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2017

Citation for published version (APA):
Zhang, H. (2017). *Multiple stressors in rotifer communities: Effects of predation, climate change, and brownification*. [Doctoral Thesis (compilation)]. Lund University, Faculty of Science, Department of Biology.

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MULTIPLE STRESSORS IN ROTIFER COMMUNITIES:

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Huan Zhang

DOCTORAL DISSERTATION

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To be defended in the Blue Hall, Ecology Building, Sölvegatan 37, Lund, Sweden on
Thursday 2nd of November 2017 at 9:00.

Faculty opponent
Dr. Steven Declerck,
Netherlands Institute of Ecology, NIOO-KNAW, The Netherlands

Organization: LUND UNIVERSITY	Document name: DOCTORAL DISSERTATION
Department of Biology	Date of issue: 2 November 2017
Author(s) Huan Zhang	Sponsoring organization: China Scholarship Council

Title and subtitle: Multiple stressors in rotifer communities: Effects of predation, climate change, and brownification

Abstract: Most organisms on Earth live in an environment where they are exposed to multiple pressures, including predation and climate change. In many aquatic ecosystems, organisms have to handle additional challenges such as brownification, co-occurring with climate warming. Despite the growing recognition of impacts of climate warming or brownification on the freshwater communities, little is known on how synergistic effects from multiple environmental changes will affect community dynamics in freshwater ecosystems. In this thesis I investigate the effects of predation, climate changes, and brownification on the rotifer community dynamics.

I show that predation has strong effects not only on population growth but also on inducible morphological defenses in rotifers. Larval fish feed extensively on rotifer prey and reduces spine length of a common rotifer (*Keratella cochlearis*) both through induction of shorter spines and selective predation on long-spined individuals. Furthermore, I demonstrate that rotifer prey can detect and respond appropriately in opposite directions to different sizes and feeding modes of predators by being plastic in spine and body size.

My studies show that rotifer community will start to establish earlier in spring under a climate-warming scenario, whereas it would also decline earlier due to increased predation pressure. Furthermore, I show that in a future climate scenario with increased temperature variations and frequency of extreme temperatures, predatory copepods benefit from heat waves due to their ability of initiating diapause at an almost adult stage and rapidly responding to temperature variation, while rotifers suffer from a higher predation pressure. Hence, in a broader perspective my studies suggest that differences in life history traits will affect predator-prey interactions, and consequently alter community dynamics, in a future climate change scenario. However, the effects of brownification on establishment and growth in the rotifer community were less pronounced, or even negligible

Key words: Climate change, community dynamic, brownification, heat wave, inducible defense, rotifer, plasticity, multiple stressors, predation, prey

Classification system and/or index terms (if any)

Supplementary bibliographical information		Language: English
ISSN and key title		ISBN: 978-91-7623-426-6 (print) 978-91-7623-427-3 (pdf)
Recipient's notes	Number of pages:129	Price
	Security classification	

Signature Huan Zhang 张欢 Date 2017-09-27

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have already been published or are manuscripts at various stages.

Cover design

Marja Boström

Layout: Huan Zhang

Proof reading: Huan Zhang

Printed by E-huset Tryck, Lund

ISBN 978-91-7623-426-6 (print)
978-91-7623-427-3 (pdf)

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SAMMANFATTNING PÅ SVENSKA

De flesta vattenlevande organismer på Jorden lever i en miljö där de samtidigt måste hantera flera olika hot och stressituationer, såsom t.ex. predation, klimatförändringar och brunifiering. Trots relativt god kunskap om varje stressfaktor för sig, vet man förvånansvärt lite om hur synergier av samtidigt förekommande hot påverkar organismer. Därför har jag i min avhandling undersökt hur predation, klimatförändringar (temperaturökning) och brunifiering (ökad humushalt) påverkar samhällsdynamiken hos min modellorganism – rotatorier. Jag visar att predation har en betydande inverkan inte bara på populationsstorleken, utan också på hur rotatorierna inducerar försvarsmekanismer. Således får fiskyngel (en stor predator för rotatorierna) längden på utskotten hos rotatorien *Keratella cochlearis* att minska, både genom inducering av kortare utskott och genom att selektivt predera på individer med långa utskott. Vidare demonstrerar jag att rotatorier kan detektera olika typer (storlekar) av predatorer och anpassa sitt försvar (utskott) så att de i möjligaste mån undgår att bli uppätna, antingen genom att sträva efter att bli mindre eller större än predatorns optimala födostorlek.

Mina studier visar också att rotatoriesamhällen etableras tidigare på våren i ett simulerat framtida klimatscenarium, men att också en dominerande predator (cyclopoida copepoder) svarar på liknande sätt och därmed håller antalet rotatorier nere. Vidare visar jag att i ett framtida klimatscenarium med ökande frekvens av extrema temperaturer, kommer cyclopoida copepoder att gynnas av ”värmeböljor” eftersom de har förmågan att låta en del av populationen vila (diapause) som nästan vuxna individer, vilka lika snabbt som rotatorier kan svara på temperaturökningar. Detta betyder att klimatförändringen sannolikt inte leder till någon ”mis-match” situation mellan byte och predator. I ett vidare perspektiv visar mina studier att skillnader i livshistoria påverkar predator-byte interaktionerna, och därmed samhällsdynamiken, i ett framtida klimatscenarium.

SUMMARY

Most organisms on Earth live in an environment where they are exposed to multiple pressures, including predation and climate change. In many aquatic ecosystems, organisms have to handle additional challenges such as brownification, co-occurring with climate warming. Despite the growing recognition of impacts of climate warming or brownification on the freshwater communities, little is known on how synergistic effects from multiple environmental changes will affect community dynamics in freshwater ecosystems. In this thesis I investigate the effects of predation, climate changes, and brownification on the rotifer community dynamics.
I show that predation has strong effects not only on population growth but also on inducible morphological defenses in rotifers. Larval fish feed extensively on rotifer prey and reduces spine length of a common rotifer (*Keratella cochlearis*) both through induction of shorter spines and selective predation on long-spined individuals. Furthermore, I demonstrate that rotifer prey can detect and respond appropriately in opposite directions to different sizes and feeding modes of predators by being plastic in spine and body size.

My studies show that rotifer community will start to establish earlier in spring under a climate-warming scenario, whereas it would also decline earlier due to increased predation pressure. Furthermore, I show that in a future climate scenario with increased temperature variations and frequency of extreme temperatures, predatory copepods benefit from heat waves due to their ability of initiating diapause at an almost adult stage and rapidly responding to temperature variation, while rotifers suffer from a higher predation pressure. Hence, in a broader perspective my studies suggest that differences in life history traits will affect predator-prey interactions, and consequently alter community dynamics, in a future climate change scenario. However, the effects of brownification on establishment and growth in the rotifer community were less pronounced, or even negligible.

