LUND UNIVERSITY

Multiple threat responses in zooplankton - from communities to individuals

Ekvall, Mikael

2015

Link to publication

Citation for published version (APA):
Ekvall, M. (2015). *Multiple threat responses in zooplankton - from communities to individuals*. Department of Biology, Lund University.

Total number of authors:
1

General rights
Unless other specific re-use rights are stated the following general rights apply:
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.
• Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
• You may not further distribute the material or use it for any profit-making activity or commercial gain
• You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: https://creativecommons.org/licenses/

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Multiple threat responses in zooplankton

—

from communities to individuals

Multiple threat responses in zooplankton

–

From communities to individuals

Mikael T. Ekvall

LUNDS UNIVERSITET

DOCTORAL DISSERTATION
by due permission of the Faculty of Science, Lund University, Sweden.

To be defended in the Blue Hall, Ecology Building, Sölvegatan 37, Lund, Sweden on Thursday 17th of September 2015 at 9:30.

Faculty opponent

Prof. Ralph Tollrian
Ruhr-Universität Bochum, Germany

Organization LUND UNIVERSITY Department of Biology, Aquatic Ecology	Document name DOCTORAL DISSERTATION Date of issue September 17, 2015
Author(s) Mikael T. Ekvall	Sponsoring organization Swedish research council (VR)

Title and subtitle
Multiple threat responses in zooplankton – from communities to individuals

Abstract

Most organisms on Earth live a life where they are exposed to multiple and variable threats. In order to maximise survival they need to be able to perceive and respond to these threats. Two common threats that crustacean zooplankton are faced with are predation and ultraviolet radiation (UVR). To cope with these threats zooplankton use different strategies such as diel vertical migration and the accumulation of photoprotective compounds.

In this thesis I study the threat responses of zooplankton when exposed to predation and UVR. I explore both inter- and intraspecific differences in the response to these threat situations. In addition to field data I also developed a new technique for tracking zooplankton using fluorescent nanoparticles, which I use to track the individual responses of zooplankton.

I investigate if accumulation of photoprotective pigmentation may affect the spatial distribution of species in nature and how individual size may affect the migratory behaviour of zooplankton. In addition I also explore how previous exposure to threats affect the behavioural responses and if some of the observed behavioural variance could be explained by consistent individual differences in behaviour.

In summary, I show that even closely related species may show large differences in their response to UVR. Intraspecific differences in pigmentation could not be related to the spatial distribution of either *Daphnia* or calanoid copepods; however, both *Daphnia* and copepods were found to perform size structured migration. I also demonstrate that previous experiences of a threat can affect how the organism responds. Some evidence for consistent individual differences in the behavioural response of *Daphnia* to UVR is presented, suggesting that individual based studies could add further to our knowledge about behavioural responses in zooplankton. Given the variability both with respect to inter- and intraspecific differences in UVR response we need to keep these differences in mind when postulating new, more comprehensive theories explaining the behaviour of zooplankton exposed to everyday threats.

Key words
Zooplankton, *Daphnia*, copepods, ultraviolet radiation, predation, multiple threats, quantum dots, tracking

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 127 / Price
	Security classification

Distribution by (name and address)

I, the undersigned, being the copyright owner of the abstract of the above-mentioned dissertation, hereby grant to all reference sources permission to publish and disseminate the abstract of the above-mentioned dissertation.

Signature  Date 2015-08-16

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 photo:

Mikael T. Ekvall

Layout: Mikael T. Ekvall & Mattias Ekvall

Proof reading: Mikael T. Ekvall

Printed by E-huset Tryck, Lund

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

Table of contents

Populärvetenskaplig sammanfattning 9
List of papers 11
introduction 13
Threats in the environment 13
Predation 13
Ultraviolet radiation 14
Zooplankton responses to threats 14
Diel vertical migration 14
Photoprotective compounds 16
Carotenoids 16
Melanin 17
Mycosporine-like amino acids 17
Interactions in threat responses 17
Interspecific differences in response to UVR 18
Tracking of small individual organisms 19
Individual variation in threat response 20
Size and previous experiences 20
Conflicting threats 22
"Personality" 23
Conclusion and future perspectives 23
References 24
Acknowledgements 31
Tack 33
My contribution to the papers 37
Paper I 41
Paper II 55
Paper III 71
Paper IV 83
Paper V 99
Paper VI 109

Populärvetenskaplig sammanfattning

Vår planet är i mångt och mycket en trevlig plats att leva på, men det är också en plats där faror och hot kan lura bakom varje hörn. Dessa hot kan vara av olika karaktär, till exempel kan det röra sig om risken att bli jagad och uppäten, att drabbas av uttorkning eller något annat obehagligt. Vår planets invånare har utvecklat en mängd olika strategier för att hantera och undvika dessa hot. En vanlig strategi, som utnyttjas av många djur, är att förflytta sig och på så sätt fly undan hotet.

I min avhandling undersöker jag hur djurplankton hanterar situationer när de utsätts för två i naturen vanligt förekommande hot, nämligen hoten av att bli uppäten och hotet att utsättas för höga doser av ultraviolett strålning. Att bli uppäten är direkt förödande för organismen och ultraviolett strålning kan skada djurets celler, vilket även det kan få förödande konsekvenser. För att hantera dessa hot förflyttar sig djurplankton dagligen upp och ner i våra sjöar och hav, de genomför en så kallad vertikal migration. På dagen när solen lyser blir de lättupptäckta byten samt utsätts för ultraviolett strålning om de befinner sig nära ytan. För att undvika detta simmar de snabbt ner mot djupare vatten, dit ljuset och den ultravioletta strålningen inte når. Först framåt natten när de inte längre hotas av ultraviolett strålning och är mindre sårbara för visuell predation återvänder de till ytan för att äta. Ett alternativt eller kompletterande skydd är att lagra på sig olika typer av pigment eller andra ämnen som skyddar djurplanktonet mot solens strålning. Denna typ av skydd har även vi människor vilket visar sig när vi solar och blir bruna till följd av att kroppen lagrar på sig pigmentet melanin för att skydda oss mot solens farliga strålning.

Men hur undersökte jag då hur mina zooplankton svarade på de två hoten? För att studera djurplanktonen mer ingående utvecklade jag bland annat en metod där djuren märks in med lysande nanopartiklar, så kallade kvantprickar. Med hjälp av denna metod kan vi följa individuella djurplankton och studera hur de svarar när de presenteras för hotsituationer. Så, vad kom jag fram till? Jag fann att bland annat att zooplanktons storlek påverkar hur starka migrationer de genomför, där mindre individer ofta uppvisar något svagare migrationer. Jag kan också konstatera att djurens tidigare erfarenheter spelar in i hur de svarar på hotsituationer, till exempel så visade det sig att individer som hade upplevt ultraviolett strålning tidigare svarade lite mer avslappnat när de utsattes för ultraviolett strålning igen. Även olika närbesläktade arter av djurplankton visade sig svara väldigt olika på hot från ultraviolett strålning, vissa arter reagerar starkt och andra nästan inte alls, detta kan sannolikt kopplas till hur djuren lever och mängden solskydd de lagrat på dig.

Jag hittade alltså skillnader mellan arter men hur ser det ut inom en art? Finns det konsekventa beteendeskillnader mellan olika individer av samma art, någonting som skulle kunna liknas vid ”personligheter”. Ja, det visade sig att det finns vissa konsekventa

skillnader mellan individer när det gäller hur de svarar på hot. Vanligtvis brukar sådan varians i beteende slätas över men baserat på dessa resultat så bör framtida försök designas med individuella skillnader i åtanke.

