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# Population regulation in the tadpole shrimp *Lepidurus arcticus*

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## Table of contents

Abstract .....	1
Introduction .....	2
Material and Methods.....	4
Study species .....	4
Distribution patterns on Bear Island and Dovrefjell.....	5
Effect of temperature and body size on growth, laboratory experiment .....	5
Sampling .....	5
Experimental design.....	6
Effect of density on final size, field experiment.....	6
Effect of system productivity and density on growth, comparative analyses of natural populations.....	7
Data analysis and statistics .....	7
Size – weight relationship .....	7
Effect of temperature and body size on growth, laboratory experiment.....	8
Effect of density on final size, field experiment .....	9
Effect of system productivity and density on growth, comparative analysis of natural populations .....	9
Results .....	11
Distribution patterns on Bear Island and Dovrefjell.....	11
Effect of temperature and body size on growth, laboratory experiment .....	11
Effect of density on final size, field experiment.....	13
Effect of system productivity and density on growth, comparative study of natural populations.....	14
Discussion .....	16
Acknowledgements .....	20
References .....	21

## **Abstract**

A metapopulation consists of several subpopulations that show limited degree of internal regulation, and are not viable alone in the long term. Instead, each subpopulation is sustained over time by migration and re-colonization from nearby subpopulations. Here, I test for internal regulation in populations of the freshwater crustacean *Lepidurus arcticus*, commonly found throughout the Arctic, and also alpine areas of mainland Norway. A survey of Arctic populations situated at Bear Island and mainland Norwegian populations situated in the Dovre area revealed a correspondence between distance between habitat patches and frequency of occurrence. The life-history and distribution pattern of *L. arcticus*, with highly ephemeral populations in fragmented habitats accordingly suggest this as a candidate species for displaying metapopulation structure. First, the occurrence of *L. arcticus* on Bear Island and Dovre was analyzed. Then, temperature and mass scaling functions were parameterized using a laboratory set-up. A field experiment was conducted to test for density-dependent growth. Finally, growth rate and density was compared among natural populations to test if population density or growth rate was affected by system productivity, or if eventual density effects on growth was modified by productivity. *L. arcticus* was more widespread at Bear Island than on Dovre. Somatic growth increased with temperature, and *L. arcticus* showed density-dependent growth in the field experiment. Neither population density nor system productivity was found to affect growth in the natural populations, but system productivity was positively correlated with population density. Density-dependent growth under experimental conditions, together with the correlation between system productivity and population density show support for internal regulation. The results suggest that the difference between Bear Island and mainland Norway are likely due to environmental factors, not a metapopulation structure.

**Keywords:** metapopulation, density dependence, population regulation, *Lepidurus arcticus*

## **Introduction**

Organisms inhabiting fragmented habitats may persist through two different mechanisms; metapopulation dynamics and internal regulation of subpopulations. Metapopulations consist of isolated subpopulations that are unstable and may go extinct due to demographic stochasticity, but become recolonized from the other subpopulations (Levins 1969). Thus, the independent subpopulations do not have to be stable, and should not be regulated so efficiently that extinctions become rare (Hanski and Gilpin 1991, Hanski 1999, Vandermeer and Goldberg 2003). Furthermore, the population dynamics of different subpopulations should not be synchronous in order to ensure that individuals can migrate from other subpopulations if one goes extinct (Hanski 1999, Begon et al. 2006). Variation in patch size or quality is also expected to affect the metapopulation dynamics. Larger or better quality patches support larger subpopulations, which have a lower extinction probability and will increase the chance of metapopulation persistence (Hanski and Gyllenberg 1993, Fleishman et al. 2002). Reduced distance to neighboring populations would also increase the probability of recolonization after local extinction, and hence the maintenance of the metapopulation as a whole (Hanski and Gilpin 1991).

The alternative mechanism of persistence, internal regulation, requires the occurrence of density dependence within subpopulations. Density dependence is usually defined as processes that cause the population growth rate to decrease with increasing density through feedback mechanisms and thus prevent the unbound fluctuation and extinction of populations (Murdoch 1994). Such negative feedback mechanisms are most commonly linked to intraspecific competition, where competition for shared resources either affects the rates of population growth through survival or through affecting rates of somatic growth, developmental time or fecundity. Competition for territories and direct interference among individuals are other density-dependent mechanisms that can affect the population, and none of these mechanisms are mutually exclusive (Begon et al. 2006). Available resources can therefore affect the upper limit of population size (the carrying capacity) either through survival or reproductive rates (Hairston et al. 1960, Arcese and Smith 1988).

Metapopulation dynamics have been observed in a variety of species, for example butterflies (Hanski et al. 1994, Hodgson et al. 2009) amphibians (Sjogren Gulve 1994, Pope et al. 2000,