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I. Zhang, H., Brönmark, C., Hansson, L.-A. 2017. Predator ontogeny affects expression of inducible defense morphology in rotifers. Ecology. DOI: 10.1002/ecy.1957

II. Zhang, H., Hollander, J., Hansson L.-A. 2017. Bi-directional plasticity: Rotifer prey adjust spine length to different predator regimes. Scientific Reports 7:10254.

III. Zhang, H., Ekvall, M. K., Xu, J., Hansson, L.-A. 2015. Counteracting effects of recruitment and predation shape establishment of rotifer communities under climate change. Limnology and Oceanography 60: 1577-1587

IV. Zhang, H., Urrutia-Cordero, P., He, L., Geng, H., Chaguaceda, F., Xu, J., Hansson, L.-A. Life-history traits buffer against heat wave effects on predator-prey dynamics in zooplankton. Submitted.

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INTRODUCTION

Almost all organisms on Earth live in an environment where they are exposed to multiple and variable pressures. The dynamics of their populations are determined by the ability of organisms to cope with their exposure to these daily stressors, including both biotic and abiotic environmental factors. Among the biotic pressure, predation stands out as an important regulator for prey population dynamics both through direct lethal effects and indirect effects through changing the behavior, morphology, or life cycles of prey organisms (Kerfoot and Sih 1987, Carpenter and Kitchell 1996), as well as a powerful selection force on prey traits.

In addition to biotic pressures, the abiotic environment limits almost all organisms to some extent, with temperature being important for all organisms. This is critical as according to the IPCC, global mean surface temperatures will likely increase between 3 -4.8 °C during the 21st century (IPCC, 2013). In addition to the increase in mean temperature, a common prediction is that extreme climatic events, such as heat waves and cold snaps, are expected to occur with increasing intensity, duration and frequency (Fischer et al. 2013, IPCC 2013). Such extreme climatic events may impose even stronger threat to organisms than a gradual increase in mean temperatures (Vasseur et al. 2014). In parallel with those future expected climate changes, other environmental drivers will co-occur in many aquatic ecosystems. A significant example is the rise in humic substances. In recent years there has been a considerable increase in the amount of humic substances reaching aquatic ecosystems, causing an increase in water color (Evans et al. 2005, Monteith et al. 2007, Hansson et al. 2013, Kritzberg 2017), thus affecting aquatic communities from primary producers to fish (Karlsson et al. 2009).

Although, the role of predation in shaping and affecting community has been widely studied (Glasser 1979, Gliwicz and Pijanowska 1989), how predator induced defensive responses would affect the population growth and community dynamics is still an open question. Despite the growing recognition of impacts of climate warming or brownification on the freshwater communities (Nicolle et al. 2012, Shurin et al. 2012, Winder and Sommer 2012, Hansson et al. 2013), little is known on how synergistic effects from multiple environmental changes will affect community dynamics in freshwater systems. As such, there are still numerous questions on the effects of predation community dynamics under large environmental change conditions.

Despite their small size, rotifers together with cladocerans and copepods constitute very important components of the pelagic food webs in aquatic ecosystems. Due to their position in the aquatic food weds, linking the microbial loop and the traditional pelagic food chain (phytoplankton, zooplankton, and fish), rotifers' responses to a changing environment have potentially large implications for aquatic ecosystem functioning. In addition, because of their short generation time and unique life cycle (box 1), rotifers are very sensitive to environmental changes and can respond rapidly. These features make them not only good model organisms for the study of micro-evolution (Declerck and Papakostas 2017), but also for detecting the effects of large-scale environmental factors, such as climate change and brownification.

In this thesis I investigate the effects of predation, climate changes, and brownification on the rotifer communities. Specifically, I have addressed the following questions: (1) Do rotifers show inducible morphological responses to vertebrate predators? How is predator ontogeny affecting the expression of rotifer inducible

Box 1. Rotifer life cycle

The monogonont rotifers have a heterogonic life cycle and generally have two types of females, amictic and mictic. The life cycle typically begins when resting eggs hatch and become amictic females (Figure B1). These amictic females produce diploid eggs developing parthenogenetically into females. Sexual reproduction is initiated when some amictic females produce mictic- female offspring. Mictic female produce haploid eggs (oocytes) that either develop parthenogenetically into haploid males or, if fertilized, develop into dark colored resting eggs (Gilbert 1974, Gyllström and Hansson 2004). Population growth occurs via diploid female parthenogenesis, and a period of bisexual reproduction leads to production of fertilized resting eggs (Gilbert 1974). Although the mechanism is not completely understood, it is generally believed that the production of resting eggs is a survival strategy of the population through unfavorable environmental conditions, such as drought or low temperature (Gilbert 1974, Pourriot and Snell 1983, Gyllström and Hansson 2004).

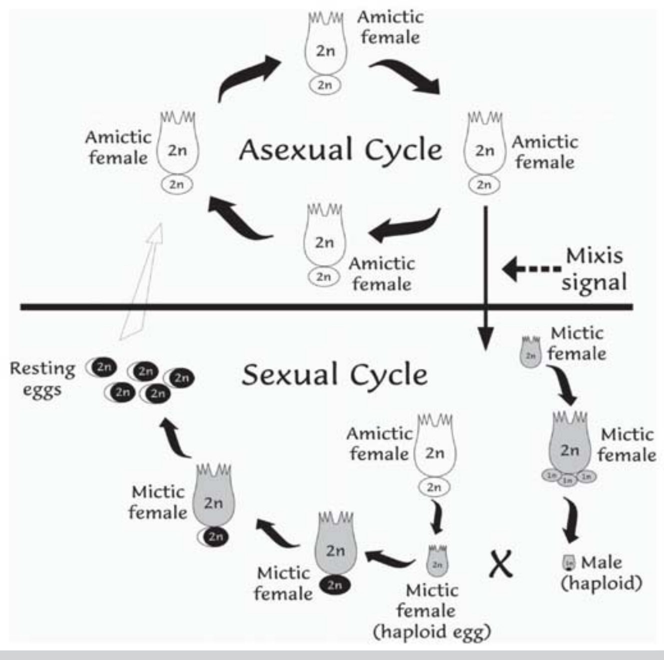

Figure B1. The life cycle of *Brachionus plicatilis* showing asexual and sexual reproduction and formation of resting eggs. From Denekamp et al. 2009 defense and population dynamics (**paper I**)? (2) How are multiple-predators affecting the inducible morphological responses in rotifer prey? Is the widely observed seasonal morphological variation in *Keratella cochlearis* related to seasonal dominance patterns among different predators (**paper II**)? (3) How are synergistic effects from climate warming and brownification affecting establishment and dynamics of rotifer communities (**paper III**)? (4) How is predation affecting establishment and dynamics of rotifer communities in a climate change scenario (**paper III & IV**)?