För att summer det hela kan jag säga att art, storlek, tidigare erfarenheter och "personlighet" spelar roll för hur zooplankton reagerar två av de faror som finns på vår planet.

List of papers

This thesis is based on the following papers, referred to by their roman numerals:

I. Ekvall, M. T., Hylander, S., Walles, T., Yang, X., Hansson, L.-A. (2015) Diel vertical migration, size distribution and photoprotection in zooplankton as response to UV-A radiation. **Limnology and Oceanography**, *In press*.

II. Hansson, L.-A., Bianco, G., Ekvall, M. T., Heuschele, J., Hylander, S., Yang, X. Instantaneous threat escape and differentiated refuge demand among zooplankton taxa. *In revision* **Ecology**.

III. Ekvall, M. T., Bianco, G., Linse, S., Linke, H., Bäckman, J., Hansson, L.-A. (2013) Three-dimensional tracking of small aquatic organisms using fluorescent nanoparticles. **PLOS ONE**, *8(11):e78498*.

IV. Hylander, S., Ekvall, M. T., Bianco, G., Yang, X., Hansson, L.-A. (2014) Induced tolerance expressed as relaxed behavioural threat response in millimetre-sized aquatic organisms. **Proceedings of the Royal Society B-Biological Sciences**, *281: 20140364*.

V. Ekvall, M. T., Palmér, T., Bianco G., Heuschele, J., Bäckman, J., Åström, K., Hansson, L.-A. Response of *Daphnia* to multiple threats from UV-A and predation. *Manuscript.*

VI. Heuschele, J[1]., Ekvall, M. T[1]., Bianco, G., Hylander, S., Hansson, L.-A. Personal invertebrates: individually consistent behaviour in *Daphnia*. *Submitted.* [1]Equal contributions

Papers I, III and IV are reprinted with permission from the publisher.

Where supplementary material is referred to in the published papers, this can be found in the online version of each of the papers.

Introduction

Most organisms on Earth live in an environment where they are exposed to multiple and variable threats. A common response when faced with a threat is to migrate or move away from the threat. In fact, many organisms move or migrate (Hansson and Åkesson, 2014) and many of these movements or migrations are triggered by threats or other factors in the environment (Hopcraft et al., 2014). With respect to threats in the environment one could say that organisms live in what could be viewed as a landscape of fear (Ripple and Beschta, 2004) and each day they need to respond to these threats in a way that maximise survival. This is true for organisms of all sizes, from the large wildebeest on the great savannahs (Hopcraft et al., 2014) to the tiny crustacean zooplankton that migrate up and down the water column on a daily basis in response to harmful ultraviolet radiation (UVR) and predation (Hansson and Hylander, 2009a, Williamson et al., 2011).

Despite their small, millimetre size, zooplankton are very important components of the aquatic ecosystem. Two of the most important groups of crustacean zooplankton are cladocerans and copepods, which are commonly found in most water bodies throughout our planet. Due to their position in the aquatic food web, linking primary production with the higher trophic levels, they constitute a important component for the life of many organisms, both aquatic and terrestrial (Brönmark and Hansson, 2005).

The aim of this thesis is to explore the threat responses in crustacean zooplankton, with respect to diel vertical migration and photoprotection, when exposed to UVR **(Papers I, II, IV, VI)** and also to the combination of UVR exposure and predation threat **(Paper V)**. The work also involves the development of a method **(Paper III)** to allow for detailed, routine based, studies on individual zooplankton in order to explore these threat responses from an individual perspective **(Papers IV-VI)**.

THREATS IN THE ENVIRONMENT

Zooplankton may face many threats in the environment; in this thesis I have focused on two of these, namely the threat from predation (from both invertebrates and from fish) and from harmful ultraviolet radiation.

Predation

Predation is probably one of the most studied fields in ecology and is known to have large impact on prey species by shaping communities and species composition, and also affecting the ecosystem as a whole (e.g. Brooks and Dodson, 1965, Ripple and Beschta, 2004). Despite a direct lethal consumptive effect, non-consumptive effects from predators can also strongly influence whole communities, in addition to individual organisms, (Peacor et al., 2012). The threat of predation is always present and given the large negative lethal effect of predation at the individual level, one individual should, at any point in time, always try to minimize the risk of being predated. To aid this, many

organisms have the ability to recognise e.g. chemical cues from predators in the surrounding environment and respond to these accordingly (Brönmark and Hansson, 2000, Engel et al., 2014, Heuschele and Selander, 2014).

Ultraviolet radiation

Ultraviolet radiation originating from the sun is the shortest wavelengths that can reach the Earth's surface. It is defined as the wavelengths between 100-400 nm and is arbitrarily divided into three different classes: UV-A (320-400 nm), UV-B (280-320 nm) and UV-C (100-280 nm). The energy of these different wavelengths increases as the wavelength decrease; making UV-C the most damaging followed by UV-B and UV-A respectively. However, the Earth's ozone layer absorbs most of the incoming UVR and UV-C is completely absorbed and does not reach the earth's surface. During most atmospheric conditions the UV-B and UV-A range of the spectrum accounts for 0.01 % and 6 % of the global radiation respectively. The visible range (400-700 nm) on the other hand accounts for 50 % of the global radiation (Kirk, 1994, Rautio and Tartarotti, 2010).

Although most of the UVR is absorbed by the atmospheric ozone layer, the amount that reaches the Earth is enough to have detrimental effects on both aquatic and terrestrial organisms (Zagarese et al., 1994, Williamson and Rose, 2010) affecting e.g. fecundity (Huebner et al., 2006), survival and growth (Bancroft et al., 2007). When UVR enters water it attenuates quite rapidly, often within the first few meters of the water column (Williamson, 1995). The attenuation of UV-A and UV-B radiation is negatively correlated with the dissolved organic carbon (DOC) content of the water, which indicates that the amount of DOC in the water is one of the most important factors influencing the attenuation of UVR (Scully and Lean, 1994, Kirk, 1994, Morris et al., 1995, Rose et al., 2009).

ZOOPLANKTON RESPONSES TO THREATS

Zooplankton have evolved several strategies for coping with threats in the environment. Below I focus on diel vertical migration and accumulation of photoprotective compounds, strategies used by both copepods and cladocerans (Fig. 1).

Diel vertical migration

The diel vertical migration of zooplankton in lakes and oceans is likely one of the largest migrations on Earth (Hays, 2003). One of the first records of this daily movement of zooplankton up and down the water column was recorded in Lake Constance by Weismann in 1877 (reviewed in Hutchinson, 1967). The normal pattern of these migrations is that organisms spend the day in the deeper and darker parts of the water column and then migrate upwards towards surface waters during night to feed (Lampert, 1989). In addition, reversed migration, or nocturnal migration, where the organisms migrate down to the deeper waters during night and occupy shallower depths during day have been shown for both copepods (Ohman et al., 1983, Minto et al., 2010) and cladocerans (Bosch and Taylor, 1973). However, not all zooplankton species perform vertical migrations, and there is

not even behavioural consistency within genera. As an example Stich and Lampert (1981) showed that *Daphnia galeata* do not perform vertical migrations, it rather stays in the surface layers all day while *Daphnia hyalina* perform migrations to deeper layers during day.