Cosentino et al. 2012) and zooplankton (Pajunen and Pajunen 2003, Haag et al. 2005). Common for these are the fragmented nature of their habitats. The subpopulations should not exhibit intense density dependence, because there is a correlation between density dependence and long term-viability of subpopulations (Hanski et al. 1996, Kean and Barlow 2000). Therefore, density dependence indicates internal regulation which violates an important assumption of metapopulation dynamics; that subpopulations are unstable and may go extinct without migration. In the present study I examine the potential for internal regulation in the crustacean *Lepidurus arcticus*, a species that inhabits lakes and small ponds in areas of the northern hemisphere (Hebert and Hann 1986, Vekhoff 1997, Rogers 2001, Hessen et al. 2004). Certain patterns in the large scale distribution may suggest that metapopulation dynamics, with local extinctions and colonization of subpopulations, plays an important role in this. More specifically, in two surveys of fishless ponds taking place at Bear Island and the Dovrefjell mountain range in 2009 and 2010, respectively, a much higher occurrence of *L. arcticus* was found in the prior area than the latter (0% vs. 65%, see result section below), despite *L. arcticus* being present in large lakes in both survey areas. Under a metapopulation framework this might be explained by density of suitable ponds at Dovrefjell, which is lower than on Bear Island (2.36 ponds per km<sup>2</sup> on Dovrefjell vs. 5.16 ponds per km<sup>2</sup> on Bear Island, see result section below), causing extinction rates to exceed colonization rates, whereas the reverse is true at Bear Island where the high density of ponds increases colonization. My approach to address this is to evaluate whether the alternative explanation for maintenance of subpopulations, namely internal regulation, can be ruled out. If not, then the difference in occurrence between the two areas may simply be due to differences in environmental conditions.

In this study, I will test for internal regulation of populations in *L. arcticus*, in order to find if metapopulation dynamics can explain why it is absent from small, fishless ponds in Dovrefjell. The study consists of four parts. First, surveys from Bear Island and Dovrefjell were used to assess the occurrence of *L. arcticus* in ponds, as well as the density of such ponds. Second, a laboratory experiment was used to calibrate models for temperature on the somatic growth rate needed to compare growth among natural populations. Third, population density was manipulated in a field experiment, to find if *L. arcticus* can exhibit density-dependent growth. Fourth, a field survey of ponds on Bear Island was carried out to find if system productivity affects population density, and if there is a relationship between population density and the somatic growth rate.

## Material and Methods

The survey of ponds on Dovrefjell was done during late summer in 2010. The laboratory experiment was conducted at the Norwegian University of Science and Technology (NTNU), Trondheim, during august of 2011. The other parts were carried out at Bear Island (74.5°N, 19.1°E), an island located in the Barents Sea, during the summer of 2009. The survey of ponds on Dovrefjell, and data from Bear Island, was used to find how many ponds *L. arcticus* occurred in, and how close the ponds were to each other in the two areas. The laboratory experiment was conducted to find the effect of temperature on *L. arcticus* somatic growth and estimate the allometric growth exponent, which was used to calculate the standardized mass-specific growth rate in the natural populations. The field experiment was conducted to find the effect of population density on somatic growth. Data collected from natural populations were used in comparative analyses to find if the somatic growth rates in a population are affected by the density, the system productivity or a combination of these. All data analyses were done in R, v. 2.14.1 (R Development Core Team 2011). Figures were created using the package *gplots* (Warnes et al. 2011).

### Study species

The study species is the freshwater crustacean *Lepidurus arcticus*, commonly known as tadpole shrimps. *L. arcticus* has a circumpolar distribution where it inhabits lakes and ponds in the northern hemisphere (Rogers 2001). Their maximum length is ca. 30 mm, and they have an annual life cycle, where most of the eggs are laid in the littoral zone in the autumn before they die. Eggs can tolerate freezing and drying, and hatch during late spring or early summer (Borgstrøm 1970, 1975, Borgstrøm and Hendrey 1976). Although they are principally benthic, they occasionally swim upwards in the water column. Tadpole shrimps feed on sediment and small organisms that live in the sediment. They also feed on zooplankton, for example species of *Daphnia* (Christoffersen 2001, Jeppesen et al. 2001). Low predation pressure is a requirement for high densities of *L. arcticus* (Borgstrøm 1970), and they are usually excluded from or kept at very low densities in lakes with significant fish populations (Jeppesen et al. 2001). *L. arcticus* creates highly ephemeral populations, which means that the role of density-dependent mechanisms is potentially low in this species. *L. arcticus* disperse by passive means, and its dispersal abilities are not well known. It is

possible that the eggs can pass through the digestive tract of birds unharmed and disperse this way, although this is not confirmed. The eggs have a sticky layer, and it is also assumed that the eggs attach to birds, or lay in mud attached to birds, for dispersal (Longhurst 1955, Hessen et al. 2004). *L. arcticus* larvae have also been found drifting in a stream down to a lake at lower altitude, a distance of 2 km (Brabrand 2010). Although genetic differences can be relatively large between ponds close to each other (Hessen et al. 2004, Wojtasik and Brylka-Wolk 2010), the presence of the same haplotype in distant regions indicates dispersal over large distances (Hessen et al. 2004).

### **Distribution patterns on Bear Island and Dovrefjell**

22 small ponds were examined on Dovrefjell during the summer of 2010, and 109 ponds were examined at Bear Island during the summer of 2009. The occurrence of *L. arcticus* in the ponds was registered. *L. arcticus* is known to occur at low densities in larger lakes in both areas. Ponds visible on 1:50000 maps were counted in a 30 km<sup>2</sup> area where the surveys on Dovrefjell and Bear Island were conducted, and ponds per km<sup>2</sup> were calculated for both areas.