Multiple stressors

Predation

Predation is a major source of mortality among zooplankton and has considerable impact on prey population dynamics, thereby shaping community composition (Sih et al. 1985). As argued above, in addition to the direct lethal effect, predators impose numerous indirect non-consumptive effects which can also have very strong effects on prey populations as well as the whole community (Miner et al. 2005). In natural systems, prey organisms are exposed to a multitude of predation pressures that vary both temporally and spatially in both intensity and mode. In order to deal with predation threats, many prey organisms have evolved anti-predator defenses in behavior (Hulthén et al. 2014), morphology, such as spines or body depth (Stemberger and Gilbert 1987b, Brönmark and Miner 1992, Laforsch and Tollrian 2004) , or life-history (Riessen 1999). These adaptive defenses can have important effects on population and community dynamics (Miner et al. 2005).

Climate change

There is a large body of scientific evidence that our planet is getting warmer and warmer. Both modelling and recorded trends predict that the increasing rate in temperature over the coming century will by far exceed those of the past (Burkett et al. 2014). The projected temperature increase on Earth will likely be between 3-4.8 °C during the 21st century depending on different greenhouse gas emission scenarios (IPCC, 2013). In addition, a recent worldwide synthesis study showed that many freshwater lakes, especially ice-covered ones, are warming faster than air temperatures (O'Reilly et al. 2015). For lake systems, a striking effect of increasing temperatures is earlier dates of ice break-up and later dates of freeze-over, which would not only increase solar energy inflow heating the water, but also affect other abiotic factors such as light conditions (Vincent 2009). Furthermore, in some regions such as Europe, the largest increase in temperature is expected to occur in winter (IPCC 2013), leading to even shorter ice-covered period and earlier spring. So temperature-governed processes in shallow lake ecosystems are expected to occur earlier in spring. For example recruitment and establishment of freshwater plankton can be strongly affected by the increasing temperatures. In addition, such altered climate has been documented to have strong impact on the phenology of various organisms in a species-specific manner (Winder and Schindler 2004a, Ekvall and Hansson 2012, Nicolle et al. 2012), causing shifts in community composition and changes in predator-prey interactions (Winder and Schindler 2004b, Hansson et al. 2013) e.g. the match/mismatch hypothesis.

Apart from the increase in mean temperatures, a common projection of climate change is that extreme climatic events, such as heat and cold waves, are expected to occur with increasing intensity, duration and frequency (Karl and Trenberth 2003, Fischer et al. 2013, IPCC 2013). Such extreme variations in temperature may impose a considerably stronger threat to organisms and their interactions than a slow and gradual increase in mean temperatures (Vasseur et al. 2014). Several studies have indicated that heat waves may trigger regime shifts (Bertani et al. 2016), fluctuation in planktonic communities (Huber et al. 2010), and the formation of cyanobacterial blooms (Huber et al. 2012). However, few studies have investigated the impact of such large environmental factors on interactions among predators and prey.

Brownification

In recent years there has been a considerable increase in terrestrially derived organic carbon running into aquatic ecosystems (Evans et al. 2005, Monteith et al. 2007, Hansson et al. 2013, Solomon et al. 2015). A large portion of the terrestrially derived dissolved organic carbon consists of humic substances causing a brown coloration of water, referred as "brownification". The underlying mechanism behind this "brownification" seems to be a combination of several different drivers, including an increase in temperature, increased carbon dioxide levels, reversed acidification and human-induced changes in land-use (Monteith et al. 2007, Kritzberg and Ekström 2012, Solomon et al. 2015, Kritzberg 2017). Regardless of the underlying mechanism, this "brownification" of the water reduces the light availability in the water column and to the sediment, affecting primary producers (Karlsson et al. 2009), predation efficiency of visual predators (Jönsson et al. 2013). Light is recognized as an important trigger for induction of zooplankton diapause (Pourriot and Snell 1983, Gyllström and Hansson 2004). So the changed light climate by brownification may affect recruitment and establishment of zooplankton. In addition to a changed light climate, brownification also adds allochthonous carbon to aquatic ecosystems which can affect bacterial production (Tranvik 1988), food web efficiency and fish production (Lefebure et al. 2013). Moreover, increases in temperature and humic substances will likely occur at the same time-scales and not independently. Despite this, there is still very little knowledge on how synergistic effects from these large environmental changes will affect community dynamics in lakes (but see e.g. Nicolle et al., (2012), Hansson et al., (2013)).

ROTIFER RESPONSE TO PREDATION

Rotifers in the freshwater ecosystem are an important link between the microbial loop and the traditional pelagic food chain, and preferable prey by many predators varying in size, taxa, and feeding mode (Williamson 1983). In order to cope with predators with different kinds of hunting and feeding techniques, rotifers have accordingly evolved various anti-predator strategies, including behavioral, as well as morphologically constituent and plastic responses. Those responses have a strong effect on the selective predation thus may affect the community composition and dynamics.

Behavioral defenses

The general predation cycle consists of: encounter, attack, capture and ingestion. Most predation behavior responses e.g. reduced activity, refuge use, migration, spatial avoidance, are operated before the encounter with a potential predator. Some responses (e.g. escaping or evasive behaviors) may be deployed to escape an approaching enemy when detected. To maximize survival, rotifers have deployed a series of behavioral responses including diel vertical migration, epizoic behavior, escape or evasive behaviors to reduce a predator's probability of success (Gilbert and Williamson 1978, Gilbert and Hampton 2001, Gilbert 2014). Diel vertical migration is a very common behavioral response to reduce predation by decreasing the encounter among zooplankton prey (Bollens and Frost 1989, Nesbitt et al. 1996). Another effective behavioral response to reduce predation utilized by some rotifers is epizoic behavior (Iyer and Rao 1995, Pena-Aguado et al. 2008), which is when an organism lives or grows on the surface of an animal species using the host only for support (Iyer and Rao 1995). It has been shown that when the rotifer *Brachionus* is epizoic on *Daphnia* it can coexist with the predator rotifer *Asplanchna* for 7 days longer than when free living with this predator. In contrast, the escape responses are very fast and triggered immediately (within several milliseconds) by physical contacts with predators (Gilbert 2014). Escape or evasive behaviors are common among *Polyarthra* and very effective in reducing capture success by certain slow swimming predators, such as *Asplanchna*, early instars of *Chaoborus* larvae (Moore and Gilbert 1987).

