water pipe. The animals were preserved in 80 % ethanol and later examined under a Wild Heerbrugg stereomicroscope at 6x magnification to the nearest 0.1 mm. The following parameters were measured: length and width of carapace (CL and CW), length of telson (TL) from carapace to the end of supra-anal plate, length of intact telson setae (TS), length of supra-anal plate (SP) and number of posterior segments not covered by the carapace (PS) (Figure 5). *L. arcticus* has been shown to have five different haplotypes (Hessen et al. 2004). A unique *L. arcticus* population occurs in the alpine Hardangervidda area, southern Norway. This special B2 haplotype population has a remarkably short telson relative to the length of carapace (Hessen et al. 2004). Therefore, the ratio of TL: CL was calculated from each individual. *L. arcticus* has two major haplotypes (A1 and B1) and only the haplotype A1 has previously been found on Spitsbergen (Hessen et al. 2004). The supra-anal plate is significantly smaller in haplotype A1 relative to the carapace length (Hessen et a. 2004). Therefore, the ratio of SP: CL was also calculated from each individual. *L. arcticus* sex and size and the number and colour of eggs were determined. The mean number of eggs was calculated from all mature females with eggs in their egg-capsules, so that it represents the mean number of eggs per mature and fertile female, not the mean egg number carried by the total female population. Differences between males and females are demonstrated in Figure 10. Animals were photographed under a microscope for later analysis of colour morphs. Red and green pigments disappeared from the *L. arcticus* body when the animals were preserved in 80 % ethanol. Therefore, colour morphs were recorded from living animals which were collected from each study population.

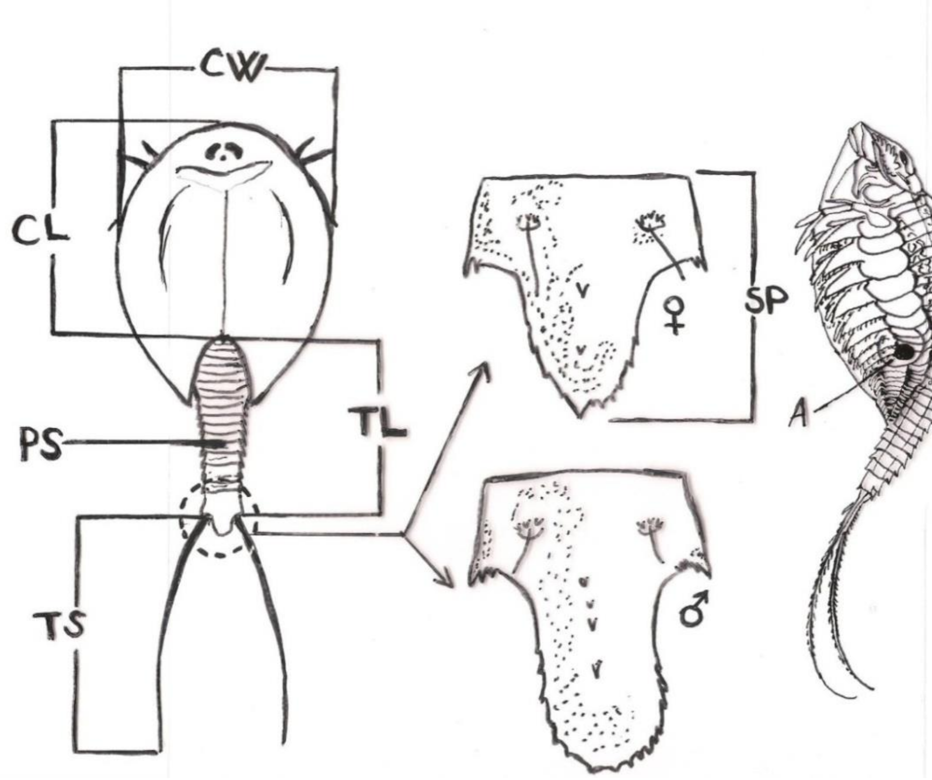


Figure 5. Examined morphological parameters of *L. arcticus* and the differences between female and male supra-anal plates and the place of female egg-capsule (A). CL=Carapace length, CW=Carapace width, TL=length of telson from carapace to the end of supra-anal plate, TS= length of intact telson setae, SP= length of supra-anal plate and PS= number of posterior segments not covered by the carapace. Modified from Hessen et al. (2004), Longhurst (1955) and Sars (1896).

2.5. Preliminary laboratory experiments

Because *L. arcticus* has been only rarely studied under laboratory conditions, it was important to first optimize the laboratory conditions before starting the actual experiment. For example, the water and air temperature, the chemical properties of the water and the diet of *L. arcticus* were optimized prior to the experiments. Preliminary experiments showed that the final experiments cannot be carried out if the animals are kept in the same container. The reason for this was the cannibalistic behaviour of *L. arcticus.* The animals seemed to be intolerant to long transportation and they required cold water. The water temperature should not rise too high at any stage of the experiment nor during the sampling or transport of *L.*

arcticus. The water used in the experiments should be taken from the home pond of the animals. The pH varies between the ponds on Spitsbergen and therefore one should pay attention where the water has been taken for the experiments.

2.6. Culturing of the L. arcticus

In the laboratory, the animals were put individually into 100 ml bottles filled with pond water. Animals were kept in a temperature controlled laboratory (air temperature 8–11 °C). The water temperature was 3.1–4.9 °C in ponds where the animals were collected. The temperature in climate room was higher than in the ponds because the temperature in UNIS climate room cannot be set below 8 °C. 24-hours sunlight is typical of the High Arctic regions and thus animals were kept in constant day light also in the laboratory. *L. arcticus* with injuries such as broken telson setae were excluded from the experiments. The broken telson setae encumbered swimming and hampered returning of *L. arcticus* from water surface back to the water column. Dead *L. arcticus* were removed after 24 hours and possible reasons for death were determined (e.g. possible diseases and failed carapace moult was recorded, and the water temperature, pH and dissolved oxygen were measured). The activity of the animals was also visually examined every 24 hours.

During the actual experiments the animals were kept in 100 ml bottles and the water was changed daily. 50 ml of water was changed on the first day and 100 ml on the second day. No air pump was used in the experiments because it seemed to decrease the water pH.

Diet was one of the most important elements in maintaining *L. arcticus* in the laboratory. Preliminary experiments showed that the more diverse diet was offered, the more animals survived in the laboratory. Not all *L. arcticus* seemed to feed on *D. pulex* as only 60 % of individuals (n=31) had eaten *D. pulex* during the 24 hour experiment. The best diet for *L. arcticus* was a four-day rotating menu switching from 1 ml of concentrated phytoplankton, to one *D. pulex* , then to one crustacean food tablet, and on the fourth day the animals were not given any food. Although four-day diet was best for the animals, a two-day rotating menu was used in the actual experiments due to the challenge of finding the right food for long experiments. In the two-day rotating menu the animals were first given one crustacean food tablet and the following day they were left without food. It should be paid attention to what kind of crustacean food tablet is used in experiments. A sinking food tablet seemed to be the best, because then the food was available for all animals, including the ones in poor condition laying on the bottom of the container, and not only for those used to forage (e.g. on *Daphnia*) in the water column. During the experiment, water was changed every day: 50 ml when the animals were fed and 100 ml on the fast day. The water was taken from the same pond as the animals. Faeces and uneaten food were removed when all the water (100 ml) was changed. *L. arcticus* should not be overfed and the containers must be kept clean to prevent bacterial and fungal growth. In the laboratory Ciliates (*Ciliophora*) began to grow easily on the surface of *L. arcticus*, because the animals had no opportunity to dig into the sediment.

2.7. Red Carapace Disease

When *L. arcticus* samples were collected from the study ponds, some animals were observed to be sick and to have a swollen, red carapace. Some healthy-looking animals became ill in the laboratory, apparently if the water temperature increased in the aquarium. The sick animals were preserved in 80 % ethanol for later examination of a possible parasite. Later the cadavers of the sick animals were autopsied and the organs and body liquids were examined under a stereo microscope. Then the animals were crushed between two 1 cm thick glass plates and examined more carefully under the stereo microscope. Since no parasite was found using this method, the preparations were made from different tissues including the fluid between the carapace and from haemolymph, egg cells and ovaries. The preparations were examined and photographed under a light microscope. Organisms with an interesting shape were found from the eggs and ovaries and therefore these organs were further examined using an electron microscope at the University of Jyväskylä, Finland.

2.8. Water chemistry in the High Arctic ponds

Water samples were collected from a total of 23 ponds in different locations around the Spitsbergen. *L. arcticus* were found in 20 study ponds. Note that *L. arcticus* was present in Adventdalen first pond, but this pond was not studied intensively because it was connected by a pipe to Adventalen second pond. Samples were collected between July 6th and September 6th in 2010. The ponds in Ny-Ålesund were sampled twice in the beginning and in the end of August. Ponds in Longyearbyen were monitored throughout the summer 2010.

In each site, water temperature was measured using a hand held thermometer held both on the bottom of the pond (at sediment surface) and approximately 15 cm below the water surface. Sediment temperature was also measured by putting the same thermometer approximately 10 cm into the sediment. Conductivity (Cond), salinity (‰), pH and the concentration of dissolved oxygen (O_2 % and mg l^{-1}) were measured using a Mettler Toledo InLab 781 conductivity meter, a Mettler Toledo Gmbtl pH meter and a Mettler Toledo In Lab 681 oxygen meter respectively. The location of the pond (i.e. latitude and longitude) was measured in the field with a handheld GPS receiver (Garmin e-trex; uses WGS84 coordinate system). The altitude and the distance from the sea and from the nearest glacier and permanent snow cover were estimated from 1:100 000 topographic maps C9 (Longyearbyen), C8 (Pyramiden), B9 (Kapp Linné) A7 (Ny-Ålesund), B4 (Reinsdyrflya) and C4 (Mosselhalvøya) published by the Norwegian Polar Institute, Tromsø.

Water samples were collected for five water chemistry variables, which were later analysed in the laboratory. Water samples were taken from the littoral zone at 15–

44 cm depth. Water samples were stored frozen. Total nitrogen (^{tot}N), total phosphorus (^{tot}P), total organic carbon (TOC) and dissolved organic carbon (DOC) were analysed at the Department of Environmental Sciences, University of Helsinki, in Lahti, Finland, using standard protocols. Marianne Lehtonen analysed the total nitrogen (^{tot}N) using the QuickChem ® METHOD 10-107-04-1-1 and the total phosphorus (^{tot}P) using the SFS 3026 standard. Nitrogen and phosphorus concentrations were measured from each pond. ^{tot}N and ^{tot}P concentrations were measured twice in three ponds (Storvatnet, Trehyrdingen 1 and Brandallaguna) in Ny-Ålesund. Santeri Savolainen analysed the total organic carbon (TOC) and the dissolved organic carbon (DOC) using the European standard SFS-EN 1484:1997. TOC and DOC concentrations were measured from all other ponds except from pond 6 in Pyramiden and from Gluudneset in Ny-Ålesund because all water was needed for the nutrient analysis and thus no water was left for the carbon analysis.

For the analysis of chlorophyll-a (Chl-a) in ponds in Kapp Linné, 80 ml of water was first filtered through a GF/F filter with a pore size of 3.0 µm and then through another GF/F with 0.7 µm pore. Unfortunately, the 3.0 µm GF/F filters were lacking and thus 2.7 µm GF/D filters were used for rest of the samples. Chl-a was extracted with methanol and filtered using the syringe filter and finally the extract was analysed with 10-AU Fluorometer. Three replicate measurements were done from each sample.

To study the amount of organic matter in the sediment of each study pond, three replicate samples were collected by digging the bottom with a 0.01 mm metal mesh. The stratification in the sediment was retained in the obtained samples. Samples were collected from different types of bottoms from 3–40 cm depth. Each sample contained 3–5 cm of surface sediment, which was homogenized before analysis. In the laboratory, 20 g of the sediment was dried in aluminium foil at 105 °C for 24 hours. Crucibles were burned at 540 °C for an hour and then let to cool in a desiccator for 30 min. Subsamples of 1–2 g of dry sediment were weighed, placed in crucible, burned at 450 °C for 4 hours, cooled in a desiccator and weighed again. The obtained results are expressed as per cent of organic matter (OM %) of the total sediment matter.

The cover of moss vegetation was estimated up to a distance of approximately 25 m from the shoreline of the pond. The moss cover around the ponds was defined into four classes: 0–10 %, 11–30 %, 31–60 % and 61–100 %. A more detailed survey of the vegetation surrounding the ponds was performed in five 40x40 cm vegetation squares, from which the number of reindeer and geese droppings was also calculated. The density of droppings at a distance up to approximately 25 m from the shoreline was used as an indicator of faecal input of barnacle geese and reindeer into the ponds. Density of goose droppings in this area was recorded using a semi-quantitative scale (none, low, medium and high) and converted into an ordinal scale ranging from 0 to 3 for statistical analyses. A similar method has been used by Van Geest et al. (2007). Fresh water ponds and wetlands are important habitats for a wide variety of birds and mammals, which can act as dispersal agents for *L. arcticus*. Hence, all observations of birds and mammals near the ponds were also recorded.

2.9. Olfaction

The olfaction experiment was carried out to find out if *L. arcticus* can trace prey using their sense of smell. The two different kinds of odour sources used were artificial algae and crushed *L. arcticus*. The artificial algae was a crustacean food tablet which is commonly used as food for freshwater shrimps maintained in aquaria. All test animals were collected from Adventdalen third pond the day before the start of the olfaction experiment. The animals were acclimated 24 hours in 100 ml bottles in the temperature-controlled laboratory until the water temperature was stabilized to 8.5–9.2 °C. Three different kinds of odour treatments were used: 1. control = no odour, 2. crushed *L. arcticus* = the odour source was crushed *L. arcticus*, and 3. algae = the odour source was artificial algae (i.e. crustacean food tablet). All odours were tested with 15 different animals and different animals were used in different treatments. The experiment was carried out in an 18x18 cm plastic container filled with 500 ml of filtered (GF/F) water. The water temperature was 8.5 °C and the water depth was 2.3 cm in the container. The water and the cotton with the source of odour were changed for each animal. The container was changed for all treatments.

The crustacean food tablet and *L. arcticus* which were used as the sources of odour were first crushed and then centrifuged to obtain clear liquid that was soaked in cotton. Four pipette tips with cotton inside were put in each corner of the three containers. After the container was filled with 500 ml of water the "smelling" cotton was placed in one corner whereas the pipette tips with clean cotton balls were put in the other corners. The pipette tips were perforated so that the odour of the liquid could diffuse from the cotton to the water. The containers were divided into nine numbered sections. The source of odour (no odour, crushed *L. arcticus* or crustacean food) was inserted to section one and the *L. arcticus* was released in the middle of the container (i.e. section five) (Figure 6A & 6B). Prior to the actual experiment the dissolution of odour substances was tested by using red watercolour and to ensure that the red pigment did not spread over other sections except the number one. It was important to put "the odour pipette" into the container after the container was filled with water. To prevent the animal from seeing the container, the animal was put into a black, bottomless bottle in the section five for one minute prior to the experiment. The experiment lasted 15 minutes. During the experiment, the sections in which the animal was moving and attaching to cotton balls was monitored (Figure 6C). Number of visits and the time that the animal spent in different sections was recorded.

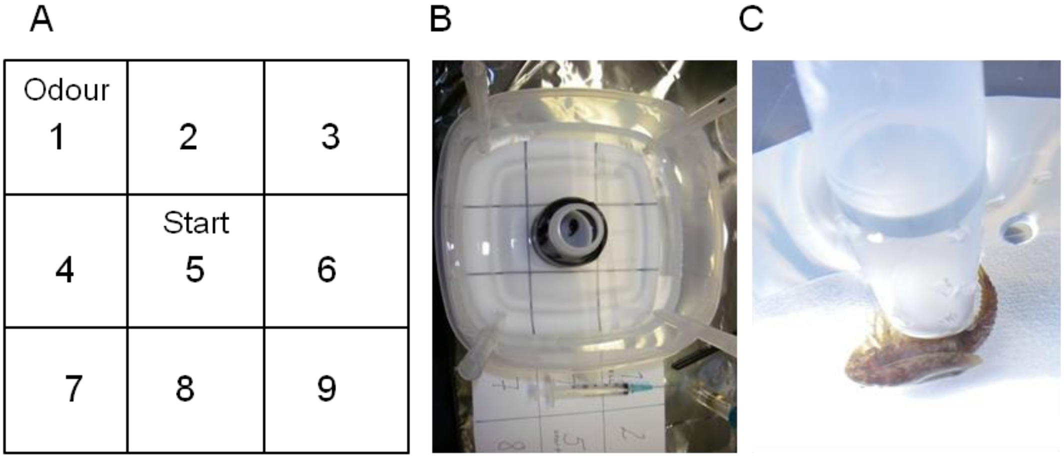


Figure 6. The study setting in the olfaction experiment. A: Experiment was done in 18x18 cm containers divided into nine sections. B: The test animal was released in the middle of the container. C: The time the *L. arcticus* was attached to the pipette tip was also monitored.

2.10. LC_{50} Salinity and pH

In this study the aim was to study the tolerance of *L. arcticus* to potential natural stressors including the water acidity (pH) and water salinity (‰). In toxicology, the median lethal concentration (LC_{50}) of a toxin or radiation is the dose required to kill half of the individuals of a tested population after a specified test duration. For the LC_{50} experiments *L. arcticus* were collected using a hand net and a spoon at 5–60 cm depth from the Adventdalen third pond in Longyearbyen. The animals were collected gently from the sediment and from the water column, placed in pond water and transported to the laboratory. The animals were acclimated 24 hours in 100 ml bottles in the temperature controlled laboratory prior to the experiments. Only animals in good condition were selected for the experiments. All animals were females, of similar size and collected from the same population. Animals were kept in 100 ml bottles during the experiment and fed using a two-day rotating menu. Fifteen *L. arcticus* were placed individually into the 100 ml exposure solutions (i.e. into different treatments), including a pond water sample for control held at temperature controlled room (air temperature 8–11 °C, water temperature 8–9.5 °C). Water was changed every day and the faeces and uneaten food was removed. 50 ml of water was changed when the animals were fed and 100 ml was removed during the fast days. Air and water temperatures were measured daily. At the beginning and in the end of the experiments dissolved oxygen, pH and salinity were measured. The survival of animals was determined as the number of dead organisms after every hour for the first two days and then once a day till the end of the experiment. LC_{50} was determined by the computer program DEBtox application. The safe salinity concentration for *L. arcticus* was calculated using empirical formula. The safe salinity concentration was defined to be equal to 96 h-LC_{50} x 0.1 (Sprague 1971).

In LC_{50}-salinity experiment, the survival of *L. arcticus* was examined in 13 different treatments with varying salinity (0.1, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12 ‰). Each treatment consisted of 15 replicates. In the salinity experiment the control group was held in water with a salinity concentration (0.1 ‰) corresponding to the salinity in the pond. Water salinity was adjusted using filtered sea water (1 μm) and confirmed using a salinity refractometer (model InLab 781 Conductivity Sensor Module, Mettler Toledo). The salinity experiment lasted for 23 days. In the LC_{50}-salinity experiment the salinity was measured every day with a digital meter (model In Lab 781 Conductivity Sensor Module, Mettler Toledo).

In LC_{50}-pH experiment, the survival of *L. arcticus* was examined in different treatments with varying pH (7.6, 8.5, 8.0, 4.5, and 4.0). Fifteen replicates of five different pH were tested. Animals maintained in the pond water with a pH of 7.6 were considered as the control group. In the LC_{50}-pH experiment the pH was measured every day using a digital meter (Mettler Toledo Gmbtl). The water pH was adjusted using HCL and NaOH and was confirmed using the same pH meter. The pH experiment lasted for two days.

2.11. O_2 consumption at different temperatures

Individual evaluations of oxygen consumption (i.e. respiration) were done by putting five *L. arcticus* individuals for each of the following temperature treatments: 3.5, 10, 16.5, 20, 25 and 30 °C. The antioxidant solution (NaOH 0.1 M and sodium ascorbate 0.1 M) were considered as a calibration sample. Filtered (2 µm) pond water was used as a control sample. The oxygen sensor was polarized because the electrolyte contains oxygen. The polarization of the oxygen sensor lasted for 3 hours until the desired signal of 11 pA (less than 20 pA) was reached. Stirring was used inside the test chambers in all treatments. A glass ring, a magnetic flea and a metal net were placed inside the 4 ml test chambers (Figure 7A). The metal net protected the animals from being damaged by the rotating magnetic flea (Figure 7A & 7B). For each treatment, animals were acclimated for 24 hours in 100 ml bottles at the temperature controlled laboratory (water temperature 8.5–9.2 °C) before starting the experiments. It was not possible to adapt the test animals into the test temperatures for longer time, because the animals died soon in 30 °C. Eriksen and Brown (1980b) also had problems to acclimate *L. lemmoni* to high water temperatures, being intolerant to 35 °C. Hence, the test animals were held only for 1 minute in the selected test temperatures before each measurement. Individual oxygen consumption measurements were determined in a 4 ml closed respirometry system filled with filtered pond water (2 µm filter). Respirometers were maintained in a water bath (Julabo F34 HL) at the selected test temperature (Figure 7C). The water in the bath was filtered through a 0.7µm filter and boiled to avoid contamination. The respiration activity experiment lasted for 15 minutes. Control value was measured in each temperature and the control value was reduced from the test result at the same temperature as the control value was measured. Oxygen consumption was measured throughout the experiment using Unisense A/S PA2000 Micro-Respiration system (Figure 7C). Oxygen consumption was determined by the computer program MicOx software.

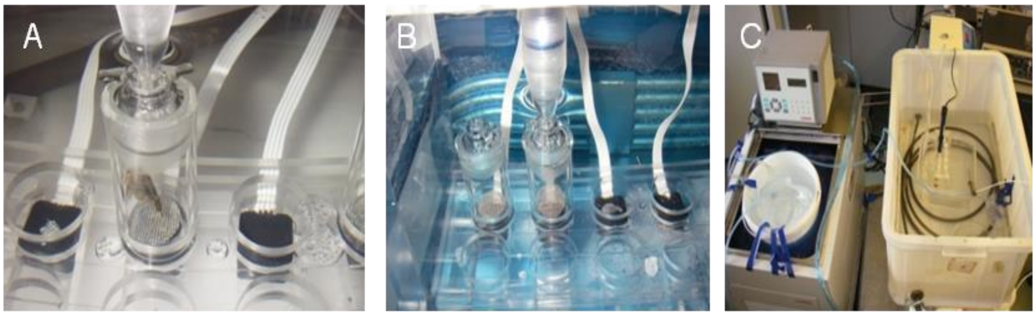


Figure 7. Oxygen consumption experiment. A: Test animal in the 4 ml chamber. B: Empty chamber with a magnet, a glass ring and a metal net. C: Unisense A/S PA2000 Micro-Respiration system and Julabo F34 HL cold and hot antifreeze circulation system.

The temperature coefficient (Q_{10}) values were calculated using the mean of the respiratory activity with the formula (1.)

(1.) $$Q_{10} = (R_2 / R_1)^{10/(T_2 - T_1)}$$

Q_{10}= the relative change of a physical property when the temperature is changed by 10 °C.

R_1= the measured reaction rate (nmol/h) at temperature T_1 (where $T_1 < T_2$).

R_2= the measured reaction rate (nmol/h) at temperature T_2 (where $T_2 > T_1$).

T_1= the temperature (°C) at which the reaction rate R_1 is measured.

T_2= the temperature (°C) at which the reaction rate R_2 is measured.

2.12. Statistical analyses

Oxygen consumption was calculated using the computer program MicOx 2.9 software and the temperature coefficient (Q_{10}) values were calculated using Microsoft Office Excel 2007. The statistical analyses were done with PASW Statistics 17 and IBM Statistics 20 software’s. All variables were tested for normality. Differences in *L. arcticus* oxygen consumption in different temperatures (3.5, 10, 16.5, 20, 25 and 30 °C) were tested using one-way analysis of variance (one-way ANOVA). When significant differences ($p < 0.05$) were found, Tukey pairwise tests were performed.

Correlations between *L. arcticus* main morphological variables (CL, CW, TL, SP, TS and PS) were studied using Pearson correlation. Regression curve estimations between CW and CL and between TS and CL were made using the power regression curve ($y = ax^{b}c$), and between TL and CL, CW and SP, CL and SP, TL and SP, number of eggs and CL, TL and water surface T (°C), TL and sediment surface T (°C) and between TL and sediment T (°C) were made using the polynomial regressions curve ($y = a + b_1x + b_2x^2+c$). Egg distributions in the right and left foot capsules were tested using Wilcoxon signed-rank test. Differences between males and females total length were tested using Mann-Whitney U-test. Non-parametric tests were used because the data did not meet the assumptions (i.e. normality and homoscedasticity) of parametric tests. Differences in total length between sick (Red Carapace Disease) and healthy animals were tested using Kruskal-Wallis –test.

In the olfaction experiment, the differences in activity of animals between treatments (algae, *Lepidurus* and control) were tested with one-way ANOVA. When significant differences were found Tukey pairwise tests were performed. Differences in animals’ swimming speed and in the use of different squares (1–9) were tested using Kruskal-Wallis -test and when significant differences were found pairwise tests (Mann-Whitney U-test) were made.

The differences of the first and second ecdysis of *L. arcticus* in different salinity treatments (control, 1 ‰, 2 ‰, 3 ‰ and 4 ‰) were tested using Kruskal-Wallis -test. When significant differences were found Mann-Whitney U-test pairwise tests were performed.

3. Results

3.1. Ecology of L. arcticus

3.1.1. Aggression and body damage

L. arcticus usually avoided other conspecifics. Cannibalism was common in *L. arcticus* populations on Spitsbergen and evasive behaviour of *L. arcticus* seemed to be a good way to avoid predation. Aggressive behaviour was common when the animals were put in the same bottle during the sample collection. Sometimes a smaller animal attacked a larger animal and started to eat it alive. *L. arcticus* often behaved aggressively towards other *L. arcticus* in the laboratory. An exception to this aggressive behaviour was only the interactions between females and males (Figure 8).

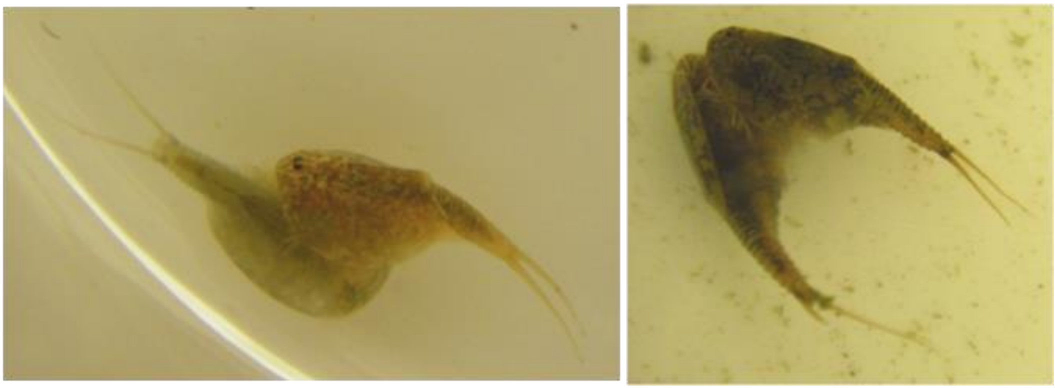


Figure 8. Interaction between *L. arcticus* female and male.

L. arcticus carapaces were sometimes injured and these injuries were observed in five study ponds: in Pond 2, in Kolhamna, in Trehyrdingen 1, in Storvatnet and in Nybyen pond. The carapaces of damaged animals had holes or cracks (Figure 9B & 9C). Damaged edges of the carapaces were darker than the healthy parts. Legs were partly or almost completely missing from three *L. arcticus* in Adventdalen second pond and Solvatnet pond (Figure 9D). A piece of telson setae was missing from several *L. arcticus*. Living animals that were lacking a piece of the tip of telson setae had difficulties in disengaging themselves from the water surface tension. An interesting discovery was that *L. arcticus* telson setae have the ability to regenerate. Damaged parts of carapaces and telson setae were darker than the healthy parts and thus they were easy to observe (Figure 9A & 9B).

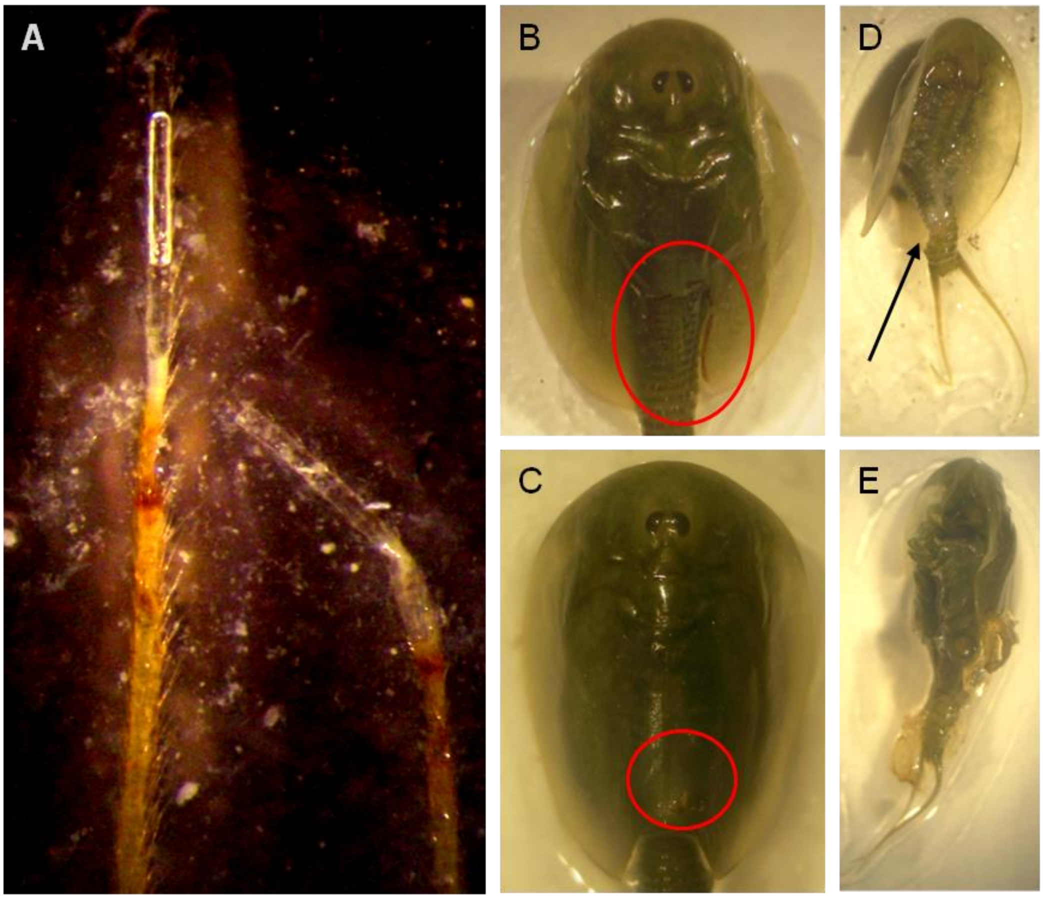


Figure 9. Pictures from *L. arcticus* injuries and recovering organs. A= regeneration of telson setae. The dark areas (rings) are injuries and the light areas are regenerated tissues. B and C= cracks in the carapace, D= injuries in the telson and missing legs, and E= moulting of *L. arcticus*.

Some of the collected *L. arcticus* were blind and had grey and blurry eyes (Table 2). One *L. arcticus* from Solvatnet pond had injuries in the head and the animal was blind. Another animal in the same pond and one *L. arcticus* in Polheim pond were also blind, but these individuals had no visible injuries in the body.

Described injuries in different body parts were likely caused by birds or other *L. arcticus*. Birds evidently feed on *L. arcticus* in Solvatnet (arctic tern), Longyearbyen (purple sandpiper), Adventdalen 2 (arctic tern and purple sandpiper) and Adventdalen 3 pond (dunlin). Bird observations are presented in Appendix 1. Birds can be significant predators of *L. arcticus* and at the same time act as dispersal vectors, because the *L. arcticus* eggs turned out to be sticky. Some *L. arcticus* had ectoparasites in the head or in the genital area (Table 2). The parasites were flat, white worms having a size of 2 mm. Some individuals had small red eggs, probably from a parasite, attached to abdomen of the carapace.

3.1.2. Male morphology

L. arcticus males are generally very rare, considerably smaller than the female, and have no special prehensile organs (Sars 1896). The mean male/female ratio was 1:16 in the six ponds where males were present. *L. arcticus* males were remarkably large on Spitsbergen. The total length of the male rarely exceeded 18 mm, but in few cases had reached a total length of 27.5 mm and a carapace length of 9.1 mm. In Brandallaguna the total length of *L. arcticus* did not significantly differ between males and females (Mann-Whitney: $U = 51.5$, $n = 33$, $p = 0.364$). Still, in mid- and late-summer males were on mean 8–30 % smaller than females in the study ponds.