Previous studies have also shown that some species tend to have different migratory behaviour depending on size. Hansson and Hylander (2009b) found that *Daphnia longispina* showed size dependent differences in migratory behaviour where *Daphnia* smaller than 0.9 mm did not migrate to the same extent as larger individuals. Similar patterns have also been observed for copepods in Italian mountain lakes (Tiberti and Barbieri, 2011). One explanation for this size structured migration pattern could be that larger zooplankton are more exposed to predation than smaller ones (Brooks and Dodson, 1965). This theory is supported by a study by Holliland et al. (2012) who saw an increase in the amplitude of the diel vertical migration in the copepod *Acartia sp.* with stage and size, suggesting an ontogenetic shift in behaviour which was attributed to an increased predation risk with size. Zaret and Suffern (1976) were among the first to identify predation as the explanatory factor for vertical migration. In many studies that followed, predator presence has been shown to elicit vertical migration in zooplankton (reviewed in Hansson and Hylander, 2009a, Williamson et al., 2011).

However, many studies have also shown vertical migrations in lakes without predators, suggesting that other factors than predation may explain the behaviour

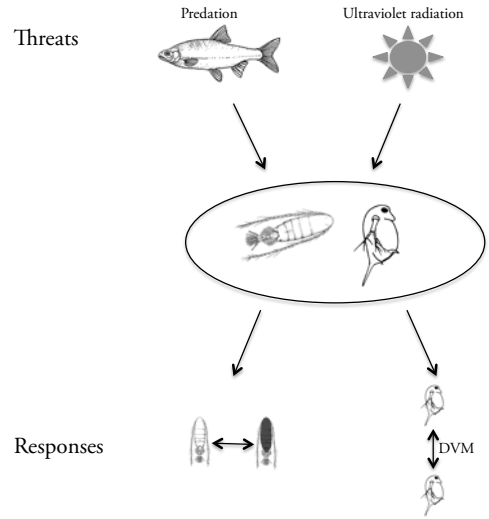

Fig. 1. Schematic overview of the response of copepods and *Daphnia* to multiple threats from ultraviolet radiation and predation. Highlighting two different strategies were copepods rely more on the use of photoprotective compounds while *Daphnia* rely more on diel vertical migration (DVM).

(Williamson et al., 2001, Hansson and Hylander, 2009a, Williamson et al., 2011). It has also been shown that *Daphnia* respond with negative phototaxis upon exposure to UVR (Hessen, 1994, Storz and Paul, 1998) and positive phototaxis to visible light (Storz and Paul, 1998). Alonso et al. (2004) also suggested that surface avoidance of zooplankton is a direct response to high levels of UVR. Dodson (1990) concluded that at least for *Daphnia*, 84 % of the variation in the amplitude of the vertical migration could be explained by water clarity, measured as secchi depth, and by moon intensity measured as per cent of the moon illuminated. Increased water transparency increases the UVR penetration depth. This has led to the transparency gradient hypothesis (Kessler et al., 2008) postulating that UVR is a primary determinant for zooplankton vertical migration in

transparent lakes with a small fish stock and that predation is the primary driver in less transparent lakes with more fish, combining the two factors as proximate cues for vertical migration. Williamson and co-workers (2011) presented a more comprehensive framework, expanding the transparency gradient hypothesis. This framework was synthesized into the transparency regulator hypothesis (TRH) where drivers are divided into dynamic and structural drivers (Williamson, 2011). Both UVR and visual predation are categorised as dynamic drivers, which may change within short time periods. The importance of these dynamic drivers will then be determined by the transparency of the system. Other factors such as food and temperature are defined as structural drivers and these are more stable over shorter time periods but may change on a seasonal basis. As dynamic factors, compared to structural factors, change within a short time period, these are more likely to be the drivers behind behavioural responses such as DVM (Williamson et al., 2011).

Photoprotective compounds

When exposed to UVR, zooplankton have several protection systems including enzymatic responses (Souza et al., 2012), DNA repair systems like nucleotide extension repair and photo-enzymatic repair (reviewed in Rautio and Tartarotti, 2010) as well as the use of photoprotective compounds (Hansson and Hylander, 2009a). For the work presented in this thesis I have included photoprotective compounds, which protect the organism from the detrimental radiation by either functioning as an antioxidant or as radiation screeners. In zooplankton there are three major groups of photoprotective compounds, carotenoids, melanin and mycosporine-like amino acids (MAAs), which are all presented below.

Carotenoids

Already several decades ago researchers were puzzled by the light blue-green or orange-red colour of various zooplankton living in mountain lakes and in the polar regions. Brehm (1938) wrote a review on the topic summarizing eleven different hypotheses that were thought to explain this red colouring of certain organisms. One of these eleven hypotheses dealt with "The shielding from ultraviolet radiation". Czeczuga and Czerpak (1966) showed that the red colour of *Diaptomidae* was due to the presence of carotenoids. When investigating the carotenoids in *Diaptomus nevadensis*, Hairston (1976) identified two compounds, astaxanthin and an ester of astaxanthin, which are the major carotenoids present in most copepods (Czeczuga, 1975, Snoeijs and Haubner, 2014) as well as in rotifers (Gilchrist and Green, 1962). In the organism, carotenoids function both as precursors for vitamin A but also as antioxidants that neutralize free radicals which are formed in cells upon exposure to radiation (Goodwin, 1986). Carotenoids cannot be produced by the zooplankton itself but needs to be obtained via carotenoid rich food (i.e. phytoplankton) (Goodwin, 1986). The photoprotective role of carotenoids have been shown in many cases, for example Ringelberg et al. (1984) showed that pigmented individuals tolerate higher levels of UVR compared to unpigmented ones. However, deeply coloured animals become more susceptible to predation from visually oriented predators

(Hairston, 1979, Luecke and O'Brien, 1981, Gorokhova et al., 2013).

Melanin

In contrast to copepods, cladocerans generally lack the red carotenoid pigmentation. Although they may have some carotenoids these are associated with pre-ovarial lipids and are allocated to eggs where they may play a role as antioxidants, but they are of minor importance for photoprotection in adults (Hessen, 1994). Instead cladocerans rely more on another type of photoprotective pigmentation called melanin, which is a black-brown or yellow-red-brown pigment that is derived from chemical and biological transformations of tyrosine and related compounds (Blois, 1978). It is the same pigment that we humans accumulate when we obtain a "sun tan" when exposing ourselves to UVR. Melanin works as a radiation screener and some precursors may also act as scavengers for free radicals (Blois, 1978, Hebert and Emery, 1990). It has been shown that pigmented *Daphnia* survive UVR much better than unpigmented individuals (Hebert and Emery, 1990, Hessen, 1994, Hessen, 1996). The melanised phenotypes are mostly found in the Arctic or high-altitude areas with clear water while unpigmented individuals occur in more coloured or turbid waters (Hebert and Emery, 1990, Rautio and Korhola, 2002, Hansson et al., 2007).

Mycosporine-like amino acids

Mycosporine-like Amino Acids or MAA:s are a family of photoprotective compounds found in many organisms (Sinha et al., 2007) and that function as UVR screeners that dissipate the solar energy as heat (Hansson and Hylander, 2009a and references therein) and are invisible in visible light (Karentz and Bosch, 2001, Tartarotti et al., 2001). Mycosporine-like Amino Acids are present in copepods and rotifers but no MAA:s, or only trace amounts, have previously been found in cladocerans (Tartarotti et al., 2001, Persaud et al., 2007), although in **Paper II** I, for the first time, found high concentrations in the cladoceran *Polyphemus*. Moeller et al. (2005) showed that MAA:s are taken up from ingested algae and that the tolerance for UVR increased 2.5-fold for UVR exposed MAA-rich copepods compared to unexposed, with low MAA. This can be compared to a 1.5-fold increase in tolerance for organisms that had accumulated carotenoids, suggesting that MAA:s are important as photoprotective compounds in copepods.