Morphological defenses

Another strategy often used by prey is morphological defenses. Several morphological features such as lorica, spine and body size are important morphological structures protecting rotifers against predators (Stemberger and Gilbert 1984, Williamson 1987, Conde-Porcuna and Sarma 1995). When feeding on rotifer prey with rigid lorica and long spines, it generally takes a much longer time for invertebrate predators, such as copepod and *Asplanchna*, to handle and ingest the prey rotifer, which reduces selective rate. For example, Cyclopoid copepods often capture individuals of *K. cochlearis*, but usually release them unharmed, being unable to reach the soft parts within their lorica. So rotifer prey such as *Keratella* and *Brachionus* are well defended against invertebrate predators because the opening of their lorica are small and protected by spines (Gilbert and Williamson 1978). The size of the rotifer prey is another factor influencing selective predation. However the effectiveness of prey size in deterring predation depends on both predator and prey size (Gilbert and Williamson 1978, Moore and Gilbert 1987). Yet there is a growing recognition on the ability of prey behavior and morphology protecting rotifers against predation, and the abilities are species-specific (Stemberger and Gilbert 1987a, Williamson 1987, Lapesa et al. 2004). However most previous studies have focused on testing the defending responses and efficiency of different rotifer prey separately in the lab (Williamson 1987), although different rotifer species would affect the selection predation rates on each other. So in **paper III**, I investigated the effects of predation and species-specific antipredator defenses on the rotifer community dynamics.

Plastic morphology defenses

Many rotifers show predator-induced plastic morphological defenses to invertebrate predators, which involve the development and elongation of spines (Gilbert 1999, 2012, 2013). Generally, the predator releases a kairomone into the environment, and the prey rotifer responds by producing daughter that has longer spines, and often a larger lorica and body size, which makes it more difficult for the predator to capture and ingest (Gilbert 1999, 2013), thus reducing predation rate by small invertebrates. For example, the *Asplanchna* induced morph of rotifer prey is much less susceptible to *Asplanchna* predation than the non-induced morph (Gilbert and Stemberger 1984, Stemberger and Gilbert 1984, Gilbert 2009).

However, as an important link between the microbial loop and the traditional pelagic food chain, rotifers are preferable prey by many invertebrate and some vertebrate predators varying in size, taxa, feeding mode, and hunting strategy calling for different responses and rapid adjustments by the prey in order to maintain fitness. For example, *Keratella tropica* develop longer spines when exposed to kairomone from *Asplanchna*; yet reduce spine length when exposed to Notonectidae (*Buenoa fuscipennis*) (Zagarese and Marinone 1992, Gilbert 2012). Prey organisms exposed to predation from gape-limited predators may grow larger than the gape-size limit of the predator and thereby escape from predation, such as the fish crucian carp (*Carassius carassius*) (Brönmark and Miner 1992), or zooplankton species that grow larger spines, neck teeth or helmets in the presence of predators (Laforsch and Tollrian 2004, Weiss et al. 2012, Gilbert 2013). Although numerous studies have reported that fish larvae feed extensively on *K. cochlearis*, no study has investigated the impact of fish larvae on the induction of morphological defense of this prey. Hence, in my thesis, I explore the expression of inducible morphological defenses in rotifers also to the vertebrate predator larval fish in **paper I**. Furthermore, I explore the morphological responses in rotifers to multiple predators in **paper II**, where I test the hypothesis that rotifer prey modify their defense responses to different predator sizes with a bi-directional adjustment in spine length in **paper II**.

Morphology defense to vertebrate predator

A common strategy of many freshwater prey species is to grow larger than the gape-size limit of the predator, thereby escaping predation (Brönmark and Miner 1992, Laforsch and Tollrian 2004, Hoverman and Relyea 2009). This has been widely studied with many rotifers developing longer spines and increasing body size in response to invertebrate predators such as the predatory rotifers *Asplanchna* and small copepods (Gilbert and Stemberger 1984, Stemberger and Gilbert 1984). However, to develop longer spines and larger body may be ineffective in the defense against large predators, such as larval fish. According to the size efficiency hypotheses (Brooks and Dodson 1965), there is a size-selective predation by large predators (e.g. fish) on large prey. Therefore, a reduction in size may instead be adaptive.

In **Paper I**, I explore the effects of a vertebrate predator, larval fish, on the induced morphology response and population dynamics of prey rotifers. I found that fish larvae fed extensively on rotifers and caused dramatic declines in the rotifer population both experimentally and in the field (**Paper I**). To examine the effects of the larval fish predation on the spine length of prey rotifers, I first conducted two lab experiments. In the first experiment *K. cochlearis* was exposed to kairomones from fish larvae testing whether the kairomones affect the development of spines in rotifers. In the second experiment, fish larvae were allowed to feed on rotifers with different size and spine length, thereby testing whether spine length affects predation rate by fish larvae. I found that *K. cochlearis* significantly reduced the spine length in response to exposure to larval fish kairomones (Fig.2 in **paper I**). This response is in accordance with the response to some other large predators, such as the ostracod *Cypris pubera* and the notonectid insect *Buenoa fuscipennis*, which both have been noted to induce a reduction in spine length of *K. tropica* (Zagarese and Marinone 1992, Gilbert 2012). I also found that larval fish predation reduced rotifer spine length through selective predation on long-spined individuals. These findings are strengthened by our field monitoring study showing that the spine length of *K. cochlearis* dramatically declined during the period when newly hatched fish started to feed on rotifers. Hence, my finding suggests that the observed changes in spine length in *K. cochlearis* during late spring might be related to the appearance and ontogeny of fish larvae and that ontogeny of a dominant predator may be a driving mechanism behind the considerable spine length variations widely observed in many rotifer taxa. My study advances our understanding on how prey may escape predation by being plastic in protective spine development, either escaping above, or below, the gape size optimum of the dominant predator.

Global scale patterns in spine length of Keratella cochlearis: A consequence of inducible defense responses to larval fish?