L. arcticus males were very rare on the Spitsbergen ponds and were not found from all ponds (Table 2). Males were only found from six ponds: from three ponds in Kapp Linné, from one pond in Longyearbyen, from Ny-Ålesund and from Reinsdyr flya. Males were found between 12th July and 23rd August, when the sampling period was between 7th July and 6rd September. On Spitsbergen the sex ratio in *L. arcticus* populations was exceptional. The male/female ratio was only 1:6–1:41 (mean 1:16) in six ponds where males were observed (Table 2). Males were not found from the other 13 *L. arcticus* ponds. However, males were found from almost all the studied areas, except from Pyramiden and Polheim Mosselhalvøya.

Table 2. Number of males and colour morphs and the occurrence of Red Carapace Disease (RCD) and parasites in the *L. arcticus* populations around the Spitsbergen.

Place and date	Number of specimens per sample	Males ♂	Number of colour morphs	Number of animals suffering from RCD	Other diseases, parasites, etc.
Kapp Linné					
Pond 1, 13.7	42	1	9	-	1 parasite
Pond 2, 12.7	43	-	10	2	1 parasite on the head
Pond 3, 13.7	34	2	10	-	-
Pond 4, 11.7	31	2	6	1	-
Pyramiden					
Pond 5, 18.7	1	-	1	-	-
Longyearbyen					
Dammyra, 31.7	12	-	1	-	1 flat worm on genitals
The north coast					
Kilneset, 2-5.8	39	4	4	-	-
Polheim, 2-5.8	38	-	1	-	1 blind, 1 sick abdomen
Ny-Ålesund					
Solvatnet, 6.8	33	-	3	1	1 parasite
Tvillingvatnet,6.8	33	-	3	2	-
Storvatnet, 8.8	35	-	5	-	-
Kolhamna, 8.8	43	-	2	-	-
Trehyrdingen 1,8.8	32	-	2	-	-
Brandallaguna, 8.8	33	5	5	-	-
Longyearbyen					
Adventdalen 2, 18.8	33	-	4	-	-
Adventdalen 3, 23.8	36	-	4	-	-
Longyearbyen 23.8	39	2	2	2	-
Ny-Ålesund					
Solvatnet 31.8	32	-	4	12	2 blind
Storvatnet 31.8	42	-	5	6	-
Tvillingvatnet 1.9	35	-	4	2	-
Trehyrdingen 1, 1.9	28	-	1	2	-
Trehyrdingen 2, 1.9	37	-	2	-	-
Brandallaguna 1.9	29	-	2	1	-
Longyearbyen					
Nybyen 6.9	31	-	1	3	-

The structure of 11th pair of legs of *L. arcticus* males is the same as than the pairs immediately preceding and following it; while females of that size, the characteristic egg-capsule is already distinctly developed (Sars 1896). Males had very strong and robust legs (Figure 10 E) and the supra-anal plate was blunt and shovel-shaped (Figure 10 A). The main differences between *L. arcticus* males and females are presented in Figure 10.

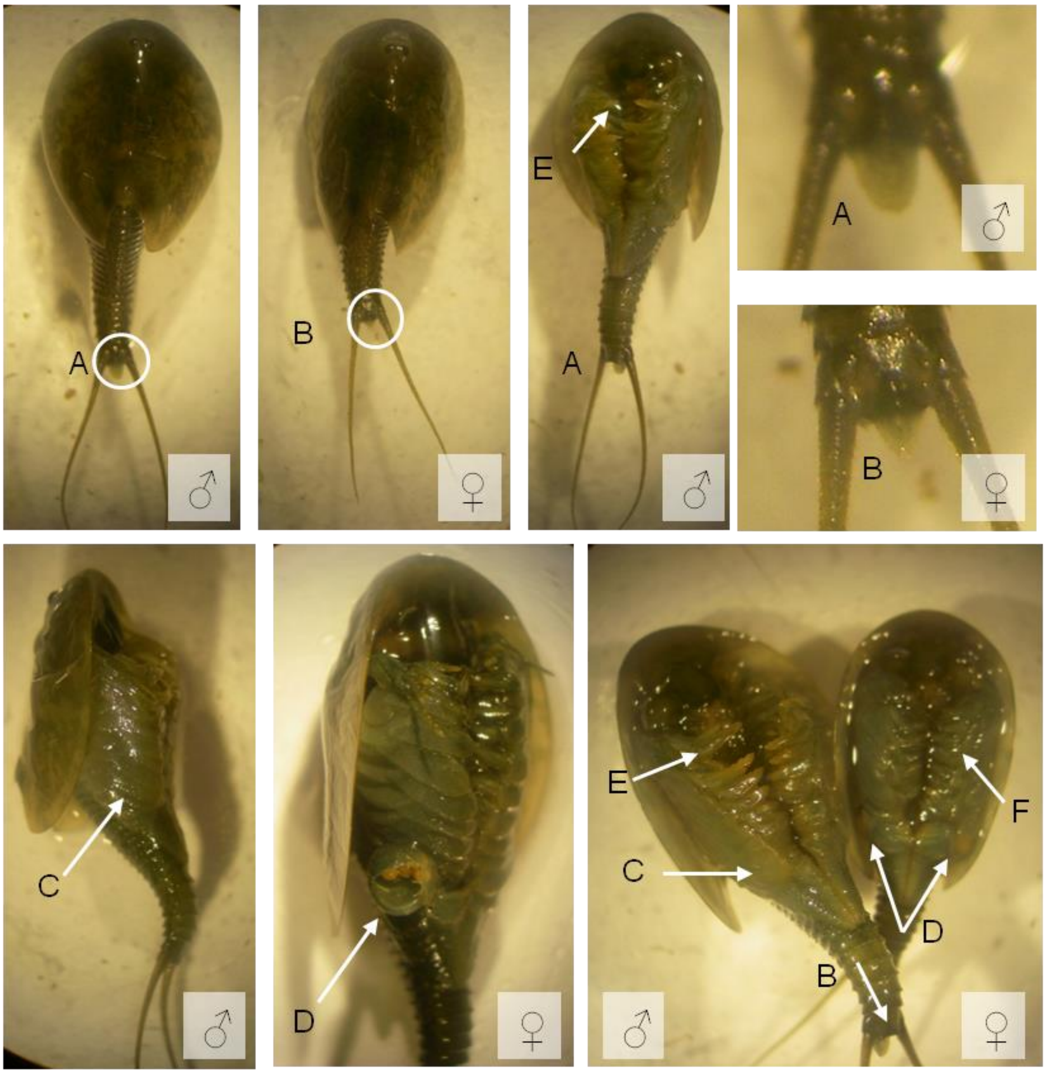


Figure 10. The main differences between the *L. arcticus* males and females. (A) Males have a blunt and shovel-shaped and (B) females have a small and sharp supra-anal plate. (C) Males have no egg-capsule, while (D) = females have an egg-capsule in the 11th pair of legs. (E) Males have stronger and more robust legs than females (F).

Males were observed in populations where females had not yet reached the sexual maturity (i.e. females had an egg-capsule in the 11th pair of legs but not yet eggs inside them). Males also occurred in the late summer (23rd August) when the females had reached the sexual maturity and were carrying eggs (Figure 11).

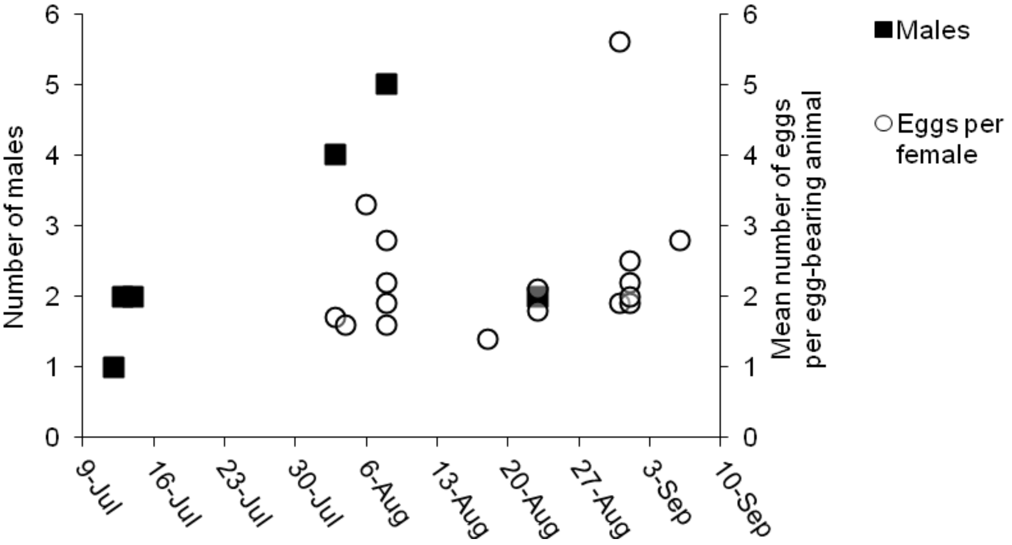


Figure 11. The number of *L. arcticus* males (solid squares; y-axis on the left) in six ponds and the mean number of eggs per mature female (open circles; y-axis on the right) in all study ponds during the summer.

3.2.3. Ratio of CL/SP and morphological differences

The ratio of carapace length to supra-anal plate ratio (CL/SP) is considered as a good way to identify *L. arcticus* species. On Spitsbergen the mean ratio of carapace/supra-anal plate of *L. arcticus* females was 14.97 %. The lowest CL/SP ratio (7.7 %) was found in Kapp Linné in early July and the highest ratio (27.6 %) was found in Solvatnet, Ny-Ålesund, in late August (Table 3). Males had a slightly higher carapace supra-anal plate ratio (mean 15.3 %) than females. The carapace supra-anal plate ratio was higher on Spitsbergen than has been observed anywhere else (Table 3).

Table 3. The ratio of supra-anal plate length to carapace length of *L. arcticus* in different northern regions. $\bar{x}$= mean ratio.

Area	Supra-anal plate length as % of carapace length	Author
Pond 1, Kapp Linné, Spitsbergen, Norway	10.00-19.35 $\bar{x}$=13.84	Present data
Pond 2, Kapp Linné, Spitsbergen, Norway	7.69-22.22 $\bar{x}$=13.42	Present data
Pond 3, Kapp Linné, Spitsbergen, Norway	10.34-17.65 $\bar{x}$=13.94	Present data
Pond 4, Kapp Linné, Spitsbergen, Norway	10.53-21.21 $\bar{x}$=14.78	Present data
Pyramiden, Pond 5, Spitsbergen, Norway	8.77	Present data
Kilneset, Reinsdyr flya, Spitsbergen, Norway	11.11-18.52 $\bar{x}$=14.38	Present data
Polheim, Mosselhalvøya, Spitsbergen, Norway	12.50-17.78 $\bar{x}$=15.09	Present data
Brandallaguna, Ny-Ålesund, Spitsbergen, Norway	8.57-19.35 $\bar{x}$=14.58	Present data
Solvatnet, Ny-Ålesund, Spitsbergen, Norway	11.94-27.59 $\bar{x}$=16.18	Present data
Kolhamna, Ny-Ålesund, Spitsbergen, Norway	10.42-25.64 $\bar{x}$=14.13	Present data
Trehyrdingen 1, Ny-Ålesund, Spitsbergen, Norway	11.11-20.69 $\bar{x}$=14.46	Present data
Trehyrdingen 2, Ny-Ålesund, Spitsbergen, Norway	11.90-20.34 $\bar{x}$=14.70	Present data
Tvillingvatnet, Ny-Ålesund, Spitsbergen, Norway	10.34-24.32 $\bar{x}$=15.97	Present data
Storvatnet, Ny-Ålesund, Spitsbergen, Norway	9.68-23.33 $\bar{x}$=14.17	Present data
Longyearbyen pond, Spitsbergen, Norway	12.82-21.28 15.53	Present data
Nybyen, Longyearbyen, Spitsbergen, Norway	12.50-20.59 15.54	Present data
Adventdalen pond 2, Longyearbyen, Spitsbergen, Norway	13.64-20.00 $\bar{x}$=16.94	Present data
Adventdalen pond 3, Longyearbyen, Spitsbergen, Norway	13.79-20.00 $\bar{x}$=16.58	Present data
Dammyra, Longyearbyen, Spitsbergen, Norway	12.68-17.72 16.15	Present data
Broughton Island, Cumberland Peninsula, Baffin Island, Canada	9.86-14.63 $\bar{x}$=11.84	Bushnell & Byron 1979
Iceland	≈12	Longhurst 1955
-	7-13	Linder 1952

A new disease called "Red Carapace Disease" (RCD) was found and it apparently affected the animal's morphology. When *L. arcticus* were suffering from RCD, the carapace/supra-anal plate ratio changed due to the swollen and risen carapace. In sick animals, this ratio was often exceptionally high (up to 34.62 %). Due to the observed RCD and sexual dimorphism, the morphological parameters (especially the carapace supra-anal plate ratio) of *L. arcticus* populations on Spitsbergen should be considered with caution.

Large morphological and size differences were observed between and within the *L. arcticus* populations. The range of key morphological characteristics of *L. arcticus* is provided in Table 4 and Figure 12. Strong positive correlations were observed between the carapace length and width, between the carapace length and supra-anal plate, between the carapace width and supra-anal plate size, between the length of telson setae and supra-anal plate, between the length of telson setae and carapace length, and between the length of telson setae and carapace width. In contrast, there was a wide scatter in carapace length and telson length and between the telson length and supra-anal plate. (Figure 12)

Table 4. Pearson correlation matrix for major morphological criteria (pooled data, n = 775). Bold denotes significant at $p < 0.05$, no bold denotes not significant at $p > 0.05$. Abbreviations: length and width of carapace (CL and CW), length of telson (TL), supra-anal plate size (SP), length of telson setae (TS) and number of posterior segments not covered by the carapace (PS).

	CL	CW	TL	SP	TS
CW	**0.93**				
TL	**0.69**	**0.76**			
SP	**0.94**	**0.93**	**0.79**		
TS	**0.87**	**0.86**	**0.72**	**0.88**	
PS	0.06	**0.14**	**0.63**	**0.20**	**0.18**

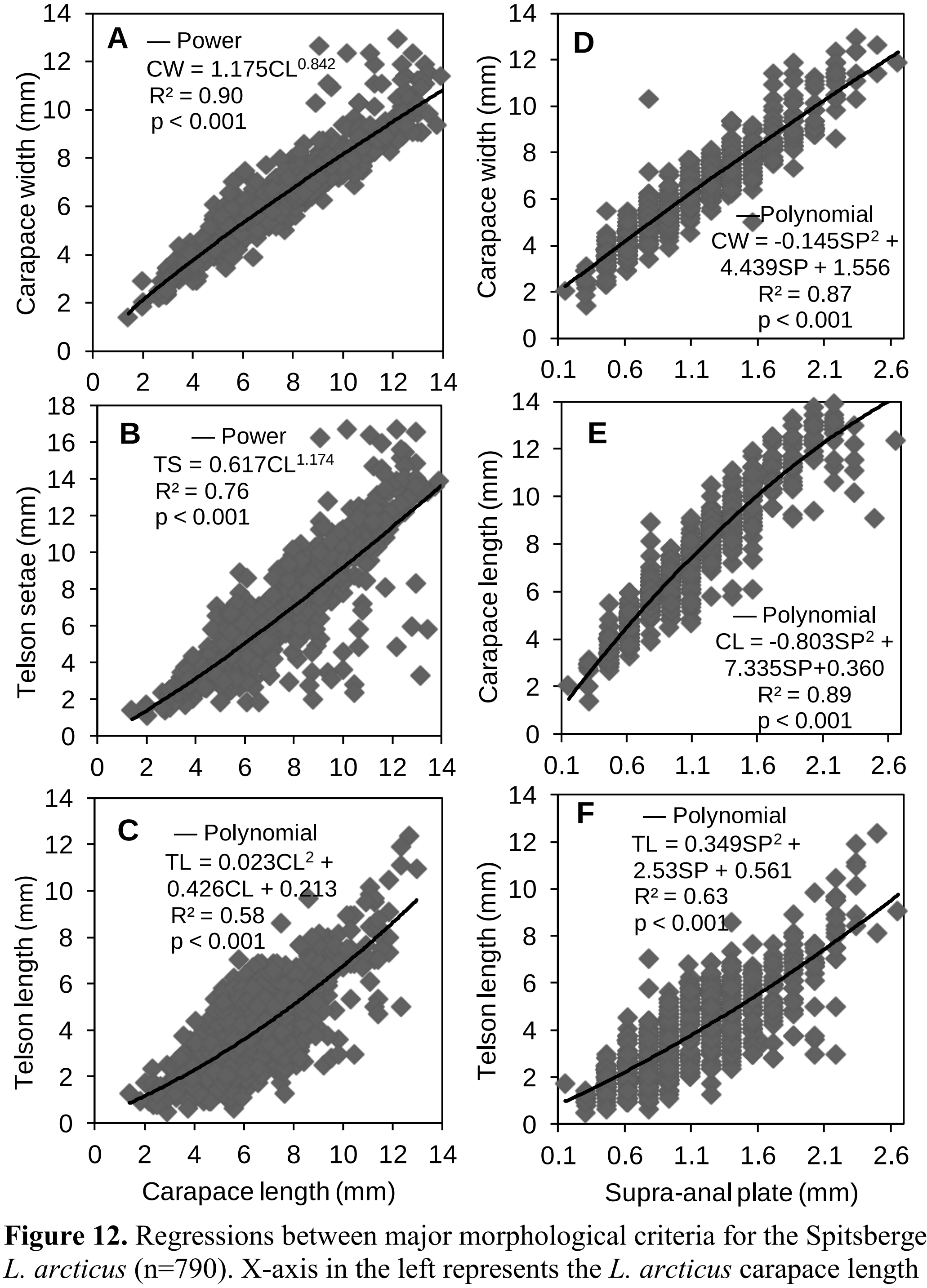


Figure 12. Regressions between major morphological criteria for the Spitsbergen *L. arcticus* (n=790). X-axis in the left represents the *L. arcticus* carapace length (mm) and x-axis in the right is the size of supra-anal palate (mm). Y-axis represents carapace width (mm; A and D), size of telson setae (mm; B), telson length (mm; C and F) and carapace length (mm; E). Black line is trend line.

3.1.4. Sexual maturity

The date of sexual maturation of *L. arcticus* females varied greatly. Normally the animals did not start to reproduce before August, but in Dammyra females were mature already in the end of July (Figure 13 A). The sexual maturation of *L. arcticus* seemed to depend on the progress of the summer as well as on the salinity and temperature of water and sediment in the ponds. The end of *L. arcticus* juvenile stage (i.e. the size when the animal started carrying eggs) was at the carapace length of ≥ 4 mm (Figure 13 B). The long-term water temperature had a major impact on the hatching time, growth and sexual maturation of *L. arcticus*. The time of sexual maturation showed great differences between the regions, but also within the same area and even within the populations (Table 5).

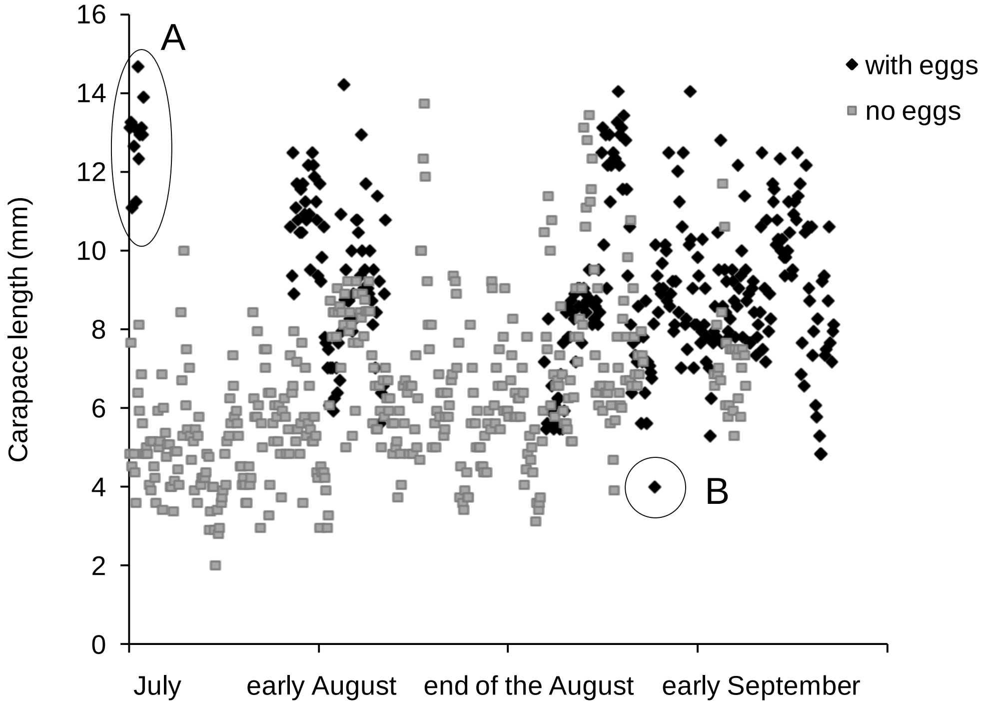


Figure 13. The carapace length (mm) of mature (with eggs) and immature (no eggs) *L. arcticus* (n=751) collected from 19 populations in different seasons (12th July – 6th September). Five of the populations were studied twice. A = the exceptionally large-sized animals in the small and slightly saline Dammyra pond. B = the exceptionally small mature *L. arcticus* in Storvatnet.

Table 5. Mean carapace length of *L. arcticus* and the occurrence of eggs in the foot capsules. (*=The animals had dropped 16 eggs from the foot capsules into the ethanol.)

Place and date	Number of specimens per sample	Mean carapace length (mm)	SD	Total of individuals carrying eggs	Total number of eggs	Egg distribution in brood pouches		Mean number of eggs per egg-bearing animal	Percentage of sample carrying eggs
						Left	Right		
Kapp Linné									
Pond 1, 13.7	42	4.9	1.12	0	0	0	0	-	0
Pond 2, 12.7	43	4.4	1.76	0	0	0	0	-	0
Pond 3, 13.7	34	4.5	1.34	0	0	0	0	-	0
Pond 4, 11.7	31	5.6	1.17	0	0	0	0	-	0
Pyramiden									
Pond 5, 18.7	1	4.8		0	0	0	0	-	0
Longyearbyen									
Dammyra, 31.7	12	12.9	1.00	12	73	41	32	6.1	100
The north coast									
Pond 10, 2-5.8	39	5.3	1.30	3	5	3	2	1.7	7.7
Pond 11, 2-5.8	38	8.3	1.23	5	8	2	6	1.6	13.2
Ny-Ålesund									
Solvatnet, 6.8	33	10.7	2.22	28	93	52	41	3.3	84.8
Tvillingvatnet ,6.8	33	4.6	1.01	0	0	0	0	-	0
Storvatnet, 8.8	35	7.0	1.69	8	13	7	6	1.6	22.9
Kolhamna, 8.8	43	7.1	1.72	19	36	18	18	1.9	44.2
Trehyrdingen 1, 8.8	32	7.1	1.96	4	11	5	6	2.8	12.5
Brandallaguna, 8.8	33	7.0	1.75	10	22	12	10	2.2	30.3
Longyearbyen									
Adventdalen 2, 18.8	33	6.3	0.91	23	33 *	14	19	1.4	69.7
Adventdalen 3, 23.8	36	8.5	0.58	29	53	30	23	1.8	80.6
Longyearbyen, 23.8	39	8.8	1.90	24	51	21	30	2.1	61.5
Ny-Ålesund									
Solvatnet, 31.8	32	12.1	1.27	22	124	65	59	5.6	68.8
Storvatnet, 31.8	42	6.8	1.30	21	40	20	20	1.9	59,0
Tvillingvatnet, 1.9	35	7.1	1.30	18	34	16	18	1.9	54.3
Trehyrdingen 1, 1.9	28	8.5	1.33	23	50	24	6	2.2	82.1
Trehyrdingen 2, 1.9	37	8.3	1.41	16	32	14	18	2.0	43.2
Brandallaguna, 1.9	29	8.5	2.20	27	67	30	37	2.5	93.1
Longyearbyen									
Nybyen, 6.9	31	10.7	0.97	29	80	45	35	2.8	93.5

The number of immature individuals was at its highest level in early summer and decreased towards late summer (Table 5 & Figure 14 & 15). Sexually mature individuals were more abundant than immature animals in the end of August and the same trend continued till September (Figure 14). Only in the Solvatnet *L. arctius* population the relative proportion (%) of mature animal was higher in early August than in the end of August (Figure 15).

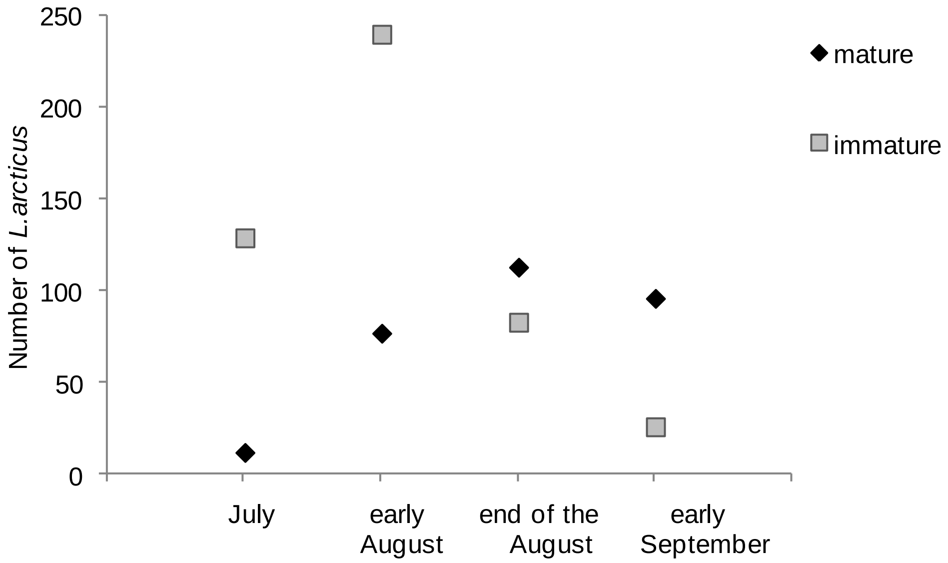


Figure 14. Number of mature and immature individuals (n=760) in different seasons (12th July – 6th September). The data is collected from 19 populations, of which five were studied twice.

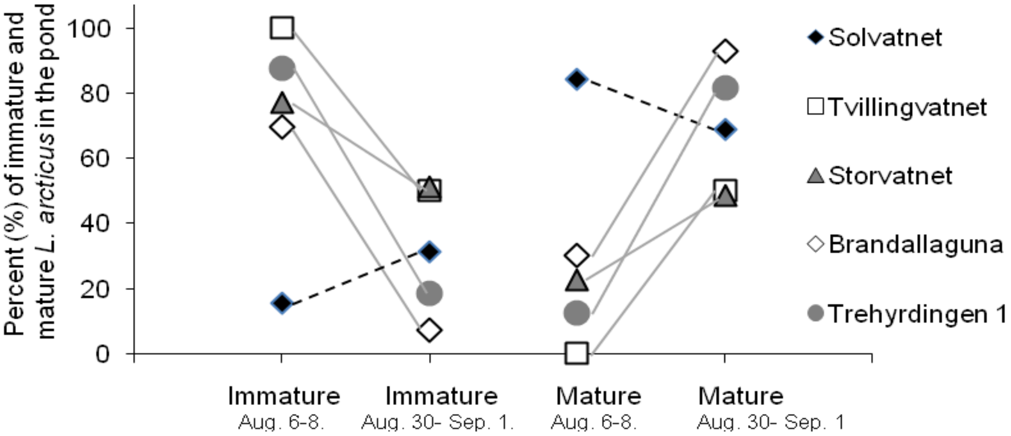


Figure 15. Shifts in the relative proportions (%) of mature and immature *L. arcticus* in five ponds in Ny-Ålesund. *L. arcticus* individuals (n=27–41) were collected twice from each study pond.

3.1.5. Reproduction and eggs

The female character (i.e. the carapace length when foot capsules appear on the 11th appendages) is reached at an exceptionally small size on Spitsbergen (Table 6). The foot capsules appear on 11th appendages in very small animals, at a carapace length of only 2.9 mm, in-mid July in Kapp Linné. Also maturity, defined by Sømme (1934) as the appearance of eggs in the foot capsules, seems to occur at a shorter carapace length and in later season on Spitsbergen than anywhere else. *L. arcticus* reached maturity already at 4.0 mm carapace length on Spitsbergen. The size of mature *L. arcticus* ranged from 4.0 mm to 9.1 mm. The size when *L. arcticus* reached sexual maturity depends on the period of the summer. It was interesting that the *L. arcticus* in Ny-Ålesund reached sexual maturity at larger size (5.9 mm) in the beginning of August than in late August (4.0 mm). The clearly smaller individuals (≤1.9 mm smaller carapace length) reached sexual maturity (i.e. carry eggs) in late autumn, than individuals in early autumn.

Table 6. Sizes at which the diagnostic female characters and the sexual maturity was reached in different *L. arcticus* populations.

Locality	Area	Carapace length at which capsules appeared on 11th appendages (mm)	Carapace length at which eggs appeared in capsules (mm)	Year	Author
Longyearbyen area 18-23.8	Spitsbergen	-	5.3 to 7.2	2010	Present data
Ny-Ålesund 6-8.8.2010	Spitsbergen	-	5.9 to 9.3	2010	Present data
Ny-Ålesund 31.8-1.9	Spitsbergen	-	4.0 to 9.1	2010	Present data
Kapp Linné 11-13.7.2010	Spitsbergen	2.9 to 8.0	-	2010	Present data
Syd Kapp	East Greenland	4.0 to 5.0	5.0	1962	Arnold 1966
Loch Fyne Fjord	East Greenland	4.5	-	1930	Sømme 1934
Myggbukta	East Greenland	4.7	6.8 to 7.4	1927-1930	Sømme 1934
Billen Bay	Spitsbergen	6 to 7	8.6 to 8.9	1896	Sømme 1934

On Spitsbergen, the total number of eggs varied between 0–12 (mean 2.6 eggs) in a single female (Table 7). Eggs were evenly distributed in the left and right foot capsules (Wilcoxon signed ranks test Z = -0.916, n = 322, p =0.360) (Table 5 & 8). *L. arcticus* females reached the sexual maturity (i.e. carry eggs) at a small body size (≥4 mm carapage length) and the sexual dimorphism begun to appear in small animals (2.9 mm carapace length) on Spitsbergen.

Table 7. The length and the egg count of *L. arcticus* in different northern regions.

Locality and time	Area	Total length in (mm) females	Number of eggs	Author
Kapp Linné 11-14.7.2010	The west coast of Spitsbergen, Norway	3.2-22.8	0	present data
Dammyra, Longyearbyen 31.7.2010	Nordenskiöld land of Spitsbergen, Norway	28.1-39.2	2-10	present data
Polheim, Mossel-halvøya, 3.8.2010	The north coast of Spitsbergen, Norway	13.4-30.8	0-3	present data
Kilneset, Reinsdyr-flya 4.8.2010	The north coast of Spitsbergen, Norway	7.3-20.5	0-2	present data
Ny-Ålesund 6-8.8.2010	The west coast of Spitsbergen, Norway	7.5-35.6	0-6	present data
Ny-Ålesund 30.8-1.9.2010	The west coast of Spitsbergen, Norway	11.4-39.4	0-12	present data
Longyearbyen 18.8-6.9.2010	Nordenskiöld land of Spitsbergen Norway	11.7-38.9	0-6	present data
Belushiya Bay 1993	Novaya Zemlya, Russia	15.8-22.1	1-2	Vekhoff 1997
Belushiya Bay 1994	Novaya Zemlya, Russia	12.3-25.6	1-4	Vekhoff 1997
Piritovyi Peninsula 1994-1995	Novaya Zemlya, Russia	15.1-29.6	1-5	Vekhoff 1997
Vaigatch Island 1995	Vaigatch Island, Russia	15.1-32.3	1-4	Vekhoff 1997
Matveev Island 1995	Near to Vaigatch Island, Russia	14.6-26.1	2-4	Vekhoff 1997

Table 8. Distribution of eggs in the left and right foot capsules of *L. arcticus*.

