Food and Parasites – Life-history Decisions in Copepods

BY

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Abstract
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In the freshwater copepod, *Macrocyclops albidus,* food availability, rearing conditions and tapeworm infection clearly affected various life-history traits and their trade-offs. I found that low food availability clearly constrained resource allocations to several life-history (often phenotypically plastic) traits, whereas high food availability either allowed for adjustments in resource allocation patterns or allowed resources to be allocated to several traits without apparent trade-offs.

Both male and female copepods allocated resources according to food availability; developing more slowly and achieving smaller adult body size when food was scarce. When food availability was low females were constrained and produced fewer eggs (in total and per clutch), and started reproduction later than females with more food available. Males under low food availability allocated relatively more to spermatophore size (current reproduction) with decreasing body size. In contrast, when food availability was high males allocated resources to body size as well as spermatophore size. Overall, at maturity, copepods of both sexes were more similar in size than in age, suggesting that large body size was more important for fitness than fast development.

In nature the prevalence of copepods infected with cestode tapeworms was found to be low (0-3%). Female copepods, experimentally infected with the cestode *Schistocephalus solidus*, showed lower overall fecundity, especially when food availability was low. However, infected females produced a larger proportion of their life-time egg production early in life than non-infected females. This might be an adaptation to reduce future fitness costs of infection. Females grown under bad rearing conditions, but with high food availability, produced their first clutch earlier than females grown under good rearing conditions, indicating an adjustment in timing of reproduction. These findings contribute to our fundamental evolutionary understanding of how environmental conditions interact with life-history traits.

Keywords: life-history, resource allocation, *Macrocyclops albidus*, cestode infection, *Schistocephalus solidus*

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List of Papers

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

I. van der Veen, I. T., Sivars Becker, L. Size and age at maturity in *Macrocyclops albidus* copepods under a high and low food regime. (submitted)

II. van der Veen, I. T., Sivars Becker, L. Resource allocation and costs of reproduction in male copepods under different food regimes. (submitted)

III. Sivars Becker, L., van der Veen, I. T. Do female copepods adjust their life-history to food availability and rearing conditions? (submitted)

IV. Sivars Becker, L., van der Veen, I. T. Seasonal variation of cestode infection and egg production in copepods in a lake and a stream in northern Germany. (submitted)

V. Sivars Becker, L., van der Veen, I. T. Reproductive resource allocation and cost of infection in copepods. (submitted)

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Contents

Introduction

All organisms are facing the dilemma of allocating their limited amount of resources to growth, reproduction and maintenance in the most beneficial way. An organism needs to reproduce to gain fitness, and in order to reproduce it needs to grow and mature, and at the same time resources need to be allocated to maintenance. When resources are allocated to one life-history trait, fewer resources will be available for other, competing, life-history traits (Stearns, 1992; Roff, 1992), which yields negative correlations between traits, i.e. trade-offs. Resource allocation decisions will have an impact on an individual's reproduction, survival and, thus, on its fitness (Stearns, 1992; Roff, 1992). Which resource allocation pattern will be most beneficial will depend on both abiotic and biotic factors, such as resource availability, competition, predation and parasitism (Hochberg *et al*., 1992; Doughty & Shine, 1998; Doums *et al.*, 1998; Candolin, 1999). Consequently organisms should be phenotypically plastic, i.e. able to vary their life-history traits when faced with environmental variability (Via & Lande, 1985; Stearns, 1992). It has been shown in various species, that individuals adjust their life-history to prevailing environmental conditions in such a way (Kaitala, 1987; Gliwicz & Guisande, 1992; Peterson, 2001; Bochdanovits & De Jong, 2003). A classical example of adaptive changes in life-history due to environmental factors, comes from Trinidadian guppies (*Poecilia reticulata*), where a difference in predation risk between rivers, so that either adults or juveniles are the target, selects for different life-histories in females in those different areas (Reznick & Endler, 1982).

It has become more and more clear that life-history trade-offs have to be studied across different species, populations and, especially, across different environments (Stearns *et al*., 1991). Allocation decisions will heavily depend on resources available and, therefore, trade-off decisions may be very different in different environments. For example, individuals might be constrained by low resource availability, to allocate in the most beneficial pattern, i.e. they are constrained to show adaptive adjustments in resource allocation patterns. On top of this, trade-offs can be difficult to detect when individuals vary in the amount of energy they can acquire (Stearns, 1992; Reznick *et al*., 2000). For example, high quality individuals may have enough resources to grow large as well as to produce many clutches, whereas individuals of lower quality might have to trade-off their resources between several life-history parameters. Such low quality individuals will grow as well as repro-

duce less, which results in a positive correlation between the traits in a population where one would expect a negative correlation, i.e. a trade-off (van Noordwijk & de Jong, 1986).

