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Zooplankton responses to multiple threats within and across generations

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List of papers

I. Sha, Y., Zhang, H., Lee, M., Björnerås, C., Škerlep, M., Gollnisch, R., Herzog, S. D., Ugge, G. E., Vinterstare, J., Hu, N., Pärssinen, V., Hulthén, K., Nilsson, P. A., Rengefors, K., Brönmark, C., Langerhans, R. B., Hansson, L.-A. 2020. Diel vertical migration of copepods and its environmental drivers in subtropical Bahamian blue holes. Aquatic Ecology. https://doi.org/10.1007/s10452-020-09807-4.

II. Ekvall, M. T.[1], Sha, Y.[1], Palmér, T., Bianco, G., Bäckman, J., Åström, K., Hansson, L.-A. 2020. Behavioural responses to co-occurring threats of predation and ultraviolet radiation in *Daphnia*. Freshwater Biology 65: 1509-1517. [1]Equal contributions.

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Zooplankton responses to multiple threats within and across generations

Yongcui Sha

LUND UNIVERSITY

DOCTORAL DISSERTATION

by due permission of the Faculty of Science, Lund University, Sweden.
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Faculty opponent
Dr. Steven Declerck,

Netherlands Institute of Ecology, NIOO-KNAW, The Netherlands

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Abstract

In their natural environments, organisms are unlikely to be distributed randomly but instead they are constantly faced with multiple and variable threats. In order to maximise survival, they need to be able to perceive the present threat level and respond accordingly. In aquatic ecosystems, two common threats for crustacean zooplankton are predation and ultraviolet radiation (UVR). Despite the growing recognition that zooplankton can plastically respond to predation and UVR within a single generation, little is known on how they evolutionarily cope with these simultaneously occurring multiple threats over generations. In this thesis, I investigate the threat responses in zooplankton when exposed to multiple threats from predation and UVR based on short-term (within a single generation) and multigenerational exposure experiments.

Alteration in behavioural traits is generally the first reaction in zooplankton to changed conditions, which allows them to escape from the threats instantly after exposure. One example of a common behavioural response in zooplankton is diel vertical migration (DVM), where they spend the day in deep, dark waters and migrate up to surface waters at night. I found that low-latitude copepods in Bahamian blue holes exhibited DVM to reduce predation risk from visually hunting fish, whereas no response was found to lake-specific differences in UVR transparency. Moreover, copepods also follow their food resources, so that they stay at the depth with rich food where predation risk and UVR may decrease to a negligible level. When exposed to conflicting threats from UVR and predation from either moving pelagic or benthic predators, *Daphnia* are able to make different risk assessments and thereby alter their behaviour in accordance with the actual threat level. I show that two *Daphnia* species respond strongly to UVR, whereas only the large prey species *D. magna* express a predator avoidance behaviour.

In addition to alterations in behaviour, *D. magna* can also change its body size and life-history to deal with multiple threats from predation and UVR. I demonstrate that *D. magna* become smaller through generations in response to fish predation, whereas they change their behaviour to avoid UVR. Individuals who have previously experienced UVR respond more relaxed when exposed to such radiation again. These individuals also produce less offspring during the first generation after exposure but the number of offspring then gradually increases through generations. Therefore, *D. magna* adopt divergent strategies over generations and become adapted to the local environmental conditions after about three generations. Exposure to UVR can induce plastic phenotypic changes in *D. magna* including alterations in behaviour and life-history shifts. However, such transgenerational effects may be modified by the evolutionary history of stress that lead to different plastic responses to UVR across generations.

Key words
Predation, ultraviolet radiation, *Daphnia*, copepods, plasticity, maternal effects, adaptation, diel vertical migration

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Yongcui Sha

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锲而舍之，朽木不折。锲而不舍，金石可镂。---苟况

Nothing happens if you stop halfway, however with perseverance,
even the most difficult things can be done. ---Xun Kuang

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List of papers

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I. Sha, Y., Zhang, H., Lee, M., Björnerås, C., Škerlep, M., Gollnisch, R., Herzog, S. D., Ugge, G. E., Vinterstare, J., Hu, N., Pärssinen, V., Hulthén, K., Nilsson, P. A., Rengefors, K., Brönmark, C., Langerhans, R. B., Hansson, L.-A. 2020. Diel vertical migration of copepods and its environmental drivers in subtropical Bahamian blue holes. Aquatic Ecology. https://doi.org/10.1007/s10452-020-09807-4.

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Author Contributions

I.   YS, HZ, ML and LAH conceived and led the study. YS, HZ, ML, RBL, LAH, CaB, MŠ, RG and SDH conducted the field work with help from GEU, JV, NH, VP, KH, PAN, KR and ChB. All authors have been actively involved in planning the study and provided logistic aid and guidance both during the research expedition and data analysis process. YS conducted the data analyses with help from RBL and LAH. YS wrote the first version of the manuscript with main contributions from LAH, RBL, ChB, KH, PAN and KR. All authors commented and provided valuable input on all versions of the manuscript.

II.   MTE, GB and LAH designed the experiment. GB and JB assembled the video system. YS conducted the experiment with help from MTE and LAH. TP and KÅ developed the tracking software. YS analysed the tracking data with help from MTE and GB. MTE and LAH wrote the first version of the manuscript. YS revised and finalized the manuscript with main contributions from MTE and LAH.

III.   YS, SVMT and LAH conceived and designed the study. YS and SVMT conducted the experiment. YS wrote the manuscript and SVMT and LAH provided comments.

IV.   YS and LAH conceived and designed the study. YS conducted the experiment. YS wrote the manuscript. LAH provided comments on the manuscript.

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Abstract

In their natural environments, organisms are unlikely to be distributed randomly but instead they are constantly faced with multiple and variable threats. In order to maximise survival, they need to be able to perceive the present threat level and respond accordingly. In aquatic ecosystems, two common threats for crustacean zooplankton are predation and ultraviolet radiation (UVR). Despite the growing recognition that zooplankton can plastically respond to predation and UVR within a single generation, little is known on how they evolutionarily cope with these simultaneously occurring multiple threats over generations. In this thesis, I investigate the threat responses in zooplankton when exposed to multiple threats from predation and UVR based on short-term (within a single generation) and multigenerational exposure experiments.

Alteration in behavioural traits is generally the first reaction in zooplankton to changed conditions, which allows them to escape from the threats instantly after exposure. One example of a common behavioural response in zooplankton is diel vertical migration (DVM), where they spend the day in deep, dark waters and migrate up to surface waters at night. I found that low-latitude copepods in Bahamian blue holes exhibited DVM to reduce predation risk from visually hunting fish, whereas no response was found to lake-specific differences in UVR transparency. Moreover, copepods also follow their food resources, so that they stay at the depth with rich food where predation risk and UVR may decrease to a negligible level. When exposed to conflicting threats from UVR and predation from either moving pelagic or benthic predators, *Daphnia* are able to make different risk assessments and thereby alter their behaviour in accordance with the actual threat level. I show that two *Daphnia* species respond strongly to UVR, whereas only the large prey species *D. magna* express a predator avoidance behaviour.

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Populärvetenskaplig sammanfattning

Vardagslivets utmaningar är inte lätta att hantera varken för oss människor eller för andra organismer. Även små, ryggradslösa djur, såsom djurplankton i våra sjöar och hav, utsätts ständigt för risken att jagas och ätas av fisk och andra rovdjur eller att utsättas för höga doser av skadlig ultraviolett strålning från solen. För att överleva i en sådan utmanande situation måste djurplanktonen kunna uppfatta den aktuella hotnivån och på ett relevant sätt svara med att skydda sig. Trots att man under senare år börjat förstå att även små, oansenliga djur kan uppvisa en palett av försvar för att hantera dessa hot under sin egen livstid, är det lite känt hur de svarar på hot över längre tid, till exempel över generationsgränser. I denna avhandling undersöker jag hur djurplankton hanterar två naturligt förekommande hot, nämligen predation, d.v.s. någon försöker äta upp dem, och ultraviolett strålning, såväl inom en generation som mellan generationer.