Place and date	Total number of egg-bearing specimens	Total number of eggs and distribution Left foot	Right foot	Mean number of eggs per animal	Author
Tuvetjern, Norway	165	183	166	2.1	Sømme 1934
Syd Kapp, East Greenland 3-25.8.1962	213	112	110	1.0	Arnold 1966
Spitsbergen, Norway 11.7-6.9.2010	319	419	406	2.6	Present data

The size of eggs where studied for 14 *L. arcticus* populations and five of these ponds where sampled twice Solvatnet, Sorvatnet, Tvillinvatnet, Trehyrdingen 1 and Brandallaguuna (Table 5). There was a large variation in the size of *L. arcticus* eggs. Eggs were found in seven different size classes (0.2, 0.3, 0.5, 0.6, 0.8, 0.9 and 1.1 mm) (Figure 15). The most common sizes of *L. arcticus* eggs were 0.8 mm and 0.6 mm. No large eggs (>0.8 mm) were observed in early spring. Small animals (carapace length 4.0–7.6 mm) were carrying only small (0.2–0.5 mm) and medium-sized (0.6–0.8 mm) eggs (Figure 15).

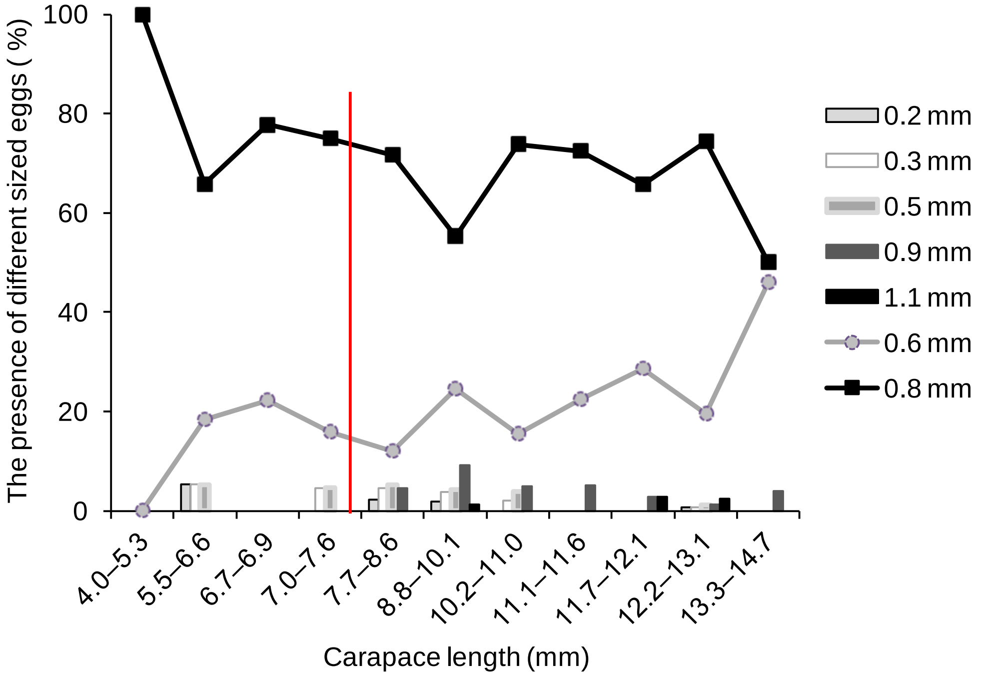


Figure 15. Contribution (%) of different egg sizes in the foot capsules of different *L. arcticus* size classes. The most common egg size was 0.8 mm. When the carapace length reached 7.7 mm (red line), animals began to have larger eggs >0.8 mm.

The number of eggs increased with increasing size of *L. arcticus* (Figure 16). When the *L. arcticus* reaches the carapace length of 4 mm they can reproduce (Figure 13). It should be noted that before reaching 8 mm in carapace length, the animals could only produce an mean of one egg.

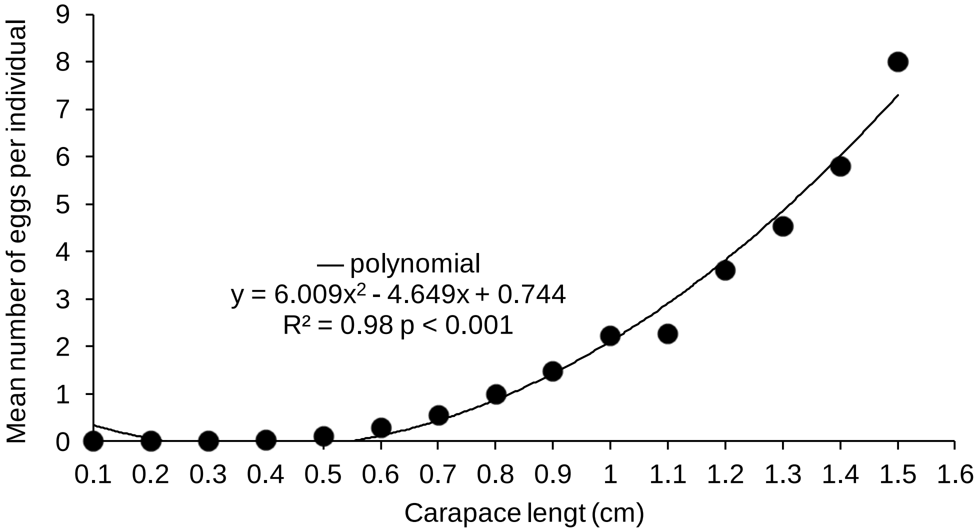


Figure 16. Mean number of eggs against the carapace length of *L. arcticus*. (n = 779).

3.1.6. Abiotic factors and body size

Water salinity seemed to have a large influence on the size of *L. arcticus*. Low water salinity seemed to speed up the growth and to enhance the development of eggs in *L. arcticus*. Females were exceptionally big in the slightly saline Dammyra pond in the end of July (Figure 13, A). The mean carapace length was 12.9 mm, even though the sediment temperature was only -1.4 °C. All females were carrying eggs and the numbers of eggs were notably high (2–12 eggs per female). Another interesting observation was that in Dammyra all females carried eggs. Other *L. arcticus* populations consisted of both immature and mature animals in the middle and late summer (Table 5). The large size did not always mean that the animal carried a lot of eggs. Some big *L. arcticus* individuals (≥ 10 mm carapace length) did not carry any eggs in late summer. These animals may have already laid their eggs or they were infertile. For example, as many as 16 eggs were found outside of the egg-capsules in Adventdalen second pond sample (n = 33 animals) in the middle of August (Table 5). In one interesting pond, Kolhamna, salinity may affect the animals' reproduction. Kolhamna was a temporal pond that dried up during the summer. In this pond the water salinity was slightly increased (0.5 ‰) before the complete drying and the animals began to reproduce more efficiently than similar-sized animals in the other permanent ponds at the same time. In Kolhamna pond, 44 % of the females were carrying eggs, while at same time in the other permanent ponds in Ny-Ålesund, only 10–31% of similar-sized animals were carrying eggs (Table 5).

Water and sediment temperatures also have a major impact on the size of *L. arcticus* (Appendices 4–9). Sediment temperature seemed to be the most important factor (R^2 = 0.41) which explain the *L. arcticus* size (Figure 17). At a particular time, *L. arcticus* were smaller in ponds located near the glacier than in ponds located close to the sea. *L. arcticus* were 41–57 % smaller in carapace length in ponds situated close to the glacier (700 m apart) than in ponds near to the sea (50 m apart).

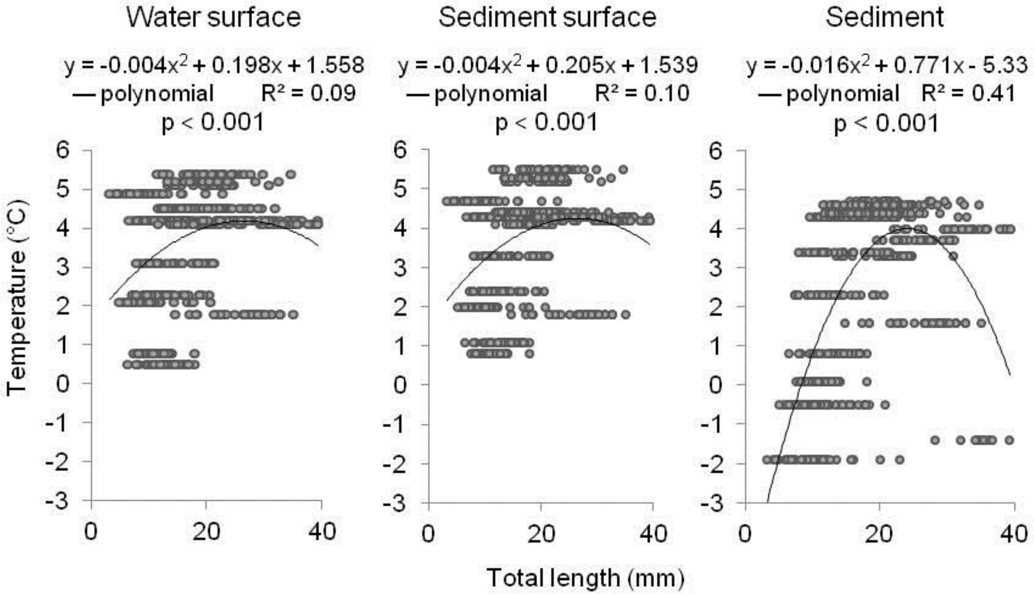


Figure 17. Regression between temperature (°C) and total length (mm). X-axis represents the *L. arcticus* total length and y-axis in the left represent the water surface temperature, in the middle sediment surface temperature and in the right sediment temperature. Black line is trend line.

3.2. Red Carapace Disease

Several individuals displayed sing of abnormal behaviour and symptoms of disease during the laboratory tests. Sick animals found in the nature and it was possible to follow the progression of the disease from different states to end under laboratory conditions. Symptoms of this disease were following: the carapace swells and turns red (Figure 18 B), the gills and the “egg sac” swells, the animal becomes exceptionally active and finally the carapace rises up. The disease named for Red Carapace Disease due to the distinct red coloration of the carapace (Figure 18).

The disease seemed to progress more rapidly in warm water, finally leading to death of the animal. Sometimes the disease developed in healthy-looking animals in the laboratory at 8–11 °C. The rise of water temperature often triggered the symptoms of the disease. This finding was supported by observations from natural *L. arcticus* populations. More sick animals were found in late summer than in early summer when the water and sediment temperature in the ponds was 1–4.3 °C higher than in the earlier seasons. Figure 19 shows the mean length of sick and healthy animals. No statistical differences or trend in size were found between sick and healthy animals. Red Carapace Disease was observed in eleven of the studied *L. arcticus* populations on Spitsbergen. In these populations, 2.7–37.5 % of the animals had the disease (Table 2).

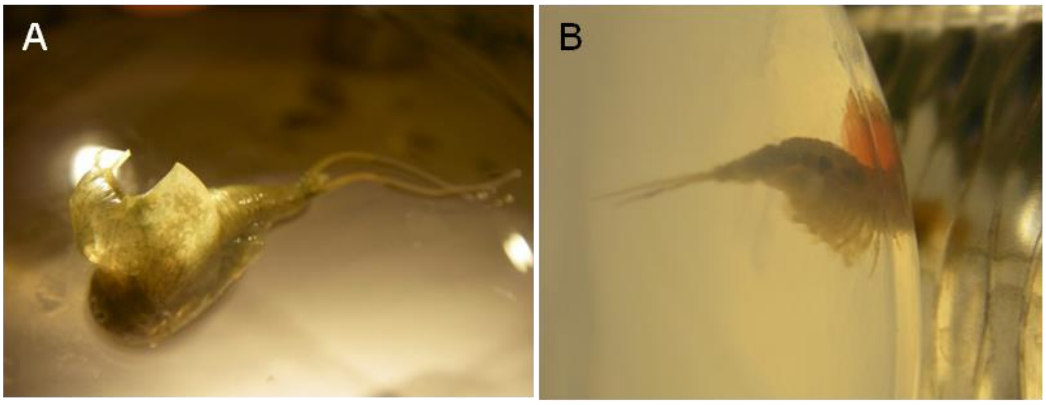


Figure 18. Photos of (A) ethanol-preserved and (B) live *L. arcticus* suffering from the Red Carapace Disease.

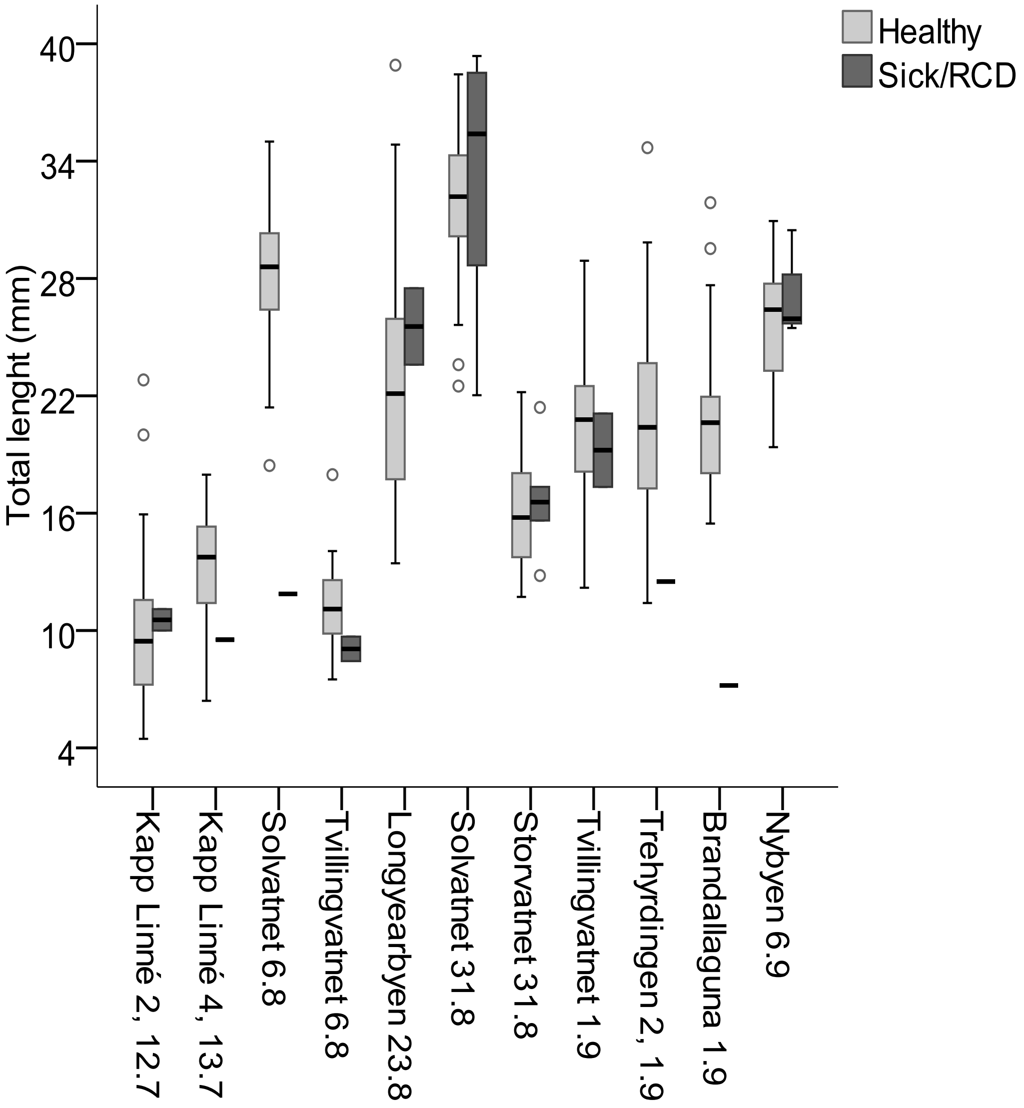


Figure 19. Box-plots showing the total length (mm) of sick and healthy animals at different times in different ponds. RCD = Red Carapace Disease. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum lengths. Circles (o) indicate the exceptionally long or short animals.

The *L. arcticus* parasite had many forms with greatly varying shape of tail and body (Figure 20, A–C). The parasite of *L. arcticus* was also found in a resting phase (Figure 20D).

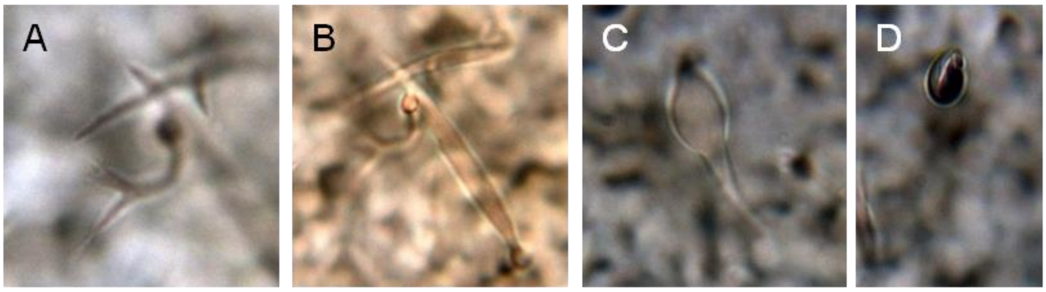


Figure 20. A possible parasite causing the Red Carapace Disease in *L. arcticus*. The variation in the parasite tail and body shape (A–C) and the resting phase of the parasite (D). The photos are cropped from pictures taken with a light microscope (100 x magnifications).

3.3. Colour morphs

Individual *L. arcticus* on Spitsbergen populations showed remarkable variation in body colour and appearance. The plain individuals had softer carapaces than the marbled animals. When the *L. arcticus* shell moult was close, the carapace shaded into translucent and soft. After the shell change, the carapace remained soft for some time. However, the light or dark colour was not only due to different stages of moulting. The colour was a unique and permanent property of individuals. In general *L. arcticus* were not able to change carapace colour in laboratory conditions with the exception of one individual from Kapp Linné that turned green. The reason for this colour change was probably the placing of the animal into too acidic water. The pH was 7.9–8.5 in the pond where the animal was collected from and only 6.3–6.4 in the water in laboratory (taken from Longyearbyen pond). The eggs of fresh *L. arcticus* were pale pink or white, and in ethanol-preserved individuals they were orange or white. The populations on Spitsbergen consisted of two major colour morphs (i.e. monochrome and marbled) and a combined colour phenotype. Remarkable spatial variation was found in the colour phenotype composition and diversity between and within the *L. arcticus* populations (Figure 21, 23).

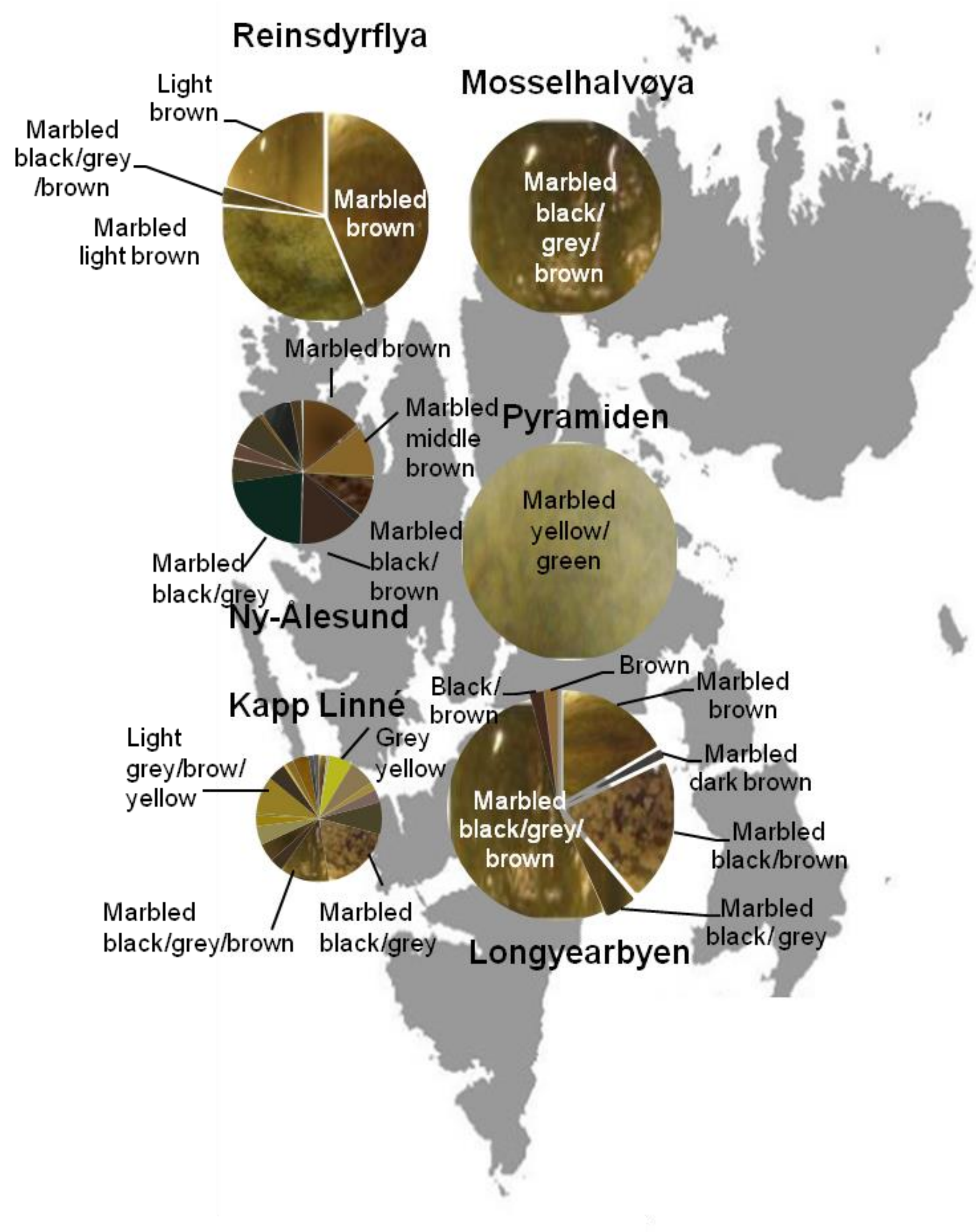


Figure 21. The existence of *L. arcticus* colour morphs in the six regions on Spitsbergen. Real colours from photographs of different colour morph are used for parts of the graphs' colour codes.

The classified phenotypes of *L. arcticus* on the Spitsbergen populations according to chromatophore pattern.

1.) Monochrome: orange, orange/grey, black, black/brown, grey, dark grey/black, grey/brown, light yellow/grey, grey/brown/yellow, light grey/brown/yellow, black/grey/brown, light/brown/yellow, brown, light brown, dark brown
2.) Marbled: light-, mellow-, middle- and dark brown, orange, light grey, light grey/yellow, yellow/green, light grey/brown/yellow, grey/brown, dark grey/brown, black, black/brown, black/grey, black/grey/brown, dark black/grey/brown and light black/grey/brown.
3.) Combination of monochrome and marbled

First, the colour morphs specialities are present in each study ponds and then focused on the purpose of different colour morphs.

Six colour morphs were observed in Tvillingvatnet in Ny-Ålesund (Figure 23). All colour morphs had black dots in the carapace in late summer (Figure 22, I). The marbled light brown individuals were exceptionally pale, almost white in the light parts of the carapace. Some individuals had an orange head. The orange colour covered 1/3 of the front side of the carapace on either side of the animal but in some individuals the orange colour was seen only on the dorsal side of the body. The preservation in 80 % ethanol changed the orange head colour into light or middle brown. The occurrence of RCD was examined carefully because this disease seemed to change the carapace colour into red. Four individuals for all studied animals in Tvillingvatnet were suffering from RCD and one of them had exceptionally small eyes. In this individual the disease had progressed into the final stage indicated by the swollen carapace that was raised to an upright position.

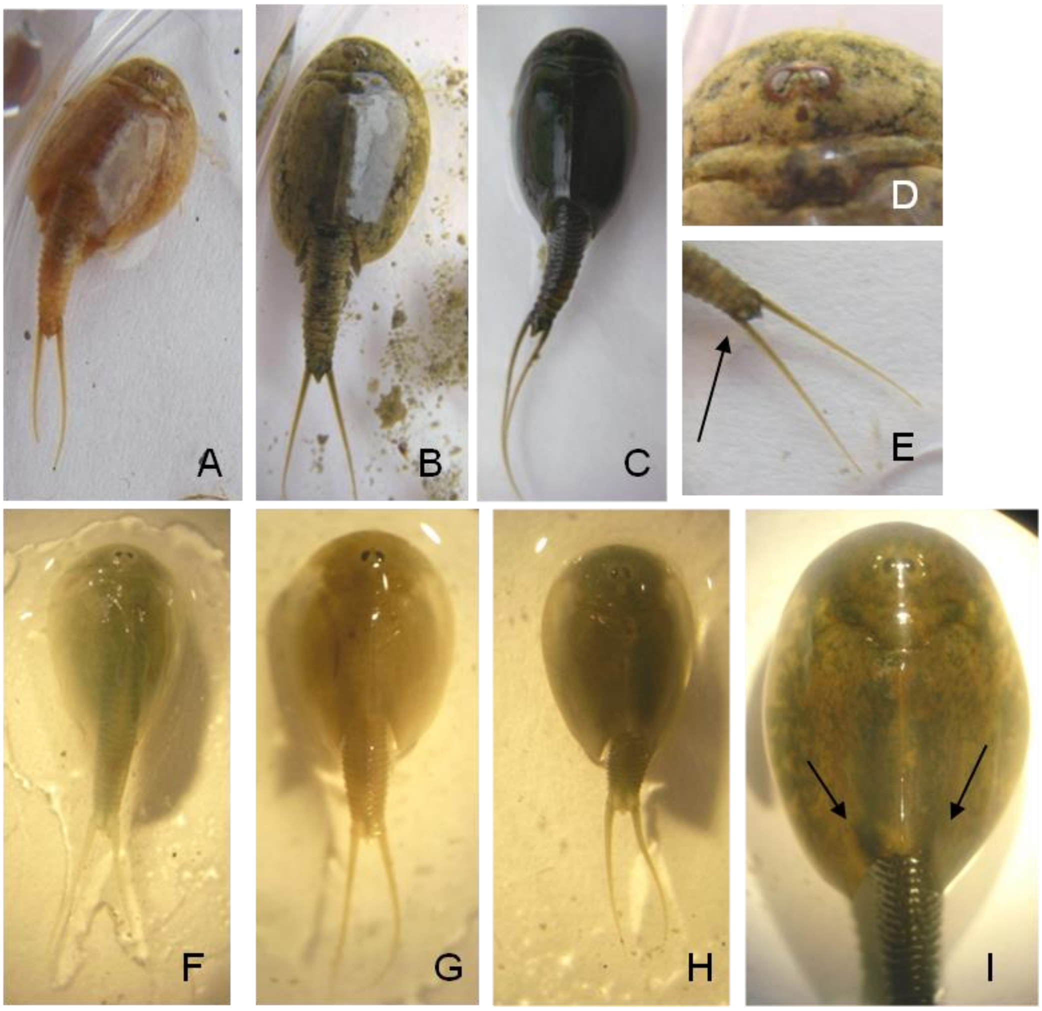


Figure 22. *L. arcticus* colour morphs. A= marbled orange, B= marbled brown, C= monochrome black, D= the red area around the eyes (red mask), E = two light spots on the supra-anal plate, F= marbled colourless, G= monochrome orange, H= grey/black, I= marbled brown/black/grey, two black spots at the lower part of the carapace. The photos A-E are taken from living *L. arcticus* while F-I are taken from animals preserved in 80 % ethanol.

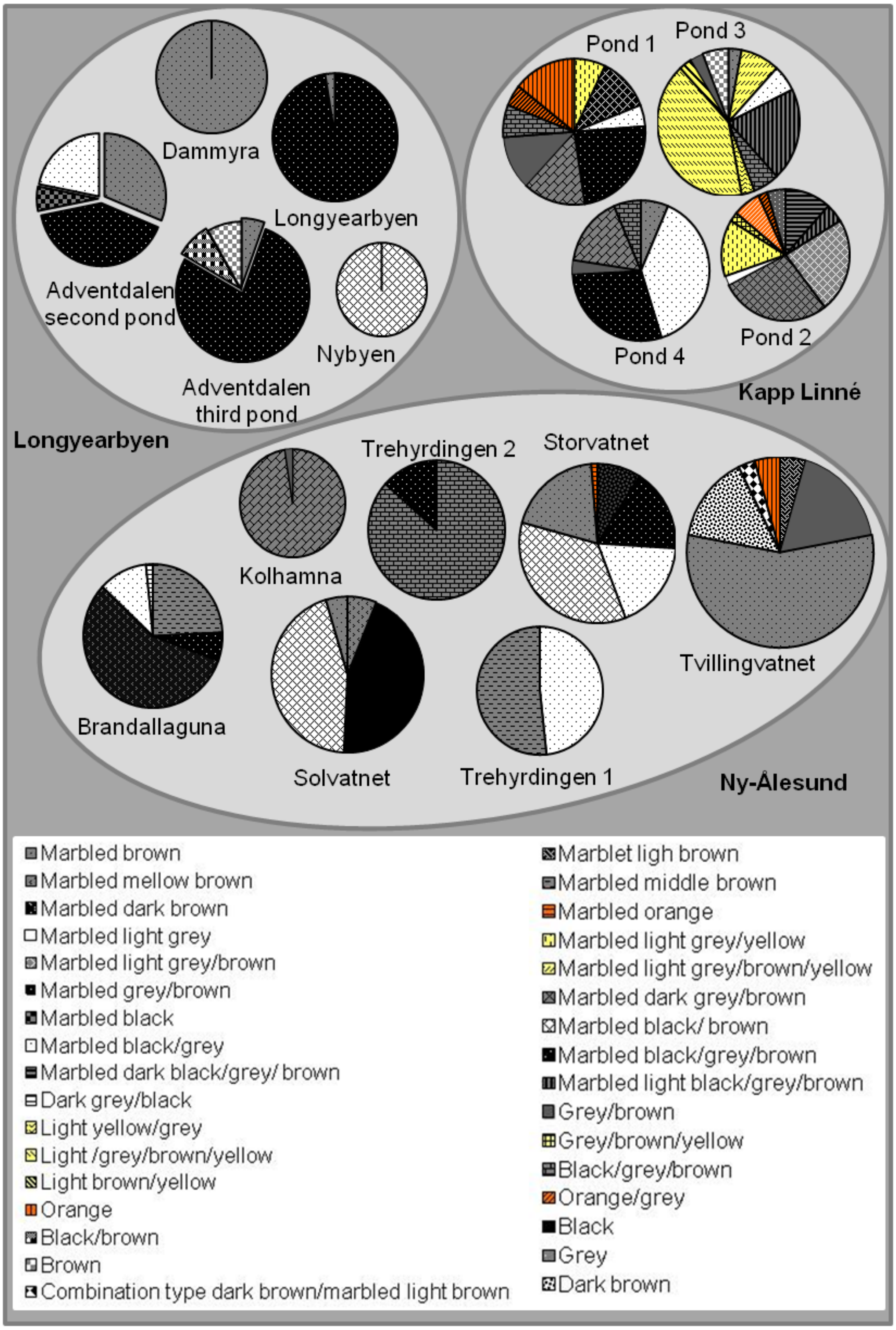


Figure 23. Occurrence of *L. arcticus* colour morphs in three main study areas (Longyearbyen, Kapp Linné and Ny-Ålesund).

Two colour morphs were observed in the temporal pond Kolhamna in Ny-Ålesund (Figure 23). Living individuals had red stripes on the both sides of the carapace. Some individuals had black spots in their carapace or light spots on their supra-anal plate (Figure 22 E & 22 I) or a protruded eye form (Figure 24 B). In this population many animals had a brownish area in their head (Figure 24 A). In the Kolhamna population, no RCD was observed but carapace injuries were very common (Figure 9 B).

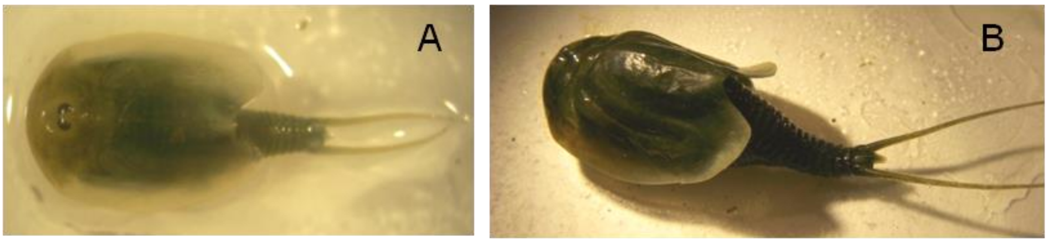


Figure 24. Individuals in temporal Kolhamna pond. A= brown head area and light spots on supra-anal plate. B= protruded eye form. The photos are taken from *L. arcticus* preserved in 80 % ethanol.