INTERACTION IN THREAT RESPONSES

The use of photoprotective compounds as protection from harmful UVR has been highlighted in several previous studies (see e.g. Rautio and Korhola, 2002, Hansson and Hylander, 2009a). In addition, zooplankton optimise their blend of photoprotective compounds according to prevailing threats in the surrounding environment (Hansson, 2004, Hansson and Hylander, 2009a). Also, the transparency regulator hypothesis (TRH) has gained support in several previous studies (Rose et al., 2012, Tiberti and Iacobuzio, 2013, Fischer et al., 2015). In **Paper I** I explore the TRH in a long-term field study in a clearwater lake with low predation pressure. In this paper I also investigate if pigmentation could

add further to the TRH by assessing the seasonal dynamics of photoprotective compounds in zooplankton at three depths along a depth gradient. I could not identify any differences in pigmentation among the different sampling depths, indicating that the zooplankton did not adjust their depth distribution according to their level of photoprotection (**Paper I**). Instead, I found indications for higher concentrations of photoprotective compounds during winter, when the UVR threat was at it lowest (Fig. 2 and 3 in **Paper I**). This finding suggests that the photoprotective compounds may provide other benefits than just photoprotection, such as providing metabolic benefits (Byron, 1981, Gorokhova et al., 2013). I did, however, find some evidence for the TRH with respect to the DVM of *Daphnia* where the strength of the DVM increased with increasing UVR intensity. The strength of the DVM of copepods was not associated to UVR intensity (Fig. 5 in **paper I**) although previous studies have shown that the daytime vertical position of copepods was related to UVR transparency (Fischer et al., 2015). This could potentially be explained by the fact that copepods seem to be less responsive to UVR than cladocerans (Leech and Williamson, 2000, Hansson, 2004). One explanation behind this difference in response may be that the two groups utilize two different strategies when it comes to the handling of these two threats. *Daphnia* show a stronger behavioural response while copepods may rely more on their photoprotective armour (Fig. 1).

INTERSPECIFIC DIFFERENCES IN RESPONSE TO UVR

Paper II explores the UVR response of five closely related zooplankton taxa (*Daphnia*, *Bosmina*, *Ceriodaphnia*, *Chydorus* and *Polyphemus*). By exposing zooplankton to UVR in a controlled laboratory environment I assessed their migratory response by manually tracking their position and quantifying their refuge demand. Refuge demand is defined as the integral of an organism's depth distribution from the start to the end of the experiment (Fig. 2). Consequently, a strong vertical migration downwards will result in a high refuge demand and a low response will result in a low refuge demand. Considerable interspecific differences in refuge demand were observed where *Daphnia* and *Bosmina* showed the strongest responses and *Chydorus* and *Polyphemus* the weakest (Fig. 2 in **paper II**). Analyses of the photoprotective compounds (i.e. melanin, carotenoids and MAA) from the two extremes (*Daphnia* and *Polyphemus*) revealed that *Polyphemus* had more than three times higher amounts of photoprotective compounds than *Daphnia* (Fig. 4 in **paper II**). Interestingly, and surprisingly, the amount of MAA was high in *Polyphemus* although, as previously mentioned, cladocerans are known to have very low amounts of MAA (Tartarotti et al., 2001, Persaud et al., 2007). The observed behaviours could be linked to the natural distribution and ecology of the two species. *Daphnia* is often found in open water where they can utilize depth as a refuge from UVR. *Polyphemus* on the other hand is often found in shallow waters (Hutchinson, 1967) where it forages close to the surface using polarized light (Odselius and Nilsson, 1983). Thus,

as refuge by downward migration is restricted in shallow water, accumulation of photoprotective pigmentation may be a more viable and adaptive option for *Polyphemus*.

TRACKING OF SMALL INDIVIDUAL ORGANISMS

Movement and behaviour are important features when studying the biology and ecology of an organism. The traditional way of studying movement and migrations of zooplankton involves quantification of abundances along a depth gradient. Although this method has proven very useful when studying DVM patterns in zooplankton there are still some questions that cannot be answered using this rather population focused method. More specifically, there are data sets on migration containing large variations in depth distribution within one species; see e.g. Stich and Lampert (1981) for a nice illustrative example. A key aspect of this is that individual organisms cause this variance in behaviour and in order to understand this variation, we are in need of individual based techniques, where we are able to follow individual organisms.

Tracking of larger animals such as mammals, birds and fish are now rather straight forward using well-established techniques and equipment such as radio- and global positioning (GPS) collars (Cagnacci et al., 2011, Mysterud et al., 2011), passive radio frequency identification (RFID) transponders (Brodersen et al., 2008, Chapman et al., 2011) or satellite telemetry (Godley et al., 2003). However, when it comes to the tracking of smaller organisms, such as zooplankton, the available equipment is most often too large and bulky. When tracking organisms to study their behaviour it is of great importance not to use equipment affecting the natural

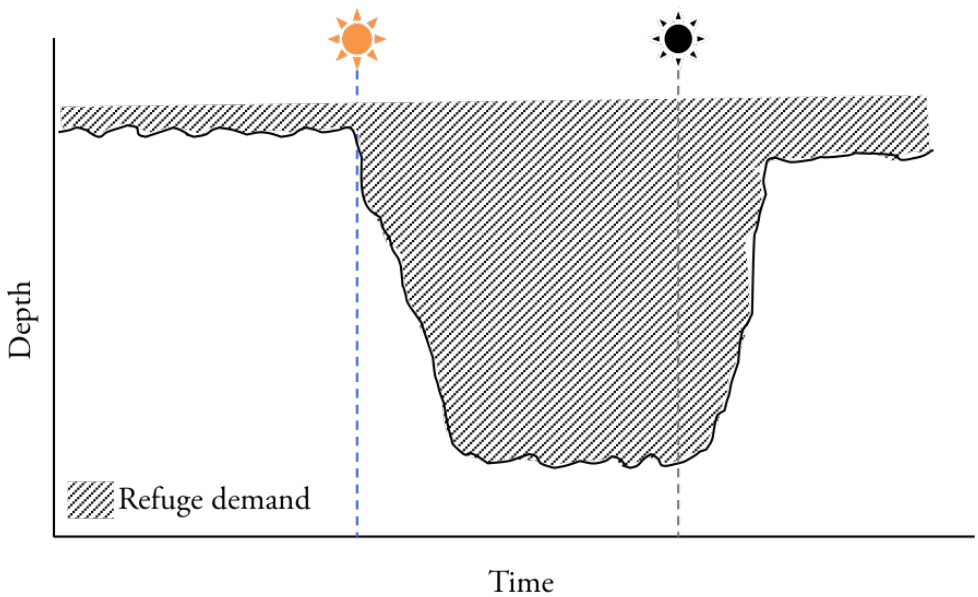

Fig. 2. Illustration of refuge defined as the organisms integrated vertical position (i.e. depth) over time. The two vertical lines indicate the switching on (left) and off (right) of the UVR threat.

behaviour, such as attaching too large and heavy devices on an organism. In **Paper III** I describe the development of a technique to label zooplankton (*Daphnia magna*) with fluorescent nanoparticles, so called Quantum dots *(Fig. 3, Box 1)*, based on a previous protocol by Lard et al. (2010). This technique was developed to facilitate studies on zooplankton individual behaviour and allows for simultaneous tracking of multiple individuals and was shown not to affect the behaviour of *Daphnia*. Quantum dots are available in a wide range of colours, which also allows for colour coding of organisms originating from e.g. different treatments. The system was also developed to allow for automated tracking which aimed at speeding up the tracking process compared to that of manual tracking (see e.g. **Paper II**).