Most of the year, small invertebrate predators dominate, suggesting that it may be adaptive for prey rotifers, such as *K. cochlearis*, to induce long spines. Since fish reproduce only once per year at high latitudes, rotifers have to respond to fish larvae during a short period of the year before the fish grow large enough to shift to larger sized food items (Hansson et al. 2007). However, at lower latitudes, fish are dominant predators during most of the year and in order to reduce predation pressure, rotifers should constantly express small body size and short spine length

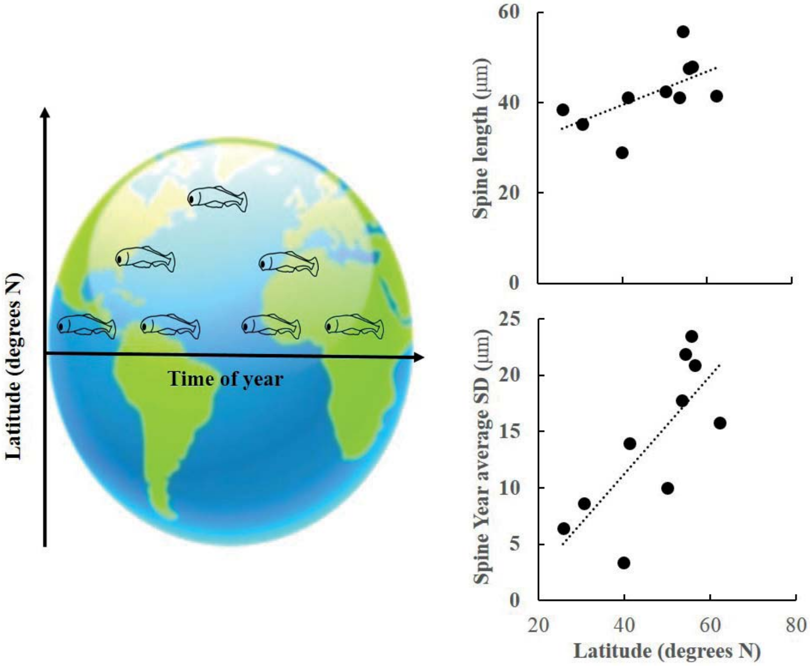

Fig. 1 Left panel: Schematic illustrating the fish reproduction pattern along latitude. Changes in annual mean (right upper panel) and standard deviation (right lower panel) of posterior spine length in *Keratella cochlearis* along a latitude gradient from 25° N to 63° N. From **paper I**.

(Fig. 1). Based on my finding that fish larvae significantly reduce spine length of *K. cochlearis*, we expected mean spine length, as well as mean yearly variance in spine length, to increase with latitude (i.e., longer spines and greater yearly variance at higher latitudes; shorter spines and smaller variance at lower latitudes). In order to test this hypothesis, I conducted a literature survey. As expected, I found a global scale pattern in spine length of *K. cochlearis*, showing an increasing variance in spine length with latitude and considerably larger seasonal variation in posterior spine lengths at higher latitudes (Fig. 1). Hence, this global scale pattern may be explained by differences in fish reproduction, although fluctuations in temperature and food availability among lakes can not be excluded as factors also affecting spine length plasticity (Lindström and Pejler 1975, Zagarese and Marinone 1992, Gilbert 2017).

Morphological defense to multiple predators

Prey may have to handle different, simultaneously occurring predators, differing in size, taxa and predation mode, calling for different responses and rapid adjustments by the prey in order to optimize fitness. Hence prey species have to form predator-specific defenses in order to improve their chances to survive a predator attack (Sih 1987, Kats and Dill 1998) and not use a general response towards all predators (Beckerman et al. 2010). Predators are, on the other hand, constrained by their prey-size choices, for

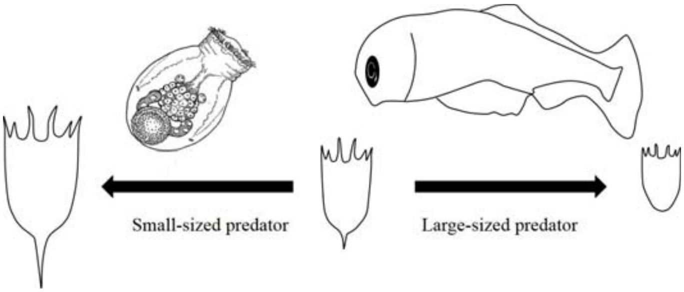

Fig. 2. A schematic illustration of expected plastic morphological responses in rotifers to a small-sized e.g. *Asplanchna* (left); and to a large-sized predator e.g. larval fish (right).

example by gape-size limitations and it has been repeatedly demonstrated that, in order to reduce the predation rate, prey respond by growing larger than the gape size limit of the predators (Brönmark and Miner 1992, Laforsch and Tollrian 2004). However, it may also be adaptive for a prey to escape from predation through avoiding the lower range of a predator's gape size, although this has rarely been demonstrated (Pastorok 1981). Since many rotifers are vunerable prey to variaous predators ranging in size from approximately two-times larger, such as *Asplanchna* spp., to more than 100 times their own size, e.g. fish larvae. Hence in **paper II**, I test the hypothesis that rotifer prey modify their defense responses to different predator sizes with a bi-directional adjustment in spine length. That is when encountering a small predator an adaptive response would be to elongate the spines, i.e. grow out of the predator's gape size. However, when encountering a large predator it may be adaptive to exhibit a smaller size, that is, reduce the spine length, thereby escaping from the predator's feeding size window (Fig. 2).

To test this hypothesis, I used three different methods. First, by exposing rotifers to kairomones from relatively large predators along a body size gradient, I assessed their inducible morphological response to large-sized predators. I found that large-sized predators induce a reduction in rotifer spine length (Fig. 3). This response is very different from the well-documented morphological responses in prey rotifers to small sized-predator such as *Asplanchna* spp. (Stemberger and Gilbert 1984, Gilbert 1999, 2013). Second, I conducted a complementary field monitoring study showing that the spine length of the prey rotifer *K. cochlearis* changed in opposite directions, in response to the shift in dominance between small-sized and large-sized predators (Fig.4). Finally, I conducted a meta-analysis on predator induced morphological defenses in rotifers covering a wide array of rotifer prey taxa and predators. The results showed that both small-sized predator and large-sized predator induced significant changes in rotifer spine length, but those changes were in opposite directions. Small-sized predator induced a significant induction or elongation of spines in rotifer prey, whereas large-sized predator induced a significant reduction (Fig. 3 in **paper II**).

Hence, by combining evidence from

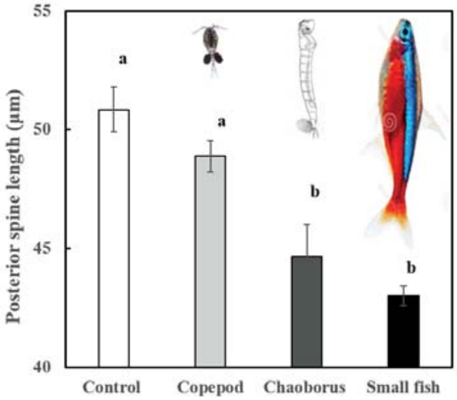

Fig. 3. Posterior spine length of *Keratella cochlearis* after 12 days of exposure to kairomone from predator-free control aquaria and relative large predators, including the copepod *Cyclops* sp., the insect larvae *Chaoborus flavicans*, and small fish (*Paracheirodon innesi*). From **paper II**. Note: Increasing gradient in size of predators.

experiments and studies in the field with a meta-analysis, I demonstrated that rotifer prey distinguish between predators and adjust their protective spine length accordingly, i.e. rapidly adjust spine length to escape either below or above the dominant predator's gape size window. In a broader perspective, these findings advance our knowledge on observed spatial and temporal variations in protective morphologies among prey organisms.