Parasitic infections introduce an additional demand for host resources (Poulin, 1998). Infections can be costly for the host through competition with the parasite over limited resources and ultimately through energy depletion caused by the parasite (Coop & Holmes, 1996), which might have an impact on the decision making and optimal resource allocation pattern of the host. The host could therefore benefit from parasite resistance by decreasing the effect of parasites or avoiding parasites. However, it has been shown that the defences used to achieve resistance can be costly (reviewed by Kraaijeveld et al., 2002; Rigby et al., 2002; Sandland & Minchella, 2003), thus, generating trade-offs with life-history traits (Sandland & Minchella, 2003).

Body size

In many organisms body size is an important life-history trait affecting fitness (Andersson, 1994). Large body size may increase an individual's competitive ability, decrease its vulnerability to predators and increase its number of offspring (Smith, 1990; Begon et al., 1996; Downes, 2002). Also in the copepod *Macrocyclops albidus* Jurine, which is studied in this thesis, size at maturity can be assumed to play an important role in determining fitness of both males and females. In male copepods, body size could be important when searching for females (described in van Leeuwen & Maly, 1991), when overcoming the initial resistance of females (desribed in Hill & Coker, 1930; Gauld, 1957; Maier, 1992; Palmer & Edmands, 2000) and when fighting with other males (Hill & Coker, 1930; Maier, 1996). Larger females produce more clutches (paper III) and more eggs per clutch (Wedekind, 1997). Larger individuals might also be better at resisting parasites (van der Veen & Kurtz, 2002; but see Wedekind, 1997).

In order to reach a large size at maturity, organisms will have to either grow fast (Metcalfe & Monaghan, 2001) or grow for a longer time (Roff, 1992; Stearns, 1992). Growing fast seems to be costly (Metcalfe & Monaghan, 2001), for example, in terms of increased predation risk at higher foraging intensities (Werner & Anholt, 1993) or physiological costs due to higher metabolic demands (Gotthard et al., 1994). Therefore, growth rates may not always be maximized. Even when growth rates are not maximized, organisms may still reach a large size at maturity by growing for a longer time, i.e. by increasing age at maturity (Roff, 1992). However, older age at maturity may also infer large costs, in terms of increased risk of infection (Minchella, 1985) or predation risk (Werner & Anholt, 1993). For example, organisms are predicted to decrease their age at maturity under predation risk

(Abrams & Rowe, 1996), simply because longer exposure to predation risk increases the chance of dying before any fitness can be obtained.

Current vs. future reproduction

Life-history theory predicts a trade-off between current and future reproduction, assuming that investment in current reproduction will be costly and, therefore, lead to a decrease in future reproduction (Williams, 1966; Roff, 1992; Stearns, 1992). For example, in several species females suffer longevity costs with increasing investment in current reproduction, which will diminish their chances of future reproduction (for example, fruitflies, *Drosophila subobscura*, Maynard Smith, 1958; collared flycatchers, *Ficedula albicollis,* Gustafsson & Pärt, 1990; humans, Westendorp & Kirkwood, 1998). The outcome of such trade-offs should depend on the relative importance of current and future reproduction. Factors affecting the relative importance of these two parts of fitness are, for example, life expectancy, and, in relation to that, expected residual reproduction (Biermann & Robertson, 1983), or the quality of the current mating partner in comparison to other potential mating partners (Sheldon, 2000). If residual reproductive value is low, allocating resources to current reproduction becomes relatively more important than allocating resources to future reproduction. On top of that, resource availability may affect longevity and thus residual reproductive value. When fewer resources are available, life expectancy may decrease and thus residual reproductive value may decrease (Lessells, 1991). Since this affects the relative importance of current and future reproduction, the trade-off between current and future reproduction will change. If the residual reproductive value (i.e. future reproduction) decreases by an increased mortality risk, life-history theory predicts more resources to be shifted to current reproduction (Fisher, 1958; Minchella & Loverde, 1981). For example, female snails (*Biomphalaria glabrata* Say*)* infected with a trematode (*Schistosoma mansoni* Sambon) increase early reproduction in response to being parasitised. It could be that by advancing their reproduction, these snails can reach higher fitness gains than if they would invest later. A later investment in reproduction involves the risk of not surviving until fitness has been gained, or being drained of resources by the parasite at the moment reproduction starts (Minchella & Loverde, 1981; Thornhill *et al*., 1986; Hochberg *et al.* 1992).