When tracking organisms one can obtain very detailed information on the positions and from these positions one can later compute a vast array of variables. With the individual organism in focus it is necessary to take the environment in which the organism lives into consideration and also how the organisms move around in this environment. In **Paper III** I developed a system that is based on three-dimensional (3D) tracking. Although two-dimensional (2D) tracking approaches have proven very useful for land-based or benthic organisms these may not be appropriate when tracking organisms that fly or swim in a three-dimensional environment (Fig. 4). Bianco et al. (2013) showed that tracking *Daphnia magna* in 2D compared to 3D gave less information regarding the swimming path and led to an underestimation of the swimming speed of up to 25% compared to when using a 3D approach.

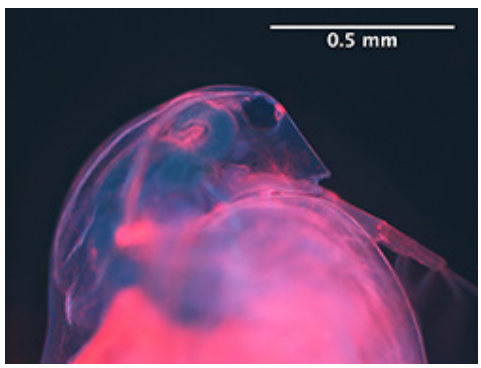

Fig. 3. *Daphnia magna* labelled with nanoparticles (quantum dots) fluorescent at 655 nm (red), picture from Ekvall et al. (2013), **Paper III**.

INDIVIDUAL VARIATION IN THREAT RESPONSE

Most individual organisms on our planet are unique in one sense or another, they do not all look or behave in the same way. In **Papers IV-VI** I further explore the responses of zooplankton to threat situations focusing on *Daphnia* as model organism. These studies were all conducted using the system and labelling method developed in **Paper III**.

Size and previous experiences

In **Paper IV** I explore the behaviour of adult and juvenile *Daphnia magna* that were either naïve or previously exposed to UVR, which I obtained by rearing them for several months either in the presence or absence of UVR. After the rearing period I then exposed the individuals to UVR to evaluate their behavioural response to the threat and also comparing this with morphological features such as individual size, previous experience (UVR/no UVR), eye size and pigmentation. Interestingly previously exposed *Daphnia* showed a more relaxed response upon UVR

Box 1. Quantum dots

Quantum dots (Qdots) are small (~10-20 nm in diameter), commercially available, nanocrystals made out of semiconductor material which have been used for a wide range of application because of their fluorescent properties and high photostability compared to conventional fluorophores (Chan and Nie, 1998), Fig. B1. Areas of use include *in-vivo* and *vitro* biomedial imaging (Ballou et al., 2007, Liu et al., 2012). In **paper III** we developed a method where we coat the Qdots with poly-L-lysine and attach them to the carapace of zooplankton. The behaviour of the zooplankton is then tracked using the fluorescence emitted by the Qdot upon excitation.

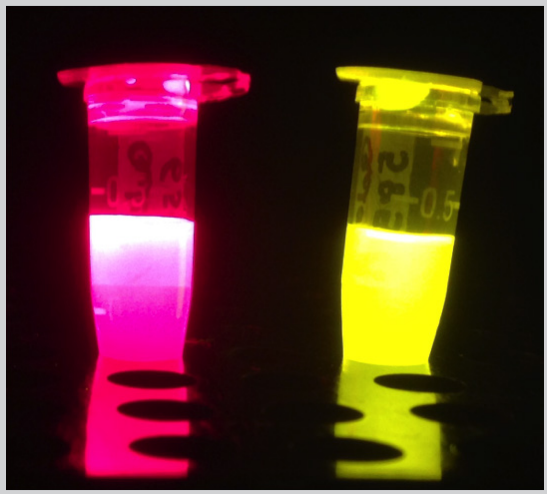

Fig B1. Tubes containing a suspension of quantum dots fluorescent at 655 nm (left) and 585 nm (right).

exposure. In **Paper I** I demonstrate evidence for size structured migration in both *Daphnia* and calanoid copepods (Fig. 6 in **paper I**), and this pattern was also seen in the study described in **Paper IV**, where smaller individuals had a lower capacity to respond behaviourally to UVR exposure compared to larger individuals. Small *Daphnia* have been shown to have lower migration amplitudes (Winder et al., 2004) and size structured migrations of zooplankton have previously been reported for both copepods (Tiberti and Barbieri, 2011) and *Daphnia* (Hansson and Hylander, 2009b). The lower capacity of smaller individuals to respond to UVR that was observed in **Paper IV** could offer an explanation to the observed phenomenon of size structured responses to UVR. Interestingly, in **Paper VI** I found that mothers (adult *D. magna*) were positioned higher in the water column compared to their daughters (i.e. younger individuals). This pattern deviates from the findings in **Papers I** and **IV** and remains puzzling and highlights the complexity of behavioural studies where multiple factors influence the observed behavioural outcome.

Comparing animals previously exposed to UVR revealed that they showed a lower response to UVR compared to naïve animals **(Paper IV**). Although the levels of photoprotective compounds could be a potential explanation for this

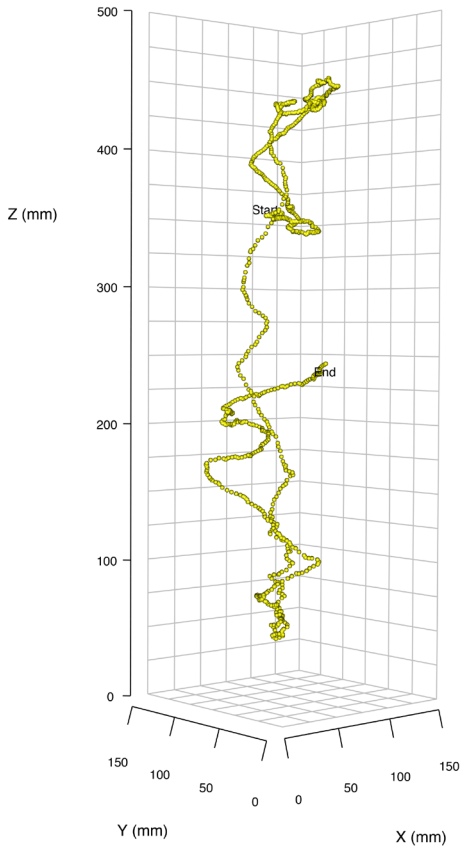

Fig. 4. Trajectory showing the vertical migration of a *Daphnia magna* in 3D when exposed to ultraviolet radiation..

observed behavioural difference (Rhode et al., 2001, Tollrian and Heibl, 2004), I found no difference in pigmentation between the populations. Interestingly, however, the eye-diameter of UVR exposed *Daphnia* was smaller compared to that of UVR naïve animals (Fig. 2 in **paper IV**). Whether or not the eye size affected the behaviour or if it was an effect of the radiation regime remains unclear, however, the reduced eye size is associated with the UVR treatment.

Conflicting threats

Conflicting threats from UVR and predation has previously been shown to induce morphological adaptations in zooplankton through changes in the composition of photoprotective compounds (Hylander et al., 2009). Hypotheses concerning DVM have, as mentioned above, highlighted predation (Lampert, 1989), UVR (Leech and Williamson, 2001) and later been compiled into a more comprehensive framework by Williamson and co-workers (2011), integrating both predation and UVR. In **Paper V** I explore the behavioural response of *Daphnia magna* and *Daphnia pulex* when presented to conflicting threats from UVR and predation. I here used either a fish (pelagic) predator or an invertebrate (benthic) predator. As mentioned earlier, the presence of a fish predator generally induces downward migration in zooplankton, while benthic invertebrate predators may induce reversed migrations where the prey favours surface waters during daytime and deeper waters during night time (e.g. Ohman et al., 1983). By presenting *Daphnia* to a UVR threat from above and a predation threat at the bottom (the invertebrate predator), I aimed to assess how *Daphnia* may trade off migration down towards the predation threat or staying higher up in the water column, but then being more exposed to UVR. I could not identify any statistically significant behavioural effects related to the presence of any of the predators, likely due to rather large variance among individuals, whereas UVR immediately induced a strong downward movement (Fig. 1 and 2 in **paper V**). Similar results was found in a field study by Tiberti and Iacobuzio (2013) and together these

results support the transparency regulator hypothesis (Williamson et al., 2011), highlighting a stronger response from UVR than from predation in clear water systems.