Hos bytesdjur, t.ex. många djurplanktonarter, är den första reaktionen på ett hot att försöka fly från hotet mot en säkrare plats. Ett systematiskt sätt för dem att fly från såväl rovdjur som skadlig solstrålning är att dygnsvandra genom att under dagen gömma sig nere vid bottnen där det är mörkt och sedan under dygnets mörka timmar röra sig upp till ytvatten där det finns mer mat. I mina avhandling visar jag att en typ av djurplankton (copepoder) företar sådana dygnsvandringar också i sjöar nära ekvatorn där den ultravioletta strålningen är stark och relativt jämn under hela året. Emellertid visade det sig att den ultravioletta strålningen från solen inte nämnvärt påverkade dygnsvandringen, sannolikt för att djurplanktonen redan för många generationer sedan investerat i pigment som skyddar mot den skadliga ultravioletta strålningen. Istället visade det sig att det främst är fiskpredationen som bestämmer hur djupt och konsekvent de vandrar. Dessutom påverkades vandringen också av var maten finns, så att djurplanktonen ibland förblir på djupt vatten om där finns tillräckligt med mat.

I en av mina studier utsattes en annan grupp av djurplankton, *Daphnia*, för hot från ultraviolett strålning i kombination med antingen predation från frisimmande fisk eller från bottenlevande rovinsekter (sländlarver). Det visade sig att *Daphnia* är kapabel att identifiera vilken typ av rovdjur det är och dessutom göra olika riskbedömningar och därigenom ändra sitt beteende i enlighet med den faktiska hotnivån och varifrån hotet kommer. Jag visar att båda de studerade *Daphnia*-arterna reagerar starkt på ultraviolett strålning, men endast den stora *D. magna* justerar sitt beteende som svar på fisk, medan den mindre arten, *Daphnia pulex*, inte reagerar nämnvärt på predatorer, sannolikt för att dess ringa storlek gör att den delvis undkommer predatorernas sökande.

Förutom förändringar i beteende kan *D. magna* också ändra sin kroppsstorlek och livshistoria för att hantera flera hot från predation och ultraviolett strålning. Jag visar att *D. magna* får en mindre storlek över generationer som svar på fiskpredation, medan de ändrar sitt beteende för att undvika ultraviolett strålning. Individer som tidigare har upplevt ultraviolett strålning svarar lite mer avslappnat när de återigen utsätts för sådan strålning, men föder också färre barn under den första generationen efter exponeringen. Emellertid ökar antalet ungar sedan gradvis över kommande generationer, d.v.s. de "vänjer sig" vid de nya förhållandena. Man kan därmed säga att *D. magna* har olika strategier över generationer och anpassar sig så småningom till de lokala miljöförhållandena efter ungefär tre generationer, vilket motsvarar mellan 1 och 2 månader. Detta betyder att exponering för ett eller flera hot kan sätta igång plastiska förändringar, såsom förändringar i beteende och i livshistoria, inte bara hos en individ, utan förändringen kan i vissa fall följa med till nästa generation,. Sådana trans-generationella effekter möjliggör en snabb anpassning till olika lokala miljöer, t.ex. olika nivå på hoten från predatorer och ultraviolett strålning, och kan vara en del av förklaringen till att dessa små djur har en nära nog global utbredning och dessutom ofta är mycket framgångsrika.

Introduction

Even for the most advanced organisms on Earth, human beings, life is always difficult with an immense stream of challenges from the surroundings, and not to mention the small aquatic prey that are constantly faced with multiple, simultaneously occurring threats in their natural environments. To be, or not to be is the question that they have to answer in order to maintain their fitness and thereby survive and persist in a rapidly changing environment. When faced with an environmental threat, the common response for organisms is generally a change in behaviour, i.e. to move or migrate away from the threat. In natural ecosystems, many animals, from the large wildebeest on the African savanna to the millimetre-sized crustacean zooplankton, move or migrate in response to different types of threats, such as predation and ultraviolet radiation (UVR) (Hansson and Åkesson 2014, Hopcraft et al. 2014). However, if migration is not an option, an organism will have to handle the set of threats present in the local environment through phenotypic plasticity, or selection that eventually leads to genetic adaptation.

Phenotypic plasticity describes the ability of a genotype to produce a range of phenotypes under different environmental conditions (Pigliucci 2001). Such plastic phenotypic changes often build up within a generation, i.e. within-generation plasticity, where individuals rapidly adjust their behaviour, morphology, or life-history traits in response to the current environmental threats (Stibor 1992, Boersma et al. 1998, Rhode et al. 2001). Within-generation plasticity can therefore enable organisms to buffer against negative impacts of their immediate environment. However, recent work has shown that phenotypic changes induced by environmental threats can be carried over across generations, so that an organism's phenotype is influenced by the experiences or actions of previous generations, most typically by its mother (Agrawal et al. 1999, Storm and Lima 2010, Bestion et al. 2014). For example, if a parent is exposed to predators, predator-induced defences in morphology may be expressed also in the offspring despite they have not themselves been exposed to predation (Agrawal et al. 1999). This phenomenon of mothers passing along information about their environment or condition to their offspring is known as maternal effects (Mousseau and Fox 1998), although these effects may persist over multiple offspring generations, i.e. environments experienced by grandparents or even earlier generations can shape the expression of traits in their descendants (Hafer et al. 2011, Walsh et al. 2014, Walsh et al. 2015, Tariel et al. 2020). This form of plasticity across generations is known as

transgenerational plasticity (TGP), which may be thought of as a specific type of maternal effects (Salinas and Munch 2012), where previous generations prime their offspring for future conditions and potentially buy time for slower genetic adaptation to catch up in the longer term (Chevin et al. 2010, Bonduriansky et al. 2012) (See Box 1 for glossary).

Box 1. Glossary

Phenotypic plasticity: the ability of a genotype to produce a range of phenotypes under different environmental conditions.

Within-generation plasticity: plastic phenotypic changes arise in response to the direct perception of environmental cues within the lifetime of an individual, synonymous with phenotypic plasticity.

Maternal effects: the phenotype of the offspring is influenced by the phenotype of its mother or the maternal environment independently of the direct effect of transmitted genes from its mother.

Transgenerational plasticity (TGP): a specific type of maternal effects that phenotypic plasticity spans across generations and occurs when environment or condition experienced by previous generations influences the phenotypic expression of their offspring.

Genetic adaptation: organisms evolutionarily adapt to the changed environment over generations with a shifting genetic composition of populations due to natural selection.

Predation is one of the most common and forceful threats present in natural ecosystems that can affect prey organisms through both direct consumption and non-consumptive effects (Lima 1998, Creel and Christianson 2008). Ultraviolet radiation (UVR) is another ubiquitous environmental threat biologically damaging to both terrestrial and aquatic organisms, such as algae, zooplankton and fish (Rautio and Tartarotti 2010). To handle these threats, organisms have to rapidly evolve or respond plastically with suites of traits by modifying their behaviour, morphology or life-history traits (Tollrian and Harvell 1999). Although such plastic responses have been widely studied in previous studies (Hansson and Hylander 2009a, Ferrari et al. 2010), a majority of them have focused on investigating single threats in isolation and typically also quantified trait responses based on short-term or within-generational experiments. Therefore, our understanding on how organisms cope with multiple, simultaneously occurring threats remains elusive, and also it is difficult to predict the role of phenotypic plasticity, including transgenerational plasticity, in promoting organisms to adapt to these multiple threats over generations.