In males the trade-off between current and future reproduction has not been studied as often as in females (but see, for example, Kotiaho & Simmons, 2003). In species where the male's first spermatophore only applies to the first mating, allocation to first spermatophore size can be interpreted as an allocation to current reproduction. On the other hand, allocation to body size, which may be important for sexual selection taking place at all matings, can be interpreted as an allocation to future reproduction. Sperm competition

is one of the major reasons for assuming high allocation to spermatophore size (Birkhead & Møller, 1992). However, we believe that sperm competition in the copepod *M. albidus*, which is studied in this thesis, is of minor importance, since females usually only mate once. Another reason may be that spermatophore size reflects paternal investment if females consume part of the spermatophore (Simmons & Parker, 1989), however, *M. albidus* females do not consume male spermatophores. The third reason why males should invest in spermatophore size is mate choice; females could have a preference for males with larger spermatophores (Møller, 1994). Male copepods can mate repeatedly (Maier, 1992; Dussart & Defaye, 1995), which indicates that there may be potential for sexual selection among males for access to unmated females and thus, for female choice. Large spermatophore size may also be an advantage when females perform post mating sperm selection (Wedekind, 1994). In *M. albidus* copepods, the time of the final moult may infer that males have to make a trade-off between allocating resources to body size or to first spermatophore size.

Aim

The degree to which biotic and abiotic factors influence the resource allocation to life-history traits in *Macrocyclops albidus* copepods is not known. From an evolutionary perspective, trade-offs between life-history traits are interesting since an individual's allocation pattern is likely to be under selection. Therefore, I have studied the effects of resource availability (paper I, II, III, V), rearing conditions (paper III) and infection status (paper V) on various life-history traits, such as age at maturity; body size at maturity; allocation to current and future reproduction; timing of first reproduction; number of clutches produced and number of eggs produced in *M. albidus* copepods. Parasitic infections are thought to greatly influence host life-history and selection pressures. Therefore, in paper IV I investigated the rate of cestode infection in two naturally infected copepod communities and in paper V I estimated the cost of cestode infection in relation to reproduction in female copepods under high and low resource availabilities.

Study species

Copepods are small water living crustaceans belonging to the arthropods (Einsle, 1993; Dussart & Defaye, 1995). They are ubiquitous components of most freshwater and marine zooplankton communities. I have studied the freshwater cyclopoid copepod species *Macrocyclops albidus* Jurine throughout this thesis (paper I, II, III & V), except for in a field survey (paper IV), where a larger variety of cyclopoid copepod species were investigated. *M. albidus* copepods are relatively large and sexually dimorphic with respect to body size. Females are larger than males, with a body size of 2.5 and 1.3 mm, respectively. This omnivorous copepod species is a common inhabitant of the freshwater littoral zone, but may also exist at deeper depths in lakes (Einsle, 1993; Dussart & Defaye, 1995). Females carry two egg sacs outside their body (Fig. 1) until the eggs hatch and free-living nauplii are released. The nauplii go through six moults where they shed the outer exuvia and grow. During the last nauplii moult they go through metamorphosis into copepodites. After additionally five moults they are adult copepods ready to engage in reproduction. In order to reproduce, males grab the female at their abdomen with their antennulae and attach a pair of spermatophores on the female's receptaculum seminis. A few hours after mating with a female, males have produced a new spermatophore that can be stored until a new mating partner is encountered. The fast production of the new spermatophore indicates that the size of the new spermatophore depends on lipid reserves and resources stored by the male at the time of mating, and is decided upon before the next mating partner has been encountered. Spermatozoa can stay alive within the female for several weeks and fertilize several clutches. Cyclopoid copepod males can mate with several females, whereas females usually mate only once, but are capable of repeated egg-production and multiple releases of nauplius larvae (Maier, 1992). When the eggs inside the female's body have been fertilized they are extruded in two egg sacs (Fig. 1).

In the experimental studies (paper I, II, III & V) *M. albidus* copepods came from a laboratory culture that was initiated with 80 females from a small river, Kremper Au, near Neustadt in northern Germany.

In paper IV, several species of copepods from two field locations were checked for presence of cestode larvae. The samples consisted mainly (> 90%) of *Eucyclops serrulatus* (Fischer), which is a cyclopoid omnivorous species (Dussart & Defaye, 1995). Females are about 1.2 mm and males

about 0.8 mm long, which is substantially smaller than *M. albidus*. *E. serrulatus* is probably, together with *Cyclops strenuus* (Fischer)*,* the most common cyclopoid copepod of central Europe (Bukvic-Ternjej *et al.,* 2001; Jersabek *et al.*, 2001). *E. serrulatus* occurs in various kinds of lakes and waters (Bukvic-Ternjej *et al.,* 2001; Jersabek *et al.*, 2001), it is polycyclic and present throughout the year (Wolf, 1905; Pesta, 1928), which also accounts for *M. albidus* (Einsle, 1993; Dussart & Defaye, 1995).

Fig. 1 Female *Macrocyclops albidus* copepod with egg sacs. © L. & C. Becker.