"Personality"

Consistent behavioural differences between individuals within and between contexts, also referred to as "personality" (Sih et al., 2004), have been shown to be important for the survival and dynamics of animal populations (Reaney and Backwell, 2007, Chapman et al., 2011). Behavioural differences allow for novel traits to become established and help species to adapt to new and more challenging conditions (Dall et al., 2004, Sih et al., 2004). Most studies regarding animal personality have focused on higher order organisms like mammals (Reale et al., 2000, Cavigelli and McClintock, 2003), birds (Bokony et al., 2012) and fish (Chapman et al., 2011, Hulthen et al., 2014), but invertebrates studies are scarce (Yli-Renko et al., 2015, Ahlgren et al., 2015). Although it may be more likely to find consistent behavioural differences in higher order organisms (vertebrates) there are several studies showing consistent behavioural types in invertebrates (Sih and Watters, 2005, Briffa and Greenaway, 2011, Ahlgren et al., 2015).

In **Paper VI** I address the question whether or not variation in the UVR response behaviour of *D. magna*, which is often considered as noise around a mean behaviour, could be caused by consistent behavioural differences between individuals (i.e. "personality"). Although *Daphnia* are clonal organisms, I found consistent behavioural differences among individuals with respect to their refuge demand and vertical distribution when exposed to UVR (Table 1 in **paper VI**). Activity in the form of swimming speed was repeatable before UVR exposure, but not during or after exposure to UVR. Altogether the results from **Paper VI** show that there are consistent behavioural differences among individual *Daphnia* and that they do not all just behave in the same way. To my knowledge, there is only one previous study investigating behavioural consistency in zooplankton and they showed individual differences in the consumption rate of marine copepods (Morozov et al., 2013). This indicates that behavioural consistency in zooplankton may be a widespread phenomenon and that variation in behaviour should, rather than be discarded as noise, be taken into consideration when evaluating behavioural data.

CONCLUSIONS AND FUTURE PERSPECTIVES

In conclusion I have here demonstrated that there are many factors influencing the threat response behaviour in zooplankton including interspecific differences (**Papers I** and **II**), size (**Papers I** and **IV**), previous experiences of threats (**Paper IV**) and that observed intraspecific variance linked to certain behaviours may be caused by consistent behavioural differences among individuals (**Paper VI**). The method developed in **Paper III** allows for detailed studies to be performed on a routine basis and can hopefully help to study some questions linked to behaviour of individuals that was previously not possible to study due to limitations in tracking techniques for smaller organisms. It may be so that predator effects take longer time to initiate

behavioural responses compared to more direct UVR effects, which could explain the lack of significant predator effects in **Paper V**. Possibly UVR is "easier" to respond to as the source of the threat is likely easier to determine in contrast to predator cues that may be diluted in the surrounding environment. Hence further studies with focus on predation likely need a higher degree of replication, as well as longer lasting experiments. Given the variability both with respect to inter- and intraspecific differences in UVR response (Fig. 1, **Paper II**) we need to keep these differences in mind when postulating new, more comprehensive theories explaining the behaviour of zooplankton exposed to everyday threats.

REFERENCES

AHLGREN, J., CHAPMAN, B. B., NILSSON, P. A. & BRÖNMARK, C. 2015. Individual boldness is linked to protective shell shape in aquatic snails. *Biology Letters,* 11.

ALONSO, C., ROCCO, V., BARRIGA, J. P., BATTINI, M. A. & ZAGARESE, H. 2004. Surface avoidance by freshwater zooplankton: Field evidence on the role of ultraviolet radiation. *Limnology and Oceanography,* 49**,** 225-232.

BALLOU, B., ERNST, L. A., ANDREKO, S., HARPER, T., FITZPATRICK, J. A. J., WAGGONER, A. S. & BRUCHEZ, M. P. 2007. Sentinel lymph node imaging using quantum dots in mouse tumor models. *Bioconjugate Chemistry,* 18**,** 389-396.

BANCROFT, B. A., BAKER, N. J. & BLAUSTEIN, A. R. 2007. Effects of UVB radiation on marine and freshwater organisms: a synthesis through meta-analysis. *Ecology Letters,* 10**,** 332-345.

BIANCO, G., EKVALL, M. T., BÄCKMAN, J. & HANSSON, L. A. 2013. Plankton 3D tracking: the importance of camera calibration in stereo computer vision systems. *Limnology and Oceanography-Methods,* 11**,** 278-286.

BLOIS, M. S. 1978. The melanins: their synthesis and structure. *Photochemical and Photobiological Reviews,* 3**,** 115-134.

BOKONY, V., KULCSAR, A., TOTH, Z. & LIKER, A. 2012. Personality Traits and Behavioral Syndromes in Differently Urbanized Populations of House Sparrows (*Passer domesticus*). *Plos One,* 7.

BOSCH, H. F. & TAYLOR, W. R. 1973. Diurnal vertical migration of an estuarine cladoceran, *Podon polyphemoides*, in Chesapeake bay. *Marine Biology,* 19**,** 172-181.

BREHM, V. 1938. Die Rotfarbung von Hochgebirgssee-Organismen. *Biol. Rev. Cambridge,* 13**,** pp. 307-318.

BRIFFA, M. & GREENAWAY, J. 2011. High In Situ Repeatability of Behaviour Indicates Animal Personality in the Beadlet Anemone *Actinia equina* (Cnidaria). *Plos One,* 6.

BRODERSEN, J., NILSSON, P. A., HANSSON, L. A., SKOV, C. & BRÖNMARK, C. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology,* 89**,** 1195-1200.

BROOKS, J. L. & DODSON, S. I. 1965. Predation body size and composition of plankton. *Science,* 150**,** 28-35.

BRÖNMARK, C. & HANSSON, L.-A. 2005. *The Biology of Lakes and Ponds,* Oxford, Oxford University Press.

BRÖNMARK, C. & HANSSON, L. A. 2000. Chemical communication in aquatic systems: an introduction. *Oikos,* 88**,** 103-109.

BYRON, E. R. 1981. Metabolic stimulation by light in a pigmented fresh-water invertebrate. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences,* 78**,** 1765-1767.

CAGNACCI, F., FOCARDI, S., HEURICH, M., STACHE, A., HEWISON, A. J. M., MORELLET, N., KJELLANDER, P., LINNELL, J. D. C., MYSTERUD, A., NETELER, M., DELUCCHI, L., OSSI, F. & URBANO, F. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. *Oikos,* 120**,** 1790-1802.

CAVIGELLI, S. A. & MCCLINTOCK, M. K. 2003. Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *Proceedings of the National Academy of Sciences of the United States of America,* 100**,** 16131-16136.

CHAN, W. C. W. & NIE, S. M. 1998. Quantum dot bioconjugates for ultrasensitive nonisotopic detection. *Science,* 281**,** 2016-2018.