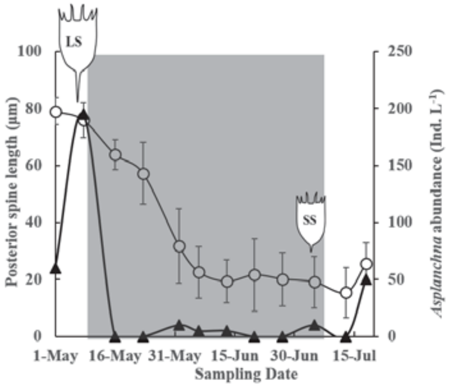

Fig. 4. Posterior spine length variations in *Keratella cochlearis* and abundances of the small sized predator *Asplanchna* from May to July 2013. The grey area indicates the period when newly hatched young-of-the-year fish feed on rotifers in Lake Krankesjön. Open circles represent posterior spine length of *K. cochlearis* and triangles represent abundances of *Asplanchna*. The symbols denote the approximate morphometric relationship between *K. cochlearis* with long (LS), and short spines SS, respectively. From **paper II**.

An example of morphological defense to multiple predators in the lake

Life is not easy, especially for prey organisms. This is very true for freshwater rotifers, which are vulnerable prey organisms and have to cope with a variety in size of predators (Williamson 1983, Gilbert 1999, 2013). Especially prey that are present almost the whole year around in many lakes, such as the widespread rotifer *K. cochlearis*, have to cope with predation pressures varying temporally and spatially in both intensity and mode. For example, in the north temperate Lake Krankesjön, *K. cochlearis* is the dominant rotifer prey during spring through summer and is present almost all year around (Hansson et al. unpublished data). *Asplanchna* is one of the most important predators on *K. cochlearis* in spring and early summer, but in late May to mid-July newly hatched fish start to feed on both *Asplanchna* and *K. cochlearis*. Since *Asplanchna* is only about 2 - 4 times as large as *K. cochlearis*, whereas fish larvae are generally more than 30 times larger than *K. cochlearis* (Hewitt and George 1987, Hansson et al. 2007), an adaptive morphological defense response of *K. cochlearis* may be to alter spine length in opposite directions. Thus, when larval fish start to feed in late spring, there should be a sharp decline in spine length and body size of *K. cochlearis*. In **paper II**, I conducted a field monitoring study on the morphological variability in spine length and body size in this rotifer prey during the period when there was a predator dominance shift between *Asplanchna* and larval fish. I found that the spine length of *K. cochlearis* dramatically decreased from 79.0 µm to 19.3 ± 7.6 µm (mean ± SD) i.e. with 75% (Fig. 4), as newly hatched fish larvae started to feed on rotifers. Simultaneously to the reduction in spine length of *K. cochlearis*, the abundance of the predator rotifer *Asplanchna* also declined (Fig 4), which is likely to be due to larval fish predation.

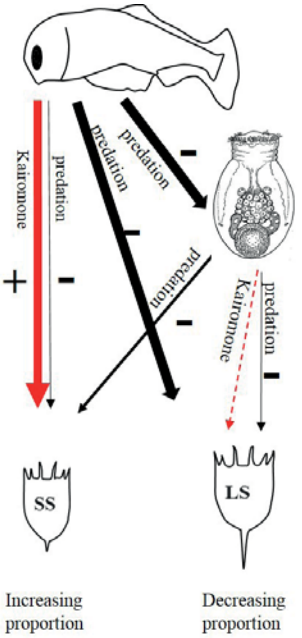

Figure 5. Schematic showing the mechanisms of dramatic reduction of posterior spine length observed in the field when fish larvae emerge. Plus (+) shows positive effect and minus (-) indicates negative effects. Thick arrow represents strong effect and thin arrow shows weak effects. Broken arrow represents unsure effect from kairomone.

The dramatic reduction in posterior spine length observed in the field may be attributed to a combination of multiple mechanisms (Fig. 5). First, omnivorous fish larvae not only feed on *K cochlearis*, but also had high selective preference on the predatory rotifers such as *Asplanchna* spp. (Ghan and Sprules 1993), which induce the increase of spine length in *K. cochlearis* (Stemberger and Gilbert 1984). Hence, fish larvae may affect the *K.cochlearis* through a trophic cascade by eliminating the predatory rotifers *Asplanchna* (Fig. 5). Second, larval fish kairomones may induce shorter posterior spine and smaller body size in *K. cochlearis* as shown in the experiment (Fig. 2 in **paper I**).

Rotifer community dynamics in future scenarios

The role of recruitment in shaping the rotifer community under multiple environmental threats

In order to escape from harsh environmental conditions, many zooplankton including rotifers can enter diapause. The termination of dormant stages can strongly affect plankton population dynamics and seasonal succession (Hansson et al. 1994, Hansson 1996, Gilbert and Schröder 2004). For freshwater rotifers, hatching of resting eggs often occurs during a short period that marks the beginning of population growth suggesting a crucial role in the establishment of the rotifer populations (Hairston, 2000; Gilbert and Schröder 2004). A number of environmental factors, such as salinity, dissolved oxygen, light, and temperature have all been reported to affect the hatching of resting eggs from the sediment (Gilbert and Schröder 2004, Gyllström and Hansson 2004, Schröder 2005). Among these factors, temperature is one of the most important triggers initiating the hatching of resting eggs (Gilbert and Schröder 2004, Gyllström and Hansson 2004, Schröder 2005). In addition, light may also be required for some taxa, although it is regarded a less important trigger for recruitment from resting stages compared to initiating resting (Pourriot and Snell 1983, Gilbert and Schröder 2004).