### **Effect of temperature and body size on growth, laboratory experiment**

#### *Sampling*

*L. arcticus* were sampled from Lake Lertjønna (62.46°N, 9.78°E) in Oppdal municipality on August 3 2011. This lake is situated at 1315 m.a.s.l., and the area has an alpine climate. Lake Lertjønna has a small introduced population of brown trout, but predation pressure appears to be sufficiently low to allow high densities of *L. arcticus*. Total length of the sampled individuals was between 7 and 17 mm. *L. arcticus* of this size are benthic, and were caught by standing on the shore using a sweep net. Sand and detritus were stirred up by motioning with the net above the bottom, and a total of ca. 150 tadpole shrimps were sampled. The tadpole shrimps were brought to the lab in 25 liter containers, and stored at 10°C before the experiments started. They swam and behaved normally after the handling.



### *Experimental design*

Five different temperature treatments (in °C, mean  $\pm$ SD: 5.3  $\pm$ 0.7, 9.0  $\pm$ 0.1, 14.7  $\pm$ 0.1, 17.7  $\pm$ 0.1 and 21.4  $\pm$ 0.3) were obtained by using a combination of climate rooms and water baths. Tubular lamps of 8 watts provided light during the day, and were switched off during the night in a cycle as done in other *Lepidurus* and *Triops* experiments (Ahl 1991, Scholnick 1995). A 15/9 L/D cycle was used here to simulate high latitude late summers. Each plastic aquarium was 0.75 l, and all water used was filtered. The water was collected from Lake Fundin, close to Lake Lertjønna; half of the water in each aquarium was exchanged daily to avoid accumulation of waste. Each aquarium contained one tadpole shrimp, and 20 individuals were used at each of the five temperatures. They were given an *ad libitum* ration of frozen chironomidae larvae and a small sliver of boiled carrot every day. Superfluous food was removed when the water was exchanged. The experiment ran for 25 days, until only ten individuals remained alive. All the tadpole shrimps were photographed when the experiment started and when they died. The photographs were used to estimate the start and end mass of the tadpole shrimps (see *size-weight relationship* below).

### **Effect of density on final size, field experiment**

In the field experiment, *L. arcticus* were sampled from a single pond in which cylindrical mesh enclosures (diameter: 45 cm, height: 45 cm) were placed at a depth of 30 cm. The mesh size was 1 mm, which allowed zooplankton to enter it as a food source. Three enclosures were placed next to each other in blocks, with 5, 15 or 75 tadpole shrimps in each. Six such blocks were placed at different sites in the pond, giving a total of 18 enclosures. The experiment ran for nine days. The tadpole shrimps were photographed at the start of the experiment. Ninety-six percent of the tadpole shrimps kept at a density of 5, eighty-five percent kept at a density of 15 and seventy-nine percent kept at a density of 75 survived to be photographed at the end of the experiment. The photographs were used to estimate the mean initial and final mass of the tadpole shrimps (see *size-weight relationship* below).

## **Effect of system productivity and density on growth, comparative analyses of natural populations**

Data from 17 ponds on Bear Island were collected to test for effects of phosphorus and density on somatic growth. Four of the ponds were deeper than 1.5 m, while the rest of the pond depths varied from 0.4 m to 1.1 m. Pond area varied from 171 m<sup>2</sup> to 14728 m<sup>2</sup>, with a mean of 4382 m<sup>2</sup>, while mean pond temperature varied from 8.0°C to 9.1°C. Size samples of tadpole shrimps were collected twice from each pond, with an interval of between 12 and 16 days, and each sample consisted of photographing tadpole shrimps from the ponds. The sample size varied from 9 to 64, and the samples were used to estimate the mass of the tadpole shrimps (see *size-weight relationship* below). Catch per unit effort (CPUE) was measured for the ponds, by doing eight z-sweeps in each pond with a sweep net, spread evenly around the pond. The unit used for CPUE was tadpole shrimp biomass per z-sweep. CPUE is an indirect measure of abundance (Harley et al. 2001, Zimmerman and Palo 2011). Phosphorus levels were used as a measure of system productivity. In lakes, phosphorus level is often a limiting resource, and therefore an indication of the carrying capacity. Growth and size parameters for various species have all increased when phosphorus was added to freshwater systems (Peterson et al. 1985, Slavik et al. 2004, Malzahn et al. 2007). Water samples were taken and the phosphorus levels in the water were measured by high-resolution ICP-MS (inductively coupled plasma mass spectrometry) at the Department of Chemistry, NTNU. Phosphorus levels were measured as micrograms per liter.

### **Data analysis and statistics**

#### *Size – weight relationship*

Throughout the study, pictures were used to obtain measurements of individual body surface, which were then transformed into body mass. To obtain a model for estimating body mass from body area, a sample of 30 individuals were photographed before being dried and weighted. A polynomial regression was used to estimate the relationship:

$$\hat{y}_i = \alpha + \beta_1 x_i + \beta_2 x_i^2 + \varepsilon \quad (1)$$

where  $\hat{y}_i$  is the estimated weight,  $\alpha$  and  $\beta$  are the fixed parameters and  $x_i$  is the area of an individual  $i$ . There was a strong correlation between *L. arcticus* size and mass ( $\alpha = 0.0002$ ,  $\beta_1 = 0.0025$ ,  $\beta_2 = 0.0082$ ,  $R^2 = 0.97$ ). This relationship was used to estimate the mass for all tadpole shrimps in the laboratory experiment, field experiment and the data from the natural populations. In the laboratory experiment, individuals that died lay in the aquariums until photographed the next day. Their bodies tended to become soft after several hours in the water, which affected the measured area of the tadpole shrimps. To adjust for the change in size caused by this, 10 live tadpole shrimps were photographed, killed, left in their aquariums overnight and photographed again. A linear regression was used to estimate the relationship:

$$\hat{y}_i = \alpha + \beta x_i + \varepsilon \quad (2)$$

where  $\hat{y}_i$  is the estimated live size,  $\alpha$  and  $\beta$  are the fixed parameters and  $x_i$  is the area after death of an individual  $i$  ( $\alpha = 0.0228$ ,  $\beta = 0.9219$ ,  $R^2 = 0.9842$ ). This regression was used to estimate the size at death for all individuals that died during in the laboratory experiment.