CHAPMAN, B. B., HULTHEN, K., BLOMQVIST, D. R., HANSSON, L. A., NILSSON, J. Å., BRODERSEN, J., NILSSON, P. A., SKOV, C. & BRÖNMARK, C. 2011. To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters,* 14**,** 871-876.

CZECZUGA, B. 1975. Carotenoids in *Eudaptomus amblyodon* Marenz (Crustacea) during ontogenetic development. *Comparative Biochemistry and Physiology,* 50A**,** 665-668.

DALL, S. R. X., HOUSTON, A. I. & MCNAMARA, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters,* 7**,** 734-739.

DODSON, S. 1990. Predicting diel vertical migration of zooplankton. *Limnology and Oceanography,* 35**,** 1195-1200.

EKVALL, M. T., BIANCO, G., LINSE, S., LINKE, H., BÄCKMAN, J. & HANSSON, L. A. 2013. Three-Dimensional Tracking of Small Aquatic Organisms Using Fluorescent Nanoparticles. *Plos One,* 8.

ENGEL, K., SCHREDER, T. & TOLLRIAN, R. 2014. Morphological defences of invasive *Daphnia lumholtzi* protect against vertebrate and invertebrate predators. *Journal of Plankton Research,* 36**,** 1140-1145.

FISCHER, J. M., OLSON, M. H., THEODORE, N., WILLIAMSON, C. E., ROSE, K. C. & HWANG, J. 2015. Diel vertical migration of copepods in mountain lakes: The changing role of ultraviolet radiation across a transparency gradient. *Limnology and Oceanography,* 60**,** 252-262.

GILCHRIST, B. M. & GREEN, J. 1962. Carotenoid pigments in *Rotifera*. *Nature,* 195**,** 905-907.

GODLEY, B. J., LIMA, E., ÅKESSON, S., BRODERICK, A. C., GLEN, F., GODFREY, M. H., LUSCHI, P. & HAYS, G. C. 2003. Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. *Marine Ecology Progress Series,* 253**,** 279-288.

GOODWIN, T. W. 1986. Metabolim, nutrition, and function of carotenoids. *Annual Review of Nutrition,* 6**,** 273-297.

GOROKHOVA, E., LEHTINIEMI, M. & MOTWANI, N. H. 2013. Trade-Offs between Predation Risk and Growth Benefits in the Copepod *Eurytemora affinis* with Contrasting Pigmentation. *Plos One,* 8.

HAIRSTON, N. G. 1976. Photoprotection by carotenoid pigments in copepod *Diaptomus nevadensis*. *Proceedings of the National Academy of Sciences of the United States of America,* 73**,** 971-974.

HAIRSTON, N. G. 1979. Adaptive significance of color polymorphism in 2 species of *Diaptomus* (Copepoda). *Limnology and Oceanography,* 24**,** 15-37.

HANSSON, L.-A. & ÅKESSON, S. 2014. *Animal Movement Across Scales*, Oxford University Press.

HANSSON, L. A. 2004. Plasticity in pigmentation induced by conflicting threats from predation and UV radiation. *Ecology,* 85**,** 1005-1016.

HANSSON, L. A. & HYLANDER, S. 2009a. Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photochemical & Photobiological Sciences,* 8**,** 1266-1275.

HANSSON, L. A. & HYLANDER, S. 2009b. Size-structured risk assessments govern *Daphnia* migration. *Proceedings of the Royal Society B-Biological Sciences,* 276**,** 331-336.

HANSSON, L. A., HYLANDER, S. & SOMMARUGA, R. 2007. Escape from UV threats in zooplankton: A cocktail of behavior and protective pigmentation. *Ecology,* 88**,** 1932-1939.

HAYS, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia,* 503**,** 163-170.

HEBERT, P. D. N. & EMERY, C. J. 1990. The adaptive significance of cuticular pigmentation in *Daphnia*. *Functional Ecology,* 4**,** 703-710.

HESSEN, D. O. 1994. *Daphnia* responses to UV-light. *Ergebnisse der Limnologie,* 43**,** 185-195.

HESSEN, D. O. 1996. Competitive trade-off strategies in Arctic *Daphnia* linked to melanism and UV-B stress. *Polar Biology,* 16**,** 573-579.

HEUSCHELE, J. & SELANDER, E. 2014. The chemical ecology of copepods. *Journal of Plankton Research,* 36**,** 895-913.

HOLLILAND, P. B., AHLBECK, I., WESTLUND, E. & HANSSON, S. 2012. Ontogenetic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia* spp. in a coastal area of the northern Baltic proper. *Journal of Plankton Research,* 34**,** 298-307.

HOPCRAFT, J. G. C., MORALES, J. M., BEYER, H. L., BORNER, M., MWANGOMO, E., SINCLAIR, A. R. E., OLFF, H. & HAYDON, D. T. 2014. Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs,* 84**,** 355-372.

HUEBNER, J. D., YOUNG, D. L. W., LOADMAN, N. L., LENTZ, V. J. & WIEGAND, M. D. 2006. Age-dependent survival, reproduction and photorepair activity in *Daphnia magna* (Straus, 1820) after exposure to artificial ultraviolet radiation. *Photochemistry and Photobiology,* 82**,** 1656-1661.

HULTHEN, K., CHAPMAN, B. B., NILSSON, P. A., HOLLANDER, J. & BRONMARK, C. 2014. Express yourself: bold individuals induce enhanced morphological defences. *Proceedings of the Royal Society B-Biological Sciences,* 281.

HUTCHINSON, G. E. 1967. *A Treatise on Limnology - Introduction to Lake Biology and the Limnoplankton,* New York, John Wiley & Sons, inc.

HYLANDER, S., LARSSON, N. & HANSSON, L. A. 2009. Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnology and Oceanography,* 54**,** 483-491.

KARENTZ, D. & BOSCH, I. 2001. Influence of ozone-related increases in ultraviolet radiation on antarctic marine organisms. *American Zoologist,* 41**,** 3-16.

KESSLER, K., LOCKWOOD, R. S., WILLIAMSON, C. E. & SAROS, J. E. 2008. Vertical distribution of zooplankton in subalpine and alpine lakes: Ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. *Limnology and Oceanography,* 53**,** 2374-2382.

KIRK, J. T. O. 1994. Optics of UV-B radiation in natural waters. *Ergebnisse der Limnologie,* 43**,** 1-16.

LAMPERT, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology,* 3**,** 21-27.

LARD, M., BÄCKMAN, J., YAKOVLEVA, M., DANIELSSON, B. & HANSSON, L. A. 2010. Tracking the Small with the Smallest - Using Nanotechnology in Tracking Zooplankton. *Plos One,* 5.

LEECH, D. M. & WILLIAMSON, C. E. 2000. Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecological Applications,* 10**,** 1530-1540.

LEECH, D. M. & WILLIAMSON, C. E. 2001. In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnology and Oceanography,* 46**,** 416-420.

LIU, Y., ZHOU, M., LUO, D., WANG, L. J., HONG, Y. K., YANG, Y. P. & SHA, Y. L. 2012. Bacteria-mediated in vivo delivery of quantum dots into solid tumor. *Biochemical and Biophysical Research Communications,* 425**,** 769-774.

LUECKE, C. & O'BRIEN, W. J. 1981. Photo-Toxicity and Fish Predation - Selective Factors in Color Morphs in Heteroscope. *Limnology and Oceanography,* 26**,** 454-460.

MINTO, W. J., ARCIFA, M. S. & PERTICARRARI, A. 2010. Experiments on the influence of *Chaoborus brasiliensis* Theobald, 1901 Diptera: Chaoboridae) on the diel vertical migration of microcrustaceans from Lake Monte Alegre, Brazil. *Brazilian Journal of Biology,* 70**,** 25-35.