The parasite

Since parasitism can have great implications for an individual's fitness, and thus selection, I have studied the effects of cestode infection in the cyclopoid copepod *M. albidus* (Fig. 1). In paper V copepod females were experimentally infected with the tapeworm *Schistocephalus solidus* (L.) (Cestoda). Cyclopoid copepods are the first intermediate host of the horizontally transmitted cestode *S. solidus* (Clarke, 1954). Copepods get infected by ingesting the free-swimming parasite larvae called coracidia. The second intermediate host is the considerably studied three-spined stickleback (*Gasterosteus aculeatus*) (Milinski, 1990; Tierney *et al.* 1996; Aeschlimann *et al.,* 2000; Øverli *et al.,* 2001; Barber & Svensson, 2003;) and as definitive host any fish eating bird is used (Fig. 2). The parasite mates either with a partner or

self fertilizes in the bird's gut and the parasite eggs are then released into the water with the bird's faeces (Clarke, 1954). In such a parasite-host system many life-history trade-offs are of particular interest and especially in relation to how resources, both limited and abundant, are allocated. However, not much is known about the parasite's influence on the first intermediate host's life-history (i.e. the copepod). Copepods are, not only first intermediate hosts for *S. solidus,* but also for several other species of cestodes (Dubinina, 1980) (paper IV). The parasites used in the experimental study were obtained from the brackish Binnenwasser, 2.5 km from the site where the copepods with which the stock culture started were obtained. The tapeworm was dissected from wild caught sticklebacks and was then cultured in an *in vitro* system to get parasite eggs, using the techniques described by Smyth (1954) and Wedekind (1997). Parasite eggs can be stored at 4 °C. Before hatching, the parasite eggs need to develop for 3 weeks at 20 °C upon which exposure to light induces hatching.
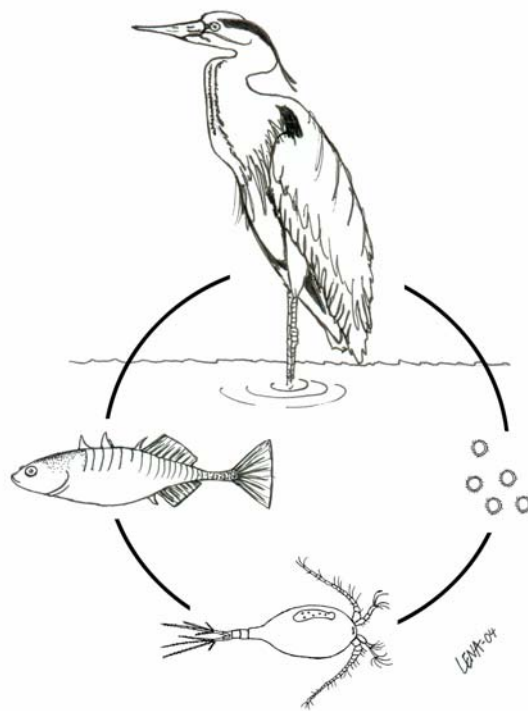

Fig. 2 The cestode *Schistocephalus solidus* has a complex lifecycle involving several hosts. The cestode larvae are ingested by a cyclopoid copepod, the first intermediate host, where it enters the body cavity and grows. The second intermediate host the three-spined stickleback (*Gasterosteus aculeatus*) ingests the copepod and the parasite continues to grow in the body cavity of the fish. In the definitive host, a fish eating bird, the parasite mainly reproduces. The parasite eggs are shed with the bird's faeces into the water. © L. Sivars Becker

General methods

The copepod cultures, from which copepods were used for the experimental studies (paper I, II, III, V) were maintained as described in van der Veen & Kurtz (2002). Copepods in the cultures where fed with *Paramecium caudatum* solution (200 cells/ml) twice a week.

In the experimental studies I took copepods (copepodite stage c1-c3 (paper I, II & V) and c1-c4 (paper III)) from the cultures and put them individually in wells of 24-well ELISA-plates. All wells were checked three times a week. When an exuvium was observed in the well, it was removed and recorded. With this information development stage and age at maturity could be estimated.

Body size of each individual was measured by means of image analysis (Scion Image, a modification of NIH Image http://rsb.info.nih.gov/nih-image). The copepod was put on its side and body size was measured as the distance from the centre of the eye to the posterior dorsal end of the cephalothorax. The same technique was used when when spermatophore size was measured (paper II).

In all experimental studies food availability and predation risk was manipulated. Copepods were either assigned to a high food regime or to a low food regime. Each copepodite was fed different amounts of newly hatched *Artemia salina* L. nauplii, depending on food regime and experimental design. Copepods in the high food regime were always fed 6 *Artemia* three times a week (18 per week) and copepods in the low food regime were fed 1-3 *Artemia* three times a week (4-7 per week depending on experimental design). In order to simulate future uncertainty I simulated predation risk by adding 0.2 ml of water from an aquarium in which sticklebacks (*Gasterosteus aculeatus* L.) were kept, twice per week to each well, resulting in a concentration of about 0.023 fish/l in each well, in all food regimes.