#### *Effect of temperature and body size on growth, laboratory experiment*

The specific growth rate for the *L. arcticus* in the laboratory experiment was calculated as:

$$G_w = (\ln W_1 - \ln W_0) / t \quad (3)$$

where  $W_0$  is the initial weight and  $W_1$  is the final weight of the tadpole shrimps after  $t$  days (Elliott and Hurley 1995). A linear regression of  $\ln G_w$  as a function of  $\ln W_0$  was performed to estimate the allometric growth exponent  $b$  (Sigourney et al. 2008). Temperature was included in the regression to find if it affected the relationship between  $\ln W_0$  and  $\ln G_w$ , and to find the effect of temperature on the specific growth rate:

$$\ln G_{wi} = \alpha + \beta_1 T_j + \beta_2 \ln W_{0i} + \beta_3 T_j \ln W_{0i} + \varepsilon_{ij} \quad (4)$$

where  $G_w$  is the specific growth rate,  $T_j$  is the temperature treatment with five levels,  $W_0$  is the start weight,  $\alpha$  and  $\beta$ s are the fixed parameters (with  $\beta_2$  being the allometric growth exponent  $-b$ ), and  $\varepsilon$  is the residual term. The indices  $i$  and  $j$  represent individuals and temperature treatments, respectively. The best model was found by model selection using log-likelihood

ratio tests. The residuals were normally distributed and showed no pattern of heteroscedasticity.

#### *Effect of density on final size, field experiment*

The mean size ( $\pm$ SD) of the tadpole shrimps at the start of the field experiment was  $0.28 \pm 0.05 \text{ cm}^2$ , and did not vary significantly among enclosures ( $F_{16,32} = 0.82$ ,  $P = 0.66$ ). The final sizes of the tadpole shrimps were therefore used as a measure of growth. A model was created using the generalized least squares function *gls* from the package *nlme* (Pinheiro et al. 2009), where density was modeled as a fixed effect. Block was also modeled as a fixed effect, as generally recommended when the numbers of observations are low. To test for enclosure effects, another model was created where enclosure was added as a random effect with the function *lme* from the package *nlme*:

$$S_{ij} = \alpha + \beta_1 D_{ij} + \beta_2 R_{ij} + \beta_3 D_{ij} R_{ij} + a_i + \varepsilon_{ij} \quad (5)$$

where  $S$  is the end size of individual  $i$  in block  $j$ ,  $D$  is the variable density and  $R$  is block. The random intercept  $a$  and the residual term  $\varepsilon$  was assumed normally distributed. A comparison was made between the *gls* and *lme* models using log-likelihood test after fitting the models with restricted maximum likelihood (REML). After the optimal random structure was found, the best model was found by model selection using log-likelihood ratio tests with maximum likelihood (ML), and was refitted with restricted maximum likelihood and validated. The residuals were normally distributed and showed no pattern of heteroscedasticity.

#### *Effect of system productivity and density on growth, comparative analysis of natural populations*

A linear regression was created to find the relationship between CPUE and the phosphorus levels of the ponds. The mean sizes of the *L. arcticus* varied between ponds both at the first and at the second size sample, and the time interval between the first and second sample varied. I therefore, based on mean size at the two sampling events, calculated a standardized mass-specific growth rate for each pond. Standardized mass-specific growth rate, under the assumption of allometric growth can be expressed as:

$$G_s = ((W_1^b - W_0^b) / (bt)) \quad (6)$$

where  $W_0$  is the initial weight and  $W_1$  is the final weight of the tadpole shrimps,  $t$  is length of the growth period and  $b$  is the allometric growth exponent estimated in the laboratory experiment (Sigourney et al. 2008). A model was created to find the effect of phosphorus and CPUE on the mean growth rate:

$$G_s = \alpha + \beta_1 C_j + \beta_2 P_j + \beta_3 C_j P_j + \varepsilon \quad (7)$$

where  $G_s$  is the standardized mass-specific growth rate,  $C_j$  is the CPUE and  $P_j$  is the phosphorus level of lake  $j$ . The standardized mass-specific growth rate and the CPUE were log-transformed to satisfy the assumptions of normality and homogeneity of residuals. The variance inflation factor (VIF) was calculated and analyzed to test if there was correlation between the predictor variables that could disturb the results (Zuur et al. 2010). No heterogeneity was found by visually checking the initial model. But because heterogeneity can be difficult to graphically assess in small datasets, several generalized least squares models were created, which added random parts that allowed for heterogeneity in the variance (Zuur et al. 2009). The models containing variance structures were tested using log-likelihood ratio tests. Two of these models assumed variance to increase as a power function with the two covariates, phosphorus levels and CPUE. Two variance structures which assumed variance to increase exponentially with the covariates, and two which assumed the variance to be proportional to a constant plus the power of the variance covariates were also tested.