In **paper III**, I investigate the impacts of climate warming and brownification on recruitment of rotifers and the consequences on their community dynamics. I conducted a mesocosm experiment (from March to May; Fig. 6) where I combined a 3 °C temperature increase with a doubling in water color (brownification), a change corresponding to modeled projections for the coming 25-75 years. Recruitment of rotifers was evaluated by setting recruitment traps at the sediment surface once they hatched from the sediment and swam up in the water column. I found that even though different genera of rotifers began to recruit from the sediment at different times, elevated temperature had a strong effect on the timing of the recruitment peak for all genera of rotifers occurring earlier in the heated, compared to ambient-temperature treatments (Fig. 1 in **paper III**). We also found that the increased temperature advanced the population development of rotifers in the water column as a result of earlier recruitment, which was also confirmed in **paper IV**. Hence, besides increased growth, a

Fig. 6. Picture of mesocosm experiment from 2014. These mesocosms were used in experiments in **Paper III & IV** in this thesis. Photo: Pablo Urrutia-Cordero.

likely mechanism behind changes in the rotifer's phenology in the water column is the advanced timing of recruitment and increased recruitment rate from the sediment in response to elevated temperatures (**paper III &IV**).

One step further, in **paper IV**, I analyzed the relationship between temperature and recruitment rate of different rotifer taxa and found that rotifer egg hatching has species-specific temperature requirements. For example, *Polyarthra* spp. resting eggs rarely hatched when water temperatures were above 15 °C, and the optimal temperature for them to hatch was between 9 and 10 °C (Fig. 7), whereas, the optimal hatching temperature for *K. cochlearis* was 14–15°C. These differences in temperature requirements likely explain the earlier establishment of *Polyarthra* spp. in the water column observed in both **paper III & IV**. Hence, the widely observed rapid seasonal succession among rotifer taxa, with some species occurring early in spring and others later in the season (Hairston Jr et al. 2000), may at least in part, be driven by taxa-specific optimal hatching temperature windows for their resting eggs.

However, even though brownification affects the light climate in the water column and on the sediment, the effects I recorded from this stressor were less pronounced, or even negligible, compared to effects

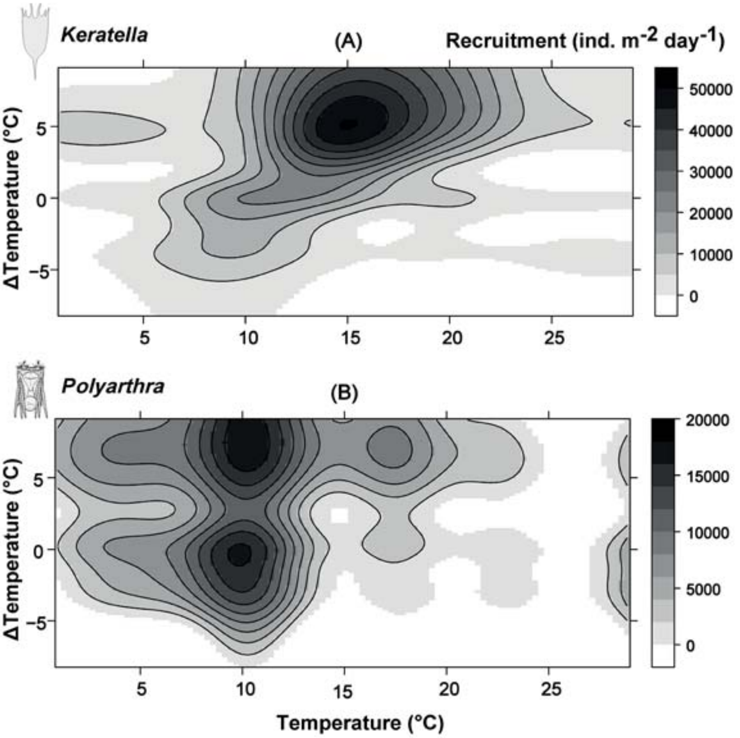

Fig. 7. Predictions of recruitment rates of *Keratella cochlearis*, *Polyarthra* spp., by GAM models along temperature levels and short term temperature variations (ΔT) gradient. From **paper IV.**

imposed by elevated temperatures. Most taxa were not affected, but one taxon (*Argonotholca*) was strongly suppressed by increased water color (**paper III**). Hence, even though light, or some other factor related to brownification, may not be crucial for the recruitment of most rotifer taxa, it may be a major cue in determining initiation in recruitment of some genera, such as *Argonotholca*.

Impacts of predation on rotifer community under climate change

All trophic levels will likely be affected by elevated temperatures in one way or another (Christoffersen et al. 2006; Nicolle et al. 2012), but interactions among organisms will likely also change, including predator-prey dynamics. In **paper III**, I found that elevated temperatures advanced establishment of rotifer communities (discussed above), but also increased predator abundances, and advanced and intensified the predation pressure (**paper III & IV**). This finding was later confirmed by Velthuis and coauthors (Velthuis et al. 2017). Apart from the increased mean temperature, I also tested the increased temperature variation and the frequency of extreme temperatures on the interactions between rotifers and their predators (**paper IV**). I found that rotifer taxa have specific temperature requirements for hatching from resting stages, and use a limited temperature window for recruitment and species-specific optimal hatching temperature for entering the water column from the sediment (as described above). However, cyclopoid copepods use the fourth stage copepodites or adult female as (resting stages) a recruitment generation to respond to rapid short-term temperature variations. Therefore, being able to diapause at an almost adult stage may constitute an evolutionary advantageous strategy, since it allows for a rapid (within days) response to improved conditions and may become even more advantageous in a climate change perspective. I also found that the predator-prey dynamics between cyclopoid copepods and rotifers expose no mismatches in a climate change scenario (**paper III & IV**). The mechanism is likely that cyclopoid copepods use late stage copepodites or adult female diapause that can, just as rotifer reproduction, rapidly respond to short term increases in temperature. Based on this we may predict that longer-lived cyclopoid copepod predators with complex life cycles are likely to benefit from more frequent temperature variations and will be able to rapidly suppress rotifer prey populations despite their far longer generation time. Rotifer prey, on the other hand, despite short generation time and high reproductive potential, will likely suffer from an even stronger predation pressure from cyclopoid copepods imposed by predicted increased temperature variation in the future.

Conclusions

Predation has strong effects not only on population growth but also on inducible morphological defenses in rotifers. In **paper I**, I found that a common predator (larval fish) present in most aquatic ecosystems, during part of their ontogeny fed extensively on rotifer prey and reduces rotifer spine length both through induction of shorter spines and selective predation on long-spined individuals. The global scale pattern on spine length of a common rotifer (*K. cochlearis*) with an increasing variance in spine length with latitude may be explained by differences in fish reproduction from once per year at high latitudes to several times per year at lower latitudes.

In **paper II,** I show that rotifer prey can detect and respond appropriately in opposite directions to different sizes and feeding modes of predators by being plastic in protective spine development, either escaping above (small-sized predator), or below (large-sized predator) the gape size optimum of the dominant predator.