MOELLER, R. E., GILROY, S., WILLIAMSON, C. E., GRAD, G. & SOMMARUGA, R. 2005. Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. *Limnology and Oceanography,* 50**,** 427-439.

MOROZOV, A., PASTERNAK, A. F. & ARASHKEVICH, E. G. 2013. Revisiting the Role of Individual Variability in Population Persistence and Stability. *Plos One,* 8.

MORRIS, D. P., ZAGARESE, H., WILLIAMSON, C. E., BALSEIRO, E. G., HARGREAVES, B. R., MODENUTTI, B., MOELLER, R. & QUEIMALINOS, C. 1995. The attentuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography,* 40**,** 1381-1391.

MYSTERUD, A., LOE, L. E., ZIMMERMANN, B., BISCHOF, R., VEIBERG, V. & MEISINGSET, E. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? *Oikos,* 120**,** 1817-1825.

ODSELIUS, R. & NILSSON, D. E. 1983. Regionally different ommatidial structure in the compound eye of the water-flea *Polyphemus* (Cladocera, Crustacea). *Proceedings of the Royal Society Series B-Biological Sciences,* 217**,** 177-189.

OHMAN, M. D., FROST, B. W. & COHEN, E. B. 1983. Reverse diel vertical migration - an escape from invertebrate predators. *Science,* 220**,** 1404-1407.

PEACOR, S. D., PANGLE, K. L., SCHIESARI, L. & WERNER, E. E. 2012. Scaling-up anti-predator phenotypic responses of prey: impacts over multiple generations in a complex aquatic community. *Proceedings of the Royal Society B-Biological Sciences,* 279**,** 122-128.

PERSAUD, A. D., MOELLER, R. E., WILLIAMSON, C. E. & BURNS, C. W. 2007. Photoprotective compounds in weakly and strongly pigmented copepods and co-occurring cladocerans. *Freshwater Biology,* 52**,** 2121-2133.

RAUTIO, M. & KORHOLA, A. 2002. UV-induced pigmentation in subarctic Daphnia. *Limnology and Oceanography,* 47**,** 295-299.

RAUTIO, M. & TARTAROTTI, B. 2010. UV radiation and freshwater zooplankton: damage, protection and recovery. *Freshwater Reviews,* 3**,** 105-131.

REALE, D., GALLANT, B. Y., LEBLANC, M. & FESTA-BIANCHET, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour,* 60**,** 589-597.

REANEY, L. T. & BACKWELL, P. R. Y. 2007. Risk-taking behavior predicts aggression and mating success in a fiddler crab. *Behavioral Ecology,* 18**,** 521-525.

RHODE, S. C., PAWLOWSKI, M. & TOLLRIAN, R. 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature,* 412**,** 69-72.

RIPPLE, W. J. & BESCHTA, R. L. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *Bioscience,* 54**,** 755-766.

ROSE, K. C., WILLIAMSON, C. E., FISCHER, J. M., CONNELLY, S. J., OLSON, M., TUCKER, A. J. & NOE, D. A. 2012. The role of ultraviolet radiation and fish in regulating the vertical distribution of *Daphnia*. *Limnology and Oceanography,* 57**,** 1867-1876.

ROSE, K. C., WILLIAMSON, C. E., SAROS, J. E., SOMMARUGA, R. & FISCHER, J. M. 2009. Differences in UV transparency and thermal structure between alpine and subalpine lakes: implications for organisms. *Photochemical & Photobiological Sciences,* 8**,** 1244-1256.

SCULLY, N. M. & LEAN, D. R. S. 1994. The attenuation of ultraviolet radiation in temperate lakes. *Ergebnisse der Limnologie,* 43**,** 135-144.

SIH, A., BELL, A. & JOHNSON, J. C. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution,* 19**,** 372-378.

SIH, A. & WATTERS, J. V. 2005. The mix matters: behavioural types and group dynamics in water striders. *Behaviour,* 142**,** 1417-1431.

SINHA, R. P., SINGH, S. P. & HADER, D. P. 2007. Database on mycosporines and mycosporine-like amino acids (MAAs) in fungi, cyanobacteria, macroalgae, phytoplankton and animals. *Journal of Photochemistry and Photobiology B-Biology,* 89**,** 29-35.

SNOEIJS, P. & HAUBNER, N. 2014. Astaxanthin dynamics in Baltic Sea mesozooplankton communities. *Journal of Sea Research,* 85**,** 131-143.

SOUZA, M. S., HANSSON, L. A., HYLANDER, S., MODENUTTI, B. & BALSEIRO, E. 2012. Rapid Enzymatic Response to Compensate UV Radiation in Copepods. *Plos One,* 7.

STICH, H. B. & LAMPERT, W. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature,* 293**,** 396-398.

STORZ, U. C. & PAUL, R. J. 1998. Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology,* 183**,** 709-717.

TARTAROTTI, B., LAURION, I. & SOMMARUGA, R. 2001. Large variability in the concentration of mycosporine-like amino acids among zooplankton from lakes located across an altitude gradient. *Limnology and Oceanography,* 46**,** 1546-1552.

TIBERTI, R. & BARBIERI, M. 2011. Evidences of zooplankton vertical migration in stocked and never-stocked alpine lakes in Gran Paradiso National Park (Italy). *Oceanological and Hydrobiological Studies,* 40**,** 36-42.

TIBERTI, R. & IACOBUZIO, R. 2013. Does the fish presence influence the diurnal vertical distribution of zooplankton in high transparency lakes? *Hydrobiologia,* 709**,** 27-39.

TOLLRIAN, R. & HEIBL, C. 2004. Phenotypic plasticity in pigmentation in *Daphnia* induced by UV radiation and fish kairomones. *Functional Ecology,* 18**,** 497-502.

WILLIAMSON, C. E. 1995. What role does UV-B radiation play in fresh-water ecosystems. *Limnology and Oceanography,* 40**,** 386-392.

WILLIAMSON, C. E., FISCHER, J. M., BOLLENS, S. M., OVERHOLT, E. P. & BRECKENRIDGE, J. K. 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnology and Oceanography,* 56**,** 1603-1623.

WILLIAMSON, C. E., OLSON, O. G., LOTT, S. E., WALKER, N. D., ENGSTROM, D. R. & HARGREAVES, B. R. 2001. Ultraviolet radiation and zooplankton community structure following deglaciation in Glacier Bay, Alaska. *Ecology,* 82**,** 1748-1760.

WILLIAMSON, C. E. & ROSE, K. C. 2010. When UV Meets Fresh Water. *Science,* 329**,** 637-639.

WINDER, M., SPAAK, P. & MOOIJ, W. M. 2004. Trade-offs in *Daphnia* habitat selection. *Ecology,* 85**,** 2027-2036.

YLI-RENKO, M., VESAKOSKI, O. & PETTAY, J. E. 2015. Personality- Dependent Survival in the Marine Isopod *Idotea balthica*. *Ethology,* 121**,** 135-143.

ZAGARESE, H. E., WILLIAMSON, C. E., MISLIVETS, M. & ORR, P. 1994. The vulnerability of *Daphnia* to UV-B radiation in the Northeastern United States. *Ergebnisse der Limnologie,* 0**,** 207-216.

ZARET, T. M. & SUFFERN, J. S. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography,* 21**,** 804-813.

Acknowledgement

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

- The Swedish Research Council (VR)

- The Centre for Animal Movement Research (CAnMove) through the Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund University

- Helge Ax:son Johnsons Foundation

- The Royal Physiographic Society in Lund

- Department of Biology/Aquatic Ecology Unit, Lund University