No indication of violation of independence from spatial correlation was found by graphical assessment either, but again because the sample size was relatively small, a random term containing spatial correlation structures was added. *Gls* models containing several spatial correlation structures were tested using log-likelihood ratio tests with maximum likelihood; exponential, gaussian, linear, rational quadratic and spherical correlation were tested (Zuur et al. 2009). After finding the optimal random structure, the best model was found by model selection using log-likelihood ratio tests.

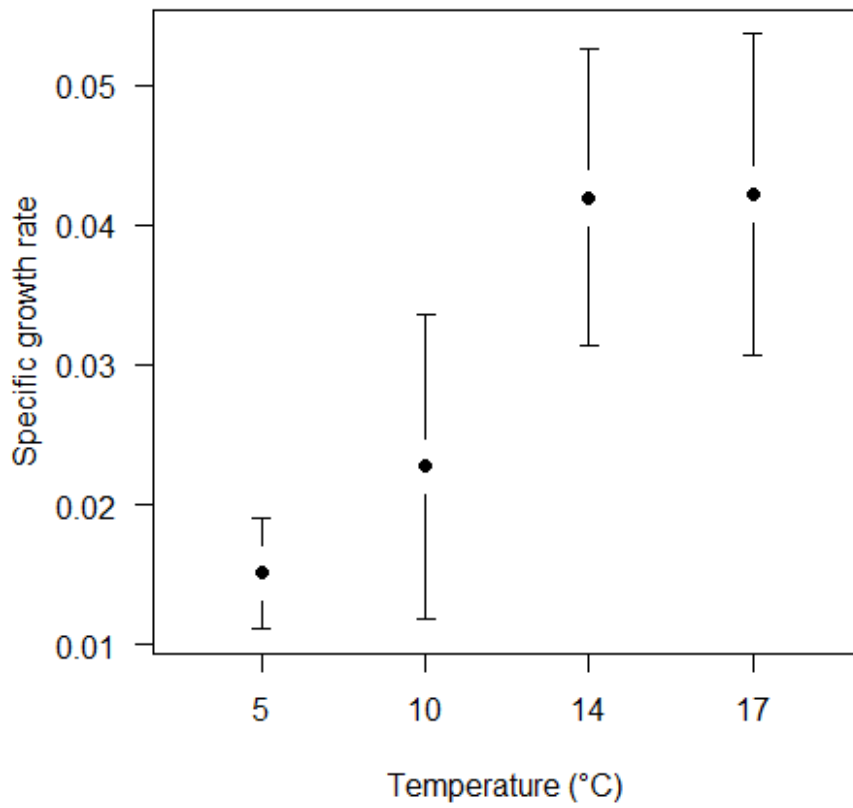
## Results

### Distribution patterns on Bear Island and Dovrefjell

*L. arcticus* occurred in none of the small ponds examined on Dovrefjell, where there were 2.36 ponds per km<sup>2</sup>. It occurred in 65% of the ponds examined at Bear Island, where there were 5.16 ponds per km<sup>2</sup>.

### Effect of temperature and body size on growth, laboratory experiment

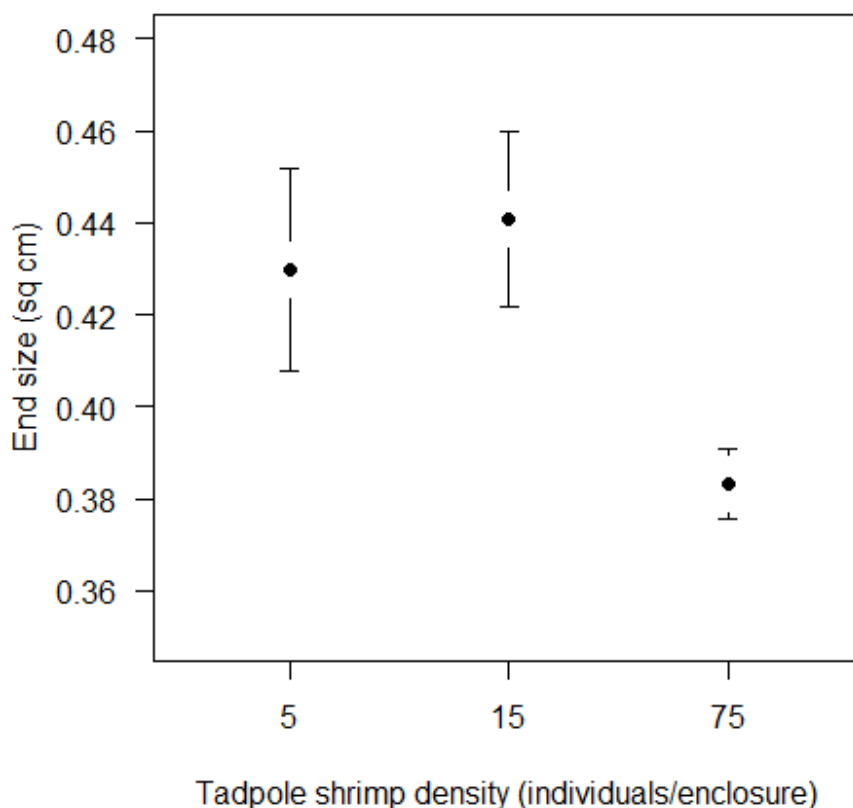
Size measurements at death started one week after the experiment started, and 43 of the initial 100 *L. arcticus* survived this long or longer (15 at 5.3°C, 8 at 9°C, 11 at 14.7°C, 7 at 17.7°C and 2 at 21.4°C). At 21.4°C, all individuals died within nine days, while they survived for an average of 10 days or more at all the other temperatures. The results from 22°C were therefore excluded from the analysis. For the analysis of growth rate, the interaction between temperature and start weight could be removed ( $P = 0.2029$ ), whereas both start weight ( $F_{1,36} = 7.227$ ,  $P = 0.0108$ ) and temperature ( $F_{3,36} = 8.834$ ,  $P = 0.0002$ ) affected the growth rate significantly. The allometric growth rate exponent was estimated ( $\pm$ SE) to  $0.4866 \pm 0.1810$ . Growth rates were lowest at 5°C, and increased with temperature (Figure 1). The significance of the results did not change when two potential outliers were removed, located between two and three standard deviations from the mean.