Cladocerans together with copepods and rotifers are three major zooplankton groups, which are widely distributed in nature and can be found in most water bodies on Earth. Despite their small size, zooplankton occupy a uniquely significant position in the aquatic food webs, linking primary producers, such as phytoplankton, and higher consumers. Due to their central position in food webs, short generation times and unique life cycle (Box 2), cladocerans of the genus *Daphnia* are frequently used as a model organism for ecological and evolutionary research, which provide opportunities to study local adaptation and micro-evolution under rapidly changing environments (Lampert 2006, Miner et al. 2012).

Box 2. *Daphnia* life cycle

The cladoceran *Daphnia* reproduce by cyclical parthenogenesis, including asexual reproduction under favorable conditions and sexual reproduction when unfavorable conditions arise (Fig. B1). The parthenogenetic cycle where female *Daphnia* reproduce amictic diploid eggs that develop directly into daughters would be continued for several generations if feeding conditions permit. Sexual reproduction occur with the production of resting eggs when triggered by external stimuli such as food shortage, overcrowding or the presence of fish predators (Pijanowska and Stolpe 1996, Gyllström and Hansson 2004). Female *Daphnia* produce two types of eggs where diploid amictic eggs develop into males and meiotic haploid eggs need to be fertilized later. After fertilization by males, those eggs are encapsulated in a thick chitinous ephippium and are able to endure extreme environmental conditions (e.g. drought and low temperature). Therefore, dormancy may be an adaptive strategy for *Daphnia* to pass the unfavorable periods and also optimizing their survival chance during passive dispersal by wind or animals (Cohen and Levin 1987).
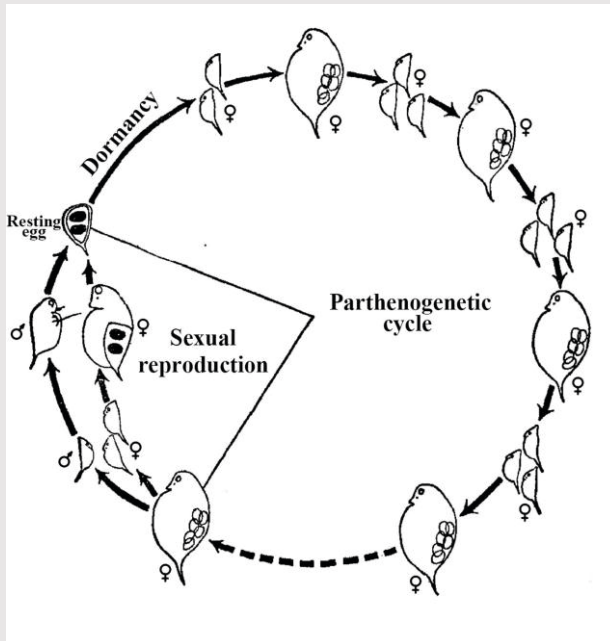

Fig. B1. The life cycle of *Daphnia* showing both parthenogenetic cycle and sexual reproduction (adapted from (Chiang and Du 1979)).

Multiple threats in the environment

In their natural environments, zooplankton are unlikely to be distributed randomly but instead they are constantly faced with multiple and variable threats, such as predation from both invertebrate and vertebrate predators, food quality and availability, competition and abiotic factors (Gyllström and Hansson 2004). In this thesis, I have focused on two of these threats, including predation from both invertebrates and fish and harmful ultraviolet radiation.

Predation

Predation is known to have a major impact on shaping structure and species composition of zooplankton communities (Sih et al. 1985, Kerfoot and Sih 1987). Besides the direct killing effect from predators, perceived predation risk alone (indirect non-consumptive effects) is powerful enough to affect the prey populations, as well as the whole communities (Peacor et al. 2012). In order to avoid being eaten, prey species have to recognize the presence of predators and then respond in a way to reduce the probability of being consumed (Lima and Dill 1990). To aid this, the prey species must either avoid its spatial and temporal overlap with the predator or develop antipredator defences such as changes in morphology or life-history to lower the susceptibility to predation (Walls et al. 1990, Lass and Spaak 2003).

Ultraviolet radiation

Although ultraviolet radiation (UVR) is not immediately lethal at low doses, it could cause many detrimental effects on organisms, both aquatic and terrestrial, owing to its highly energetic short wavelengths (Rautio and Tartarotti 2010). UVR reaching the Earth's surface can be arbitrarily divided into two classes according to the wavelength: UV-B (280-320 nm) and UV-A (320-400 nm) (Rautio and Tartarotti 2010), where UV-B shows stronger damaging effects than UV-A. Most of the UVR originating from the sun can be absorbed by the atmospheric ozone layer but still a large amount of the radiation reaches the Earth's surface. Especially in recent years, the levels of UVR reaching the Earth's surface have been increasing due to the reduction and depletion of stratospheric ozone layer and climate change (McKenzie et al. 2003, Häder et al. 2007, Häder et al. 2015). The strong oxidative stress caused by UVR may lead to negative impact on fitness not only in individual organisms (Rautio and Tartarotti 2010), but also affect the whole community structure of zooplankton (Williamson et al. 2001, Marinone et al. 2006).

However, the UVR regime in the water column differs from that reaching the ground. The penetration of UVR into water is strongly associated with the amount of dissolved organic carbon (DOC) in water. Strong negative correlation between the

concentration of DOC and UVR attenuation in water was found (Scully and Lean 1994). Especially, in some humic lakes with high DOC concentration, UVR attenuates quickly within the first few meters (Kirk 1994), whereas UVR can penetrate much deeper in oligotrophic transparent lakes (Rose et al. 2009, Williamson and Rose 2010). Therefore, the effects of UVR on aquatic organisms are variable depending on the lake conditions.

Zooplankton responses to threats

Zooplankton are very sensitive to environmental changes and have developed several strategies for coping with threats in order to sustain their fitness. Below I focus on changes in behaviour, mainly through diel vertical migration, in both cladocerans and copepods (Fig. 1), and also morphological defences and life-history strategies adopted by the cladoceran *Daphnia* in response to predation and UVR.