To study allocation to reproductive traits in adult copepods the copepods had to mate. Each female was put together with two males (paper II & III) or with one male at the time (paper V) until mating occurred. In order to study allocation to current reproduction and cost of reproduction in males, spermatophores were measured before and after mating (paper II).

In paper V I used individual copepods with similar genetic background i.e. siblings from the same 14 families in all treatments, to compare effects of infection on reproduction in different food regimes. By assuring a similar genetic background I reduced the risk of large quality differences between food regimes and infection statuses.

In order to study female reproduction, i.e. timing of first reproduction, number of clutches produced (paper III & V), eggs in each clutch, and total egg production (paper V), females were put individually in a floating net in nalgene cups (200 ml) in 150 ml of water in which hay had been boiled. Each female was observed every second day and presence of egg sacs or loss

of egg sacs were recorded. If the female had lost her eggs she was transported to a new container to keep track of her clutch production and prevent her from eating her progeny.

In the field study (paper IV) two locations: Wedeler Au, Hamburg, and Trammer See, Plön, were examined for the presence of cestode infected copepods. Samples were taken at regular intervals during the spring and summer season. Each copepod was scanned under a microscope for the presence of parasite larvae and the presence of egg sacs (Fig. 1).

Results and Discussion

Age and size at maturity – paper I

In paper I, I assessed resource dependent patterns of copepod body size and age at maturity. Large size at maturity has a positive effect on fitness in many organisms (Andersson, 1994). On the other hand, older age at maturity usually has a negative effect on fitness (Werner & Anholt, 1993). As stated earlier, since large size at maturity can be reached by increasing the age at maturity, a trade-off between age and size at maturation is predicted from a theoretical point of view (Stearns & Koella, 1986).

Resource availability is likely to affect the outcome of such life-history trade-offs (Stearns *et al.*, 1991). For instance, with higher resource availability, more resources could be allocated to growth. This could either result in larger size at maturity or lower age at maturity, both of which could positively affect the fitness of an organism. The outcome of allocation decisions in such a trade-off will depend on the relative benefits of each of the components in the trade-off (Roff, 1992; Stearns, 1992). When one trait in a trade-off is more affected by resource availability than another, one can assume that the trait with the lowest variability is the trait with the largest fitness benefits. This can be assumed because it has been shown that the higher the impact of a certain trait on the fitness of individuals, the lower the variation in that trait should be in the population (Gustafsson, 1986).

In paper I, I show that resource availability affected age and size at maturity of *M. albidus* copepods. Under a low food regime copepods were smaller as adults and took longer time to develop from the c4 copepodite stage to the adult stage than under a high food regime. This seems to be a general pattern for copepods, i.e. in several copepod species lower food quality or quantity results in smaller size and older age at maturity (Santer & van den Bosch, 1994; Twombly & Burns, 1996; Twombly *et al.*, 1998; Makino & Ban, 2000; Twombly & Tisch, 2000), and this is also one of the predicted possible outcomes in theoretical studies (Roff, 1992).

When both traits were standardized, size at maturity showed a smaller difference between the two food regimes than age at maturity (Fig. 3). Since traits that have a large effect on fitness can be expected to show low variation (Gustafsson, 1986), one could argue that, under these experimental conditions, size at maturity may have been more important for fitness than age at maturity. Similar results have been found for naupliar development in

copepods, i.e. naupliar development time was found to be more variable than size at transformation from nauplia to copepodite (Twombly, 1993, 1995, 1996). Interestingly, such analyses have, to my best knowledge, not been done for copepodite development before.
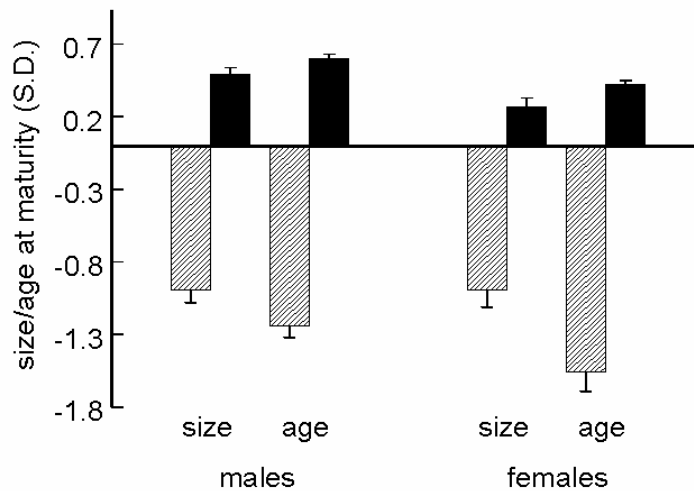

Fig. 3 Size and age at maturity (estimated as the time from copepodite stage 4 to adult) expressed in standard deviations (S.D.) from the mean. Standard deviations and means were calculated per trait and per sex, by pooling the high and low food regimes. In this way size and age at maturity can be compared on the same scale. A smaller difference between the high (black bars) and the low food regime (hatched bars) for size than for time indicates that that trait is more variable and consequently one could argue that it is less important for fitness.