**Figure 1:** The effect of temperature on the growth rate of *L. arcticus* in the laboratory experiment. Plots represent the mean specific growth rate, with error bars representing the 95% CIs.

## Effect of density on final size, field experiment

When modeling variation in final size, adding enclosure as a random component to the initial model significantly increased the log-likelihood of the model ( $P = 0.0007$ ). The main effect block was removed from the model, as removing it did not cause a significant decrease in the log-likelihood ( $P = 0.0645$ ). Density had a significant effect on the final size ( $F_{2,15} = 4.6009$ ,  $P = 0.0277$ ), and was included in the best model. Removing two potential outliers, both located more than four standard deviations from the mean, did not change the effect of density ( $F_{2,15} = 4.7628$ ,  $P = 0.0250$ ). High density decreased the growth of the tadpole shrimps (Figure 2), and the individuals kept at a density of 75 were on average 10.7% smaller than those kept at a density of 5. The random effect of enclosures contributed to 14.7% of the total variation.

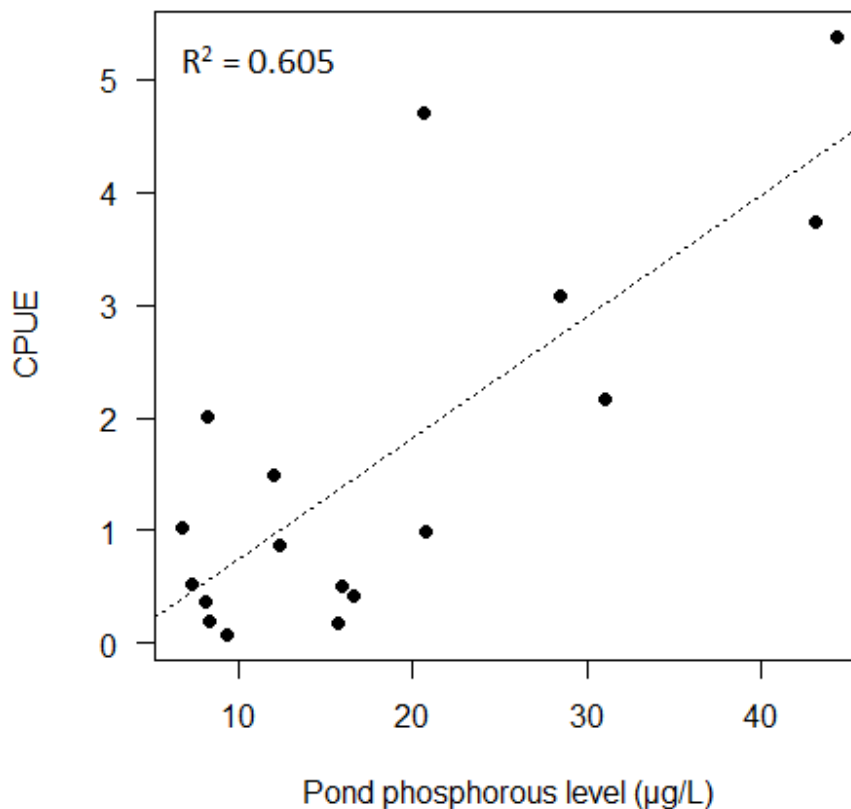


**Figure 2:** The effect of population density on *L. arcticus* growth in the field enclosures. Plots represent the mean end size, with error bars representing the 95% CIs.