Behavioural responses

Changes in behaviour give organisms the possibility of reacting almost instantly to an appearing threat, and may therefore reduce the risk of the threat by instant movement or migration. Additionally, behavioural changes are easily reversible when the threat vanishes. Diel vertical migration is a well-known defensive behaviour found in zooplankton, where tons of biomass migrates up and down in the water column of lakes and oceans on a daily basis, probably representing the largest migratory movement on Earth with respect to biomass (Hays 2003). Predator avoidance is originally assigned as the ultimate reason for this behaviour (Lampert 1993, Hays 2003), as zooplankton, including cladocerans and copepods, which constitute preferred prey for numerous organisms, can escape from encountering the visually oriented hunting predators, e.g. fish, by migrating downwards to deeper and darker waters during the day and then migrate upwards to surface waters at night when predation risk from fish diminishes (Fig. 1). A reversed migration, where zooplankton favour surface waters during daytime and migrate downwards at night, may also provide protection against benthic invertebrate predators (Ohman et al. 1983, Nesbitt et al. 1996). However, during the vertical migration, individuals may exhibit variable behaviours, such as sinking down to different depth refugia according to their body size, when exposed to size-selective predators, such as fish, who preferentially feed on large-sized prey organisms (Brooks and Dodson 1965). This pattern has been shown for both cladocerans (Hansson and Hylander 2009b, Ekvall et al. 2015) and copepods (Tiberti and Barbieri 2011, Holliland et al. 2012, Tiberti and Iacobuzio 2013) in previous studies that larger zooplankton tend to migrate strongly by residing at deeper depths during the day as compared to smaller species and/or individuals.
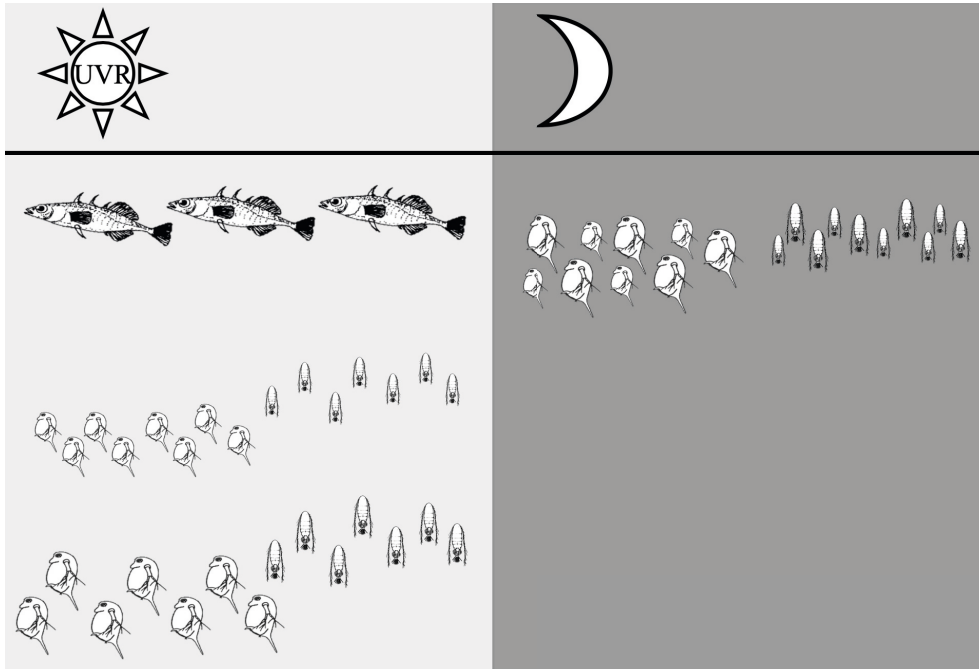
Fig. 1. A schematic illustration of diel vertical migration in *Daphnia* and copepods. During the day, they migrate down to deeper waters in order to reduce the risk of being detected by visually hunting fish predators, as well as to avoid high exposure to harmful UVR. Larger sized species or individuals always stay deeper than smaller ones during the day because they are more vulnerable to fish predators. However, during the night, all individuals migrate to warmer and food rich surface waters for feeding.

Vertical migration can also be an adaptive strategy for zooplankton to cope with UVR, where they leave well-lit surface waters during the day to reduce the high exposure to the dangerous radiation (Rhode et al. 2001, Hansson and Hylander 2009a, Williamson et al. 2011). It has been shown that the cladoceran *Daphnia* are equipped with ultraviolet photoreceptors in their compound eyes (Smith and Macagno 1990) and generally elicit strong behavioural responses by moving out of the surface waters when exposed to UVR (Leech et al. 2005), although those with photoprotective pigmentation, such as melanin, may migrate less distance than unpigmented individuals (Rhode et al. 2001, Hansson and Hylander 2009a). In contrast, when exposed to UVR, the magnitude of such behavioural responses among copepod species may vary ranging from attraction to avoidance to no response (Overholt et al. 2016). These varied responses of copepods could be due to their level of pigmentation, such as carotenoids, or other protective, non-pigment compounds such as mycosporine-like amino acids (Hansson and Hylander 2009a, Hylander 2020), which may compensate for the potential damaging effects of UVR when dwelling at shallower depths. Accumulation of pigments, such as melanin and carotenoids, may help zooplankton, including cladocerans and copepods, to combat UVR damage, but may also make them more conspicuous to visually hunting

predators (Hansson and Hylander 2009a). Therefore, when exposed to conflicting threats from predation and UVR, zooplankton may have to hierarchically evaluate the threat situation and respond accordingly by blending the cocktail of behaviour and photoprotective substances in different ways (Hansson et al. 2007, Hylander et al. 2009, Hylander and Hansson 2013).

In addition to changes in depth distribution, the presence of predators may also induce altering of speed in prey organisms (Schoeppner and Relyea 2009, Langer et al. 2019), as O'Keefe et al. (1998) found that when faced with similar sized *Daphnia* clones, fish predators selected individuals with faster swimming speed. Accordingly, Langer et al. (2019) found that *Daphnia* individuals decreased their swimming speed in the presence of predator cues. Prey organisms with slow swimming speed may decrease the encounter rates with visual predators, such as fish (Gerritsen and Strickler 1977), and therefore give them an advantage to avoid predation risk. However, the presence of UVR may induce zooplankton to change their speed in an opposite direction, as shown in previous studies that the cladoceran *Daphnia* increased their swimming speed to swim down to deep waters instantly after exposure to UVR (Ekvall et al. 2013, Hylander et al. 2014, Heuschele et al. 2017). As UVR attenuates with depth (Scully and Lean 1994), a faster downward speed allows zooplankton individuals to escape from this detrimental radiation and reach at a safer depth rapidly.

Morphological responses

When faced with predators, another strategy adopted by prey species is morphological defences. There are reports on the formation of neckteeth, helmets and crests in *Daphnia* species in response to *Chaoborus* sp. and notonectid predators (Agrawal et al. 1999, Riessen and Gilbert 2019, Diel et al. 2020). These alterations in *Daphnia* head shape are thought to interfere with the predator's mouthparts or handling organs leading to a reduced efficiency of capture and consumption of prey (Dodson 1974, Laforsch and Tollrian 2004). However, the elongated morphs with neckteeth, helmets and crests may be less efficient to thwart large predators such as fish since their gape size is large enough to ingest most zooplankton prey without any difficulty. The size efficiency hypothesis predicts that size-selective predation by fish can eliminate large-bodied cladocerans and lead to a zooplankton community dominated by smaller species (Brooks and Dodson 1965), suggesting that reducing body size may be adaptive for zooplankton where the large-sized predators (e.g. fish) are dominant. Such morphological changes in body size have previously been found in several *Daphnia* species when exposed to size-selective fish predators (Fisk et al. 2007, Collins and Wahl 2018) or fish kairomones (Dodson 1989, Stoks et al. 2016). Although both vertical migration and reduction in body size reduce the vulnerability to visual fish predators, zooplankton seems unlikely to exhibit the combination of these two antipredator defences at the same time because

the food level is generally low at deeper depths and larger individuals are shown to be more resistant to starvation than smaller ones (Threlkeld 1976). As argued above, the selective pressure to migrate to deeper waters in the presence of visual predators is generally stronger on larger *Daphnia* species, or larger sized individuals, since they are more exposed to predation than smaller ones (Hansson and Hylander 2009b).

Life-history strategies

In addition to behavioural and morphological responses, *Daphnia* can also undergo a life-history shift following exposure to predators and UVR. Predator-induced changes in life-history traits have been observed in different *Daphnia* species as response to kairomones from invertebrate as well as vertebrate predators (Lass and Spaak 2003). Generally, *Daphnia* mature earlier at a smaller size and produce higher numbers of smaller eggs when exposed to large size-selective predators such as fish, whereas invertebrate predators like *Chaoborus* may induce *Daphnia* to delay maturation at relatively larger size accompanied with a decreased clutch size (Riessen 1999). By adaptively allocating energy between growth and reproduction, the impact of predation risk can be reduced and the chance of successful reproduction before being consumed by predators is increased. *Daphnia* may also use diapause as an adaptive strategy to reduce predation risk (Hairston 1987) by switching from asexual parthenogenesis to sexual reproduction with the formation of ephippia (Box 1) in order to avoid the predators in time instead of facing the enemy through behavioural or morphological defences.