Even though the copepods were more similar in size at maturity than in age at maturity in both sexes, this effect tended to be stronger in females than in males, although not significantly so (Fig. 3). In females, food (high or low) affected age and size at maturity more differentially than in males. This means that in females size at maturity can be assumed to be relatively more important for fitness than age at maturity, as compared to in males. Sexual size dimorphism, with females being larger than males, is strong in this species (1.41 (Maier, 1994), 1.40 this study). Such size dimorphism is in agreement with the suggestion that size may be more important for fitness in females than in males.

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Resource allocation in males – paper II

In paper II, I investigated the cost of mating in male *M. albidus* copepods and how males allocate their resources to body size and first spermatophore size, depending on resource availability. As stated earlier, the relative importance of current and future reproduction will affect the outcome of the trade-off. The interesting aspect of this trade-off is that first spermatophore size is only applicable to the first mating (i.e. allocation to current reproduction), whereas adult body size is a fixed trait, which applies to all matings during a male's life (i.e. allocation to future reproduction). I showed that when food availability was high spermatophore size increased with body size, which indicates that when male copepods had plenty of resources they allocated to current as well as to future reproduction (Fig. 4). This is in line with the theory that when an individual has high resource availability, i.e. when it has enough resources to allocate to all traits, it may not have to trade-off between different life-history traits (van Noordwijk & de Jong, 1986). On the other hand, in males with low food availability body size and spermatophore size were not significantly correlated (Fig. 4). However, relative spermatophore size (spermatophore/body size) increased with decreasing body size, which indicates that males allocated relatively more to current reproduction with decreasing body size at low food availabilities.
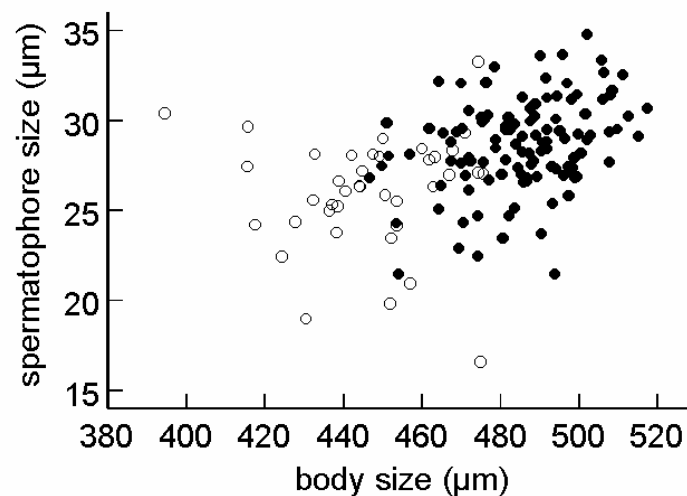

Fig. 4 The relationship between adult body size and first spermatophore size of *M. albidus* males in the low (open circles) or the high food regime (filled circles). In the high food regime adult body size and first spermatophore size were significantly positively related (slope = 0.056, t_1 = 3.68, p = 0.0004), whereas this was not the case in males from the low food regime (slope = 0.0023, t_1 = 0.08, p = 0.93).

I believe that this negative significant relationship between body size and relative spermatophore size is due to constraints. When resources are limiting, individuals have to make trade-offs (van Noordwijk & de Jong, 1986; Roff, 1992; Stearns, 1992).

However, the question remains why allocation to current reproduction increases relative to allocation to future reproduction with decreasing body size in the low food regime. Firstly, it may be that when food is limited, life expectancy and thus, residual reproductive value decreases (Biermann & Robertson, 1983). When body size is positively correlated to individual quality (van der Veen & Kurtz, 2002) the decrease in residual reproductive value may be stronger in smaller males, because low quality individuals may not be as good as high quality individuals at surviving bad circumstances. In that case, with decreasing body size, the allocation to current reproduction should increase relative to the allocation to future reproduction, which is what I observed. However, small individuals may not necessarily suffer a lower life expectancy when food is limited. Large individuals may have higher metabolic demands and may therefore, when resources are limiting, suffer higher physiological costs than small individuals (Gotthard *et al*., 1994). If this would be the case, residual reproductive value should decrease with increasing body size in the low food regime, and males should allocate more to current reproduction (spermatophore size) relative to future reproduction (body size) with increasing body size. This is the opposite of what I found and thus a less likely explanation. A second possible explanation may be that when body size is under sexual selection, large males may have a higher future fecundity than small males (Andersson & Iwasa, 1996). Although no data are available on this for copepods, as I proposed in the introduction, there are many stages of the mating behaviour during which sexual selection for large body size might take place, i.e. searching for females (van Leeuwen & Maly, 1991), overcoming the initial resistance of females (Hill & Coker, 1930; Gauld, 1957; Maier, 1992; Palmer & Edmands, 2000), or fighting with other males (Hill & Coker, 1930; Maier, 1996). If body size would be under sexual selection, small males would have low prospect for mating in the future and, in order to optimise their fitness, should therefore allocate more resources to current reproduction than to future reproduction, which is what I observed. It may be that above a certain amount of resources available, an allocation to body size may start to pay off in terms of residual reproductive value, and then the best strategy is to allocate relatively more to future reproduction.