## Effect of system productivity and density on growth, comparative study of natural populations

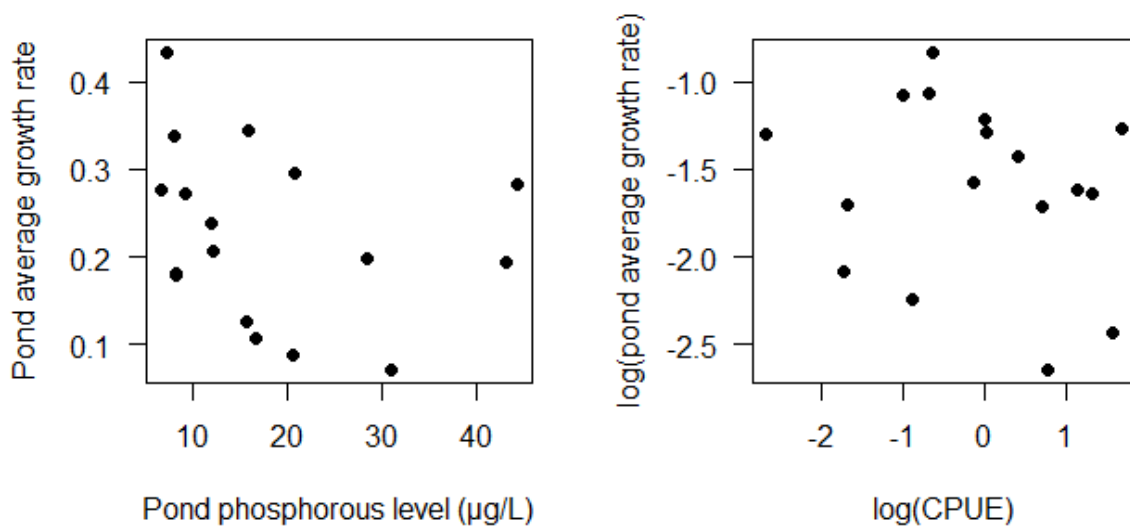
There was a clear positive relationship between the phosphorus level in a pond and the catch per unit effort (CPUE) of *L. arcticus* ( $F_{1,15} = 22.983$ ,  $P = 0.0002$ ; Figure 3).



**Figure 3:** The relationship between the catch per unit effort (CPUE) and the phosphorus levels of the ponds.

For the analysis of the growth rate in the ponds, the variance inflation factor (VIF) was 2.53 for the predictor variables. When the random parts containing different variance structures were added to the model, all failed to significantly increase the log-likelihood of the model ( $P \geq 0.3186$  for all), indicating that the homogeneity of variance assumption was not violated. Again, when the random parts containing different correlation structures were added to the model, all failed to significantly improve the model ( $P \geq 0.7647$  for all), indicating that the independence assumption is not violated. In the model comparison, the model with an interaction between CPUE and phosphorus level was found to be significantly better than one without ( $P = 0.0492$ ). However, the model estimate for the interaction was not significant ( $P$

= 0.0914). Furthermore, the interaction showed a higher growth rate for a given density when the phosphorus level was low than when it was high, contrary to what might be expected. Thus, the evidence for the interaction between CPUE and phosphorus level in this model was not convincing, and was therefore excluded from the model. Neither the main effect of phosphorus level nor the main effect of CPUE affected the growth rate significantly (Figure 4;  $P = 0.5332$  and  $P = 0.7642$ , respectively), and were removed from the model. Thus, the null model was found to be the best model.



**Figure 4:** The relationship between pond phosphorus levels and pond CPUE and the average standardized mass-specific growth rate in each pond. Growth rate was not significantly affected by phosphorus level or CPUE.

## Discussion

This study shows that *L. arcticus* is more widespread on Bear Island than in the study area on Dovrefjell, and that the density of ponds on Bear Island is more than twice that of Dovrefjell. Temperature within the tested temperature range affected the growth rate positively, although mortality was exceptionally high at 21.4°C. *L. arcticus* exhibited density-dependent growth in the field experiment, and an analysis of the natural populations showed that population density was correlated with the phosphorus levels in the ponds. Neither phosphorus levels nor population density was found to affect the growth in the natural populations.

The observed density-dependent growth, and the positive correlation between population density and system productivity among natural populations, indicate that intraspecific competition for resources does occur in this species. This causes the system productivity to determine population density in habitats without natural predators, such as those studied here. In other species, competition for resources have been known to cause density-dependent growth (Jenkins et al. 1999, Post et al. 1999, Lorenzen and Enberg 2002) or density-dependent survival or recruitment (Craig et al. 2007, Martino and Houde 2012). The results from the present study suggest regulated subpopulations in *L. arcticus*, contradicting metapopulation theory. Therefore, it seems unlikely that metapopulation dynamics can explain the observed differences in occurrence in ponds between the two study areas.

Several environmental factors may contribute to the observed differences in distribution patterns between areas. The closely related species *Triops australiensis* is widely distributed in the southern Australia, but is excluded from the northern part, and a study of this species found evidence which suggests that its distribution is limited by localities with suitable climate (Williams and Busby 1991). Likewise for *L. arcticus*, climatic conditions differ between regions. Bear Island is positioned in the middle of the Barents Sea, and is ca. 12° latitude further north than the more continental Dovrefjell. The annual average temperature on Bear Island is around -4°C, compared to ca. 0°C on Dovrefjell (Sollid et al. 2003, Norsk Polarinstitut 2010). Also, the maximum temperatures during 2011 was 13.2°C on Bear Island, and 23.7°C at Hjerkin observation station which is located at Dovrefjell at 1012 m.a.s.l., both measured during late summer (yr.no 2012a,b). It has been suggested that the distribution of *L. arcticus* is limited by too warm winter temperatures. *L. arcticus* has been

found at lower altitudes after lakes have become regulated, probably because the littoral zone dries and temperatures tend to decrease in the winter after regulation (Brabrand and Saltveit 1980). The littoral zone is where most of the eggs are deposited, and freezing might be beneficial to the eggs, although this is not clear (Borgstrøm 1997). It is also known that temperature can play a vital role in the physiological performances of ectotherms. Scholnick (1995) found that the growth rate and mortality rate of the related species *Triops longicaudatus* is highly dependent on the diurnal oscillations in temperature and oxygen conditions of its environment, although this species inhabits ephemeral pools in warmer climates. It is possible that the climatic conditions in Dovrefjell can cause unfavorable conditions for *L. arcticus*, and thereby limit its distribution, perhaps because of periodical high temperatures in smaller ponds during summer. The high mortality rate at 21.4°C in the laboratory experiment and the large differences in temperatures between regions suggest that such conditions might limit the distribution, particularly in small ponds, which fluctuates more with fluctuations in air temperatures than larger lakes.