However, exposure of *Daphnia* to UVR is always associated with reduced growth rates due to its strong oxidative stress (Rautio and Tartarotti 2010). In order to minimize the negative effects from UVR, *Daphnia* develop different alternative strategies, including avoidance behaviour, accumulated photoprotective compounds as well as photoenzymatic repair systems (Hansson and Hylander 2009a). Recently, modifications in life-history traits, such as earlier age at reproduction and producing resting eggs, have also been found among *Daphnia* species as an adaptive strategy to handle UVR threat (Hylander and Hansson 2010, Fernández et al. 2018). For example, Fernández et al. (2018) found that *Daphnia* populations historically exposed to high UVR reproduced at an earlier age with a higher fecundity than those historically exposed to low UVR. The authors argued that allocating more energy into reproduction may compensate for the higher mortality caused by UVR, which enabled them to maintain fitness. It is important to mention that evidence for this reaction norm so far is still very limited and it is not justified to consider such UVR-induced life-history strategies as a general phenomenon in *Daphnia*.

Responses across generations

Most of above-mentioned studies are mainly investigating inducible defensive strategies driven by phenotypic plasticity within a single generation, but now there is growing evidence showing that phenotypic changes induced by environmental threats can span multiple generations (Uller 2008, Jablonka and Raz 2009, Bonduriansky et al. 2012). Therefore, experiences by mothers or even earlier generations in the past environment have the potential to modify the phenotypes of their descendants through a range of nongenetic processes such as maternal effects (Agrawal et al. 1999, Storm and Lima 2010, Bestion et al. 2014) or transgenerational plasticity (Walsh et al. 2014, Walsh et al. 2015, Tariel et al. 2020).

Several previous studies have shown that predation can trigger maternal effects on offspring antipredator behaviour, where parental or grandparental exposure to predator cues caused offspring to alter their behaviour, for example longer time spent immobile among crickets, greater dispersal ability in lizards and increased escape behaviour in snails (Storm and Lima 2010, Bestion et al. 2014, Tariel et al. 2020), allowing a pre-adaptation to the presence of predators. However, to the best of my knowledge, evidence of predator induced modifications in vertical migration among zooplankton offspring are very scarce. In aquatic ecosystems, *Daphnia* serve as an important prey for both vertebrate and invertebrate predators, but they are not passive victims of their enemies. To maximise survival, they may produce plastic defensive strategies within a single generation by altering their morphology or life-history traits, which have been repeatedly reported in previous studies (Riessen 1999, Ferrari et al. 2010). However, in order to reach the maximum morphological change, *Daphnia* may require several generations of exposure to fish cue (Tanner and Branstrator 2006). Moreover, parental exposure of *Daphnia* to predation can also significantly alter the offspring phenotypes, such as induction of defensive morphologies (Agrawal et al. 1999), or modification in various life-history traits (Walsh et al. 2015). Therefore, it is important to take into account the long-term or transgenerational effects of predation when investigating how organisms adapt to a rapidly changing environment.

To date, an extensive number of studies have investigated the within-generation impacts of UVR on zooplankton behaviour or life-history traits (Hansson and Hylander 2009a, Fernández et al. 2018), although parental exposure to UVR may also have the potential to influence the traits among offspring. For example, when parents are exposed to UVR, the detrimental effects of UVR can be accumulated over generations leading to significantly decreased survival and reproduction in their offspring (Huebner et al. 2009). However, parental exposure to UVR may also increase the resilience of their offspring to counteract the negative effects of the threat (Ghanizadeh Kazerouni et al. 2017). Maternal effects, including transgenerational plasticity, can adjust offspring phenotypes and have the potential to program offspring with appropriate defences in order to tolerate future stressful

conditions. However, more studies are needed to investigate the consistency of such transgenerational effects.

Aims of the thesis

In this thesis, I have aimed to investigate how crustacean zooplankton handle multiple threats from predation and UVR within and across generations. I investigated their behavioural responses to these threats both in the field and in the laboratory to further the understanding of diel vertical migration and its underlying mechanism. I have also studied the phenotypic changes of *Daphnia*, including behaviour, morphology and life-history traits, over generations when exposed to predation and UVR based on the multigenerational exposure experiments. Specifically, I have addressed the following questions:

(1) How do copepods handle daily threats from predation and UVR through diel vertical migration in low-latitude freshwater systems? Which are the possible drivers behind such behavioural responses? (**paper I**)

(2) How do differently sized *Daphnia* species behaviourally respond to multiple conflicting threats from predators with different feeding habitats and UVR? (**paper II**)

(3) How do *Daphnia* cope with multiple threats from fish predation and UVR across generations? Can *Daphnia* adapt to the challenging environment after three generations of exposure? (**paper III**)

(4) How does the environment experienced by previous generations affect the phenotypes of their descendants when exposed to UVR? Does the evolutionary history of stress affect such transgenerational responses to UVR? (**paper IV**)

Behavioural responses to multiple threats

Behavioural traits are very labile and can be changed instantly after exposure to a threat. However, in natural environments with complex and heterogeneous habitats, zooplankton often require different behavioural responses in order to balance various conflicting selective pressures. Hence, in **Paper I-II** I explore the behavioural responses of zooplankton to multiple threats from predation and UVR based on the field study and laboratory experiment.

Diel vertical migration in low-latitude freshwater systems

Diel vertical migration (DVM) is the most common behaviour phenomenon in zooplankton, where organisms significantly change their depth distribution on a daily basis by migrating to deep waters during the day and returning back to surface waters at night (Fig. 1) (Lampert 1993, Hays 2003). Such a behavioural response is generally considered as an adaptive strategy for zooplankton to reduce fish predation and harmful solar radiation (UVR) (Hansson and Hylander 2009a, Williamson et al. 2011). To date, an extensive number of studies have been performed to evaluate zooplankton DVM, but a majority of them have focused on systems under strong seasonality at higher latitudes, leading to a limited understanding on how low-latitude zooplankton behaviourally avoid daily threats from fish predators and UVR through DVM.

In **Paper I**, I explore patterns of vertical distribution in copepods in six subtropical Bahamian blue holes that vary in predation pressure and water transparency (differ in UVR exposure). I compared differences in the copepod abundances at six depths between day and night to investigate whether low-latitude copepods perform DVM. Similar to numerous observations in high-latitude/high-elevation systems (Fortier et al. 2001, Berge et al. 2009, Tiberti and Iacobuzio 2013, Fischer et al. 2015), copepods in low-latitude Bahamian blue holes performed DVM, characterized by a downward migration during the day and upward migration to surface waters at night. However, there was an exception that did not follow this pattern, where calanoid

copepods in one of the blue holes (Hubcap) did not migrate and mainly resided at a constant depth well below the Secchi depth during both day and night. This could potentially be explained by the relatively low water transparency and deeper chlorophyll maximum in this specific blue hole, so that copepods can remain stationary at the food rich medium depth where threats from visually hunting fish predators and UVR may also remain at negligible levels.