In **paper III**, rotifer community establishment via recruitment and population can be predicted to occur earlier under a climate change scenario, whereas it would also decline earlier due to increased predation pressure. However, the effects from brownification on establishment and growth in the rotifer community were less pronounced, or even negligible, compared to effects imposed by elevated temperatures. Hence, some expected large-scale environmental changes, such as elevated temperatures, may be more important than others, such as brownification.

In **paper IV**, I show that in a future climate scenario with increased temperature variations and frequency of extreme temperatures, copepods benefit from heat waves, while rotifers suffer from a higher predation pressure. Hence, in a broader perspective my studies suggest that differences in life history traits will affect predator-prey interactions, and thereby may alter community dynamics, in a future climate change scenario.

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ACKNOWLEDGEMENT

I would like to thank all the funders that made my PhD-studies and this thesis possible:

- The China Scholarship Council (CSC)

- The ERA-Net BiodiERSA project LIMNOTIP through the Swedish Environmental Research Council for Spatial Planning and the Environment (FORMAS).

- Department of Biology/Aquatic Ecology Unit, Lund University

Thanks! Tack! 感谢！

2nd of September 2013, I moved to Sweden and started my adventure as a Ph.D. student at Lund University. I knew little about rotifer and Sweden, and I had no idea about what the future would bring. Now, after four years, I know a lot more about rotifers and lovely people in Sweden. I have also gained so many wonderful memories. This book is the result of the adventure which I could not have made without you.

My supervisors

Lars-Anders, I don't know how I can put into words the gratitude for the support you have provided to me through the past four years. You have given me freedom to develop and pursue my passion (e.g. the meta-analysis and inducible defense). I really appreciate how you helped and trained me to become an independent researcher especially during the last year. I am very grateful that you always keep an open ear to my questions, anxieties and even my homesickness (sometimes) and you have taught me, supported me, encouraged me, praised me and comforted me when needed. I really appreciate the numerous encouragement you have given to me during those depressing and frustrating days and taught me how to cope with them. Thank you so much for being such a fantastic supervisor! I will never forget your incredible kindness and hospitality, and hope I can pay back in the future, living up to the great example as a great person and a great researcher that you have set for me.

Karin, thank you very much for your guidance, support and nice scientific discussion and input. I am really grateful that you shared your extensive knowledge about the hatching of plankton resting stage with me and that you arranged the rotifer taxonomy training workshop for me in Uppsala.

Jun, you have become an unofficial co-supervisor during this thesis. Thank you so much for inspiring me to pursue my Ph.D. in Sweden. I really appreciate the great help and all the inspiring suggestions on the research proposal for my Ph.D. project you have given to me. Without your help and guidance, I would never make it here. I am also very grateful for the encouragement and insightful suggestions on statistics for my manuscripts. And I would also like to thank you for setting a true example of consistency and enthusiasm for research.

My collaborators and colleagues

Pablo U, I am really lucky to have you who is always filled with endless passion and enthusiasm as my project companion and friend. It has been so much fun to work, discuss, and exchange ideas with you.

Mattias, thanks a lot for being a great guide of conducting mesocosm experiments. I am so grateful that you taught me so many useful techniques at the start of Ph.D. which really helped me a lot. Thank you!

Christer, thank you for your constructive inputs and insightful suggestions on the manuscripts and being so supportive to students!

Johan H, thank you for all the help with statistics and inspiring discussion on meta-analysis. I appreciate your valuable input on the manuscript.

All the Limnotip members: **Pablo U**, **Mattias, Jens**, **Margarida**, **Fernando**, **Ioana**, **Tim**, **Mariana**, **Hong**, **Zhongqiang**, **Liang**, **Valentina**, **Mikael**, **Rebecca** thank you a lot for your great efforts ! I am sure I forgot to mention someone here, sorry!

Jens, thank you for being a perfect guide of my first Limnotip sampling trial. It has been so much fun to work with you both in the lab and field.

Tobias, thank you for sharing your knowledge on rotifer taxonomy with me. You are so nice and selfless to spend those days just for training me. The knowledge I have learned from you is really helpful for the whole Ph.D. Thank you a lot!

The **"Bahamas Group",** thank you very much for all the inspiring discussion and great research ideas.

Mikael, thanks for lending me algal food for my rotifers!

Marja, thank you for painting this beautiful cover for my thesis and making me feel welcomed when I started

Hong, thank you for sharing your knowledge on rotifers with me.

Marcus, I really appreciate your helpful feedback on the "kappa".

Simon, thank you very much for being so encouraging and helpful, for sharing sweet photos, stories of **Vera** and sweet Swiss chocolates with me. I would also like to thank you for all the interesting discussion about everything from Fe to politics. You are a fantastic officemate and friend.

Marie, I remembered the first time I met you Lasse said "Marie knows everything" .You do Marie! I would like to thank you for making me feel welcomed at the beginning, for encouraging me during the depressing days, for being my "baking teacher" and organizing the great baking workshops, for teaching me the taxonomy of rotifers, for answering all my questions, for sharing various great stuffs from food to Swedish history. My four years here in Sweden would have been much less fun without you. You are wonderful!

Aquatic Ecology, thank you all in the Unit for making this place such a friendly, supportive, and creative working environment. Thank you for all the scientific discussion, fikas, and great parties. It has been so great to study and work here during the past four years. I have gained so much lovely memories.

我的家人

亮，这一路走来，感谢有你的陪伴、鼓励和支持，分享我的成就和喜悦，分担我的艰难和压力。

爸爸妈妈和弟弟妹妹们，感谢有你们永远无条件的信任、支持和爱！每次研究受挫或实验进展不顺的时候，是你们的鼓励给了我极大的动力。

My contributions to the papers

I. Predator ontogeny affects expression of inducible defense morphology in rotifers

HZ and LAH designed the study and all authors were involved in conducting the study. HZ wrote the manuscript with contributions from LAH and CB.

II. Bi-directional plasticity: Rotifer prey adjust spine length to different predator regimes

HZ and LAH conceived and designed the meta-analysis and the field study. HZ, JH and LAH designed the lab experiment. HZ conducted the lab experiment. LAH and HZ conducted the field study. HZ analyzed data and drafted the manuscript. All authors contributed to the writing of the manuscript.

III. Counteracting effects of recruitment and predation shape establishment of rotifer communities under climate change.

ME, LAH designed and conducted the mesocosm experiment. HZ, LAH designed the lab experiment and HZ conducted the lab experiment. HZ and JX analyzed data. HZ wrote the manuscript with contributions from all other authors.

IV. Life-history traits buffer against heat wave effects on predator-prey dynamics in zooplankton

HZ and LAH conceived and designed the study. HZ, PUC and LAH conducted the experiment. HZ and LH analyzed data. HZ wrote the manuscript with contributions from all other authors.

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