Different species composition may also cause differences in the distribution pattern, by predation or competition from other species. A greater diversity of species is expected to occur at Dovrefjell, due to its more southern location. A shift in the species composition may also be a reason why *L. arcticus* thrives at lower altitudes on the Norwegian mainland after lakes become regulated. It has been shown that macrophytes, macrobenthos and fish richness have all decreased in regulated lakes (Palomaki and Koskenniemi 1993, Hellsten 2001, Aroviita and Hamalainen 2008, Sutela and Vehanen 2008), and potential predators and competitors may therefore be excluded, particularly in the regulation zone which dries during winter. Differences in climate and differences in species composition are of course not mutually exclusive; they are most likely correlated, and may both contribute to the difference in distribution patterns between Bear Island and Dovrefjell.

Although there was a clear correlation between phosphorus levels and population density in the natural populations, phosphorus levels did not affect the growth rates. There was also a clear density-dependent effect on growth in the field experiment, but not in the ponds. Two mutually non-exclusive factors may contribute to this: the regulation may happen at different stages in *L. arcticus* lifecycle, and there may be sources of failure in the model or measurements that could disturb the results. While the *L. arcticus* measured in the survey were benthic adults, the lowered population density in low productivity ponds might be the

result of density-dependent mortality in early, planktonic stages of the tadpole shrimps lifecycle. Density-dependent mortality in early life-stages has been found in fish, and can possibly modify patterns in abundance (Craig et al. 2007). Another possibility is that the populations are regulated by lowered fecundity. Food availability has been found to affect fecundity in a variety of taxa from birds (Hogstedt 1981, Arcese and Smith 1988, Nagy and Holmes 2005) to fish (Clifton 1995). Likewise, the number of *L. arcticus* eggs might be affected by food availability. In an ephemeral population like that of *L. arcticus*, attaining large enough body size to start laying eggs before the end of the season must be of utmost importance to the individuals. It is therefore possible that the *L. arcticus* growth rate at benthic stage remains largely unaffected by system productivity, but that less resources result in higher juvenile mortality and/or lower individual egg number. Similarly, the failure to detect density-dependent growth might also be caused by population regulation on other demographic traits, leading to weak density-dependent growth. Density-dependent growth occurred only at the highest test density in the field experiment, which means that internal regulation by density-dependent growth could occur to a lower degree at lower densities, not detected in the natural populations.

Sources of failure in the model or measurements may also disturb the results. There is uncertainty around the standardized mass-specific growth rate used in the model. The allometric growth rate exponent used in the calculation of the growth rates was estimated from the laboratory experiment, by individuals from Dovrefjell. Also, the average growth rates in the ponds do not take individual tadpole shrimp differences into consideration. Newly laid *L. arcticus* eggs can hatch without diapause (Vekhoff 1997), and adds to the uncertainty of the estimate of the average growth rate. In addition, there is a correlation between phosphorus levels and population density, which can disturb their effect on the average growth rate when modeled together (Zuur et al. 2010). The variance inflation factor (VIF) is a measure of the severity of the collinearity, and was 2.53 between the variables phosphorus levels and population density. Zuur et al. (2010) advocate using a VIF value of 3 as the limit for including two correlated predictor variables in a single model, which means that VIF values below 3 should not disturb the results. However, they also state that VIF values as low as 2 can cause non-significant parameter estimates if the ecological signals are weak. Thus, although effects of phosphorus and density may have an influence on *L. arcticus* growth rate in natural populations, detecting these may be problematic due to the correlation between the two predictor variables.

For a species to exhibit metapopulation dynamics, fragmented subpopulations that have realistic chances of extinction are necessary (Hanski 1999, Begon et al. 2006). Therefore, the independent populations in a metapopulation should not be regulated so efficiently that extinctions become rare; it would indicate that the populations are independent (Hanski 1999). This study shows that *L. arcticus* can exhibit density-dependent growth, and that there is a correlation between system productivity and population density, indicating internal regulation of populations. This suggests that the subpopulations in ponds are indeed able to survive for a long period, and therefore, that classic metapopulation dynamics are not required to explain the maintenance of small, fragmented *L. arcticus* populations. Failure to detect effects of population density and system productivity on growth in the natural populations might be due to the regulation happening at a different stage in the *L. arcticus* lifecycle, not included in my tests. The difference in occurrence on Bear Island vs. Dovrefjell is perhaps more likely explained by environmental differences between the two regions. Warmer temperature and predation by or competition from other species are plausible reasons for the lack of *L. arcticus* in ponds at Dovrefjell.

## **Acknowledgements**

I would like to thank my supervisors Sigurd Einum at NTNU and Anders Finstad at NINA for providing me with data, and for the help, guidance and valuable comments they have given me during fieldwork, statistical analysis and writing. Thanks to Reidar Borgstrøm for supplying information on a relatively unknown species, and to my fellow students for companionship. And last, but not least, thank you Kaia for being a marvelous and supportive person.

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