The transparency-regulator hypothesis argues that UVR should be more important than fish predation in determining zooplankton vertical distribution in more transparent lakes (Williamson et al. 2011), which has been confirmed in studies performed in high-latitude/high-elevation lakes (Kessler et al. 2008, Tiberti and Iacobuzio 2013, Fischer et al. 2015). However, this scenario seems unlikely in those low-latitude blue hole systems since the daytime depth of calanoid copepods increased with both predation risk and depth of food resources (Chlorophyll *a*), but was seemingly unaffected by the UVR threat (Fig. 2), suggesting that fish predation and food availability are likely drivers of the vertical migration in copepods. I also found a size-structured depth segregation in copepods, where larger individuals stayed at deeper depths than smaller ones during the day, which further strengthens the suggestion that predation is the major driving force for DVM at low-latitudes. Although copepods in those low-latitude freshwater systems are constantly exposed to UVR across seasons, they may have established photoprotective compounds to handle this threat. Hence, my study advances our understanding on DVM of zooplankton in low-latitude freshwater systems and adds to the current knowledge by showing that the mechanism behind DVM behaviour may vary among systems, but also systematically by latitude.
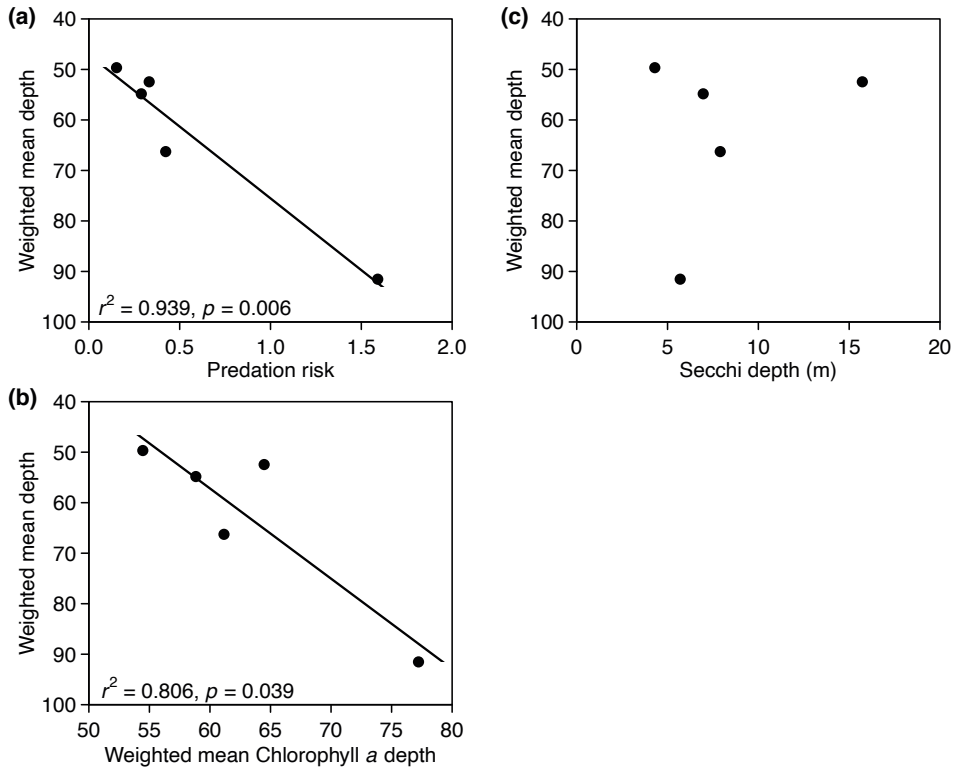
Fig. 2. Relationship between daytime weighted mean depth of calanoid copepods and predation risk (a), and weighted mean Chlorophyll *a* depth (b), and Secchi depth (an estimate of UVR strength) (c), respectively. From **Paper I**. Note that the normalised depth scale (y-axis), where 100 indicates the maximum depth surveyed for each blue hole.

Interspecific differences in response to conflicting threats

Organisms in the wild are faced with multiple threats and a common response is a change in behaviour to move or migrate away from the threat. At the population level, trade-offs between behavioural responses to conflicting threats from predation and UVR have previously been observed in the freshwater zooplankter *Daphnia* (Boeing et al. 2004, Kessler et al. 2008, Leech et al. 2009, Tiberti and Iacobuzio 2013). Despite their small size, clonal *Daphnia* individuals are far from behaving like identical robots, but instead exhibit variable behaviours, such as swimming differently in speed when exposed to a predation threat (Langer et al. 2019). However, the existing devices, such as GPS collars or PIT tags, are successfully used to track individual behaviour in large animals, such as mammals, birds and fish (Brönmark et al. 2008, Hansson and Åkesson 2014), but are impossible to apply to

small organisms such as *Daphnia* because such devices are too large and heavy to allow the mm-sized organisms to act normally. Therefore, in contrast to fish and bird migrations, our knowledge of movements and migration by mm-sized individual invertebrates within and among species in response to multiple threats is still elusive.

In **Paper II**, I explore the behavioural responses of two differently sized prey taxa, *Daphnia magna* and *Daphnia pulex*, when exposed to conflicting threats from UVR and a predation threat in the form of either a pelagic fish or a benthic invertebrate predator, using an advanced tracking method based on nanotechnology. After being labelled with fluorescent nanoparticles (Qdots) (Ekvall et al. 2013), each *Daphnia* individual was tracked in three dimensions both under conditions resembling night (no UVR) and day (UVR) in combination with three predation treatments, i.e. no predator, bottom-dwelling damselfly larvae and fish (See Fig. 3 for the procedure of behavioural assay). I aimed to assess how *Daphnia* make potential trade-offs in their behaviour when faced with simultaneously occurring threats from different directions.
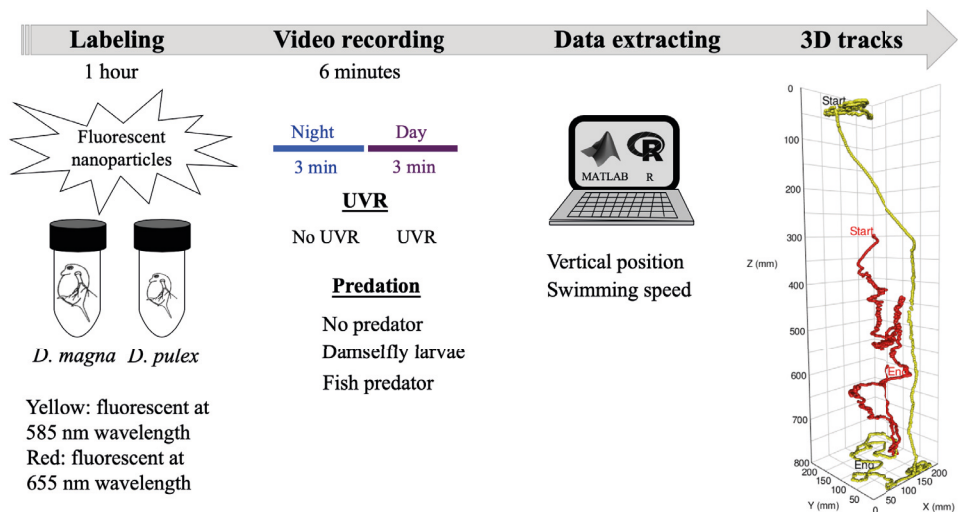
Fig. 3. Schematic layout of the behavioural assay: The daphniids were labelled with fluorescent nanoparticles before the behavioural analysis. After labelling, *Daphnia* individuals were placed into the video recording setup and filmed their behaviour in the absence and presence of UVR for 6 minutes when exposed to three predation treatments, i.e. no predator, bottom-dwelling damselfly (*Calopteryx* sp.) and fish (stickleback, *Pungitius pungitius*) predators. Each video recording was analysed in MATLAB and R software to extract the vertical position and swimming speed. See methods section of **Paper II** for further details.