Two colour morphs were found from Trehyrdingen 2 pond in Ny-Ålesund (Figure 23). All marbled grey/black/brown individuals had light dots on the supra-anal plate, whereas the other colour morph had both dotted and dotless individuals. The living marbled grey/black/brown morph had a delicate green shade on their carapace. Some monochrome grey/black/brown individuals had light dots in middle part of the carapace (Figure 25). The monochrome had a soft and the marbled animals had a hard carapace. The orange area around the eyes and the black supra-anal plate was a unique feature of this population. One *L. arcticus* was suffering from RCD in this population.

Figure 25. Light dots on middle part of carapace were a unique feature of seven individuals in Trehyrdingen 2.

Two colour morphs were found in Trehyrdingen 1 pond in Ny-Ålesund (Figure 23). The contrast was very clear between dark and pale areas of carapace. This population differed from the one in the nearest pond Trehyrdingen 2 because the eye area of the animals was not orange or red. The eye area mask was a bit lighter than the area around it, but not orange (Figure 26). This population was also characterized by a protruded eye form. Two animals had paler eyes than the others and in some animals the posterior part of the carapace was grey. Major differences were found in the length and thickness of individuals' telson setae (Figure 27). The telson setae were orange at marbled middle brown morph, which was also uncommon feature among Spitsbergen *L. arcticus* populations (Figure 26). RCD was not found in this population, but one individual had an injured carapace.

Figure 26. Marbled middle brown colour morph of *L. arcticus* in Trehyrdingen 1. Contrast between the pale and dark brown areas of the carapace are very strong, the supra-anal plate is black and has two light dots, the telson setae are orange, and the eye area is protruded, not red or orange. The photo is taken from a living *L. arcticus.*

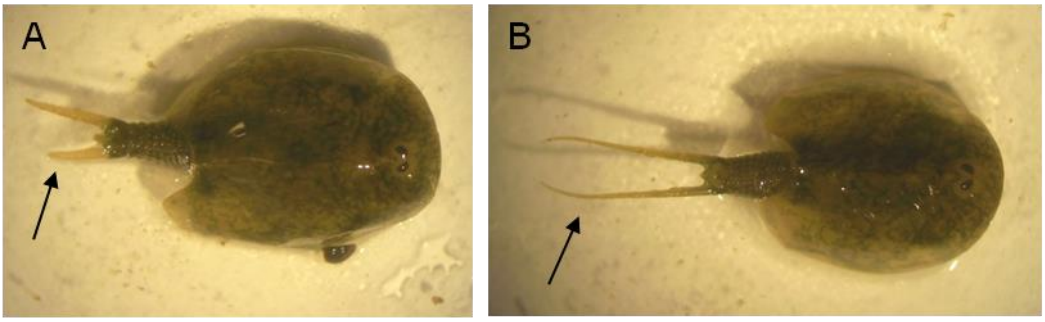


Figure 27. Similar-sized *L. arcticus* individuals in the same population can be very different by their morphology. A= the robust telson setae. B= the long and thin telson setae. The photos are taken from ethanol-preserved *L. arcticus* samples from Trehyrdingen 1 population.

Five colour morphs were found from Brandallaguna pond in Ny-Ålesund (Figure 23). The main colour morphs were marbled middle brown and marbled dark brown (Figure 28). All morphs had a dark supra-anal plate. Some animals had light dots on their supra-anal plate. The red mask was typical for the middle brown morph. *L. arcticus* had an unusual eye structure. The dorsal surface of the head bears a pair of compound eyes, an ocellus and the dorsal organ. Immediately in front of the compound eyes lies the ocellus which detects light. An unpaired and oval-shaped dorsal organ with unknown function located behind the compound eyes. The dorsal organ was exceptionally red and clearly visible at the head of middle brown morph (Figure 28 C). The red mask and dark supra-anal plate were also observed in *L. arcticus* population in Trehyrdingen 2. One animal suffered from RCD and three animals had broken telson setae.

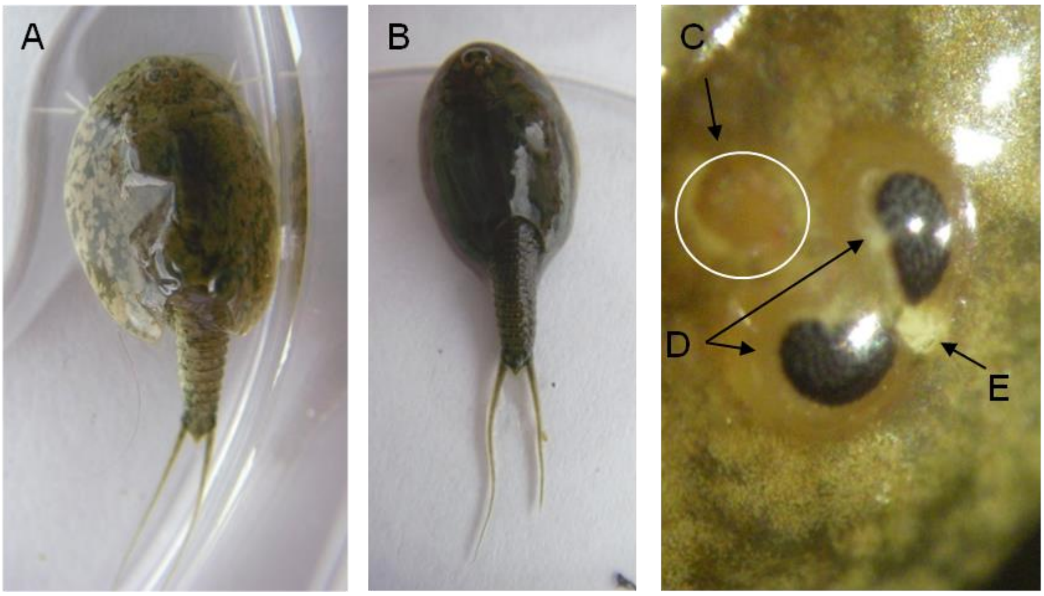


Figure 28. Two main colour morphs in pond Brandallaguna and the structure of the eyes and dorsal organ. A= marbled middle brown colour morph, B= marbled dark brown colour morphs, C= dorsal organ, D= pair of compound eyes and E= ocellus. Note the exceptionally visible dorsal organ and the red eye mask of the middle brown morph (A). Photos are taken from living *L. arcticus.*

Four colour morphs were observed in Solvatnet pond in Ny-Ålesund (Figure 23, 29). The most common morph was black. Carapace of black morph was soft and lumpy. Marbled brown morph had a small yellow ring around the dorsal organ. Animals of different colours and sizes were living in different parts of the pond. The *L. arcticus* dietary habits were observed on different habitat types (on soft sediment and among water moss) in the field. Dark animals were often living on soft sediment and preyed upon *D. pulex* at about 1 m depth. Animals with marbled colour were living among the water mosses and preyed upon Chironomidae larva. Animals in this population had many kinds of injuries including broken telson setae, missing egg-capsule, head injuries and eye problems (blind animals). RCD was very common in this population (20 % animals were sick).

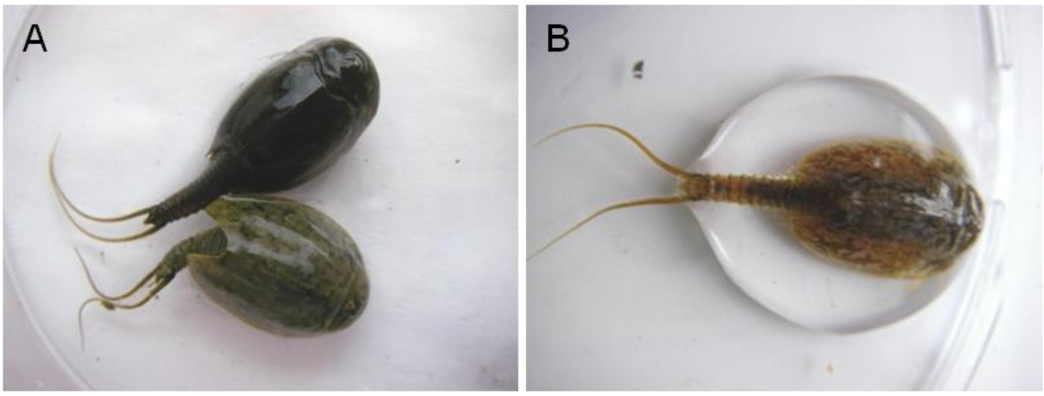


Figure 29. Three colour morphs in Solvatnet in Ny-Ålesund. A= Black and marbled brown colour morphs. B= Marbled mellow brown colour morph. Photos are taken from living *L. arcticus.*

Six colour morphs were found in Storvatnet pond in Ny-Ålesund (Figure 23). All morphs had a red mask but the mask was more visible in light than in the dark animals. Some individuals also had a dark supra-anal plate. Discovery of the orange morph in Ny-Ålesund pond was a big surprise (Figure 30 A), because this morph was typical only in the Kapp Linné area. Many animals had several injuries on their carapace and six animals were suffering from RCD.

Only one *L. arcticus* was found from Pond 5 in Pyramiden (Figure 21). The marbled colour of the animal was a combination of yellow and green (Figure 30 B).

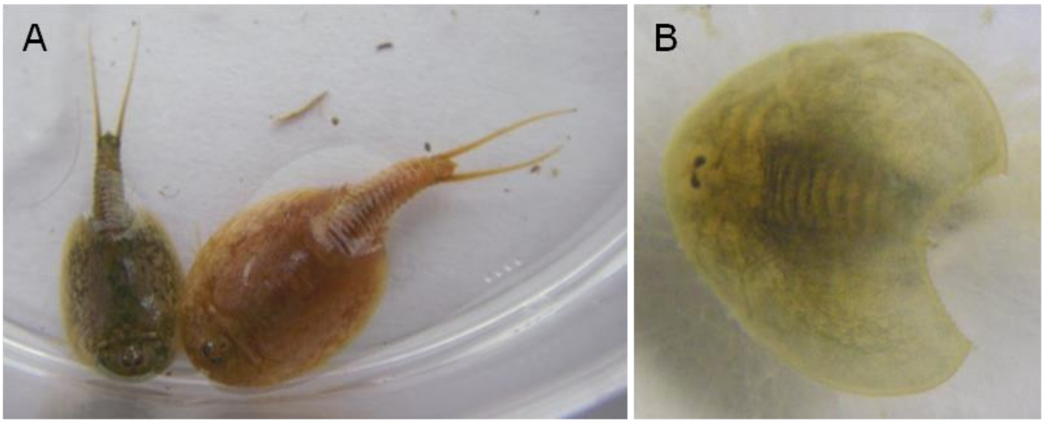


Figure 30. Untypical *L. arcticus* colour morphs were found from Ny-Ålesund and Pyramiden. A= untypical marbled orange morph was found from Storvatnet in Ny-Ålesund. B= the *L. arcticus* colour in pond 5 in Pyramiden was an extraordinary combination of yellow and green.

One colour morph was found from the pond Polheim (Mosselhalvøya) on the northern coast of Spitsbergen (Figure 21). Animals in this population had brown head areas and light brown mouth parts. Some animals had light dots on the supra-anal plate. RCD was not observed in this population.

Four colour morphs were observed in pond Kilneset (Reinsdyrflya) on the northern coast of Spitsbergen (Figure 21, 31). All individuals were slightly orange. Some dark animals had light dots on the supra-anal plate. RCD was not observed in Kilneset population. Two individuals had broken telson setae.

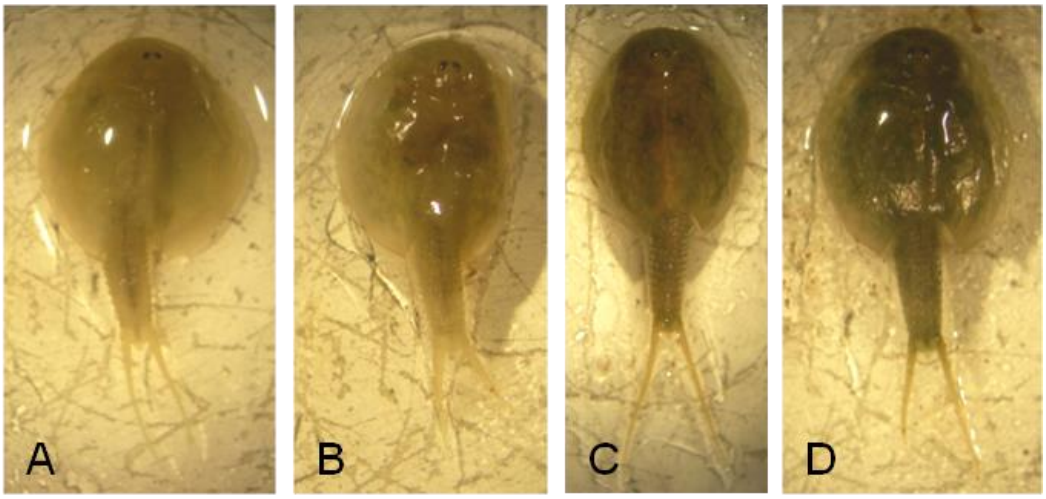


Figure 31. Four colour morphs in Kilneset on the north coast of Spitsbergen: A= light brown, B= marbled light brown, C= marbled brown and D= marbled black/grey/brown. Photos are taken from ethanol-preserved *L. arcticus*.

The presence of several colour morphs was a distinctive feature for all *L. arcticus* populations in Kapp Linné area. Also the abundant presence of orange morph was an unique feature in this area (Figure 32).

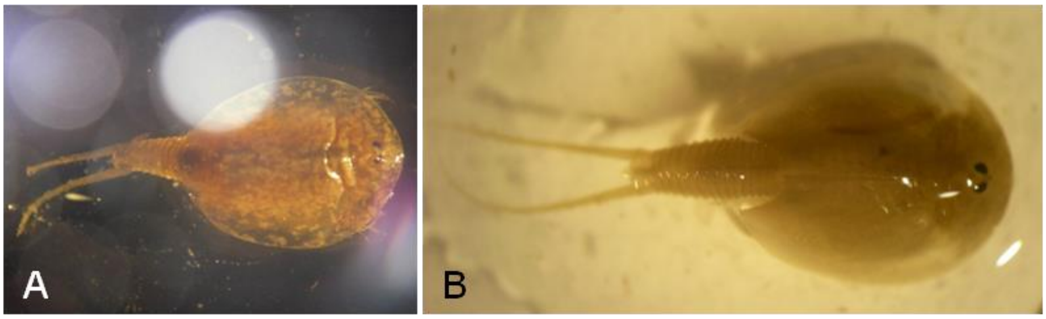


Figure 32. Orange colour morphs were common in Kapp Linné area. A= the marbled orange colour morph (living individual), B= the monochrome orange colour morph (preserved in 80 % ethanol).

Nine colour morphs were found from Pond 1 in Kapp Linné (Figure 23). The marbled light grey/yellow individuals were almost colourless. RCD was not observed in this population. Ten colour morphs were found from Pond 2 in Kapp Linné (Figure 23). Note that some differences in colours (dark and light) could be explained by different moulting times. Holes in carapaces and broken telson setae were common in this population. Two animals were suffering from RCD. Ten colour morphs were found from Pond 3 in Kapp Linné (Figure 23). RCD was not observed in this population. Six colour morphs were observed in Pond 4 in Kapp Linnè (Figure 23). One *L. arcticus* had RCD.

Two colour morphs were observed in Longyearbyen pond in Longyearbyen (Figure 23). Most individuals had light dots on the supra-anal plate. Two animals were suffering from RCD.

One colour morph was found from Nybyen in Longyearbyen (Figure 23). Some individuals had a red mask, but the most interesting feature was the colour of telson. Both sides of the telson were lighter than the dorsal and ventral surfaces and the dorsal side of the telson was slightly orange (Figure 33). The dark supra-anal plate had two light dots. Only one animal had injuries in the carapace. In Nybyen pond three animals were suffering from RCD.

Figure 33. The marbled black/brown morph in small Nybyen pond. The colouring of telson was unique in this population. Photos are taken from living *L. arcticus.*

Four colour morphs were found in Adventdalen second pond in Longyearbyen (Figure 23). Mouth area 1/3 of both side of carapace was red, but legs were brown. The red mask, the two black spots at the lower part of the carapace (Figure 22 D & 22 I) and the red area on the distal part of the telson were typical features for *L. arcticus* in Adventdalen second pond. Physical injuries were observed for this population. Almost all legs were missing for two animals. Four colour morphs were found from nearby Adventdalen third pond in Longyearbyen (Figure 23).

One colour morph was observed in Dammyra in Longyearbyen (Figure 23). In this population the large females were characterized by a protruded eye form and by a light dot on the carapace that was not observed in any other population (Figure 34). One animal had RCD.

Figure 34. A light dot on the lower part of the carapace was an unique feature for *L. arcticus* in the small saline Dammyra pond.

The occurrence of the three main colour morphs (black, brown and orange) in different habitat types (sand/sludge, bryophytes and cyanobacteria) is presented in Table 9. The sand/sludge and bryophytes habitats were found in all *L. arcticus* ponds. The surface colour of sand/sludge sediment was often grey or light brown, while the bryophyte vegetation was green or brown. More detailed description of the sediment colour and quality is presented in Appendix 3. The orange cyanobacteria mat, which grew on the stones, was not so common habitat type (Table 9). This orange cyanobacteria habitat was found in half of the ponds where orange *L. arcticus* morph was present and also in the ponds where orange morph was not found.

Table 9. The occurrence of three main habitat types (sand/sludge, bryophytes and cyanobacteria) and three *L. arcticus* colour morphs (black, brown and orange) in the five regions on Spitsbergen. Here the colour morphs include all the variety of black, brown and orange colouration. N/A = data is not available, N/L = *L. arcticus* is not present in the pond.

Area	Longyearbyen						Kapp Linné				Pyramiden		Ny-Ålesund									Northern coast of Spitsbergen	
Pond name	Longyearbyen	Dammyra	Adventdalen 1	Adventdalen 2	Adventdalen 3	Nybyen	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6	Solvatnet	Tvillingvatnet	Storvatnet	Kolhamna	Trehyrdingen 1	Trehyrdingen 2	Brandallaguna	Geese pond	Gluudneset	Kilmeset	Polheim
Habitat colour types																							
 Sand/sludge	X	X	N/A	X	X	X	X	X	X	X	X	N/L X	X	X	X	X	X	X	X	N/L X	N/L X	X	X
 Bryophytes	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X
 Cyanobacteria							X		X	X		X			X		X	X					X
L. arcticus colours																							
 Black	X			X	X	X	X	X	X	X			X		X	X	X	X	X			X	X
 Brown	X	X		X	X		X	X	X	X			X	X	X	X	X		X			X	
 Orange							X	X						X	X								

The orange or yellow colour morphs do not mimic any aposematic invertebrate or crustacean species living in the Arctic, but may instead mimic the shape and colour (orange and yellow) of polar willow (*Salix polaris*) autumn leaves (Figure 35). *S. polaris* turns into autumn-colour early (Rønning 1996) and it is a common plant near the study ponds (Appendix 2).

Figure 35. The orange and yellow morphs may mimic the colour of an autumn coloured polar willow (*S. polaris*) leaves. Note the similarity of shapes between *L. arcticus* carapace (right and left) and the *S. polaris* leaves.

3.4. Olfaction

Differences were observed between the treatments in the placement of the test animals in separate sectors of the test container (Figure 36). Squares 7, 8 and 9 were among the most popular squares in all the treatments (Figure 36). In the treatment with crushed *L. arcticus*, the odour corner (square one) was the most popular square (Figure 36). Also in the treatment with algae, the odour corner was more popular than in the control treatment (Figure 36). In the treatments with algae and crushed *L. arcticus*, the animals did not at all attach to the corner three. Animals in the algae and crushed *L. arcticus* treatments most often attached themselves to the corner one, where the source of odour was located (Figure 36). Nine animals in crushed *L. arcticus* treatment, eight animals in algae treatment and four animals in control treatment were attached to the "odour" corner. Animals in the control treatment attached most often to the corner seven.

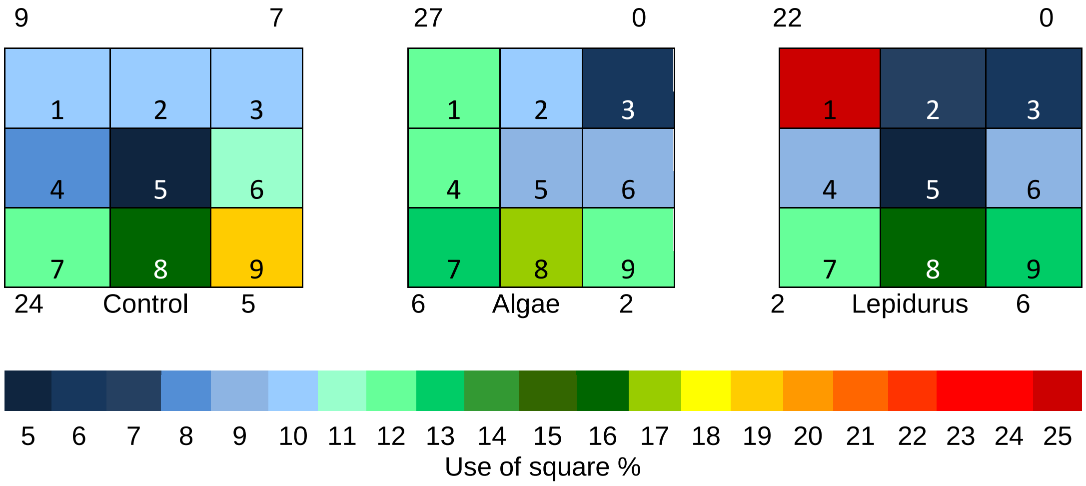


Figure 36. The figure shows how much time *L. arcticus* spent in different areas of the aquarium in the control, algae and crushed *L. arcticus* treatments in the olfaction experiment. The colours represent the relative proportion (%) of time the animals spent in each square. The numbers inside the grid are square numbers. The numbers outside the grid indicate how many times the animals caught the tip of the pipette in corner of the aquarium. Square one was the odour corner in the algae and crushed *L. arcticus* treatments.

By examining the number of squares *L. arcticus* visited in different treatments, *L. arcticus* was found to be most active in the treatment with crushed *L. arcticus*. Numbers of visit in different squares (pc) were calculated. Mean number of visits in different squares were 285 (max 459 visits, min 95 visits) in crushed *L. arcticus* treatment, 117 (max 185 visits, min 9 visits) in algae treatment and 139 (max 369 visits, min 24 visits) in control treatment. The animal activity differed significantly between the treatments (one-way ANOVA, F=15.393; p<0.001). Animals were more active in the crushed *L. arcticus* treatment than in the other treatments (Tukey p<0.001). This exceptionally active behaviour in the crushed *L. arcticus* treatment was seen as high numbers of visits in different squares and as avoidance of animals to stay in a single square for a long time (Figure 37 and 38). One *L. arcticus* in the control treatment was unusually active and visited different squares exceptionally frequently (Figure 37).

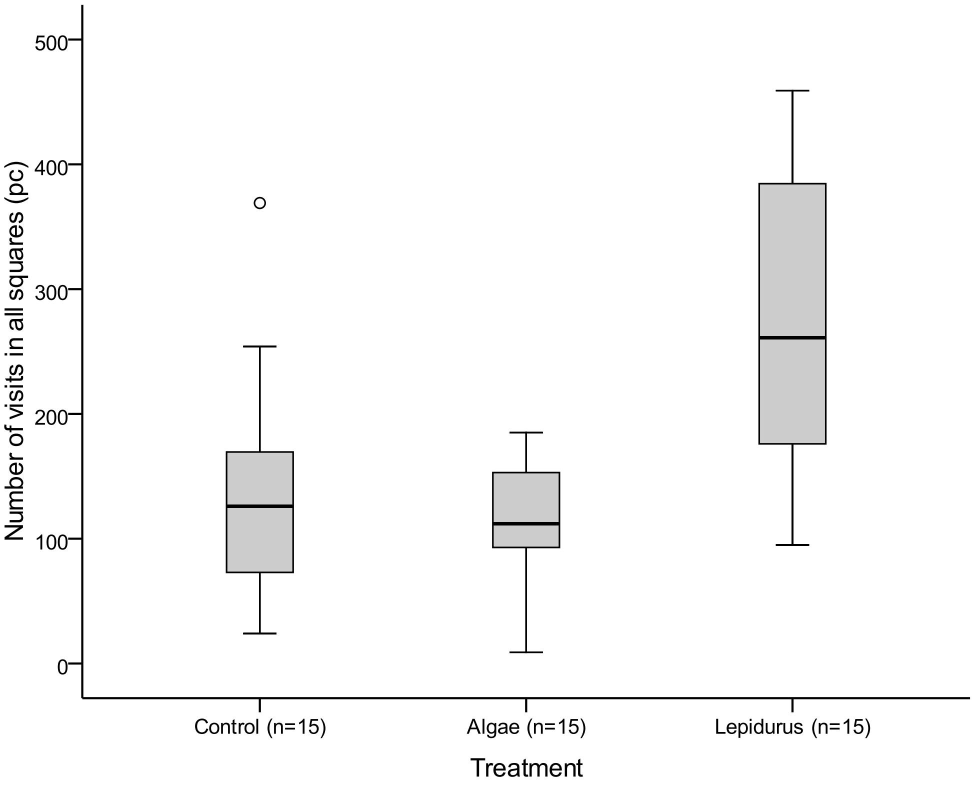


Figure 37. *L. arcticus* activity in the different olfaction treatments. Y-axis shows how many times animals visited in different squares during the 15 minute test. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values. The circle (o) indicates the exceptionally active animal in the control treatment.

Increased activity in the crushed *L. arcticus* treatment was also reflected to increase in *L. arcticus* swimming speed. The mean times (seconds, s) the animals spent in a single square were 3.1 s (range 1.9–5.0 s) in crushed *L. arcticus* treatment, 8.5 s (range 5.3–28 s) in algae treatment and 6.9 s (range 2.4–11.8 s) in control treatment (Figure 38). The *L. arcticus* swimming speed (activity) differed significantly between the treatments (Kruskal–Wallis -test: p<0.001). In the crushed *L. arcticus* treatment, animals spend less time in a square (i.e. swam faster) than in the other treatments (Mann-Whitney U-test: p<0.005) (Figure 38). One *L. arcticus* in the algae treatment was exceptionally calm and spend a mean of 28 s in each square.

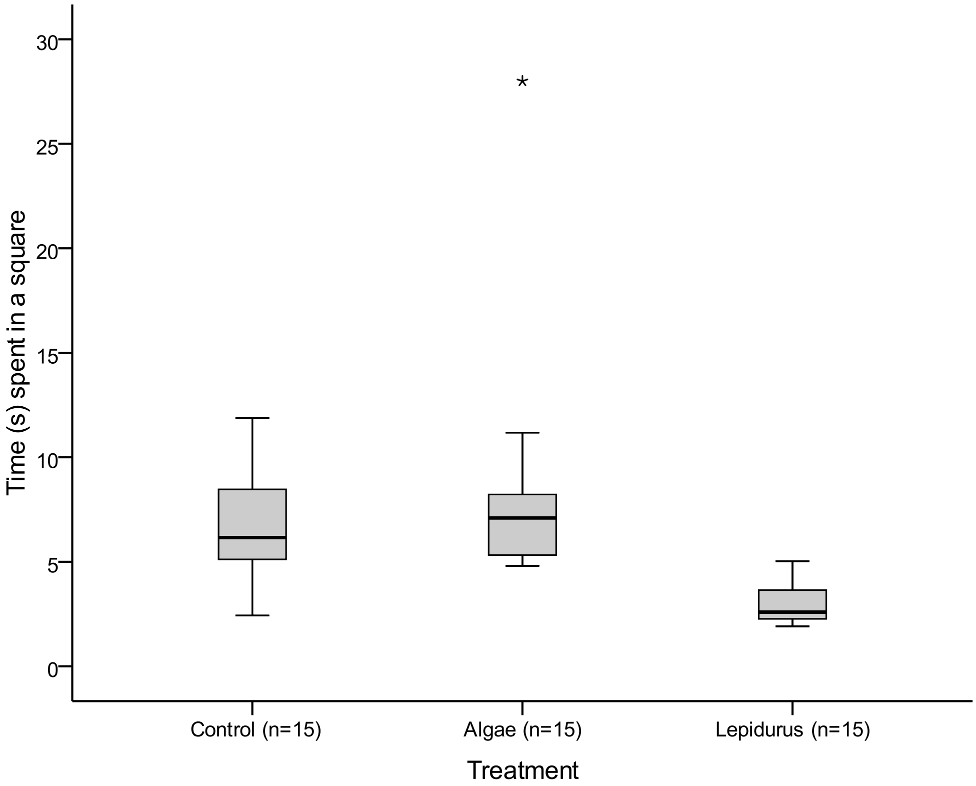


Figure 38. Box-plot showing the even mean time (s) animals spent in one square. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values. Star (*) indicates the exceptionally behaved animal in algae treatment that spend an mean of 28 s per square.

The time the animals spent in central square differed significantly between the treatments (Kruskal–Wallis -test: p = 0.009). The test animals in the algae treatment spent significantly more time in the middle of the container than animals in the control or in the crushed *L. arcticus* treatments (Mann-Whitney U-test: algae vs. control p=0.012; algae vs. Lepidurus p=0.06; Figure 39). The animals in control and in crushed *L. arcticus* treatments spent on mean 32–35 % less time (i.e. on mean half a minute less) in the middle of the container than animals in algae treatment.

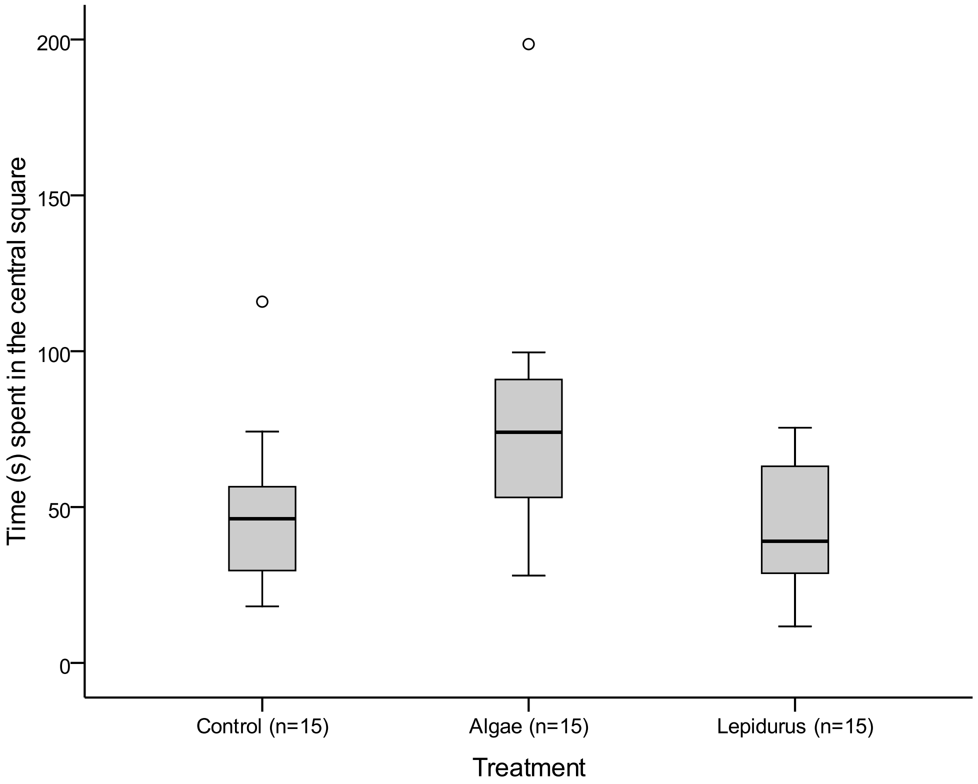


Figure 39. Time (s) spent in the central square in the olfaction test. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values. Circles (o) indicate two animals that spent unusually long time in the middle square.

There were no significant differences between the treatments in the time the animals spent in the odour corner (Kruskal–Wallis -test: p = 0.515). However, three animals in crushed *L. arcticus* treatment spent a considerably longer time in the square one than any individuals in the other treatments (Figure 40). These three animals spent 52–53 % of the time in the odour corner, while the other animals in the same treatment spent only 14 % of the time in odour corner.