Males produced significantly smaller spermatophores after having mated with a female, suggesting that mating is costly in this species. The effect of the consecutive spermatophore being smaller was stronger in males in the low food regime than in the high food regime. Thus, it seems that when food availability is low males pay a higher cost of mating than males in the high food regime. However, it is important to note that males in this study were

mated with females from their own food regime, which means that the larger decrease in spermatophore size after mating in the low food regime may be the result of males tailoring their allocation to subsequent spermatophores to the quality of the female previously encountererd instead of being costs of mating. Theoretically it has been predicted that males should tailor their sperm allocation to female quality (Galvani & Johnstone, 1998), which, for example has been found in the coral reef fish *Thalassemia bifasciatum* (Shapiro *et al.,* 1994).

This difference in allocation pattern between males with different re-source availabilities also points out the importance to study allocation patterns under more than one level of food availability, and in both sexes.

Female life-histories and food availability – paper III

In this experimental work I have studied changes in female life-history traits (i.e. body size, time to first reproduction, adult life span and number of clutches) to different food availabilities (high and low) and rearing conditions (good and bad) in female *M. albidus*. In this paper I used data from two successive experiments. The rearing conditions for copepodites differed between those two experiments, which affected adult body size and mortality. I based my denomination for good and bad rearing conditions on those differences in body size, and mortality between these two experiments.

Since rearing conditions affected survival (i.e. future reproduction) I expected females from different rearing conditions to differ in resource allocation to various life-history traits. Females are expected to allocate more to current reproduction (i.e. adjust the timing of reproduction to an earlier date) when the future is uncertain, for example, due to increased mortality risk (caused by worse rearing conditions) (Fisher, 1958; Minchella & Loverde, 1981). As stated earlier, food availability was manipulated in order to study if the allocation pattern is resource dependent. When food availability is low, females might be constrained in their resources and thus have to trade-off between future and current reproduction. On top of that, if resource availability is low females might also have had low prospects for current reproduction. As predicted, females under bad rearing conditions produced fewer clutches than females under good rearing conditions, and they differed in the timing of first reproduction. Females took longest to start their reproduction under bad rearing conditions and low food availability (Fig. 5). However, in the same rearing conditions but with higher prospects of current reproduction (higher resource availability) females were the fastest to reproduce (Fig. 5). An adjustment in timing of reproduction could be a way for the females to compensate for the lower life expectancy, when rearing conditions were bad, and an adaptation to ensure higher fitness gains. Females, with high food availability and good rearing conditions, that might have had higher

prospects for both future and current reproduction, took intermediate time to start reproduction (Fig. 5).
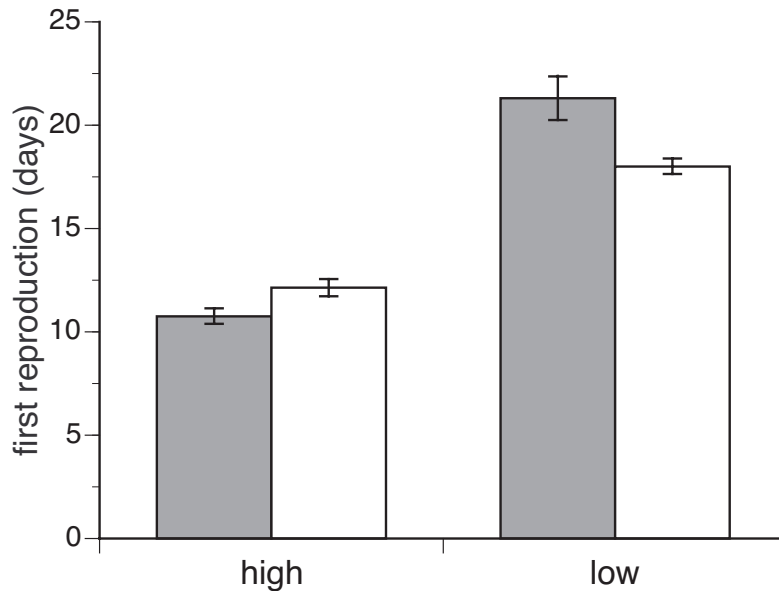

Fig. 5 The effect of food availability (high and low) and rearing conditions (bad – grey bars; good – white bars) on the timing of the first reproduction i.e. days from adult moult to the production of the first egg sacs.