I found that both *D. magna* and *D. pulex* responded strongly to UVR, whereas only the large *D. magna* adjusted their behaviour in accordance with the level of predation risk (Fig. 4). When exposed to UVR, both *Daphnia* species showed a strong downward migration with an increased swimming speed, allowing them to rapidly escape the threat from this damaging radiation (Fig. 4). However, during the UVR exposure, the presence of predator did not lead to any additional changes in the depth distribution of daphniids, suggesting that UVR is the major force driving the vertical migration of *Daphnia* in this clearwater systems (Williamson et al. 2011). Interestingly, in **Paper I**, I found that the vertical migration of low-latitude copepods were mainly determined by the fish predation and food availability, which is in stark contrast to the finding observed in **Paper II**. This could potentially be explained by the different strategies utilized by the two zooplankton taxa, as copepods may rely more on the use of photoprotective compounds to counteract UVR threat, while *Daphnia* generally show stronger behavioural responses to avoid this threat, which has also been reported by Ekvall et al. (2015).
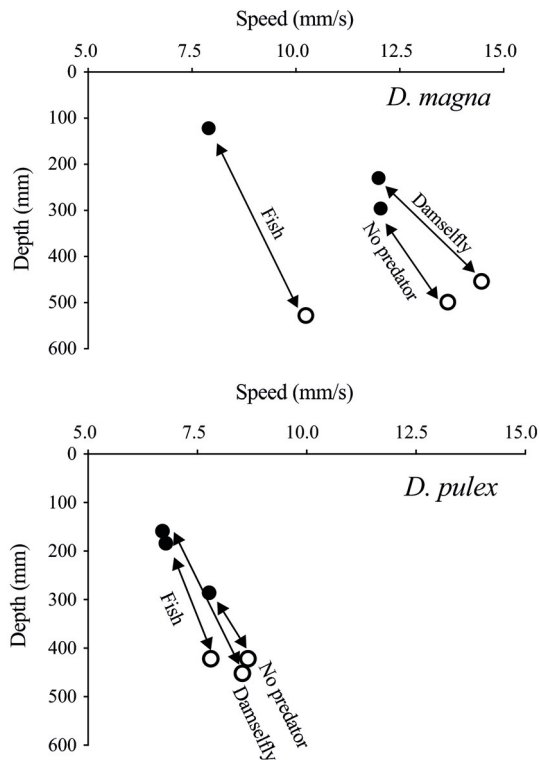
Fig. 4. Combined response in position and speed. A two-dimensional overview of the behavioural response variables depth (mean; mm) and speed (mean; mm/s) of *Daphnia magna* (upper panel) and *Daphnia pulex* (lower panel) during night (black symbols) and day (open symbols). Arrows connect mean values in depth and speed responses for day (with UVR) and night (no UVR) conditions when exposed to: no predator; bottom-dwelling damselfly (*Calopteryx sp.*) and fish (stickleback, *Pungitius pungitius*) predators. Variance measures are omitted for clarity. From **Paper II**.

In accordance with the size efficiency hypothesis (Brooks and Dodson 1965), there is a size-selective predation by predators on prey organisms with larger size. To test this hypothesis, I measured the actual predation rates by different predators on both *D. magna* and *D. pulex*. I found that fish imposed a far stronger predation risk than damselfly for both species, but the predation pressure imposed on large *D. magna* was almost 10 times stronger than the small *D. pulex*. Interestingly, I found that the two investigated *Daphnia* species behaved in accordance with the actual threat levels, where the large prey species in this study (*D. magna*) responded strongly to fish cues with both reduced speed and a more restricted water volume explored, while small prey species *D. pulex* showed no response to predators. Hence, my finding suggests that the mm-sized invertebrate *Daphnia* are able to identify predators with different feeding efficiency and respond accordingly based on the level of predation risk due to size-selective predation.

In **Paper I**, I demonstrate evidence for a size-structured depth segregation in copepods, and this pattern was also found in the study described in **Paper II**, where the small species, *D. pulex*, swam slower and stayed at a relatively shallower depth compared to large *D. magna*. Moreover, in **Paper III**, I also found that *D. magna* individuals reared under predation displayed different behavioural responses to UVR, where larger individuals stayed at deeper depths in the water column compared to smaller ones. Such size-structured migration has previously been observed in both copepods (Tiberti and Barbieri 2011, Tiberti and Iacobuzio 2013) and *Daphnia* (Hansson and Hylander 2009b, Ekvall et al. 2015), which may be a common phenomenon in natural systems due to the size-selective predation by large predators (e.g. fish). Therefore, differently sized prey taxa may rank multiple threats in accordance with the actual threat levels based on their size and respond accordingly.

Variation in threat responses across generations

In order to cope with harsh environmental conditions, the cladoceran *Daphnia* have accordingly developed various strategies, including alterations in behaviour, morphological changes or shifts in life-history patterns. Some aspects of these defensive strategies have been extensively discussed as a plastic response within an individual's lifetime, so-called phenotypic plasticity (Tollrian and Harvell 1999, Pigliucci 2001). However, such plastic responses may span multiple generations so that information about the past environmental conditions may potentially alter the phenotypes of future generations (Mousseau and Fox 1998, Agrawal et al. 1999), leading to different responses across generations. In **Paper III-IV**, I explore the transgenerational responses of *Daphnia* to multiple threats from predation and UVR and also reveal the consistency of such transgenerational effects when exposed to UVR.

Diverging responses to multiple threats

In **Paper III**, I investigate the transgenerational changes in behaviour, morphology and reproductive output of *Daphnia magna* that were exposed to control, predation, UVR and the combination of predation and UVR over three consecutive parthenogenetic generations. After reared under the respective treatment for 30-40 days, I evaluated the behavioural responses by *D. magna* from each treatment when again exposed to UVR for each generation. I quantified the refuge demand and swimming speed during the exposure to UVR to assess the behavioural differences in the UVR avoidance between individuals from each treatment and each generation. Refuge demand is calculated as the integral of an individual's depth position over time, where large values are associated with individuals that behaviourally avoid UVR, and a small value indicates that the animals stay high up in the water column despite exposure to UVR. I also measured the body length for each individual and recorded its reproductive output for each treatment and each generation. I found that *D. magna* were able to detect and distinguish between different types of threats and adopted divergent strategies over generations to handle the multiple threats from predation and UVR.

When exposed to UVR, all individuals displayed a rapid downward migration, but the strength in response differed between treatments where individuals reared under UVR conditions had a smaller refuge demand and also swam slower than their naïve siblings (Fig. 5). This suggests that individuals previously exposed to UVR acquire tolerance and show a less pronounced behavioural response when again exposed to this threat. Such UVR-tolerant behaviour has also been observed in previous studies for both copepods and *Daphnia* (Hylander et al. 2014, Overholt et al. 2016), which was also confirmed in **Paper IV**. In contrast to the treatment effects on behaviour, generation had no effect on either refuge demand or speed for any treatment, suggesting that when exposed to UVR, offspring responded in a similar way as their mothers.
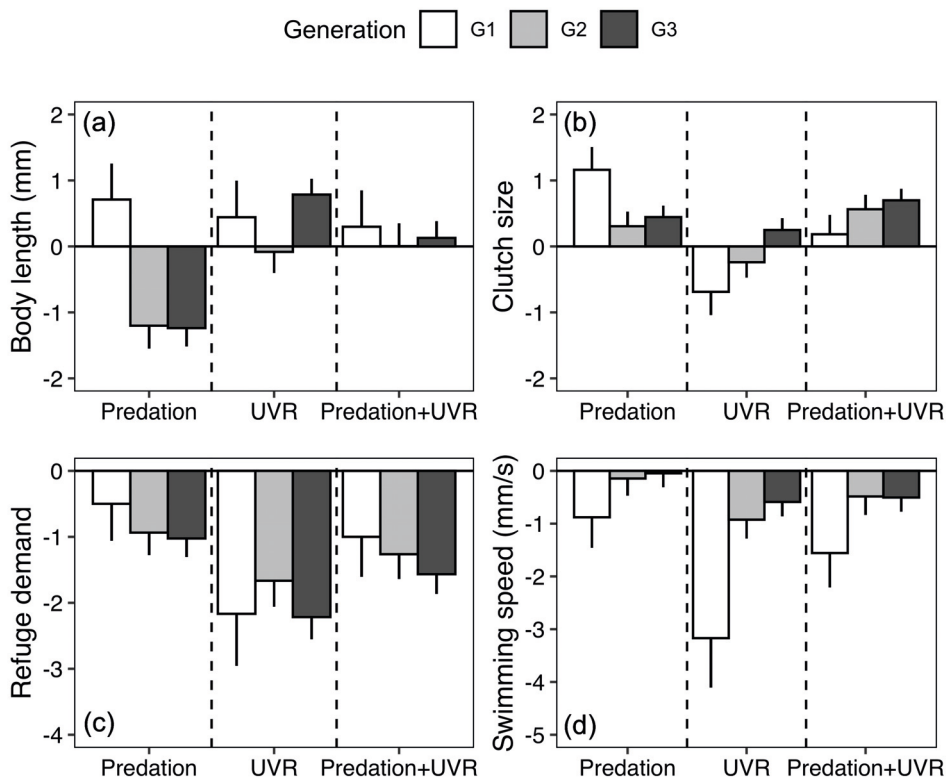
Fig. 5. The mean effect sizes (Cohen's *d*) of (a) body length, (b) clutch size, (c) refuge demand, and (d) speed for *Daphnia* individuals under treatments of predation, UVR, and the combination of predation and UVR. Bars show the development during three consecutive generations (G1, white bars; G2, light grey bars; G3, dark grey bars), which were normalized using the mean value of control individuals as zero baseline. Error bars are standard errors. From **Paper III**.