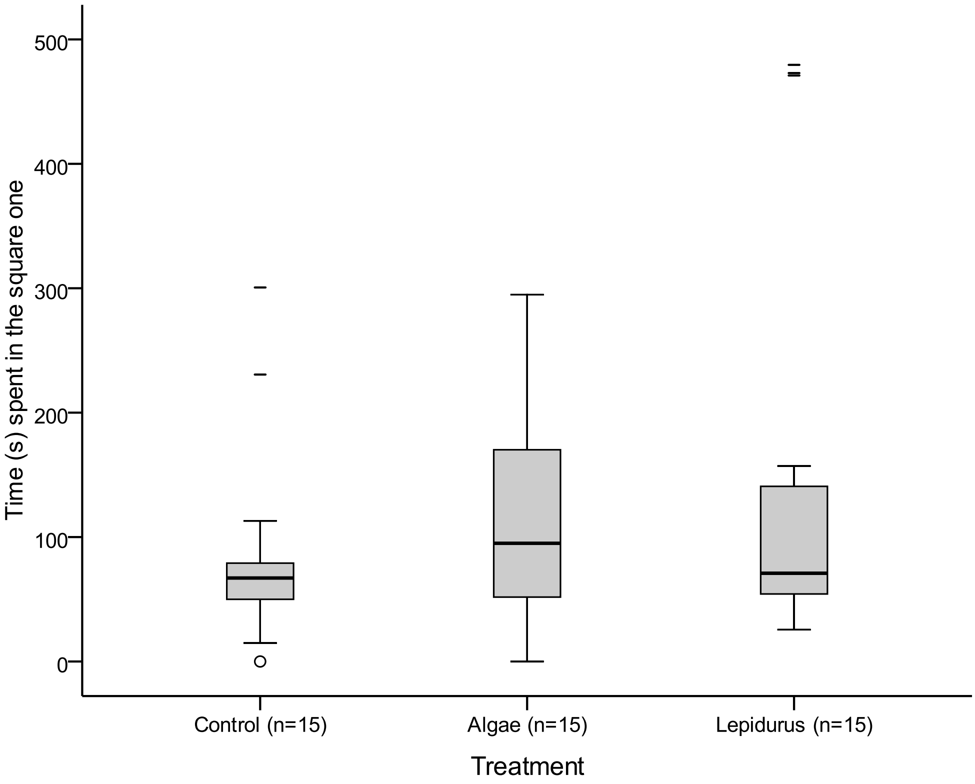


Figure 40. The use of square 1 ("the odour corner") in the olfaction test. Olfaction experiment observed how much time (s) animals spend in the "odour corner" (square 1) with no odour, algae (i.e. crustacean food made of algae) or crushed *L. arcticus* added. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values. The lines (–) indicate the animals that spent unusually long time in the square one. The circle (o) indicates the animal in control treatment that did not visited the square one at all.

3.5. Water chemistry in the High Arctic ponds

L. arcticus was present in 20 ponds, but 19 ponds were included to this water chemistry summary because Advendalen first pond was excluded. The mean oxygen concentration in these ponds was 51 %. The mean surface temperature of water and sediment was 3.4 °C, and the mean sediment temperature was 2.5 °C. The water pH varied between 6.3 and 8.5. The mean water conductivity was 412 µS/cm and the mean salinity was 0.2 ‰. The physical and chemical characteristics of the 23 study ponds are summarized in Table 10. More detailed description of the water chemistry data can be found in the Appendix 4 (Longyearbyen), Appendix 5 (Kapp Linné), Appendix 6 (Pyramiden), Appendix 7 (the northern coast of Spitsbergen) and Appendices 8–9 (Ny–Ålesund).

Table 10. Physical and chemical characteristics of the 23 study ponds, including ponds with and without *L. arcticus*. More details are given in Appendices 4–8.

	Area a	Water T °C	Salinity ‰	pH	Cond. µS cm^{-1}	Chl µg L^{-1}	TOC mg L^{-1}	DOC mg L^{-1}	^{tot}N mg L^{-1}	^{tot}P µg L^{-1}
Mean	220	3.4	0.2	7.8	656	1.68	6.5	5.6	0.4	28.3
Max.	1380	5.4	2.8	8.5	5230	9.04	52.0	57.0	1.1	89.0
Min.	0.06	0.2	0.0	6.3	84	0.13	0.9	0.6	0.1	3.6

The high TOC and DOC concentrations indicated high runoff of allochthonous matter from the catchments. TOC ranged from 0.9 to 52.0 mg l^{-1} (mean 6.5 mg l^{-1}), while DOC ranged from 0.6 to 57.0 mg l^{-1} (mean 5.6 mg l^{-1}). Three ponds in Ny-Ålesund (Storvatnet, Trehyrdingen 1 and Brandallaguna) were sampled twice to study seasonal variation in TOC and DOC concentrations. Exceptionally high TOC (52.0 mg l^{-1}) and DOC (57.0 mg l^{-1}) were measured from Brandallaguna in Ny-Ålesund (Figure 41), where the large glacial river Bayelva flows near the pond.

The sediment organic matter (OM %) ranged from 2 to 54 % (mean 17 %). Low sediment organic carbon per cent was measured from Pond 4 (2 %) and Pond 1 (4 %) in Kapp Linné, from Nybyen (4%) and Adventdalen second pond (9 %) in Longyearbyen, from Pond 5 (6 %) in Pyramiden, from Tvillingvatnet (4 %) and Brandallaguna (5 %) in Ny-Ålesund and from Polheim (2 %) in Mosselhalvøya. Very high OM % was measured from Pond 2 (54 %) in Kapp Linnè, from Dammyra (44 %) in Longyearbyen and from Solvatnet (31 %) in Ny-Ålesund.

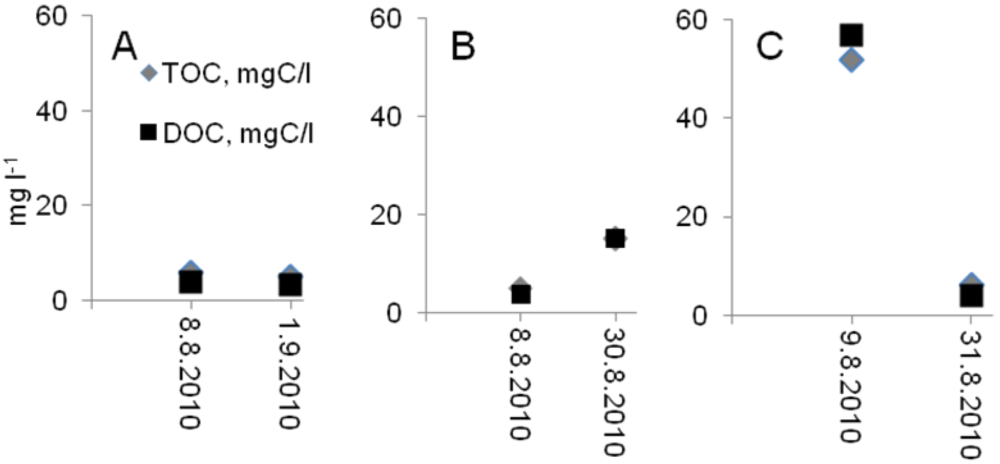


Figure 41. Changes in the total organic carbon (TOC) and dissolved organic carbon (DOC) in three study ponds in Ny-Ålesund. A = Storvatnet, B = Trehyrdingen 1 and C = Brandallaguna.

Relatively low concentrations of total nitrogen (^{tot}N) were observed in the study ponds on Spitsbergen. The ^{tot}N ranged from 0.065 to 1.050 mg l^{-1} with a mean of 0.367 mg l^{-1}. Remarkably low ^{tot}N was measured in Tvillingvatnet (0.065 mg l^{-1}), which is the drinking water pond in Ny-Ålesund. The highest ^{tot}N levels (1.050 mg l^{-1}) were measured only 1.2 km away from the Tvillingvatnet. Solvatnet was a nitrogen-rich pond located very close to the sea.

Total phosphorus (^{tot}P) ranged from 3.6 to 89.0 µg l^{-1} (mean 28.3 µg l^{-1}). Even 46 % of the ponds showed a relatively high ^{tot}P concentration (>25 mg l^{-1}). The highest ^{tot}P concentrations were measured from "Geese pond" (89 µg l^{-1}) and Storvatnet (51 µg l^{-1}) in Ny-Ålesund and from Dammyra (66 µg l^{-1}) in Longyearbyen. No *L. arcticus* were found living in Geese pond. A lot of barnacle goose (7–48 pc) was seen near these phosphorus-rich ponds (Appendix 1). *L. arcticus* were exceptionally large in Dammyra and in Solvatnet. Exceptionally low ^{tot}P low concentrations (4–11 µg l^{-1}) were measured from five ponds: from pond 3 in Kapp Linné, from pond 6 in Pyramiden, from Tvillingvatnet and Kolhamna in Ny-Ålesund and from Adventdalen third pond in Longyearbyen. No barnacle geeses were observed near the phosphorus-poor ponds Kolhamna, Pond

3 and Pond 6 (Appendix 1). The total phosphorus/total nitrogen ratio (TN: TP) ranged from 4:1 to 39:1 with a mean of 17:1.

Chlorophyll-a (Chl-a) concentrations were consistently low ranging from 0.13 to 9.04 with a mean of 1.68 µg l^{-1}. The highest Chl-a concentration was measured from Pond 4 in Kapp Linné. Chl-a concentrations were measured from two size fractions (normal ≥2.7 µm and small size 2.7–0.7 µm). Proportions of smaller size Chl-a were between 0.9 % to 12.6 % (mean 5.1 %) of the total Chl-a concentration.

3.6. Sensitivity of L. arcticus *to changes in water salinity*

The resistance of *L. arcticus* to osmotic shock due to increase in water salinity was studied in a LC_{50} experiment measuring the lethal concentration in which 50 % of the animals die within 48 hours. All animals died within 48 hours when the water salinity was increased to 11 ‰ or 12 ‰ (Figure 42). However, all animals survived 48 hours in the control and in the 1 ‰, 2 ‰ and 6 ‰ treatments, whereas 93 % of the animals survived when the water salinity was increased to 3–5 ‰ or to 7–8 ‰. Survival of *L. arcticus* was poor in 5–12 ‰ treatment, being less than 34 % after seven days. Low salt concentrations (0–2 ‰) were well tolerated. *L. arcticus* tolerated the 12 ‰ salinity for five hours, 11 ‰ for 12 hours, 10 ‰ for 48 hours, 9 ‰ for two days, and 8 ‰ and 7 ‰ for a maximum of five days. The *L. arcticus* safe salinity (0.471 ‰) was defined to be equal to 96 h-LC_{50} x 0.1. A salinity of 1.85 ‰ had no significant effect on the mortality of *L. arcticus*. Findings from the laboratory tests were supported by observations from natural *L. arcticus* populations. A good example of the *L. arcticus* salinity tolerance was the Dammyra population living in a pond with a water salinity of 1.5 ‰.

Mortality occurred in the control group in the three weeks salinity experiment; therefore, control mortality was reduced from other treatments. During the experiment five animals died due to the Red Carapace Disease. One animal failed to change shell and died when the old shell was stuck around the telson.

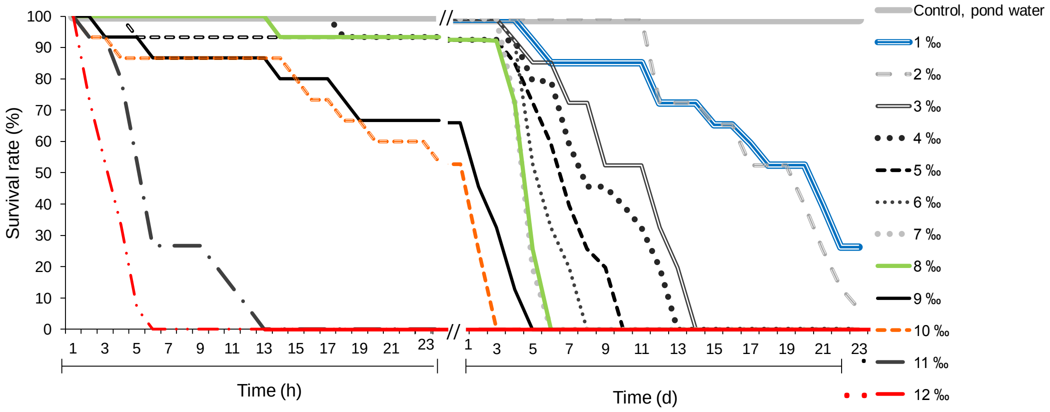


Figure 42. Survival rate of *L. arcticus* in different salinity treatments. Y-axis indicates the percentage of survived animals and the x-axis shows the hours (left) and days (right) after the start of the experiment. Treatment mortality is adjusted by mortality from the control group.

A low salinity had an effect on *L. arcticus* growth. In the beginning of the experiment no significant difference in the day of the first ecdysis was observed between the low-salinity treatments (Kruskal-Wallis -test: p=0.081; Figure 43). In the control group, the first ecdysis occurred on the eighth day after the start of the experiment (mean 8.1, SD ± 1.05 days). In the 1 ‰ salinity, the first ecdysis occurred on the sixth day (mean 6.5, SD ± 1.57 days). In the 2 ‰ salinity, the first ecdysis occurred on the eighth day (mean 8.2, SD ± 2.61 days). In the 3 ‰ salinity only one animal survived from the first ecdysis. The first and only ecdysis in the 3 ‰ salinity occurred on the sixth day after the start of the experiment. In the 4 ‰ salinity two *L. arcticus* survived from the first ecdysis. The first and only ecdysis in the 4 ‰ salinity occurred on the seventh day.

There were significant differences in the start of second ecdysis between the treatments (Kruskal-Wallis -test: p=0.045). A low salt concentration (1 ‰) significantly speeded up the second ecdysis of *L. arcticus* during the LC$_{50}$-salinity experiment (Figure 43). In the control (0.1 ‰), animals changed shell later than in 1 ‰ salinity concentration (Mann-Whitney -test: p=0.008). The second ecdysis occurred on the eight days after the first edysis, in the control group (mean 8.3, SD ± 1.49 days), on the sixth day of the 1 ‰ salt treatment (mean 6.7, SD ± 0.95 days) and on the seventh day of 2 ‰ salt treatment (mean 7.0, SD ± 3.5 days). This mean that the *L. arcticus* exchange their shell every 7–11 days in fresh water, every 5–9 days in 1 ‰ salt water and every 2–10 days in 2 ‰ salt water.

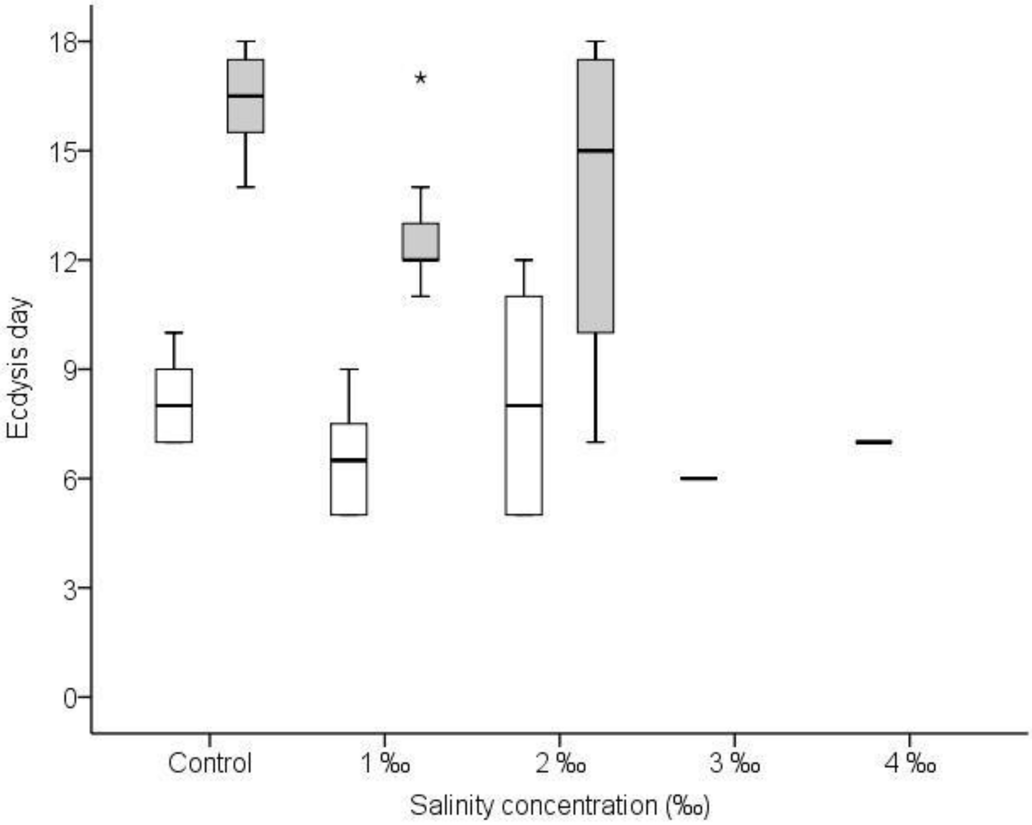


Figure 43. The day of the first ecdysis (white) and second ecdysis (grey) of *L. arcticus* in different salinity treatments in the LC_{50}-salinity experiment. Star (*) indicates one individual in 1 ‰ salinity concentration that changed the shell exceptionally late. Salt concentration was 0.1 ‰ in the control treatment. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values.

3.7. Sensitivity of *L. arcticus to changes in water pH*

The tolerance limit of *L. arcticus* was tested in different water pH levels (4.0, 4.5, 8.0, 8.5 and control pH 7.6). *L. arcticus* tolerated a short-term (48 h) acidification of water up to pH ≥4.5. No mortality was observed in the control group suggesting that natural death of *L. arcticus* or other external factors not influenced the result of the experiment. Mature *L. arcticus* began to die when the animals were exposed to very low pH (pH 4) (Figure 44). In pH 4 the animals reached 50 % mortality in 18 hours and all died by the end of the experiment. In mature females no-effect pH-time was pH 4.941–13.5 days. In the other treatments (pH 8.49–4.5) none of the *L. arcticus* died during the experiment.

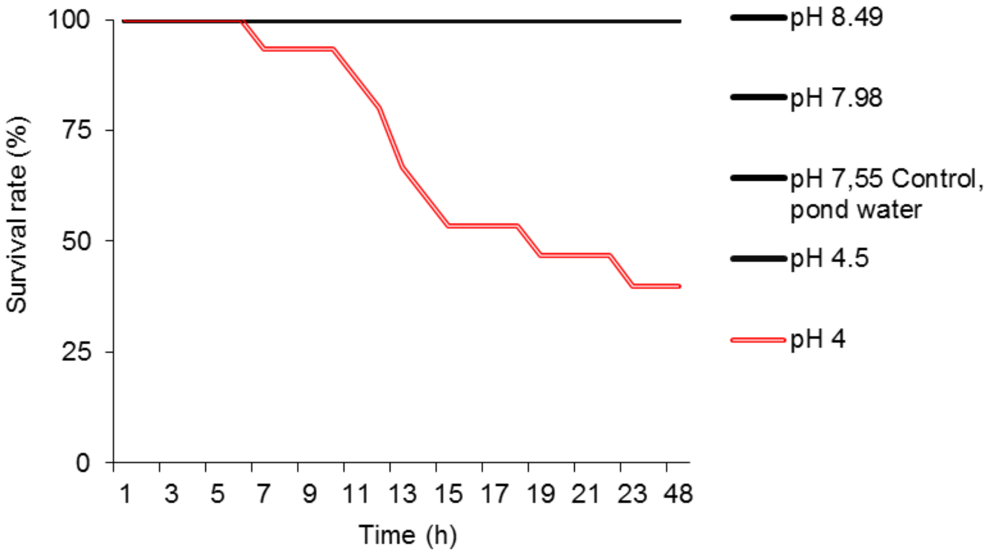


Figure 44. Survival of *L. arcticus* in different pH treatments in the LC_{50}-pH experiment. Y-axis represents the survival percentage and the x-axis is the time in hours.

The natural pH in *L. arcticus* ponds varied between 6.25 and 8.84 (mean 7.76) (Appendices 4–9 & Table 11). The lowest pH values were measured from ponds in Longyearbyen (Appendix 4). The lowest pH value (6.25) was measured near a dog kennel in Adventdalen. The pH was also low (6.33–6.45) in the

Longyearbyen pond in early summer, when no *L. arcticus* were observed in the pond. In contrast, in late summer, higher pH values (7.6–7.9) were measured from Longyearbyen pond and at that time *L. arcticus* were also found abundantly.

Table 11. The influence of water pH to the occurrence of *L. arcticus* in ponds on Spitsbergen and in other northern regions.

Place	*L. arcticus* does not occur pH and year	*L. arcticus* occur pH and year	Author
Longyearbyen, Svalbard, Norway	–	6.25–8.06 (2010)	Present data
Pyramiden, Svalbard, Norway	6.92–7.96 (2010)	6.58–7.31 (2010)	Present data
Kapp Linné, Svalbard, Norway	–	7.94–8.41 (2010)	Present data
Ny-Ålesund, Svalbard, Norway	8.28–8.75 (2010)	7.14–8.84 (2010)	Present data
Mossel halvøya, Svalbard, Norway	–	7.76–8.09 (2010)	Present data
Reinsdy-flya, Svalbard, Norway	–	7.95–8.12 (2010)	Present data
L.Svartavastjørni outlet, Norway	5.17–7.27 (1993–2000)	6.10–7.11 (2001–2004)	Fjellheim et al. 2007
L.Svartavatnet outlet, Norway	5.18–6.70 (1993–1998)	6.26–6.89 (1999-2004)	Fjellheim et al. 2007
Jåttolako, Padjelanta national park, Sweden		7.7–7.8 (1994)	Blomkvist 1995
–		6.1–6.8	Borgstrøm et al. 1976
Sweden		6.3–7.0	Borgstrøm & Larsson 1974
Greenland		6.2–8.0	Röen 1962

3.8. The effect of increase in water temperature to the oxygen consumption of L. arcticus

There were significant differences between the temperature treatments (one-way ANOVA, F=6.221, p = 0.001). However, only the oxygen consumption in 10 °C differed significantly from the other treatments ($p=<0.05$), except from the 16.5 °C treatment. The final oxygen consumption values were corrected for control baselines. The respiration rate reached its peak at 10 °C and then declined sharply with increasing temperature (Figure 45). Three animals began to die rapidly when the water temperature was 30 °C. The concentration of dissolved oxygen decreased with increasing water temperature. In 30 °C the oxygen concentration was 235.9 µmol l^{-1} and this concentration was lethal for *L. arcticus*. *L. arcticus* seemed to have a temperature optimum at around 10 °C, but survived when the water temperature varied between 3.5 and 20 °C. All *L. arcticus* populations lived in a very cold water (0.2–5.5 °C) in ponds on Spitsbergen.

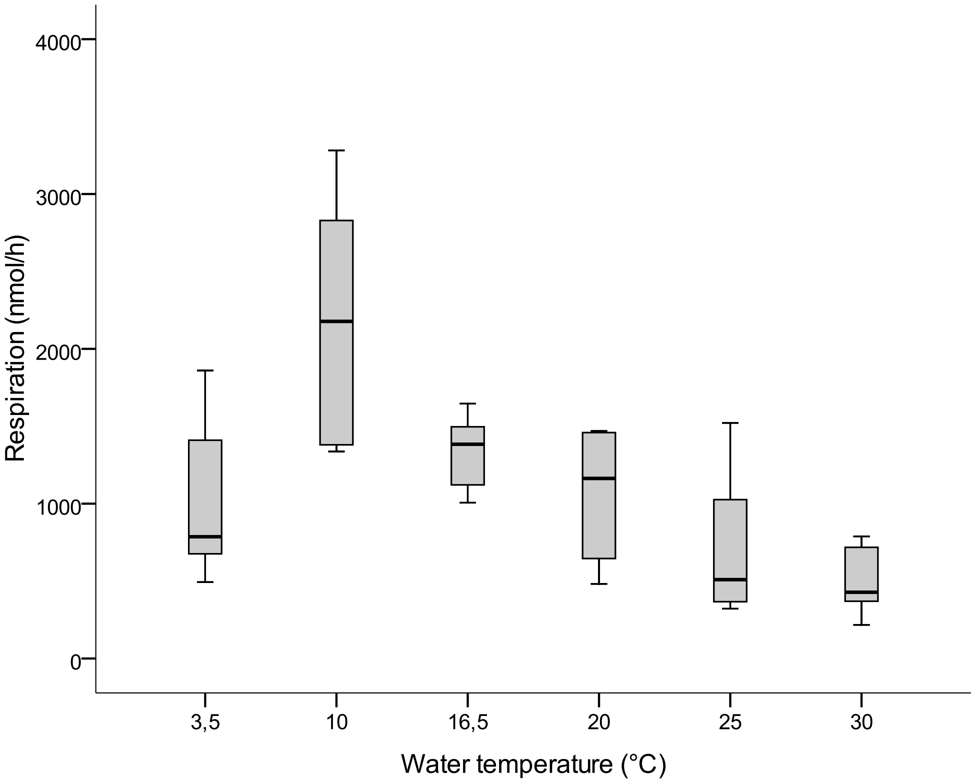


Figure 45. The oxygen consumption (nmol/h) of *L. arcticus* (n = 5 per treatment) in different temperatures. In the box-plots, lines indicate the median, boxes show the upper and lower quartiles and whiskers stand for the observed minimum and maximum values.

The temperature coefficient Q_{10} is a convenient way to examine the temperature dependency of the oxygen consumption process. *L. arcticus* showed considerable sensitivity to temperature, responding to rising temperature with a rapidly descending Q_{10} values. Q_{10}`s ranged from 0.45 to 3.15 (Figure 46). The Q_{10} was 3.15 when the water temperature changed from 3.5 to 10 C°. Q_{10} on physiological reaction is usually between 1.5 and 2.5, sometimes even higher (Tirri et al. 2001). The sharp decline in the respiratory activity of *L. arcticus* at higher temperatures (16.5–30 °C) was reflected to a low Q_{10} value (< 0.53). The exceptionally low Q_{10} values were measured when the temperature changed from 10 to 16.5 °C, from 16.5 to 20 °C, from 20 to 25 °C and from 25 to 30 °C (Figure 46).

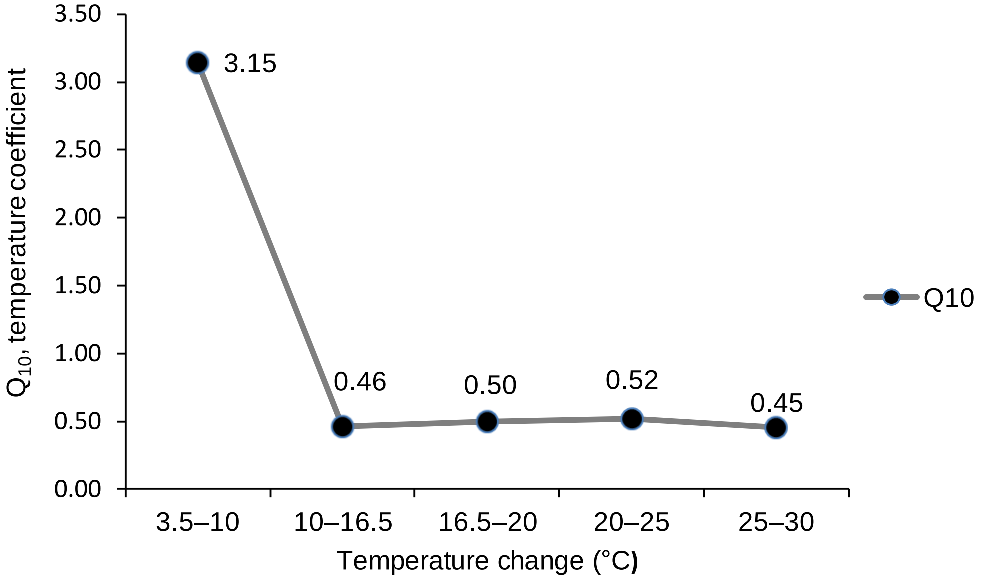


Figure 46. The temperature coefficient (Q_{10}) values represent the factor by which the respiration rate (R nmol/h) increases when the temperature (T) is raised by 10 °C. Note that T_1 and T_2 do not need to be exactly 10 °C apart in order to use the equation. The respiration rate increases with increasing temperatures only at low temperatures (3.5-10 °C). The (Q_{10}) values were calculated using the equation $Q_{10}=(R2/R1)^{10/(T2-T1)}$ (Tirri et al. 2001).

The sensitivity of *L. arcticus* to selected environmental variables is summarized in Table 12. The values are threshold values for the *L. arcticus* long-term exposure to selected environmental stressors.

Table 12. Tolerance limits of *L. arcticus* to different environmental stressors.

	No change	Reduced	Extinct
Temperature	occurs 0.8–19 °C	16.5–20 °C	>20 °C
pH	>7	7-6.1	<6.1
pH and TOC	pH>7 & TOC ?	pH<7 & TOC<1.5mg/l	pH<6.1 & TOC<1.5mg/l
Salinity	0-1 ‰	1-2 ‰	>2 ‰
O_2	>315 µmol/l	>258 µmol/l	≤258 µmol/l

4.2. Colour morphs

Different environmental variables such as UV-radiation and food availability may influence the colouration of *L. arcticus* on Spitsbergen. The selective advantages (e.g. the ability to avoid predation or harmful effects from UV) of different colour morphs likely depends on the depth and heterogeneity of the habitat and on the biotic diversity of the community. These elements are strongly affected by different abiotic factors.

The *L. arcticus* populations on Spitsbergen showed a great diversity in colour patterns. The function of these diverse colour patterns may include protection against visual predators such as birds, fish or cannibalistic conspecific or/and against UV-radiation (Figure 47). The colour pattern may reflect fitness of an individual and help *L. arcticus* to find a mating partner. The newly hatched larvae of *Lepidurus* species may be densely coloured with carotenoid pigments (Longhurst 1955). For example, the colour of *Triops cancriformis* larvae is very variable and probably depends on the feeding and nutrition of the parents: well-fed females can have pink eggs with carotenoids while starving females usually have white eggs (Fox 1949). Note that the *L. arcticus* eggs are pink or white but the ethanol preserved eggs are orange or white.

The variability of colour patterns among *L. arcticus* provides an exceptional example of biological diversity in High Arctic region. Cryptic individuals, like marbled orange and marbled brown living on orange cyanobacteria mats or among water mosses, respectively, are not easily detected by predators. The black morph, which distinctly contrasts with their light grey habitat, may instead protect animal against UV-radiation (Figure 47).

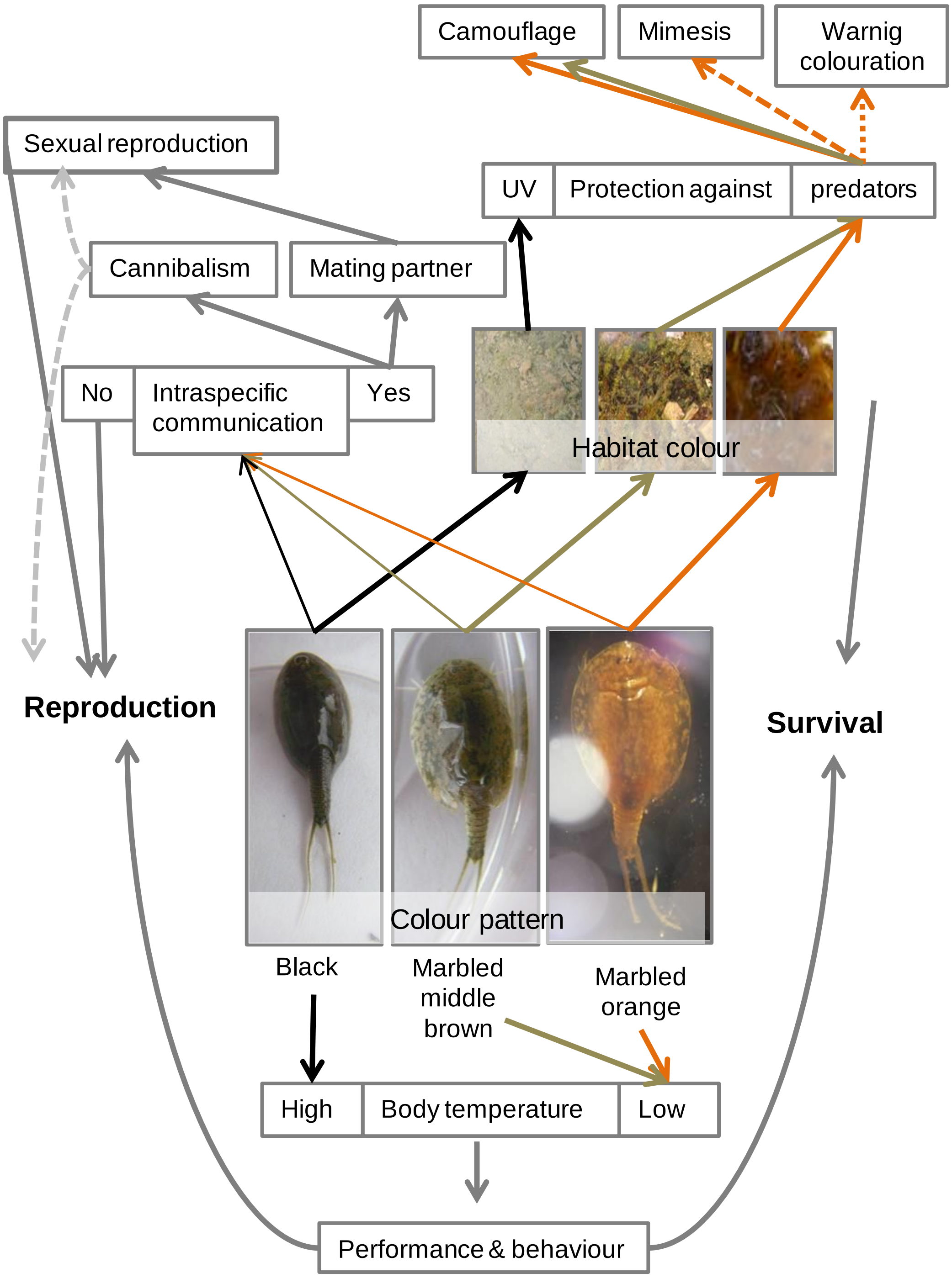


Figure 47. Function of protective colouration. The occurrence of three *L. arcticus* colour pattern (black, marbled middle brown and marbled orange) in different habitats types (sand, moss and cyanobacteria) and the possible influence of colour pattern on reproduction success and survival of *L. arcticus*.