Interestingly, when exposed to fish cue, *D. magna* adopt a different strategy by gradually reducing their body size across generations in order to counteract predation risk (Fig. 5). I found that *D. magna* from the third generation showed the smallest mean body size, which were 3 and 11% smaller than their mothers (G2) and grandmothers (G1), respectively. These results are consistent with previous studies based on short-term experiments (Dodson 1989, Riessen 1999, Zhang et al. 2017). However, my study adds to previous understanding by showing that prey organism induces a smaller body size to become less vulnerable to predation since fish predators are generally size-selectively feeding on larger prey, but the maximum morphological changes may require several generations of exposure (Tanner and Branstrator 2006). Surprisingly, when *D. magna* were simultaneously exposed to predation and UVR, they did not change their body size through generations. Although UVR may affect the efficiency of fish cue (Sterr and Sommaruga 2008), UVR may also interact with predation (Alton et al. 2010) and indirectly reduce the zooplankton survival under predation by suppressing the development of inducible morphological defences.

In addition to changes in behaviour and morphology, exposure to predation and UVR also altered the reproductive strategy of *D. magna* but in different ways (Fig. 5). I found that individuals reared in the presence of fish cue responded with increased clutch size compared to control individuals. Allocating more energy into reproduction and meanwhile maturing at a smaller size may enhance the chance of *D. magna* survival in a situation with large predators, such as fish. Although UVR-exposed individuals showed a lower behavioural response to UVR, such UVR tolerance was associated with a cost of reduced clutch size especially for the initial exposure period (generation 1). Interestingly, the clutch sizes eventually increased through generations and *D. magna* reared under UVR were able to reproduce and behave in a similar way as naïve siblings after three generations of exposure to UVR. Transgenerational plasticity likely explain this pattern as it may buffer negative effects of environmental threats and thereby promote organisms to persist and rapidly become successful in a changing environment.

Asymmetric responses to UVR

An individual's phenotype can be altered by direct contact with environmental cues (within-generation plasticity) (Pigliucci 2001), but also by environmental features experienced by previous generations (transgenerational plasticity) (Agrawal et al. 1999, Galloway and Etterson 2007, Salinas et al. 2013). There is a growing recognition that phenotypic plasticity including transgenerational plasticity may be different depending on the environmental context. Such context-dependent effects have been documented in several studies when investigating threats of salinity, food

availability or predation (Plaistow et al. 2006, Groot et al. 2016, Walsh et al. 2016), although similar studies related to UVR are quite rare.

In **Paper IV**, I address the question whether or not variation in the UVR induced plastic response of *D. magna* across generations could be caused by the stress history of the previous or ancestral generations. I found that the environment experienced by previous generations including parents and grandparents significantly influenced the phenotypes of their descendants. In line with previous studies (Hansson and Hylander 2009a, Fernández et al. 2018), exposure to UVR induced plastic phenotypic changes in *D. magna* including alterations in behaviour and life-history shifts, although such transgenerational effects of UVR was context-dependent due to the evolutionary history of stress, as well as to the traits considered. I found that naïve *D. magna* showed strong behavioural responses to the UVR threat, but individuals quickly changed their behaviour according to the current rearing environment which would show an UVR tolerant behaviour with low refuge demand when they had been experienced with UVR within their lifetime. Although the levels of photoprotective compounds could be a potential explanation for this UVR tolerant behaviour (Rhode et al. 2001, Hansson et al. 2007), I found no difference in pigmentation among individuals from different treatments. Similarly, I also found that *D. magna* delayed the maturation after two consecutive generations of exposure to UVR, however, there was no change in the number of offspring through generations. In contrast to the naïve population, *D. magna* that had been reared under UVR for more than 150 generations kept the tolerant behaviour through generations even when the UVR threat was absent, that is, individuals exhibited similar behavioural and life-history responses as their mothers or grandmothers irrespective of their own rearing environment. My study suggests that *D. magna* populations with different stress histories show asymmetric responses to UVR across generations.

Effects of UVR on life-history variables of *D. magna* are demonstrated in **Paper III**, where *D. magna* exposed to UVR initially showed a smaller clutch size but they gradually increased the clutch size through generations. This pattern deviates from the finding in **Paper IV**, as I found that individuals reared under UVR for at least three generations always produced lower number of offspring. The differences between these two findings is likely due to the individual or clonal variation in threat response (Connelly et al. 2016, Walsh et al. 2016), highlighting the complexity of transgenerational studies where multiple factors may influence the observed outcome.

Conclusions

In conclusion, I have here demonstrated that zooplankton have the ability to perceive the present threat level and respond by reducing the risk through changes in their behaviour, morphology or life history traits. Alteration in behavioural traits is generally the first reaction in zooplankton to changed conditions, allowing them to escape from the threats instantly after exposure. In **Paper I**, I found that low-latitude copepods in Bahamian blue holes performed diel vertical migration (DVM), characterized by a downward migration during the day and upward migration to surface waters at night. Despite the constant exposure to UVR, predator avoidance and food availability are the major drivers of copepod DVM at those low latitudes, suggesting that the underlying mechanism behind DVM behaviour may vary by latitude. When exposed to conflicting threats from UVR in combination with either moving pelagic or benthic predators, *Daphnia* are able to make different risk assessments and thereby alter their behaviour in accordance with the actual threat level. Two *Daphnia* species responded strongly to UVR by migrating downwards to deeper depths with a faster swimming speed. However, only the larger species, *D. magna*, showed predator avoidance behaviour, whereas the smaller, less vulnerable, *D. pulex* did not respond to predator cues (**Paper II**).

Results of **Paper III** indicate that *D. magna* adopt divergent strategies over generations through modifying morphology, behaviour or life-history traits and thereby become adapted to multiple threats from predation and UVR after three generations of exposure to the threat. Exposure to UVR had persistent, transgenerational consequences for offspring phenotypes that could span at least three generations. Evolutionary history of stress may affect the expression of such effects leading to different plastic responses to UVR across generations (**Paper IV**).

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