Zooplankton have been shown to develop protective pigmentation against the harmful ultraviolet (UV) radiation in the clear and shallow high-latitude ponds, where solar radiation can penetrate through the whole water column (Rautio et al. 2009). High-latitude water bodies often have a low concentration of coloured dissolved organic matter (CDOM) and hence a deep penetration of ultraviolet (UV) radiation into water column (Schindler et al. 1996, Laurion et al. 1997, Molot et al. 2004). Most diverse colour morphs were found in Kapp Linné ponds where dissolved organic carbon (DOC) and total organic carbon (TOC) concentrations were low. Red, brown and black pigments are typical for high-latitude zooplankton protecting against the UV radiation (Brehm 1938). In Kapp Linné, orange, yellow, brown and black pigments were typical for *L. arcticus* populations. Dark colour morphs absorb more heat than light colour morphs, and thus dark animals may have higher body temperature than the lighter individuals. The higher body temperature may be a crucial factor allowing faster metabolic rate in cold High Arctic ponds. The marbled light grey/yellow individuals were almost colourless, which may be a sign of leucism, because their eyes were black and not red like the eyes of albinos.

The orange colour pattern may also be a warning colouration for visual predators. Ang and Newman (1998) demonstrated that orange flatworm (*Phrikoceros baibaiye*) possess a recognisable signal (i.e. colour pattern) that the visual fish predator (*Thalassoma lunare*) clearly avoided. The orange and yellow *L. arcticus* morphs may also mimic the colour and shape of an autumn coloured polar willow (*S. polaris*) leaves. Leaf insects (Phylliidae) and dead leaf butterfly (*Kallima sp.*) use camouflage to take the appearance of a leaf (Nijhout 2001 & Hennemann et al. 2009). Mimesis of leaves is well documented in other taxa (Eigenmann & Allen 1921, Hennemann et al. 2009), but the ability of *L. arcticus* to mimic a real leaf may be the first documented crustacean leaf mimesis in the aquatic environment. The mimicry in colour, shape and movements is very close to the polar willow leave, the photographs and drawings of the dead specimens scarcely doing it justice. A leaf mimicking fish (*Monocirrhus polyacanthus*) outline is similar to that of an asymmetrical leaf and when swimming it resembles a drifting leaf (Eigenmann & Allen 1921). The spinning swimming movement of *L. arcticus* is also similar than a drifting leaf in the water column.

Rautio et al. (2009) showed that *L. arcticus* has five pigments. One of them is fucoxantinthin that originates from brown algae giving them a brown or olive-green colour (Tirri et al. 2001). Zeaxanthin is another and one of the most common carotenoid pigments giving plant tissue a yellow colour (Tirri et al. 2001). The third pigment canthaxanthin (also called Carrophyll Red and C.I. Food Orange 8) is used for colouring fish flesh orange and chickens skin yellow (European commission 2002). Canthaxanthin is also a carotenoid pigment that is widely distributed in nature and found e.g. from green algae (Czygan 1968), blue-green algae (Hertzberg and Liaaen-Jensen 1966), bacteria (Saperstein and Starr 1954) and mushrooms (Haxo 1950). A fourth pigment found from *L. arcticus* is astaxanthin, a dark-red pigment found e.g. from *Hematococcus pluvialis* green microalgae (Boussiba & Vonshak 1991). The primary carotenoid pigment in *L. arcticus* is cyanobacterial pigment called echinenone (Rautio et al. 2009). The existence of different colour morphs in *L. arcticus* populations on Spitsbergen may simply reflect variable food sources of individuals and populations. For example, orange animals may have eaten food containing more red and orange pigments (e.g. green algae *Hematococcus sp.*, blue green algae, or bacteria) than the brown or black *L. arcticus*. Bacteria probably make a substantial contribution to the *L. arcticus* diet because the most abundant pigment comes from this source (Rautio et al. 2009). It is possible that the organism causing the RCD disease synthesizes the red pigment (canthaxanthin) because the sick animal's carapace turns to red. *L. arcticus* may get the RCD from their food and spread the infection to cannibalistic conspecifics.

Food type not only likely affects the colour but also the hardness of the *L. arcticus* carapace. The plain, dark individuals had soft shells and were observed to feed on *Daphnia* about 1 m depth. *Daphnia* were found between the legs of the black *L. arcticus*. Actively swimming *L. arcticus* can benefit from the soft, flexible carapace when hunting *Daphnia* in the water column. The marbled individuals had harder shells and were found preying on chironomids among water mosses in the shallow water. These individuals may benefit from the hard carapace when they are pushing through the water mosses. It is also possible that chitin from chironomid head capsules affects the hardness of the *L. arcticus* carapace. Since *L. arcticus* can eat its own shell, eating the chironomid head capsules should not be a problem for the species. The hard carapace and a good protective colour is really useful for *L. arcticus* living among the water mosses in quite shallow water, where they are otherwise easily caught by birds including arctic tern and purple sandpiper.

4.1. Red Carapace Disease

The temperature active disease of *L. arcticus* on the Spitsbergen High Arctic region was an important result. Unfortunately, the cause of the disease has not yet been discovered, but it is likely a parasite. The parasite is not a parasitic worm of *Acanthocephala,* but could be a member of the *Apicomplexa.*We was looking for a parasitic worm in laboratory experiments, but no *Acanthocephala* was found in the tissues of sick animals. In other crustaceans, the parasitic *Acanthocephala* worm typically causes a red spot in the infected animal. The helminth larva of *Polymorphus paradoxus* is identifiable by colour, shape and size of the carapace of living amphipods, *Gammarus lacustris* (Bethel & Holmes 1973). The size and shape of the *L. arcticus* parasite suggests that it most likely to belong to the *Apicomplexa*. The symptoms of the RCD suggest that the parasite life cycle may include many host species and the parasite needs to change the host to complete the life cycle. A nematode (*Skrjabinoclava morrisoni*) can manipulate the behaviour of its intermediate host (the amphipod, *Corophium volutator*) to increase the likelihood of transmission to its final host (the semipalmated sandpiper, *Calidris pusilla*) (McCurdy et al. 1999). The amphipods parasitized by nematodes increase their surface activity during daytime, when sandpipers feed visually. The red colour of the *L. arcticus* carapace and the active behaviour suggests that the main host of the parasite could be a bird (e.g. arctic tern or purple sandpiper) or a fish (e.g. Arctic char). The swelling of egg sacs suggests that the parasite ensures that *L. arcticus* drops the eggs before disease kills the animals. It is also possible that the observed mortality in laboratory experiments can partially be explained by the existence of RCD. No sick animals were observed in five populations where males occurred. Sick animals were observed in only one population in which males were present. The *L. arcticus* populations that reproduce sexually may show larger genetic variation making them less susceptible to RCD.

Increase in temperature seemed to speed up the progression of the disease. Because this disease can thus create a significant threat to *L. arcticus* populations due to global warming, it should be investigated more intensively in the future.

4.3. Injuries

Some *L. arcticus* in the studied populations were missing legs or had broken telson setae or injuries to the carapace. Hessen et al. (2004) found darkened “rings” on the distal part of the telson setae in one *L. arcticus* population on Spitsbergen and similar dark areas were also observed in this study (Figure 9, A). The darkened rings were likely broken and regenerated telson setae rather than a distinctive feature of the population. Bushnell and Byron (1979) found variation in the number of legs on the right and left side of the *L. arcticus* body in the Cumberland Peninsula region, Broughton Island, Canada. Morphological examinations in the same study revealed that eight individuals showed a discrepancy between the number of legs on the right and left side of the body. Bushnell and Byron (1979) did not notice scar areas or other indication of broken or adrift legs. However, it is likely that the reported injuries in *L. arcticus* body are caused by predators.

L. arcticus has three main predators in the fishless pond on Spitsbergen: arctic tern (*S. paradisaea*), purple sandpiper (*C. maritima*) and cannibalistic *L. arcticus*. According to Summerhayers & Elton (1923) the stomachs of two young purple sandpipers had remains of *L. arcticus* in Prince Charles Foreland, Svalbard. Hartley & Fisher (1936) also found *L. arcticus* in stomachs of arctic tern on West

Spitsbergen. Here, a new finding is that dunlin (*C. alpina*) can also eat *L. arcticus*. Waders can only eat *L. arcticus* in shallow water, while arctic terns are able to catch *L. arcticus* from the deeper central parts of ponds. Arctic terns were seen to fly above the ponds and to make quick plunges into the water. Waders were only looking for food from the soft bottoms and among the water mosses near the shoreline. Dead *L. arcticus* were observed in two ponds in Ny-Ålesund, Solvatnet and Brandallaguna. In Solvatnet pond, there were many arctic terns catching *L. arcticus* and thus it is likely that the dead animals had died due to a failed bird attack. The carapaces of dead animals were damaged but the soft body parts were undamaged. It was surprising that other *L. arcticus* had not eaten the dead conspecifics, because cannibalistic behaviour was very common in the laboratory. This would suggest high food availability for *L. arcticus*, because dead animals were found from these ponds and *L. arcticus* were larger than in other ponds in Ny-Ålesund at the same. It is also possible that predation by birds had decreased the population size of *L. arcticus* and thus more food resources had been available for the remaining animals, possibly explaining the large size of the animals.

4.4. Olfaction

This experiment clearly demonstrated that *L. arcticus* has an olfactory ability. Crustaceans are generally sensitive to gravity, pressure, sound, light, temperature, touch and chemicals (Thorp & Covich 2001). In this olfaction experiment, nine female *L. arcticus* were strongly attracted to crushed *L. arcticus* and three of the animals spent half of the test time in the “odour corner”, suggesting that the dissolved chemicals released from injured animals (e.g. haemolymph) may help *L. arcticus* to locate injured or dead animals. However, there were no statistical differences in the time animals spent in the odour square (Figure 40). Significantly increased activity and swimming speed in crushed *L. arcticus* treatment may explain why no statistical differences were observed. It is possible that animals were searching for food in the crushed *L. arcticus* treatment, which may explain why they were swimming so fast. The odour source was also placed near the water surface and not on the bottom of the aquarium. In nature, dead animals were always found on sediment surface and not floating in the water column or at the surface. The odour of dead animal coming from an unusual direction (i.e. near the surface) may confuse the test animals and thus explain the active searching behaviour in the crushed *L. arcticus* treatment.

Johansen (1911) and Arnold (1966) noted that *L. arcticus* specimens which died in the tanks were rapidly eaten by other conspecifics. It remains unclear whether all individuals are capable of cannibalism, but instead it is clear that this feeding behaviour is a common feature of the populations on Spitsbergen. It seems likely that only some adult individuals are specialized to prey on members of their own species. This idea is supported by observations in the field where smaller-sized *L. arcticus* were observed to attack larger conspecifics and start to eat them right away. Thus, cannibalism in *L. arcticus* is not size-dependent so that larger individuals would always consume smaller ones. The behaviour changes of *L. arcticus* individuals were observed when several animals were placed in the same bottle. Some of the animals (1–2 pcs.) usually floated at the surface and thereby avoided encounters with others when five animals were placed in a 200 ml bottle. The best physical fitness may solve who can be a cannibal and who cannot. The adult *L. arcticus* were also eating their own shells after moulting in laboratory conditions. The shell may actually contain essential nutrients for growth. Another factor supporting the idea of cannibalistic behaviour is the large number of empty shells of *L. arcticus* in ponds in the spring time. Poulsen (1940b) noted that *L. arcticus* do not hibernate and only one generation is present annually in East Greenland. Scholander et al. (1953) reported that *L. arcticus* are mechanically damaged and killed by freezing into ice. Johansen (1911, 1922) also saw dead adults as soon as the ice surface began to form on the lakes, but when the ice became thicker, more and more *L. arcticus* were frozen and died. It seems likely that the *L. arcticus* juveniles may eat the remains of *L. arcticus* from past year if they are available. If this behaviour is true, it could partly explain differences in the population sizes in early spring. It is also possible that only the shells of dead animals have been preserved over the winter, and some other animals have eaten the soft tissues.

Animals in the algae treatment spent significantly more time in the middle of the container than animals in the control or in the crushed *L. arcticus* treatment. This behaviour may indicate that algae odour may calm *L. arcticus*. Aquatic vegetation (Bryophyta) is an important habitat for *L. arcticus* on Spitsbergen (Appendix 3). *L. arcticus* may hide from visually hunting birds inside these bryopyte ferryes. Familiar odour may calm animals as was observed in algae treatment, or induce predation behaviour as was seen in crushed *L. arcticus* treatment. *Daphnia* has also been shown to have potential to distinguish between ecologically relevant odours (Van Gool & Ringelberg 1996). In the same study, two *Daphnia* species were attracted by the odour of edible algae but not by the odour of toxic algae.

Similarities were observed between the treatments in the placement of the test animals in squares 7, 8 and 9 (Figure 36). These squares were among the most popular squares in all the treatments. The animals' behaviour was observed behind these (7, 8, 9) squares. Observation may have influenced the *L. arcticus* behaviour and thus explain why these squares were so popular. The animals were most likely hiding behind of the aguarium front glass, even when the observations were made by wearing a white laboratory jacket (the walls around the aquarium were white) and avoiding unnecessary movement. However, the observer seemed to have an unwanted effect on the test animals' behaviour. This issue should be taken into account when planning similar odour experiments. It is recommended that the test aquarium is placed inside of a glass box where the test animal cannot see outside but the obsever can see inside.

Olfaction may play a very important ecological role in *L. arcticus* population dynamics, because it helps animals to find food or to localize injured or dead animals. Christoffersen (2001) demonstrated that *L. arcticus* are active and efficient predators of planktonic prey. Olfaction may be extremely important for young *L. arcticus* and for sexually mature females that carry eggs, because these animals have a high nutrient demand. The animal activity significantly increased in crushed *L. arcticus* treatment. The increased activity can be explained by active searching for food or by an escape reaction for some animals. Failed bird attacks can injure or kill *L. arcticus* on the Spitsbergen ponds. Because of this predator–prey relationship, *L. arcticus* can benefit from their capability to locate injured or dead conspecifics offering an easy and large-sized prey. Relatively large-sized catches and good nutritional value is important for short-lived but fast-growing Arctic crustacean. Some individual *L. arcticus* on Spitsbergen were blind or they had a "cataract". These individuals probably used more olfactory and tactile senses in feeding than the healthy animals. The discoveries of the blind animals in natural populations suggest that *L. arcticus* uses a variety of senses in foraging. Miller (1980) reported that being a predator is the only way how *L. arcticus* can get enough food to maintain such a high growth rate. *L. arcticus* individuals are exceptionally large, and reach sexual maturity at small sizes on Spitsbergen. It seems likely that cannibalistic behaviour partly explains the unique characteristics of *L. arcticus* (large body size and high reproductive capacity) on Spitsbergen.

The chemical signatures of different natural food sources of *L. arcticus* may be extremely complex, varying not only in composition but also in the concentration of specific components. These odour signatures undoubtedly experience both short- and long- term changes in response to the life cycle of *L. arcticus* prey organisms and the natural seasonal event. Different salmonid species and American eels (*Anguilla rostrata*) can use their olfaction to identify and return to their home stream or lake (Dittman & Quinn 1996, Barbin 1998). Minnow, which can predate on *L. arcticus* (Borgstrøm et al. 1985), respond fast to Schreckstoff, a chemical alarm signal located in their skin when wounded by a predator (Krause 1993). In the experiment the minnows moved closer to each other and tended to be surrounded by the conspecifics. The hunting *L. arcticus* can apply their olfactory memory to discriminate odours from different food sources. The one injured *L. arcticus* and several healthy animals were placed in same container in the study of Arnold (1966). The healthy animals rapidly attacked towards the injured animal and after this the injured animal was eaten alive. Injured *L. arcticus* probably secreted some recognizable component which attracted other

conspecifics. In nature, the turbulence of water may impair the responses of *L. arcticus* to different odours.
In summary, I suggest that *L. arcticus* can locate food using olfaction but in nature they usually find their food using visual and tactile senses in combination with olfaction. It can be concluded that *L. arcticus* has the potential to be an effective predator of injured *L. arcticus* due to olfaction. The presence of *L. arcticus* in Arctic ponds and lakes may play an important role in nutrient cycling because they can eat dead and injured animals.

4.5. L. arcticus sensitivity to water salinity

It can be concluded that *L. arcticus* can tolerate small changes in water salinity and a slightly increased salinity (1 ‰) may speed up the growth and ecdysis of the species.

The salinity of freshwater ponds is normally 0 ‰, while the salinity is 34.7 ‰ in coastal areas of the Barents Sea. *L. arcticus* tolerated a salinity increase of 2 ‰, but many animals were able to tolerate up to 8 ‰ increase in salinity for at least 48 hours. The available field data shows that *L. arcticus* can naturally live in ponds with 1.5 ‰ salinity. Climate change can affect the salinity and/or water temperature and therefore the composition of aquatic invertebrate communities (Verschuren et al. 2000). *L. arcticus* is probably adapted to small changes in water salinity. A large proportion of the large branchiopods live in fresh water. However, some species of *Branchinella*, *Streptocephalus*, and *Thamnocephalus* and all species of *Parartemia* and *Artemia* live in saline inland waters (Brendonck et al. 2008). The salinity tolerance of California clam shrimp (*Cyzicus californicus*) seems to be similar to that of *L. arcticus*, because 95 % of *C. californicus* survived in 1.8, 3.5 and 5.3 ‰ salinity for 48 hours (Eriksen & Brown 1980a), while 93 % of *L. arcticus* survived 48 hours in 3, 4, 5, 7 and 8 ‰ salinity. Along a salinity gradient, many cladocera exhibit a unimodal response in abundance owing to their limited ability to osmoregulation (Frey 1993). For some metals such as cadmium (Cd), the sensitivity of *Diporeia* spp. amphipod increases with both increasing temperature and decreasing salinity (Gossiaux et al. 1992). Thus, the *L. arcticus* salinity tolerance may also be linked to metal toxicity or parasitism. In slightly saline water (1.2 ‰), ectoparasites (flat worms) were found from *L. arcticus* heads and genital areas. The saline water seemed to speed up the ecdysis and thereby improve the resilience of *L. arcticus* to ectoparasites as the parasite exposure time is shortened.

The increased growth rate of *L. arcticus* in slightly saline water may be an adaptation to the life in temporary ponds. The catchments of the temporal ponds were typically small, the sources of water were mainly thawing snow and the water salinity increased as the ponds dried. Water salinity in closed basin typically increases by evaporation (Wetzel 2001). In slightly saline water, *L. arcticus* may need to produce new eggs as efficiently as possible before the pond dries up. This finding was supported by two observations: Firstly, the faster growth to a large size increased the reproductive efficiency on *L. arcticus,* because bigger *L. arcticus* can produce larger and more eggs than the smaller animals. A low salt concentration (1 ‰) significantly speeded up the second ecdysis of *L. arcticus*. Secondly, the smaller animals started to produce more eggs in slightly saline temporary ponds than in permanent ponds.

4.6. Sensitivity of *L. arcticus to changes in water pH*

The pH experiment was carried out because many *L. arcticus* populations in Norwegian mainland have become extinct due to acidification (Fellheim et al. 2001). *L. arcticus* have not been found from waters with a pH below 6.1 (Röen 1962, Borgström & Larsson 1974, Blomkvist 1995, Borgström et al. 1976, Fjellheim et al. 2007, Table 11). On Spitsbergen the lowest pH levels were measured in Longyearbyen (pH 6.3–8.0) and in *L. arcticus* ponds in Pyramiden (7.0–7.4). These areas are or used to be subjected to coal mining activity. Low pH did not always explain the absence of *L. arcticus* in a pond. For example, in pond

Gluudneset the pH 8.4 was optimal for *L. arctius* but the water salinity level of 2.8 ‰ was apparently too high. In areas where human disturbance was evident, the pH of pond water was often lower than in areas with little or no human activity. Low water pH due to human disturbance was observed in Longyearbyen, Pyramiden and in some areas of Ny-Ålesund with common coal mining areas. However, in some ponds on Spitsbergen, the pH was relatively high compared to other previously studied *L. arcticus* habitats (Table 11). The highest ever reported pH in a *L. arcticus* pond (pH 8.84) was measured from Solvatnet, Ny-Ålesund, in early August.

Borgstrøm & Hendrey (1976) observed increased mortality and delayed moulting of the first larval stages of *L. arcticus* at pH <5.5. Experiments conducted in Canada revealed a significant increase in mortality below pH 4.5 (Havas & Hutchinson 1982) and the internal levels of Na and Cl decreased when *L. arcticus* were kept under acid stress (Havas & Hutchinson 1983). Similar results were obtained in the present LC50-pH experiment. Strong acid stress at pH 4 caused significant mortality of the mature *L. arcticus*. Other aquatic species have been observed to have similar problems in acid waters. For example, the circumpolar *G. lacustris* amphipod have been shown to be stressed in high temperature and the presence is restricted to lakes with pH ≥ 6.6 (Økland & Økland. 1986). Schindler & Turner (1982) and France (1983) reported reduced calcification of the exoskeleton of *Orconectes virilis* crayfish at pH 5.6 and increased parasite infections. Combined effects of acidification, parasites and increased temperature are and will be serious threats to *L. arcticus* populations in Arctic waters. However, it must be taken into account that *L. arcticus* can burrow in the sediment (≈1 cm) and therefore may benefit from the acid-neutralizing capacity of the sediment. Acid lakes often have a relatively higher proportion of species living in the sediment (in-fauna), where they are somewhat isolated from the pH conditions in water column as compared to species belonging to the epifauna (Økland & Økland 1986). *L. arcticus* can inhabit both benthic and pelagic habitats although the *L. arcticus* usually spend most time close to the sediment. *L. arcticus* may avoid too acid water by staying near or in the sediment or by occupying a habitat near a source (e.g. spring) of acid-free water. The monitoring data of Fjellheim et al. (2001) from exceptionally acid Svartvatnet, South Norway, indicated that *L. arcticus* have probably survived in small refuges either near inflowing groundwater or in the littoral zone below the more acidic surface layer.

The *L. arcticus* on Spitsbergen may be exposed to short-term drop of pH during the heavy run-off and snow melt in spring. It is possible that the dry and wet fallouts contain acidic compounds that are flushed into ponds and drop the water pH in spring. Small lakes are generally more sensitive to acid precipitation than the large lakes (Tammi et al. 2003). In Longyearbyen pond, the pH rose from 6.4 in early season up to 7.8 in late summer. Acidification in fresh waters is particularly linked to atmospheric deposition, but may also have terrestrial origins and be related to effluents from mining industries (Økland & Økland 1986). Mining was clearly the dominant economic activity on Spitsbergen in the 20th century (Stange 2009). In Longyearbyen there have been seven coal mines and one of them (Gruve 7) is still operating. Coal mining in Ny-Ålesund stopped in 1962 and all mining activities in Pyramiden were stopped in 1998. In areas that still have mining activities a particular attention should be paid to the water acidity. The coal mine drainages from 49 abandoned mines were studied in the Santa Catharina region, Brazil (Silva et al. 2011). The mean pH of these drainage waters were alarming low and varied between 2.44 and 3.88. Spread of coal dust from mines and coal trucks to the environment was clearly seen around the ponds in Longyearbyen and coal was even found from the pond sediments. Fine coal particles may remain in the air and be dispersed by winds. More attention should be paid on the coal dust spread by the wind on Spitsbergen. Coal trucks should be covered during transport to prevent the dust from spreading to the environment.

Many metals become bioavailable within the range of pH 5.0–5.5 (Stumm & Morgan 1981). However, crustaceans are known to be fairly tolerant to copper, which is an essential element in their haemolymph (Maund et al. 1992, Gerhardt 1995). In physiological respect, the acid water impedes the ecdysis of adult *L. arcticus* and therefore reduces the animal’s potential to produce eggs during the short Arctic summer. Several ecdyses are needed before the *L. arcticus* reaches large enough body size to start producing eggs. *L. arcticus* is extremely sensitive to acid water (Fjellheim et al. 2001), but adults may survive in short-term acid stress. In the past decades, the distribution of *L. arcticus* has shrunk notably due to acid precipitation in Norway (Fjellheim et al. 2001). People have attempted to re-introduce *L. arcticus* to their original and restored acidified habitats. In these cases, the acid lakes and their catchments have been treated with liming to improve water quality (Fjellheim et al. 2001). Different life stages of *L. arcticus* have different tolerances to pH and the local populations may also have different sensitivities to acid stress. Calcium regulation is especially important to crustaceans and there is clear evidence for a weakened calcium uptake at low pH (Økland & Økland 1986). As several studies have shown, acid water can have several unwanted effects on *L. arcticus*. The absence of *L. arcticus* can be used as early warning signals of acidification of some ponds and lakes in High Arctic.

There are also other factors that may affect aquatic ecosystems on Spitsbergen. The dumping ground of Longyearbyen is located in the Adventdalen region and may affect the water chemistry in the ponds as well as in Lake Isdammen from which local people obtain their drinking water. Several habitats of Notostaca have been spoiled by refuse dumping in Austria (Löffler 1993). Moreover, the excessive use of Isdammen water may result in lower water level and consequently in the changes in water chemistry and/or desiccation of several shallow ponds and pools near to Isdammen. Another factor likely affecting the water chemistry is dog kennels located in Adventdalen. The dogs secrete acid urea that may have declined the water pH in Adventdalen ponds. The measured pH of 6.3 is close to the lowest pH level of 6.1 tolerated by *L. arcticus*. Hence, the nutrient-rich and acid dog faeces should not be placed close to water bodies but instead so that the spring runoff and snow melt would not transport them into waterways. A slight drop (0.1–1.0) in pH can wipe out the local *L. arcticus* populations in Longyearbyen and Pyramiden ponds. Such local extinctions of *L. arcticus* populations may have unwanted effects on the upper trophic levels such as birds feeding on *L. arcticus*.

4.7. Oxygen consumption

All large branchiopods can regulate their oxygen consumption and live at low oxygen concentrations (Thorp & Covich 2001). This study showed that relatively low oxygen concentration (235.9 µmol O_2/l) and high temperature (30 °C) were together lethal to *L. arcticus*. Eriksen & Brown (1980b) demonstrated that *L. lemmoni* had a minimum oxygen tolerance and showed inability to regulate oxygen consumption at low oxygen concentrations. Q_{10} values for *L. lemmoni* varied from 2.1 to 5.1 (Eriksen & Brown 1980b), whereas in this study the Q_{10} values for *L. arcticus* ranged from 0.45 to 3.15. Such low Q_{10} values are rarely measured from aquatic poikilotherms (Pattee 1965, Wolvekamp & Waterman 1960). According to Thorp & Covich (2001), the Q_{10} values for metabolic rate are 2–3 in the majority of ectotherms. Thus, the Q_{10} values outside of this range indicate active metabolic regulation: values <1.5 suggests active metabolic suppression and >3.5 active metabolic stimulation with temperature change. The present results indicate that the active metabolism of *L. arcticus* is outstandingly suppressed with increasing temperature. The results suggest that *L. arcticus* has adapted to live in cold water.

The amount of oxygen reduces when the water temperature rises. *L. arcticus* lived in ponds where the oxygen concentration is 456.6– 398.9 µmol O_2/l. The *L. arcticus* optimal temperature was 10 °C, when the water oxygen concentration was 352.6 µmol O_2/l. *L. arcticus* therefore seems to tolerate well 11 % lower oxygen content than observed in their natural habitats. However, the 33 % decrease in oxygen concentration (from 352.6 µmol O_2/l at 10 °C optimum to 235.9 µmol O_2/l at 30 °C) was lethal for *L. arcticus*.

O_2 consumption of *L. arcticus* declined rapidly with increasing temperature, suggesting that the species has adapted to live in cold water. *L. lemmoni* occur in warm water ponds (7.7–24.5 °C) in the western USA (Lynch 1966). The metabolic rate of *L. lemmoni* reached the maximum at 27.8 °C (Eriksen & Brown 1980b), while the maximum respiration rate for *L. arcticus* was seen at 10 °C. *L. arcticus* is clearly a species that requires a high oxygen concentration and cool water. *L. arcticus* showed poor tolerance to increased temperature, with a mean Q_{10} value of about 0.48 in the high temperature treatments. Another factor that supports the idea of the limited acclimation of *L. arcticus* to high temperatures was the high mortality rate while acclimating animals to 16.5, 20, 25 and 30 °C. *L. arcticus* has undoubtedly lived under stable environmental conditions for a very long time and thus the need for temperature acclimation has probably been limited. The water temperature in *L. arcticus* ponds on Spitsbergen ranged from 0.5 to 5.5 °C, while the water temperature in lakes studied by Arnolt (1966) ranged from 3 to 19 °C in Greenland. In July *L. arcticus* were abundant despite the low sediment temperature (-0.5 – -1.9 °C) in some study ponds. It may be possible that the *L. arcticus* lay their eggs among aquatic vegetation rather than on sediment, since the temperature of the sediment is so low in early summer. It can be concluded that the *L. arcticus* are living below the physiological temperature optimum on Spitsbergen waters. *L. arcticus* is a species that is capable of living only within a narrow temperature range. Among Notostraca, *L. arcticus* should be considered stenothermal.

4.8. Differences in the external morphology of *L. arcticus* *– an important tool for identification of the species?*

The size of *L. arcticus* has dramatically increased over the last 114 years. The mean size of males has increased since by 50 % and female size has increased by 15 % compared to Sars studies in 1896. The largest female was 64 % larger (in total length) than any of those studied 114 years ago. Organisms can generally reach larger final body sizes when the development time increases (Roff 1992). However, global warming has been demonstrated to reduce the body size of some aquatic organisms (Daufresne et al. 2009). Nevertheless, the *L. arcticus* size has increased notably. Observed changes in the size of *L. arcticus* may be caused by global warming (e.g. a longer growing season), or simply by the fact that the animals were collected at different times of the year. *L. arcticus* lives below its temperature optimum on Spitsbergen and thus may benefit from higher summer temperatures and longer growing season in the present climate conditions. Some previous studies do not present the time when the animals were collected, although this is a particularly important parameter when studying the size and growth rate of High Arctic animals. Nevertheless, the morphology (size and reproduction) of *L. arcticus* is very unique on Spitsbergen.

Sars (1896) defines *L. arcticus* as a species with the number of posterior segments not covered by the carapace varying between 12–18. In this study the number of these segments varied between 2–21. Sars (1896) also states that *L. arcticus* males rarely exceed 12 mm in total length. Mean total length of *L. arcticus* male was 18 mm on Spitsbergen. Males were considerably smaller than females, but were able to reach up 27.5 mm in total length. In the studies conducted by Sars (1896), the biggest male was only 13 mm long. The same phenomenon was also seen in the size of females. The largest female observed by Sars (1896) was 24 mm, while in this study the largest female was 39.4 mm. The total length (23 mm) of *L. arcticus* must be considered as the mean size for fully-developed females.

The size of the supra-anal plate and the CL/SP ratio are considered as good tools to identify *L. arcticus* species. The size of the supra-anal plate varies between *Lepidurus* species (Longhurst 1955). The *L. arcticus* supra-anal plate is very small, but the size of the supra-anal plate showed large variability. Hessen et al. (2004) showed that *L. arcticus* has two major haplotypes (A1 and B1) on Bear Island and one (A1) on Spitsbergen. The supra-anal plate of the haplotype A1 was significantly smaller than the haplotype B1´s supra-anal plate (Hessen et al. 2004). As significant differences in morphology can be observed within the same species, one should be rather careful in identifying this species by using only a single morphological variable. This study has shown a lot of new information about the morphological variables of the *L. arcticus* on Spitsbergen. The carapace supra-anal plate ratio (mean CL/SP = 15) was higher on Spitsbergen than has been observed anywhere else (Table 3). This probably means that the majority of animals were of haplotype A1 on Spitsbergen. Haplotype A1 is also found in the mainland Norway and in the Bear Island (Hessen et al. 2004). Another interesting observation was the small size of the carapace (≤15 mm). The carapace should be 20 mm long and CL/SP ratio should be then around 12 in adult animals (Longhurst 1955). Such large carapaces were not observed on Spitsbergen. A small carapace length and a high CL/SP ratio may mean that the *L. arcticus* allocate resources for soft tissues rather than for hard shells (carapace and supra-anal plate) on Spitsbergen. It is important to note that *L. arcticus* individuals were also unusually large on Spitsbergen, the observed maximum total length being 39.4 mm.

In this respect, the identification key of *L. arcticus* should be revised. Large morphological differences were also observed between and within different *L. arcticus* populations. These distinctive features can be explained e.g. by reproductive isolation, niche differentiation, historical isolation due to different glacial refuges (Hessen et al. 2004) and differences in temperature and salinity. *L. arcticus* may be considered as a relict species over its southern range of distribution for example in mountains in Norway (Hessen et al. 2004, Sars 1896). Some of the observed morphological differences are due to gender and age. Sømme (1934) showed that the supra-anal plate of males is longer than in females, and the same observation was made in this study. The morphological measurements of juveniles and sick animals should be regarded with caution. Hessen et al. (2004) hypothesised that the *L. arcticus* juvenile stages from different geographical locations may show pronounced morphological variability. The hypothesis of Hessen et al. (2004) was correct, but there also seems to be a large variation in morphology of juvenile and adult *L. arcticus* within the populations. The morphological plasticity in *L. arcticus* makes this species challenging for identification. The most important thing would be to examine the animal supra-anal plate shape and size (Figure 10) as well as to calculate the number of body segments (26–28 pcs). By doing so the *L. arcticus* can be identify correctly.

L. arcticus remains have been found in lake sediments on Spitsbergen and in Greenland (Bennike & Hedenäs 1995, Jeppesen et al. 2001). By measuring the remains (e.g. supra-anal plate) and using the Figure 12 formulas it is possible to calculate the carapace size of the historical animals. By doing so, it could be possible to find out if the animals have reached sexual maturity (carapace size 4.0–9.1 mm); if the carapace length is ≥8 mm, the animal has propably been large enough to produce at least one egg. Thus, future paleolimnological studies could use *L. arcticus* remains more to evaluate the historical ecology of the species.

4.9. Seasonal variation in egg production of L. arcticus

Number of eggs of the *L. arcticus* species is easy to calculate, because the eggs are large and orange in ethanol preserved samples and the animals carry only a few eggs (≤12 eggs). *L. arcticus* were able to carry more eggs than is ever before observed in any studies. The number of eggs produced by a female *L. arcticus* can depend on a variety of abiotic and biotic factors such as temperature, salinity, oxygen, food and population density. *L. arcticus* were carrying more eggs on Spitsbergen than has previously been observed in Novaya Zemlya Archipelago, Russia (Vekhoff 1997), in Syd Kapp, East Greenland (Arnold 1966), and in Tuvetjern, Norway (Sømme 1934) (Table 7 & 8). Animals were carrying an mean of 2.6 eggs on Spitsbergen, whereas in previous studies the mean numbers were 1.0 in East Greenland (Arnold 1966) and 2.1 in Tuvetjern, Norway (Sømme 1934) (Table 8).

The *L. arcticus* on Spitsbergen seem to be able to carry more eggs than has been observed in any previous studies. On Spitsbergen the total number of eggs varied between 0–12, while in the study of Vekhoff (1997), *L. arcticus* were found to carry only 1–5 eggs in Novaya Zemlya, 1–4 eggs in Vaigatch Island and 2–4 eggs in Matveev Island, Barents region of Russian Arctic (Table 7). The low number of eggs observed in other studies can be due to a combination of factors. The present study provides evidence that at high temperatures female *L. arcticus* may become mature at a smaller size than at lower temperatures. There seemed to be a connection between the rate of reproduction and the water temperature in Storvatnet and in Kolhamna in Ny-Ålesund. The water temperature was 3.1 °C and 23 % of animals were carrying eggs in Storvatnet, while the water temperature was 4.2 °C and 44 % of similar-sized animals were carrying eggs in Kolhamna at the same time. This observed phenomenon may be associated with more rapid metabolism in warmer water. This assumption was supported by the respiration activity experiment. The respiration activity of the animals increased with increasing temperature from 3.5 to 10 °C. Increase in water salinity may also speed up animal's growth. This assumption was confirmed by observations from both laboratory experiments and natural populations. The salinity issue is discussed more in chapter 4.5.

The timing of open water period can also have an influence on the sexual maturation of *L. arcticus*. The start of ice free period in ponds and lakes on Spitsbergen depends greatly on the distance from the sea and glaciers. At a larger scale, the importance of altitude and latitude is highlighted when contemplating the species distribution at their southern limits. *L. arcticus* is a boreo-alpine relict in Scandinavia, existing at greater altitudes towards the south and close to the sea-level in the Arctic (Sømme 1934). Temperature differences can be notable between ponds located only 1.2 km away from each other. The importance of pond's distance from the sea and glaciers on the timing of *L. arcticus* sexual maturation can be clearly seen in lowland areas on Spitsbergen. The small body size of *L. arcticus* will naturally restrict the egg carrying capacity of the females. Therefore, the timing of sampling has a strong influence on the results. It is recommended to collect *L. arcticus* samples in August. Animals are usually mature and more easily detected because they are larger in August than earlier in the summer. Sampling date influences the result and therefore it is important to measure water and sediment temperature, pH and salinity at the same time. The date of the collection of samples should always be reported to be able to compare the result with other studies. Animals and other data which were collected at different times, made the comparison of the present results complicated. It would be useful to collect samples from the same pond several times.

Eggs were evenly distributed in the left and right foot capsules of *L. arcticus* (Table 8) as was also previously found by Arnold (1966) and Sømme (1934). In warmer water the time needed to reach maturity is short and the advantage of becoming mature earlier seems to be more important than the advantage of producing large numbers of eggs at least in temporary ponds. Effective reproductive capacity also seemed to reflect other features of the *L. arcticus* populations on Spitsbergen, where females seemed to reach sexual maturity and the sexual dimorphism appeared at exceptionally small body size (Table 6), potentially as a consequence of local adaptation to abiotic and biotic conditions. These differences can be explained by varying water and sediment temperatures and salinity conditions (Appendices 4–9). For example, the slight increase in salinity or temperature in temporal ponds seemed to speed up the growth of *L. arcticus*. The water and sediment temperatures were exceptionally low in ponds where the animals had not yet reached the maturity. The immature stage of *L. arcticus* lived in remarkably low water temperatures (0.5–4.9 °C) and in the freezing sediment (-1.9–0.8 °C) in Kapp Linné ponds in early season (11–12th July). The immature animals lived in cold water (0.8 °C) and among almost freezing sediment (0.1 °C) in Tvillingvatnet in early August. The season does not explain why no sexually mature *L. arcticus* were observed in this pond, because sexually mature females were found at the same time from five other ponds in the same area. The more likely reason for the absence of mature females in Tvillingvatnet was the low water temperature which had delayed the beginning of ice-free period and thus shortened the growing season in relation to other ponds in the same area. Hydrologic processes are both spatially and temporally highly variable in catchments surrounding High Arctic ponds, so that ponds location between sea and glaciers has a great influence on water and sediment temperatures. Ice and snow melts offer a cold water supply throughout spring and summer if glaciers or snow-capped mountains are near enough to the pond's catchment. Tvillingvatnet was located near three glaciers: eastern Brøggerbreen

(0.7 km), western Brøggerbreen (1.5 km) and western Lovenbren (1.2 km). This partly explains the low water and sediment temperatures observed in late season. The cold winds from the glaciers can also explain the low temperatures. The length of ice free period and water and sediment temperatures is very important for *L. arcticus* growth, because the temperature is optimal for development of *L. arcticus* for such a short time. The timing of phytoplankton bloom can also be an important factor for the planktonic juvenile stages of *L. arcticus*. The sediment temperature can affect at least the timing of benthic algal bloom and probably also the phytoplankton bloom. Sediment can absorb a large amount of heat from the water during the warmer periods of the year and transmit heat to the water during the winter (Wetzel 2001). In shallow lowland lakes, the importance of temperature in algae bloom dynamics must be considered (James et al. 2009). Thus, it would be important to measure the sediment temperature and not only the water temperature in permafrost area, because the timing of algal bloom and the sediment temperature can be strongly linked in High Arctic ponds.

The ponds on Spitsbergen freeze solid in winter and thus *L. arcticus* spend winters as resting eggs on the bottom of the pond. The hatching of *L. arcticus* eggs coincides with the spring snowmelt in Lake Svartvatnet located at 1213 m a.s.l. in South Norway (Fjellheim et al. 2001). *L. arcticus* hatch at a later stage of development than *T. cancriformis* and *Lepidurus apus* and the eggs of *L. arcticus* are much larger compared to those of other species in the family (Longhurst 1955). In the present study, a new observation was that *L. arcticus* can produce eggs of different sizes and the size of eggs can also show seasonal variation. Small animals carried only small or medium-sized eggs in early season. When the animals reached up the carapace length of 7.7 mm, they began to carry big (>0.8 mm) eggs. The large eggs of the species may play an important role in the success of hibernation in harsh condition. The observed congruent differences in the egg sizes and water temperatures may explain the occurrence of different-sized individuals in early spring. The small adults may be those which have been starving at the juvenile stage and thus can only produce small eggs. Nevertheless, it is good to produce large eggs but small eggs are better than none. The eggs of

Simocephalus vetulus (Cladocera) are much larger in Greenland than in England, even when the British specimens are reproducing at lower temperatures than the conspecifics at the summer temperatures in Greenland (Green 1966). It seems likely that the function of large eggs is to improve the survival of *L. arcticus* in areas where the sediments of lakes and ponds are frozen in winter. In cold water the large eggs ensure the maximum speed of maturation in the following spring. The deep-sea prawn (*Pandalus borealis)* produces bigger and heavier eggs at high latitudes on Spitsbergen than at lower latitudes in Bergen (Clarke et al. 1991). Young *L. arcticus* most likely have a better chance to survive through poor food conditions when they are well-nourished at the beginning of life. The observed great variation in egg sizes may ensure the maximum increase in the population size because different-sized animals can feed on various sizes of food.

Fox (1949) reported that the eggs of *L. arcticus* were able to hatch after drying, indicating that in many cases the eggs of this genus must be resistant to drought (Longhurst 1955). The same assumption was supported by the present findings from two ponds that dried up during the summer but still had abundant populations of *L. arcticus*. *L. arcticus* in these ponds were often carrying more eggs than the similar-sized animals in permanent ponds at the same time. *L. arcticus* seemed to be remarkably flexible in terms of reproduction. A slight increase in water-ion concentration seemed to have a positive effect on growth and start of egg production in *L. arcticus*. It seems that salinity triggers *L. arcticus* maturation in drying ponds. *L. arcticus* need to lay eggs quickly before the water disappears from these ponds. Many previous studies have focused on the number of individuals and have not studied the reproduction of *L. arcticus*. Reproduction capacity of animals (number of mature animal and eggs, and the presence of males) reflects better to the condition and size of a *L. arcticus* population than the number of collected animals in population alone.

4.10. Dispersal agents in permanent and temporal ponds

Arnold (1966) suggests three dispersal mechanisms for *L. arcticus*: (1) adhesion of the eggs to the feet of waders, (2) transmission via the faeces of birds, and (3) accidental dropping of living specimens by avian predators. *L. arcticus* have limited potential for active dispersal. The species is a poor swimmer (Arnold 1966) and unable to fly to new areas. *L. arcticus* seemed to be unable to resist water currents in ponds. This was seen on windy days, when the undercurrent often carried *L. arcticus* near to the pond shore. Strong waves and undercurrent together sometimes pushed *L. arcticus* to dry land. Purple sandpipers fed on *L. arcticus* on the sediment near to the pond shore and adult *L. arcticus* were remarkably easy to pick up on the dry land in the windy days.

Water currents and winds are probably important dispersal agents, resulting in passive movement of resting eggs and even adult animals. Water may be an important abiotic factor for the transport and movement of *L. arcticus* eggs in Arctic ponds. Spring runoff may transport *L. arcticus* eggs and autumn runoff can affect the local distribution of adult *L. arcticus*. *L. arcticus* occurred also in small shallow pools (≤1.5 m in diameter and ≤10 cm in depth) near the ponds but these pools were not connected to ponds. It seemed that the animals were either hatched in these pools or some abiotic or biotic vectors had carried them. *L. arcticus* individuals were not able to escape unfavourable conditions (UV, bird predators or lack of food) and seek out new locations in these shallow pools. In summer 2010 precipitation was very low (40 mm) on Spitsbergen (Norwegian Meteorological Institute 2011) and thus prevented flooding near the ponds. It is possible that the melting snow and ice and the water masses from Glacier Rivers can transfer eggs, juveniles and even adult *L. arcticus* in local scale. Since the *L. arcticus* are evidently unable to swim upstream (Arnold 1966), the water can be an important vector for the short- and even long-distance dispersal.

Some ponds dry out temporarily on Spitsbergen. The bottom sediments of temporal ponds are exposed to winds during the dry season, which can actually be good for wildlife. Spitsbergen is a windy area, where the lack of trees allows the wind to act as an effective dispersal vector. The wind dispersal may play a part in the distribution of the dry eggs of Branchiopoda (Clark & Wootton 1972). It is possible that the wind transports *L. arcticus* eggs from the sediments of temporal ponds to new areas. Because the eggs of *Lepidurus* sp. and *Triops* sp. are able to hatch after drying (Fox 1949, Longhurst 1955), the potential dehydration of eggs is unlikely a dispersal barrier to the species. Temporal ponds are an important and highly threatened habitat type on Spitsbergen. Temporal ponds are important for wildlife because the occasional droughts kill all the fish (i.e. one of the main predators of *L. arcticus* and invertebrates) and thus allow other species to thrive. Hence, it is important to remain these ponds in pristine state and not make them permanent-like, because they have a unique and specialised *L. arcticus* population.

Ponds on Spitsbergen are closely linked to the surrounding terrestrial landscape. The ponds are important water sources for terrestrial animals (e.g. arctic fox and Svalbard reindeer), which can then act as dispersal agents for *L. arcticus*. *L. arcticus* eggs were found to be sticky and able to attach even to the parents own carapace. The sticky eggs may thus travel to new areas among the mammals' fur or birds' feathers.

Waterfowl can be important predators of large branchiopods in shallow ponds (Dodson and Egger 1980), and this is also true in the High Arctic regions of Norway. The major predators of *L. arcticus* in shallow Arctic ponds on Spitsbergen are arctic tern and purple sandpiper. Dunlins were also occasionally seen to feed on *L. arcticus* in a shallow temporal pond in Longyearbyen. *L. arcticus* eggs have been found from the foot of ringed plover (*Charadrius hiaticula*) (Salomonsen & Johansen 1950). Ringed plover were nesting in the same areas where the *L. arcticus* were present in Kapp Linné and Longyearbyen. Birds can be significant predators of *L. arcticus* and at the same time act as dispersal vectors. Wingstrand (1951) suggested that all *L. arcticus* individuals in an isolated Swedish pool were transported as eggs by water birds from Herschel Island, north coast of Canada. The same *L. arcticus* haplotype has also been found from Spitsbergen, Bear Island and Russia (Hessen et al. 2004). It is unknown whether the eggs are resistant to digestion of birds or fish, but at least they are able to withstand desiccation (Fox 1949) and low temperatures. These dormant eggs have likely facilitated the present broad distribution as well as the ability to future dispersal of *L. arcticus.*

Migrating fish may also act as a dispersal vector of *L. arcticus* in ponds and lakes connected by rivers. The sticky eggs may adhere on the body of fish. Arnold (1966) highlighted that *L. arcticus* was almost certainly unable to swim upstream in rivers. For this reason, the fish may be important for short-distance up-stream dispersal in river systems. The eggs' dormancy facilitates the long-distance dispersal of the species from one water body to another. It can be concluded that the three main dispersal vectors of *L. arcticus* are via water currents, wind and phoresy with fish, mammals and birds.

4.11. Coexistence of *L. arcticus and fish*

Fish predation can be important for the survival of *L. arcticus* (Sømme 1934, Borgstrøm et al. 1985, Jeppesen et al. 2001). However, this study did not focus on the coexistence of fish and *L. arcticus*. The role of fish predation must be taken into account when planning the conservation of *L. arcticus*. Therefore, the occurrence of fish and *L. arcticus* is described in more details in this section.

L. arcticus is generally most abundant in shallow ponds and lakes that freeze solid during the winter and thus lack fish. However, this species can coexist with fish in some deep lakes (Borgstrøm et al. 1985) and in shallow cold lakes (Primicerio & Klemetsen 1999). *L. arcticus* lives in <14 °C epilimnetic temperature in shallow lake Strømsli-Lombola, northern Norway, with a maximum depth of 9.5 m

(Primicerio & Klemetsen 1999). The winter temperatures have been argued to restrict *L. arcticus* to cold climates, supposedly reflecting that winter eggs are unable to tolerate higher winter temperatures than those prevailing in Arctic lakes (Aass 1969). It seems likely that the presence of *L. arcticus* highly depends on the water temperature during the short growing season and not so much on the winter temperatures, because the adults die in winter. According to the respiratory experiment the optimum temperature for *L. arcticus* was 10 °C. All the present study ponds on Spitsbergen inhabited by *L. arcticus* were cold with water temperature never exceeding 5.6 °C during the study in summer 2010. The presence of *L. arcticus* in shallow ponds and temporary pools may be due to the prevailing environmental conditions on Spitsbergen. However, climate conditions are expected to change in the future (IPCC 2007). *L. arcticus* lives in stagnant permanent ponds or in temporal ponds which may freeze solid on Spitsbergen High Arctic. Lack of unfrozen water in the winter and the fact that some ponds probably dry out in summer prevents the formation of permanent fish stocks on Spitsbergen ponds. However, current global circulation models predict 2–2.4 ºC increase in summer temperatures in Svalbard (IPCC 2007). If air temperature increases fewer Arctic ponds and lakes will freeze to the bottom and the High Arctic waters will have an increased number of ice-free days.

In a Norwegian reservoir *L. arcticus* has been found to virtually disappear from the diet of brown trout (Hesthagen & Sandlund 2010) probably due to strong predation of minnow (*P. phoxinus*) on the planktonic stages of *L. arcticus* (Borgstrøm et al. 1985). Non-native fish species or populations of foreign genetic origin have been widely stocked in Nordic countries (Tammi et al. 1999). It is important that minnows do not spread to the areas where *L. arcticus* are present, because they can eat all small *L. arcticus* before they start to reproduce. *L. arcticus* has a short adult life span and starts producing eggs in late summer. Minnows have not been found from the Faroe Islands, Iceland and Greenland (Hesthagen & Sandlund 2010) and thus it is unlikely they could spread to Svalbard. However, three-spined sticklebacks (*Gasterosteus aculeatus)* have been observed in some lakes in Svalbard due to stockings by human (Martin Svenning and Steve Coulson personal communication). If human transfer Arctic char or other fish species to fishless lakes and ponds in Svalbard, the fish may totally wipe out the local *L. arcticus* populations. *L. arcticus* can survive in the challenging environment of Svalbard, but the fish predation could be disastrous for the species in High Arctic waters.

L. arcticus has an interesting relationship with its fish predators. *L. arcticus* may not only be vulnerable to fish predation, but can also act as a controller of coexisting fish by consuming fish eggs (Sars 1896). Arctic char can form ecologically distinct morphs that may have different spawning times and habitats (Klemetsen et al. 2003). In Fjellfrøsvatn, northern Norway, the littoral and profundal char morphs are extraordinarily segregated by spawning time (September vs. February) and place (littoral vs. profundal) (Klemetsen et al. 1997, 2002). Fjellfrøsvatn is connected to the shallow lake Strømsli-Lombola, where immature, planktonic stages of *L. arcticus* have been found (Primicerio & Klemetsen 1999). In this lake, *Daphnia* sp. dominates and brown trout is the most abundant fish species (Primicerio & Klemetsen 1999). Trout spawns on the stone and gravel bottoms, usually in running waters, although lake spawning populations also occur (Klemetsen 1967, Scott & Irvine 2000, Schneider 2000, Brabrand et al. 2002). Trout reproduces in autumn or winter, earlier at higher latitudes and altitudes (Klemetsen et al. 2003). The overlap of fish spawning time and the presence of *L. arcticus* may be important for both species. Fish eggs would be probably good food for the *L. arcticus* which may increase the *L. arcticus* own reproduction success. In lakes where Arctic char, brown trout or other fish species spawn in the shallow littoral zone and stagnant water in the autumn before the lake is covered with ice, it is possible that *L. arcticus* may feed on fish eggs. Thus, *L. arcticus* may affect the density of and predation pressure from their own predator, thereby possibly preventing the formation of a permanent fish stock in a lake or pond dominated by *L. arcticus*.

4.12. L. arcticus effects on the physico-chemical environment of the High Arctic ponds

Adult *L. arcticus* stir up sediment as they move and search for food on the bottom. Sometimes the animal may bury itself completely or slowly progress forwards in the sediment, leaving behind a distinctive trail (Arnold 1966). Such trails were frequently observed to traverse in all directions in the undisturbed areas of the ponds on Spitsbergen as well as in ponds studied by Arnold (1966) in East Greenland. *L. arcticus* can thus likely cause sediment resuspension (i.e. return of bottom material back to water column). The sediment resuspension is likely beneficial for *Daphnia* that is an efficient macrofilter feeder strongly affecting other planktonic herbivores (Primicerio & Klemetsen 1999). The sediment resuspension causes the transition of nutrients from the sediment to water column where the nutrients are available for phytoplankton (e.g. primary production). *Daphnia* can drastically reduce and even eliminate rotifers and cladocerans and also negatively affect copepod nauplius (Bengtsson 1987, MacIsaac & Gilbert 1989, Tessier 1986, Conde-Porcuna et al. 1994). Wind-induced sediment resuspension is common in shallow ponds on Spitsbergen. The sediment resuspension coupled with phytoplankton succession can led to liberation of phosphorus from resuspended particles, which in turn can result in high ${}^{tot}P$ concentrations and low TN: TP ratio (Niemistö 2008). This phenomenon and bioturbation together probably explains the high phosphorous content (66 µg l^{-1}), low TN:TP ratio (4:1) and high chlorophyll-a concentration (3.08 µg l^{-1}) in a small *L. arcticus* pond Nybyen. Wind- and bioturbation-induced sediment resuspension may also explain the high phosphorus (23.3–69.5 µg L^{-1}) and low TN:TP ratios (6:1–11:1) observed in six other *L. arcticus* ponds on Spitsbergen.

The sediment resuspension during strong algae blooms (pH>9) can lead to aerobic release of phosphorus (Niemistö 2008). The pH is naturally high (mean 7.8) on Spitsbergen ponds. In one *L. arcticus* pond, Pond 4 in Kapp Linné, an exceptionally high concentrations of Chl-a (9.04 µg L^{-1}) and ${}^{tot}P$ (48 µg L^{-1}), a low

TN:TP ratio (11:1) and a high pH 8.3 was measured in early July. In this pond, the sediment temperature was above freezing (0.8 °C) and the water temperature was 0.5–1.1 °C, whereas in other ponds nearby the sediment temperatures were below zero (-0.5 – -1.9 °C) and the water temperatures were between 2.0 and 4.9 °C at the same time. I assume that in this pond, the measured high Chl-a concentration was due to a phytoplankton bloom. However, *L. arcticus* may also detach benthic algae from the sediment and thereby alter the Chl-a concentration in the water. The phytoplankton in High Arctic ponds may bloom when the sediment temperature is above zero, since phytoplankton is not able to always actively control its own place in the water column. In the clear-water Arctic ponds and lakes, the sediment temperature can be a more crucial controller of phytoplankton growth than the sunlight, partly because the frozen bottom prevents the release of sedimented nutrients. As there is enough light in the whole water column, the light does not inhibit the photosynthesis in transparent waters. Sediment temperature can be a one important factor affecting the timing of Arctic phytoplankton bloom.

4.13. Water chemistry in High Arctic ponds

L. arcticus is benthic for the most part of its adult stage. *L. arcticus* may serve as a food source for birds and fish, affect the decomposition rates of organic material and take part to the recycling of inorganic nutrients. *L. arcticus* may also have a strong influence on bioturbation in Arctic ponds. Changes in the occurrence of *L. arcticus* may have unwanted influence on the transfer of energy in ponds, lakes and even in the surrounding Arctic tundra.

Water chemistry was exceptional in some *L. arcticus* ponds possibly indicating on-going changes in the freshwater ecosystems on Spitsbergen. The observed median concentrations of TOC (3.1 mg l^{-1}) and DOC (2.5 mg l^{-1}) were typical for oligotrophic lakes (2.2 mg l^{-1} and 2.0 mg l^{-1}, respectively; Wetzel 2001).

Nevertheless the water carbon concentrations (TOC and DOC) indicate that not all Svalbard ponds are oligotrophic. Nine ponds were oligotrophic; eight ponds were mesotrophic and three ponds even shows signs of eutrophication (Brandalaguuna, Trehyrdingen 1 and Solvatnet in Ny-Ålesund). The TOC seems to have doubled in twelve years in three ponds in Ny-Ålesund. In 2010, the concentrations of TOC were 2.0–2.3 times higher in Storvatnet and Solvatnet and 1.6–13.0 times higher in Branddallaguna than was previously measured by Van Donk et al. (2001). The observed high TOC and DOC concentrations in Brandallaguna in August 2010 may be caused by glacial runoff or goose faeces. Brandallaguna is situated in a wetland area where there are two shallow ponds and a glacier river called Bayelva (Figure 3). Wetlands are among the most abundant and biologically productive aquatic ecosystem in the Arctic (Mitsch & Gosselink 1993, Moore et al. 1981). The quality of melting waters may also have major influence on the concentration of cations, anions, nutrients and dissolved organic matter in the receiving water bodies, and even on the fate and behaviour of toxic pollutants (Prowse et al. 2006). Another possible reason for high concentrations of DOC and TOC in Brandallaguna could be the abundant faeces from barnacle geese and reindeer seen on the pond shore. Over the past few decades a dramatic increase in the breeding populations of geese has been observed on Spitsbergen (Van Geest et al. 2007). Barnacle goose may have a major effect on the water quality and vegetation near to the Arctic ponds. Increasing numbers of lesser snow geese (*Chen caerulescens caerulescens*) has led to loss of vegetation and partial erosion of sediment in the coastal marshes of Canada (Jefferies et al. 2006). The vegetation mosaic near the Arctic ponds may disappear, leading to fast shifts in vegetation states. Barnacle geese stay close to the ponds because they provide shelter against predators such as arctic fox. Geese seemed to drop faeces directly into the water and around the pond catchment where they were grazing and breeding. The occurrence of birds may partly explain the high amounts of organic matter in the sediments of some ponds. For example, the percentage of sediment organic matter was high (54 %) in the bird sanctuary area in Kapp Linné. Significantly lower contents of soil organic matter (5–25 %) are more typical for the bioclimate subzone B on Spitsbergen (Jónsdóttir 2005).

The incoming waters are usually warmer than water in the lakes and thus they tend to pass through the lake without significant mixing (Prowse et al. 2006). This was not the case in Longyearbyen pond where the incoming water was coming from a glacier and thus was colder than water in the pond. All study ponds were shallow and thus experienced frequent mixing during windy weather. Internal loading can be problematic in some ponds, if the number of geese or other possible external loadings will not decrease. Increase in nutrient concentrations will inevitably lead to change in the trophic state of the pond (from oligotrophic to mesotrophic), especially if the pond is situated near to the ocean where the sediment temperature may rise rapidly in early spring. In such case, the nutrient-rich sediment would be unfrozen for a longer time period and thus the sediment could release nutrients in the water column throughout the summer.

Small amounts of organic carbon in the sediment and the high TOC and DOM concentrations in the water created amazing features in Brandallaguna. A lot of gas, probably methane, was released from the pond bottom when *L. arcticus* samples were collected from 1–1.5 m depth. Smaller bubbles were rising constantly, whereas a large bubble of about 50 cm diameter rose to the surface when the samples were collected from the eastern side of the pond. The decomposition process of the soil is mainly dependent on the characteristics of the organic matter, the environment conditions and activity of microorganisms and soil fauna (Loureiro et al. 2006). I assume that the food web in Brandallaguna may get part of their energy from methanogenic bacteria. This assumption was supported by an exceptional presence of *L. arcticus* in the deep water and the gas leak from the bottom of the pond. Swarms of large *Daphnia* were not seen in deep area of the pond where the *L. arcticus* were found. In the study of Van Geest et al. (2007), the presence of *L. arcticus* was not related to *Daphnia* biomass or nutrient content of the ponds on Spitsbergen.

Concentrations of TOC or aluminium may influence the distribution of invertebrates in relation to pH and calcium (Hämäläinen and Huttunen 1990, Sutcliffe et al. 1986, Hobaek and Raddum 1980). TOC concentrations are often especially low (< 1.5 mg/l^{-1}) in the sites inhabited by species with a low tolerance for acidic water (Lien et al. 1996). Reported pattern indicates that clear water sites having low concentrations of TOC must have higher pH and/or calcium concentrations in order to support a diverse fauna. TOC and pH values were low in Longyearbyen pond (0.94 mgC/l^{-1} and pH 6.4) and in Adventdalen second pond (0.86 mgC/l^{-1} and pH 6.3) in Longyearbyen, and in Pond 5 (1.4 mgC/l^{-1} and pH 7.0) in Pyramiden. One should pay great attention to the development of water chemistry in these three ponds because the *L. arcticus* populations are in great danger of extinction.

In the present study ponds the mean total phosphorus (^{tot}P) concentration was exceptional, i.e. higher than have been measured in other similar limnological surveys in High Arctic. In contrast, relatively low concentrations of total nitrogen (^{tot}N) (mean 0.367 mg l^{-1}) were measured on Spitsbergen ponds. The TN: NP ratio suggested a P-limitation (≥17:1) at 58 % of the study sites and the rest of the sites the ratio suggested N-limitation. Mean total phosphorus concentration on Spitsbergen (28.3 μg l^{-1}) was similar to the phosphorus concentration in New Zealand (29 μg l^{-1}; Jeppesen et al. 2003). On Spitsbergen, the mean total phosphorus concentrations were higher than previously measured from lakes in northeast Greenland (10.2 μg l^{-1}; Jeppesen et al. 2001), in Greenland (11 μg l^{-1}; Jeppesen et al. 2003), and in Ellesmere Island (9.1 μg l^{-1}) and in Prince Patric Island (16.5 μg l^{-1}) in Canadian High Arctic (Antoniades et al. 2003). Similar low ^{tot}P concentration (10 μg l^{-1}) was measured in *L. arcticus* lake Strømsli-Lombola in mainland Norway (Primicerio & Klemetsen 1999). Sediment resuspension may explain the exceptionally high concentration of phosphorus on Spitsbergen. The sediment resuspension during algae blooms (pH >9) may lead to aerobic release of phosphorus (Niemistö 2008). *L. arcticus* live under exceptionally high ^{tot}P concentrations on Spitsbergen waters compared to ^{tot}P concentrations in other High Arctic regions. However, according to Wetzel´s (2001) classification scheme based on ^{tot}P and ^{tot}N concentrations, all study ponds were still ultra-oligotrophic.

Chl-a concentrations were low in all areas on Spitsbergen except in pond 4 in Kapp Linné. On Spitsbergen, the Chl-a concentrations varied between 0.13–9.04 μg l^{-1} (mean 1.68 μg l^{-1}) and resembled those measured from Greenland (range 0.2–5.4 μg l^{-1}, mean 1.26 μg l^{-1}) by Jeppesen et al. (2003). Antoniades et al. (2003) measured Chl-a concentrations from two locations in Canadian High Arctic region. In their study the Chl-a concentrations were between 0.1–2.6 μg l^{-1} (mean 1.1 μg l^{-1}) in Ellesmere Island and between 0.1–6.9 μg l^{-1} (mean 0.8 μg l^{-1}) in Prince Patrick Island. Thus, the Chl-a concentrations on Spitsbergen seem to correspond more to those measured from Greenland than from freshwaters in Canadian High Arctic. According to Wetzel´s (2001) classification scheme based on Chl-a concentrations, 95 % of the study ponds on Spitsbergen were classified as oligotrophic, which is typical for High Arctic water bodies. An abnormally high Chl-a concentration (9.04 μg l^{-1}) was measured from only one pond in Kapp Linné and this pond (Pond 4) was thus classified as mesotrophic. In general, the low Chl-a, ${}^{tot}P$ and ${}^{tot}N$ concentrations indicate that the pelagic primary production is low in all the study ponds.

4.14. Climate change

Temperature is one of the most important ecological parameters. The current global climate models predict warmer summer and winter temperatures and increasing precipitation on Spitsbergen which will lead to changes in annual runoff (IPCC 2007). It is probable that the runoff in many glacier- and snow-fed rivers increases and the spring peak discharge will happen earlier. Increased cloudiness may lead to lesser insolation and change the evaporation-precipitation dynamics and thereby affect water temperatures in aquatic systems during the short Arctic summer. Changes will occur in High Arctic aquatic systems in the future. These potential changes include: longer ice free season, enlargement and increased number of glacial lakes and changes in top predators of the food web (IPCC 2007). This study highlights the ongoing changes in the fitness (e.g.

increase body size and improve reproduction capacity) of a High Arctic top predator *L. arcticus* and discloses the alarming eutrophication of the Spitsbergen ponds.

Mosses in tundra ecosystems may become the dominant vegetation in terms of total biomass and form a continuous cover over large areas of the Arctic landscape (Beringer et al. 2001). Mosses are particularly important in the discontinuous permafrost zone, where the mean annual temperature is near 0 °C (Nicholas & Hinkel 1996). Mosses often dominate vegetation in areas near to the High Arctic ponds and annual air temperature is below zero on Spitsbergen. If mosses and the underlying peat layer are removed by fire or mechanical disturbance, the depth of active layer increases because more heat is conducted into permafrost (Nicholas & Hinkel 1996, Mackay 1995, Dyrness et al. 1986). Two of the study ponds (Adventdalen second pond and Tvillingvatnet) were heavily tilled by excavators and the vegetation was completely destroyed near the Adventdalen second pond. Ultimately, thawing of permafrost may lead to thermokarst (i.e. collapse of the ground surface) and inundation of lower soil layers with water, which may have large ecological and economic consequences (Nisbit 1989). However, permafrost melting is not expected to happen in Svalbard in the immediate future.

Vegetation, especially mosses, has an important role in shorelines of Arctic ponds. Moss acts as an insulate layer producing cooler summer temperatures (6.9 °C lower at depth of 0.5 m) and warmer winter temperatures (2.3 °C higher at depth of 0.5 m) when compared with a homogenous loam soil column (Beringer et al. 2001). It seems likely that vegetation, especially mosses, is a significant factor affecting thermal and hydrological properties of Arctic ponds. Higher soil temperatures resulting from the disturbance of the moss layer or high-latitude warming could increase decomposition rates, potentially changing these systems from being a sink to become a source of CO_2 to the atmosphere (Serreze et al. 2000, Cialis et al. 1995, Grulke et al. 1990) and creating a positive feedback to warming (Oechel et al. 1993, Billings et al. 1982). Furthermore, an increased depth of active layer may lower the water table, causing greater aeration and even warmer temperatures that may further increase decomposition of soil carbon (Beringer et al. 2001). Lower water levels may lead to increased development of true macrophytes, filamentous algae and benthic microalgae because of improved light conditions at the lake bottom, thereby favouring benthic chydorids (Crustacea) at the expense of zooplankton (Jeppessen et al. 2001). Climate warming can lead to higher primary production and thereby increase the amount of food (e.g. chironomids) to *L. arcticus*, but at the same time also cause problems if the growing green algae mats capture and kill prowling *L. arcticus*. Evidence of the existence of this phenomenon was obtained when the pond Solvatnet was studied in Ny-Ålesund. *L. arcticus* individuals became entangled in the algae mats. However, combined neo- and paleoecological studies have shown that invertebrates respond to changes in substrate availability (e.g. macrophytes, mud and sand) or in lake chemistry (e.g. salinity and pH) rather than to changes in water level (Verschuren et al. 2000). It is important to note that climate warming affects aquatic ecosystems both through indirect effects, such as change in catchment processes (e.g. thicker active layer because of permafrost melting, decreased snow and ice cover) and direct temperature effects (e.g. water temperature increases). On Spitsbergen, the degree of human influence varies regionally, being less evident in uninhabited northern areas than in mining towns. All human activities that have an effect on the Arctic ponds (e.g. acidification, eutrophication, land use and plant cover) may also potentially affect the survival of *L. arcticus*. To protect the waters and *L. arcticus* in High Arctic, people should avoid damaging vegetation near the ponds and lakes and releasing nutrients or chemicals in waters (e.g. waste waters and pollutants from coal mines, landfills and dog yards).

The described recent changes in *L. arcticus* size and reproduction capacity suggest that *L. arcticus* populations on Spitsbergen have already dramatically responded to elongation of growing and ice-free season and probably also to increased algal productivity due to climate warming. These ecological changes in Arctic regions may induce migrations of invertebrates from temperate and mid-latitude to high-latitude regions. Recent changes in ecological conditions of natural habitats have often been fatal to the branchiopods. For example, Löffer (1993) reported that eight of the sixteen known Austrian large branchiopod species are extinct, primarily due to agricultural activities and artificial changes in hydrologic conditions. Large branchiopods have been used for the assessment of the quality and function of temporary wetlands (Brendonck et al. 2008). In this study I identified water chemistry variables that could be used as indicators of the condition and responses of *L. arcticus* populations to changes in High Arctic ponds (Table 12). These general requirements for indicator species applying to *L. arcticus* include:

1. Sensitivity to the environmental factors, in this case pH, temperature and salinity
2. Common occurrence and distribution over the entire survey area
3. Easily visible and rapidly surveyed by non-expert workers
4. Species for which experimental data are available, and
5. Information on *L. arcticus* is available from the end 1800s to the present.

L. arcticus is a good indicator species of the on-going habitat and climate change. It seems likely that the *L. arcticus* populations have been in a steady-state with the present water chemistry. However, some populations may survive for some years and then become extinct, which might be due to several reasons. For example, *L. arcticus* may disappear if the pH drops below 6.1, the salinity increases to >2 ‰, or if the pond dries up before the *L. arcticus* reach sexual maturity. Global warming is likely to exacerbate environmental conditions on Spitsbergen. *L. arcticus* will face many challenges, if the current change in climate and environment in the Arctic will continue.

These studies add to the developing information base necessary to understand the relationship between the environmental stresses and the potential pollutant impact from anthropogenic contaminants. Rise in water temperature, salinity or acidification can lead to extinction of *L. arcticus*. Here, the studies of *L. arcticus* ponds on Spitsbergen increase our limited knowledge about the relationships between different natural and anthropogenic stressors and the ecological condition of key aquatic organisms in High Arctic regions.

5. Conclusions

A list summarizing the the main conclusions of the thesis are given below. Each section is based on the initial four study hypotheses (H1–H4).

H1: Acidification and increased water salinity and temperature induced by global warming can lead to higher mortality and potential extinction of *L. arcticus* in Arctic ponds.

1.) The condition of *L. arcticus* was strongly related to the water pH, interaction between TOC and pH, temperature and water salinity.
2.) *L. arcticus* tolerated small changes in water salinity. A slight increase in salinity (1 ‰) seemed to speed up the ecdysis of *L. arcticus*.
3.) *L. arcticus* were not found in waters with pH below 6.1 and a strong acid stress at pH 4 caused rapid mortality of the mature females.
4.) *L. arcticus* populations are in danger of disappearing due to acidification of two ponds in Longyearbyen and one pond in Pyramiden on Spitsbergen. A slight drop in pH (0.1–1.0 units) may wipe out these *L. arcticus* populations. Thus, water pH and TOC should be monitored in these ponds and the input of acidifying substances should be prevent.
5.) A new disease (named as Red Carapace Disease) was discovered from *L. arcticus* on Spitsbergen. This disease is likely caused by an unknown parasite and seemed to activate with increasing temperature.

H2: *L. arcticus* can be used as an indicator species of environmental change in Arctic regions.

1.) *L. arcticus* can be used as an indicator species of climate change and acidification in the Arctic region (Table 12).

2.) *L. arcticus* is clearly a species that reguires a high oxygen concentration and cool water. Among Notostraca, *L. arcticus* should be consider as stenothermal.

H3: *L. arcticus* is cannibal and can use chemical cues to localize injured conspecifics.

1.) *L. arcticus* may use olfaction to find food including injured conspecifics.
2.) The main *L. arcticus* predators seemed to be arctic tern, purple sandpiper and other cannibalistic *L. arcticus* individuals.

H4: Camouflage is an important characteristic for *L. arcticus* and this crustacean´s colouration varies within and between Arctic ponds.

1.) The existence of different colour morphs monochrome and marbled in different colours (black, brown and yellow) was an unknown characteristic of this High Arctic crustacean species.
2.) *L. arcticus* populations showed a great diversity in the composition and diversity of colour morphs between and within the Arctic ponds.

Furthermore:

1.) *L. arcticus* females reach sexual maturity at a smaller body size and sexual dimorphism begins to appear in smaller animals on Spitsbergen than anywhere else.
2.) Males occur in some *L. arcticus* populations on Spitsbergen. Sexual reproduction in *L. arcticus* is likely more common than was previously believed.

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Appendix 1. Bird and mammal observations near the ponds in Longyearbyen, Kapp Linné , Pyramiden, Ny-Åledund and Northern coast of Spitsbergen. The bird and mammal observation were made near the ponds. **= large numbers (>10) of birds, ***= large flock (>15) of birds, x= sound of geese was heard near the pond and – = vertebrate not seen near to the pond.

Area	Longyearbyen						Kapp Linné				Pyramiden		Ny-Ålesund									Northern coast of Spitsbergen	
Pond name	Longyearbyen	Dammyra	Adventdalen 1	Adventdalen 2	Adventdalen 3	Nybyen	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6	Solvatnet	Tvillingvatnet	Storvatnet	Kolhamna	Trehyrdingen 1	Trehyrdingen 2	Brandallaguna	Geese pond	Gludneset	Kilmeset	Polheim
Birds												–											
Branta leucopsis, adult	9	***			6		8	2					8	13	48		5		11	9		48	x
Branta leucopsis, chick	4						5						3	10					10				
Sterna paradisaea				5	3		6	1	2	**			4							5	***		1
Calidris maritima	1					1		2								2		4	3	1			
Calidris alpina			1																				
Phalaropus fulicarius							1			1													
Stercorarius parasiticus				1			1								4		1	3	5			1	
Pagophila eburnea								1	1	1													
Rissa tridactyla								19		13			1										
Larus hyperboreus							1						7										
Northern fulmar													2										
Somateria mollissima										1			2										
Plectrophenax nivalis	2	**						1			1					2							
Cepphur grylle								1															
Gavia stellata							2																
Clangula hyemalis							2																
Mammals																							
Alopex lagopus	1					1								1	1	1							
Rangifer tarandus platyrhynchus	1						3						2						3				
Ursus maritimus									1														

Appendix 2. Vegetation type, moss cover, plants observations near the ponds in Longyearbyen, Kapp Linné , Pyramiden, Ny-Åledund and Northern coast of Spitsbergen. The vegetation observation were made 0–25 m from the pond shore. N/O= not observation made, – = higher plant not seen near to the pond, H= high moss cover, M= medium moss cover, L= low moss cover.

Area	Longyearbyen						Kapp Linné				Pyramiden		Ny-Ålesund									Northern coast of Spitsbergen	
Pond name	Longyearbyen	Dammyra	Adventdalen 1	Adventdalen 2	Adventdalen 3	Nybyen	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6	Solvatnet	Tvillingvatnet	Storvatnet	Kolhamna	Trehyrdingen 1	Trehyrdingen 2	Brandallaguna	Geese pond	Gludneset	Kilmeset	Polheim
Vegetation type			N/o																	N/o	N/o		
Moss tundra community							x	x	x	x	x	x	x		x				x			x	
Mountain Sorrel community																							x
Willow-field horsetail community	x	x				x								x				x					
Shore-meadow community					x																		
Poorly developed vegetation				x												x	x						
Moss cover	H	H	N/o	L	L	M	H	M	H	H	M	M	H	L	H	L	L	L	M	N/o	N/o	H	L
Plants			N/o					–				–	–		–	–				N/o	N/o	–	
Oxyria digyna											x												x
Saxifraga oppositifolia							x							x					x				
Saxifraga cespitosa							x		x	x				x			x		x				
Saxifraga rivularis										x													
Saxifraga cernua						x																	
Saxifraga foliolosa																	x						
Salix polaris	x	x				x	x							x				x					
Poa arctica						x																	
Deschampsia						x																	
Grass	x	x			x				x	x													x
Green algae				x																			
Lichen														x				x					x
Fungi													x										
Cyanobacteria mat																x							

Appendix 3. The bottom quality (range of 0–3; 0 = none, 1 = few, 2 = common, 3 = plenty), the sediment colour and the largest primary producerse in the ponds. ▨ = predominat type, N/A = data is not available

Area	Longyearbyen						Kapp Linné				Pyramiden		Ny-Ålesund									Northern coast of Spitsbergen	
Pond name	Longyearbyen	Dammyra	Adventdalen 1	Adventdalen 2	Adventdalen 3	Nybyen	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6	Solvatnet	Tvillingvatnet	Storvatnet	Kolhamna	Trehyrdingen 1	Trehyrdingen 2	Brandallaguna	Geese pond	Gludneset	Kilmeset	Polheim
Bottom quality			N/A																		N/A		
Blocks (>200 mm)	0	0		1	0	1	1	1	0	1	2	1	1	1	1	0	0	1	1	0		0	1
Large stones (60–200 mm)	1	0		2	0	1	**3**	2	**2**	**2**	1	1	1	**3**	1	1	2	2	1	0		0	**3**
Small stones (20–60 mm)	1	1		1	0	1	2	2	2	2	1	2	2	2	2	**2**	**3**	**3**	2	1		0	3
Gravel (2–20 mm)	0	0		1	1	0	1	2	1	1	1	2	1	2	0	1	1	0	1	1		1	1
Sand (0.02–2 mm)	1	0		1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1		1	1
Clay/sludge	**3**	**2**		**3**	**2**	**3**	2	**3**	1	1	**3**	**3**	**3**	1	**3**	1	2	1	**3**	**3**		**3**	1
Fine detritus	1	1		0	0	1	0	1	2	1	0	0	1	1	0	1	1	1	1	1		0	0
Coarse detritus	0	2		0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1		1	0
*Timber, (*plank, +bark)*	+1	0		0	0	0	0	0	0	0	0	0	*2	0	0	0	1	0	0	0		0	0
Coal	1	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0
Sediment colour			N/A											N/A						N/A			
Black	x	x		x	x		x	x	x	x			x		x	x	x				x	x	
Dark grey									x			x			x	x	x	x					
Grey									x									x					x
Dun											x												
Dark brown				x	x				x														
Brown								x	x	x						x	x	x	x				
Light brown							x											x			x		
Tan							x																
Reddish orange																x	x						x
Reddish brown												x											
Reddish																						x	
Green									x						x	x	x						
Aquatic "vegetation" e.g. photosynthetic mosses, bacteria and algae																							
Bryophyta	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x
Cyanobacteria							x		x	x		x			x		x	x					x
Green algae balls				x									x										
Green algae mats								x		x			x			x			x				

Appendix 4. Logyearbyen water chemistry and sediment property. N/A = value not available, Longye. = Longyearbyen, Advent. 2 = Adventdalen second pond, Advent. 3 = Adventdalen third pond.

Site	Water surface T °C	Sediment surface T °C	Sediment T °C	Salinity ‰	Cond. µS cm^{-1}	pH	O^2 %	O^2 mg L^{-1}	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Longye.	1.0	0.9	0.3	0.1	201.1	6.4	46.8	4.5	4.2	1.7	7.7.2010	78°12.147´	015°34.457´
Dammyra	4.2	4.3	-1.4	1.2	2453.3	7.2	47.3	5.2	2.8	5.5	31.7.2010	78°12.171´	015°45.877´
Advent. 2	4.1	4.1	4.3	0.1	277.7	6.3	52.1	6.5	0.3	5.0	18.8.2010	78°13.130´	015°41.483´
Advent. 3	N/A	N/A	N/A	0.2	484.7	8.0	58.0	6.4	0.3	5.1	23.8.2010	78°13.004´	015°42.344´
Nybyen	4.2	4.3	3.7	0.1	288.7	7.2	55.1	7.1	3.5	1.7	6.9.2010	78°11,824´	015°34,993´
Mean	2.9	3.0	1.8	0.5	741.1	7.1	51.5	5.8	2.2	3.8			
Median	3.6	3.8	2.7	0.2	288.7	7.2	51.7	5.9	2.8	5.0			
Maximum	4.2	4.3	4.2	1.5	2453.3	8.0	58.0	7.1	4.2	5.5			
Minimum	0.2	0.2	-1.4	0.1	201.1	6.3	46.8	4.5	0.3	1.7			

Site	^{tot}N mg L^{-1}	^{tot}P µg L^{-1}	TN:TP	TOC mg L^{-1}	DOC mg L^{-1}	OM %	Sediment moisture content %	Chl > 2.7 µm µg L^{-1}	Chl 2.7–0,7 µm µg L^{-1}	^{tot}Chl µg L^{-1}	Moss cover % 25 m	Goose droppings 25 m	*L. arcticus* density m^2
Longyea.	0.155	23.3	7:1	0.9	1.0	15.8	42.3	N/A	N/A	N/A	61–100	medium	0
Dammyra	0.555	16.0	35:1	8.7	6.6	43.8	89.2	N/A	N/A	N/A	31–60	high	N/A
Advent. 2	0.440	30.3	15:1	0.9	0.7	8.9	39.4	N/A	N/A	N/A	11–30	low	1
Advent. 3	0.345	11.0	31:1	5.5	4.3	11.5	47.7	N/A	N/A	N/A	11–30	low	N/A
Nybyen	0.285	66.0	4:1	3.8	2.8	4.4	39.6	3.08	0.17	3.24	31–60	low	0.5
Mean	0.387	28.0	19:1	4.0	3.1	16.9	51.6						
Median	0.393	22.4	20:1	3.8	2.8	11.5	42.3						
Maximum	0.555	66.0	35:1	8.7	6.6	43.8	89.2						
Minimum	0.155	11.0	4:1	0.9	0.7	4.4	39.4						

Appendix 5. Kapp Linné water chemistry and sediment property.

Site	Water surface T °C	Sediment surface T °C	Sediment T °C	Salinity ‰	Cond. μS cm^{-1}	pH	O^2 %	O^2 mg L^{-1}	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Pond 1	4.2	4.3	-0.5	0.1	271.7	8.2	42.4	4.6	0.3	4.5	12.7.2010	78°04.272´	013°42.294´
Pond 2	4.9	4.7	-1.9	0.1	260.7	8.3	49.4	5.7	0.3	4.5	12.7.2010	78°04.375´	013°42.423´
Pond 3	2.1	2.0	-0.5	0.1	265.7	8.2	45.5	4.7	0.4	4.3	12.7.2010	78°03.632´	013°40.345´
Pond 4	0.5	1.1	0.8	0.1	321.7	8.3	46.0	5.0	0.1	5.2	11.7.2010	78°03.411´	013°36.716´
Mean	2.9	3.0	-0.5	0.1	279.9	8.3	45.8	5.0	0.3	4.6			
Median	3.2	3.2	-0.5	0.1	268.7	8.3	45.7	4.9	0.3	4.5			
Maximum	4.9	4.7	0.8	0.1	321.7	8.3	49.4	5.7	0.4	5.2			
Minimum	0.5	1.1	-1.9	0.1	260.7	8.2	42.4	4.6	0.1	4.3			

Site	^{tot}N mg L^{-1}	^{tot}P μg L^{-1}	TN:TP	TOC mg L^{-1}	DOC mg L^{-1}	OM %	Sediment moisture content %	Chl > 3 μm μg L^{-1}	Chl 3–0.7 μm μg L^{-1}	^{tot}Chl μg L^{-1}	Moss cover % 25 m	Goose droppings 25 m	*L. arcticus* density m^2
Pond 1	0.130	25.5	5:1	1.9	1.3	28.5	66.9	2.01	0.19	2.20	61–100	medium	4-8
Pond 2	0.290	36.5	8:1	2.9	2.1	1.7	66.3	0.90	0.04	0.94	31–60	low	2-14
Pond 3	0.117	7.1	17:1	2.0	1.3	3.6	28.0	3.18	0.21	3.39	61–100	low	5-7
Pond 4	0.515	48.0	11:1	2.5	1.7	54.2	84.5	7.92	1.11	9.04	61–100	medium	18
Mean	0.263	29.3	10:1	2.3	1.6	22.0	61.4	3.50	0.39	3.89			
Median	0.210	31.0	9:1	2.3	1.5	16.0	66.6	2.59	0.20	2.79			
Maximum	0.515	48.0	17:1	2.9	2.1	54.2	84.5	7.92	1.11	9.04			
Minimum	0.117	7.1	5:1	2.9	1.3	1.7	28.0	0.90	0.04	0.94			

Appendix 6. Pyramiden water chemistry and sediment property. N/A = value not available.

Site	Water surface T °C	Sediment surface T °C	Sediment T °C	Salinity ‰	Cond. µS cm^{-1}	pH	O^2 %	O^2 mg L^{-1}	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Pond 5	3.1	3.0	2.1	0.1	140.5	7.0	51.6	5.7	3.6	2.8	16.7.2010	78°39.360´	016°10.795´
Pond 6	2.4	2.4	1.2	0.1	200.2	7.4	52.2	5.9	3.3	2.5	16.7.2010	78°39.271´	016°11.343´

Site	^{tot}N mg L^{-1}	^{tot}P µg L^{-1}	TN:TP	TOC mg L^{-1}	DOC mg L^{-1}	OM %	Sediment moisture content %	Chl > 2.7 µm µg L^{-1}	Chl 2.7–0.7 µm µg L^{-1}	^{tot}Chl µg L^{-1}	Moss cover % 25 m	Goose droppings 25 m	*L. arcticus* density m^2
Pond 5.	0.195	15.5	13:1	1.4	1.0	6.2	26.2	0.34	0.01	0.34	31–60	high	N/A
Pond 6	0.190	11.3	17:1	N/A	N/A	18.7	40.0	0.12	0.00	0.13	31–60	high	none

Appendix 7. The northern coast of Spitsbergen, Kilneset and Polheim water chemistry and sediment property. N/A = value not available.

Site	Water surface T °C	Sediment surface T °C	Sediment T °C	Salinity ‰	Cond. µS cm^{-1}	pH	O^2 %	O^2 mg L^{-1}	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Kilneset	2.3	2.4	2.3	0.1	253.5	8.0	45.7	55.4	0.4	12.2	4.8.2010	79°42.176´	013°22.594´
Polheim	5.1	5.2	3.3	0.0	84.4	7.9	46.9	5.1	0.1	6	3.8.2010	79°53.395´	016°02.337´

Site	^{tot}N mg L^{-1}	^{tot}P µg L^{-1}	TN:TP	TOC mg L^{-1}	DOC mg L^{-1}	OM %	Sediment moisture content %	Chl > 2.7 µm µg L^{-1}	Chl 2.7–0.7 µm µg L^{-1}	^{tot}Chl µg L^{-1}	Moss cover % 25 m	Goose droppings 25 m	*L. arcticus* density m^2
Kilneset	0.340	26.0	13:1	3.1	2.5	21.1	44.5	0.45	0.00	0.45	61–100	medium	4
Polheim	0.310	13.5	23:1	3.0	2.0	1.6	18.3	2.11	0.03	2.14	11–30	low	N/A

Appendix 8. Ny-Ålesund water chemistry and sediment property 6–9.8.2010. N/A = value not available, Tvillingv.=Tvillingvatnet, Storvat.=Storvatnet, Kolhamn.=Kolhamna, Trehyrd1.=Trehyrdingen 1, Brandall.=Brandallaguna, Geese p.=Geese pond and Gluudne.=Gluudneset

Site	Water surface T °C	Sediment surface T °C	Sedi-ment T °C	Salinity ‰	Cond. $\mu S\ cm^{-1}$	pH	O^2 %	O^2 $mg\ L^{-1}$	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Solvatnet	1.8	1.8	1.6	0.2	499.3	8.5	79.3	10.1	0.05	2.1	6.8.2010	78°55.´34.22´	011°56´21.0´
Tvillingv.	0.8	0.8	0.1	0.1	163.6	7.4	47.8	5.6	1.2	0.7	7.8.2010	78°55´00.6´	011°52´25.9´
Storvat.	3.1	3.3	3.4	0.1	251.7	8.1	49.7	6.5	0.45	1.4	8.8.2010	78°55´25.9´	011°52.54.1´
Kolhamn.	4.2	4.3	4.3	0.5	973.3	8.0	51.5	6.5	0.1	2.1	9.8.2010	78°56´01.8´	011°50´55.2´
Trehyrd1.	N/A	N/A	N/A	0.5	978.3	8.2	49.9	6.3	0.9	1.7	8.8.2010	78°56.02´0´	011°49.11´8´
Brandall.	N/A	N/A	N/A	0.1	217.0	8.4	50.5	6.5	0.5	1.9	9.8.2010	78°56.27.4´	011°49´22.6´
Geese p.	4.8	3.6	2.7	0.2	408.0	8.7	52.1	6.0	0.26	2.0	7.8.2010	78°55´31.4´	011°55´21.8´
Gluudne.	3.9	4.0	2.2	2.8	5230.0	8.4	52.2	5.7	0.05	1.2	6.8.2010	78°914.6959´	012°0633493´
Mean	3.1	3.0	2.4	0.6	1090.2	8.2	54.1	6.6	0.44	1.6			
Median	3.5	3.5	2.5	0.2	453.7	8.3	51.0	6.4	0.36	1.8			
Maximum	4.8	4.3	4.3	2.8	5230.0	8.7	79.3	10.1	1.20	2.1			
Minimum	0.8	0.8	0.1	0.1	163.6	7.4	47.8	5.6	0.05	0.7			

Appendix 8 continues. Ny-Ålesund water chemistry and sediment property 6–9.8.2010. N/A = value not available.

Site	^{tot}N mg L^{-1}	^{tot}P µg L^{-1}	TN:TP	TOC mg L^{-1}	DOC mg L^{-1}	OM %	Sediment moisture content %	Chl > 2.7 µm µg L^{-1}	Chl 2.7–0.7 µm µg L^{-1}	^{tot}Chl µg L^{-1}	Moss cover % 25 m	Goose droppings 25 m	*L.arcticus* density m^2
Solvatnet	1.050	50.5	21:1	13.0	8.5	30.8	64.8	2.19	0.03	2.23	61–100	medium	0
Tvillingv.	0.065	3.6	18:1	0.9	0.6	3.6	24.7	0.26	0.01	0.28	11–30	low	0
Storvatnet	0.445	69.5	6:1	6.0	3.9	N/A	N/A	N/A	N/A	N/A	31–60	low	1.6
Kolhamna	0.340	8.6	39:1	2.8	1.8	15.6	69.2	2.54	0.04	2.58	11–30	low	1.6-3.3
Trehyrdingen1	0.410	18.5	22:1	4.9	3.7	N/A	N/A	N/A	N/A	N/A	11–30	none	2.2
Brandallaguna	0.315	20.0	16:1	52.0	57.0	N/A	N/A	N/A	N/A	N/A	31–60	medium	N/A
Geese pond	0.315	89.0	4:1	4.1	3.0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	none
Gluudneset	0.540	30.5	18:1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	none
Mean	0.435	36.3	18:1	12.0	11.2	16.7	52.9	1.66	0.03	1.70			
Median	0.375	25.3	18:1	4.9	3.7	15.6	64.8	2.19	0.03	2.23			
Maximum	1.050	89.0	39:1	52	57	30.8	69.2	2.54	0.04	2.58			
Minimum	0.065	3.6	4:1	0.9	0.6	3.6	24.7	0.26	0.01	2.23			

Appendix 9. Ny-Ålesund water chemistry and sediment property 30.8–2.9.2010. N/A = value not available, Storvat.=Storvatnet, Tvillingv.=Tvillingvatnet, Trehyrd1.=Trehyrdingen 1, Treyrd2.=Trehyrdingen 2, Brandall.=Brandallaguna and Kolham.=Kolhamna.

Site	Water surface T °C	Sediment surface T °C	Sedi-ment T °C	Salinity ‰	Cond. µS cm^{-1}	pH	O^2 %	O^2 mg L^{-1}	Distance from the sea (km)	Distance from the glacier (km)	Date	Latitude (°N)	Longitude (°W)
Solvatnet	4.1	4.2	4.0	0.2	409.7	7.9	53.0	6.9	0.05	2.1	31.8.2010	78°55.´34.22´	011°56´21.0´
Storvat.	4.5	4.4	4.4	0.1	270.0	7.8	51.9	7.7	0.45	1.4	1.9.2010	78°55´25.9´	011°52.54.1´
Tvillingv.	4.5	4.4	4.4	0.1	223.2	7.4	51.9	7.1	1.2	0.7	2.9.2010	78°55´00.6´	011°52´25.9´
Trehyrd1.	5.2	5.3	4.6	0.1	190.0	7.9	51.8	6.8	0.9	1.7	30.8.2010	78°56.02´0´	011°49.11´8´
Trehyrd1.	3.3	3.4	3.7	N/A	N/A	N/A	N/A	N/A	0.9	1.7	1.9.2010	78°56.02´0´	011°49.11´8´
Trehyrd2.	5.4	5.5	4.6	0.03	84.0	7.2	53:2	7.0	1.3	1.3	31.8.2010	78°56.54.5´	011°48´51.4´
Trehyrd2.	3.7	3.7	3.5	N/A	N/A	N/A	N/A	N/A	1.3	1.3	1.9.2010	78°56.54.5´	011°48´51.4´
Brandall.	4.5	4.4	4.7	0.13	309.0	8.1	52.2	7.5	0.5	1.9	31.8.2010	78°56.27.4´	011°49´22.6´
Brandall.	3.1	3.2	3.4	N/A	N/A	N/A	N/A	N/A	0.5	1.9	1.9.2010	78°56.27.4´	011°49´22.6´
Kolham.	N/A	N/A	4.9	N/A	N/A	N/A	N/A	N/A	0.1	2.1	30.8.2010	78°56´01.8´	011°50´55.2´
Mean	4.3	4.3	4.2	0.1	247.6	7.7	52.4	7.2	0.72	1.6			
Median	4.5	4.4	4.4	0.1	246.6	7.8	52.1	7.1	0.7	1.7			
Maximum	5.4	5.5	4.9	0.2	409.7	8.1	53.2	7.7	1.3	2.1			
Minimum	3.1	3.2	3.4	0.03	84.0	7.2	51.8	6.8	0.05	0.7			

Appendix 9 continues. Ny-Ålesund water chemistry and sediment property 30.8–2.9.2010. N/A = value not available.

Site	^{tot}N mg L $^{-1}$	^{tot}P µg L $^{-1}$	TN:TP	TOC mg L $^{-1}$	DOC mg L $^{-1}$	OM %	Sediment moisture content %	Chl > 2.7 µm µg L $^{-1}$	Chl 2.7–0.7 µm µg L $^{-1}$	^{tot}Chl µg L-^{1}	Moss cover % 25 m	Goose droppings 25 m	*L.arcticus* density m^2
Solvatnet	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.61	0.07	0.69	61–100	medium	N/A
Storvatnet	0.365	14.0	26:1	5.1	3.3	16.3	61.3	0.62	0.06	0.68	31–60	medium	0
Tvillingvatnet	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.23	0.01	0.24	11–30	low	N/A
Trehyrdingen1	0.420	23.9	18:1	15.0	15.0	26.8	58.1	0.58	0.04	0.62	11–30	none	N/A
Trehyrdingen1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	11–30	none	N/A
Trehyrdingen2	0.235	27.5	9:1	1.9	1.3	13.4	51.0	0.75	0.04	0.79	11–30	low	0.6
Trehyrdingen2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	11–30	medium	N/A
Brandallaguna	0.630	29.3	21:1	6.3	4.0	5.0	36.4	0.21	0.01	0.21	31–60	medium	N/A
Brandallaguna	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	31–60	medium	N/A
Kolhamna	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	11–30	low	N/A
Mean	0.435	36.3	18:1	12.0	11.2	16.7	52.9	0.50	0.04	0.54			
Median	0.375	25.3	18:1	4.9	3.7	15.6	64.8	0.60	0.04	0.65			
Maximum	1.050	89.0	39:1	52	57	30.8	69.2	0.75	0.07	0.79			
Minimum	0.065	3.6	4:1	0.9	0.6	3.6	24.7	0.21	0.01	0.21			