With low food availability female *M. albidus* copepods became smaller as adults (see also paper I), which has also been found in other copepod species (Ban, 1994; Santer & van den Bosch, 1994; Hart *et al.*, 1995; Twombly & Tisch, 2000; but see also Makino & Ban, 2000). Besides their smaller size, females in the low food regime also took longer time to their first reproduction and produced fewer clutches, which was what I expected. As already mentioned, body size can affect the fitness of organisms (Andersson, 1994). For example, in the copepod *M. albidus* large females produce more eggs per clutch (Wedekind, 1997). Many other studies have also found a strong positive effect of food availability on egg production in copepods (paper V; Durbin *et al.*, 1992; Santer & van den Bosch, 1994; Hart *et al.*, 1995). In contrast, adult life span seemed to be less affected by food availability, even though females with low resource availability were older at maturity than females with high resource availability (Paper I). I expected females in the high food regime to have a longer adult life span than females in the low food regime, due to their higher resource availability and younger age at maturity, however, this was not the case. One appealing explanation for this could be the higher clutch production in the high food treatment. It has been shown that reproduction is costly in terms of survival, for example, in male fruit flies *Drosophila melanogaster* Meigen (Partridge & Farquhar, 1981) or

in the plant Ragwort *Senecio jacobaea* L. (Gilman & Crawley, 1990). In my study, females in the high food treatment produced significantly more clutches than females in the low food treatment. Maybe the higher clutch production by females in the high food treatment was costly in terms of survival, and thus I do not find any differences in adult life span between females in the two food treatments. The extra resources females in the high food treatment had compared to females in the low food treatment, might have been allocated to reproduction instead of survival.

A field study – paper IV

In this field study (paper IV) the natural rate of cestode infection and egg production in copepods was monitored over a spring and summer season in two water bodies in Northern Germany: Wedeler Au, in Hamburg, which is a nutrient rich stream and Trammer See, Plön, which is a clear, more nutrient poor lake. Both copepod populations of *Eucyclops serrulatus* had low prevalence of cestode infection, over the season (0.5% and 0.8%, respectively, ranging from 0-3%). In the nutrient poor lake there was a peak of 3% cestode infected copepods in early June when temperatures were elevated, whereas no clear peaks could be observed in Wedeler Au. The overall parasite prevalence found in this study is in the lower range of what has been reported in previous field studies (Sysoev, 1987; Zander *et al.*, 1994; Pasternak *et al.*, 1995; Dörücü, 1999), which indicates large differences between seasons and between water systems. However, the prevalence of cestodes in copepods is known to increase with water temperature (Sysoev, 1987; Dörücü, 1999), which was also the case in my study. Since it, to my knowledge, is impossible to distinguish cestode species visually in copepods I do not know with what cestode species the copepods at the two sites were infected. It is likely that the cestode species at the two sites were not the same. In Wedeler Au in September, 48% of the sticklebacks were infected with the cestode *Proteocephalus filicollis* (Rudolphi), and in Trammer See 60% of the sticklebacks were infected with *Valipora campylancristrota* (Wedl) (Kalbe *et al.*, 2002), both of which have cyclopoid copepods as intermediate hosts. This indicates that there were at least two different cestode species at the two sites.

The relationship between cestode prevalence and copepod reproduction, measured as the percentage of copepods carrying egg sacs among infected and non-infected copepods, differed between the two sites. Infected copepods carried less often egg sacs than non-infected copepods in the nutrient poor lake (Trammer See), but in the nutrient rich stream (Wedeler Au) this pattern was reversed; in Wedeler Au infected copepods carried egg sacs more often than non-infected copepods (Fig. 6). There may be several explanations for this effect, two of which I would like to focus on. Firstly, there

might be different cestode species at the two sites, having different effects on their hosts (Forbes, 1993). Some cestode species severely deplete the host of resources, whereas others may not affect host energy expenditure as strongly. Such species differences may have an effect on the amount of resources the host can allocate towards reproduction and thus on the percentage of infected copepods with egg sacs that occur in a population (Forbes, 1993; Perrin & Christe, 1996). Secondly, since infected copepods face an increased predation risk (Wedekind & Milinski, 1996; Pulkkinen et al., 2000) it may be beneficial for infected copepods to reproduce as quickly as possible (Minchella & Loverde, 1981; Minchella, 1985; Thornhill et al., 1986; Hochberg et al., 1992; Forbes, 1993). It has previously been shown that under experimental (i.e. well fed) conditions copepods infected with the cestode S. solidus developed egg sacs more often than non-infected copepods (Wedekind, 1997). By producing egg sacs faster, the infected copepods may get higher fitness gains than when they would postpone investment in reproduction to an uncertain future (McCurdy et al., 1999).
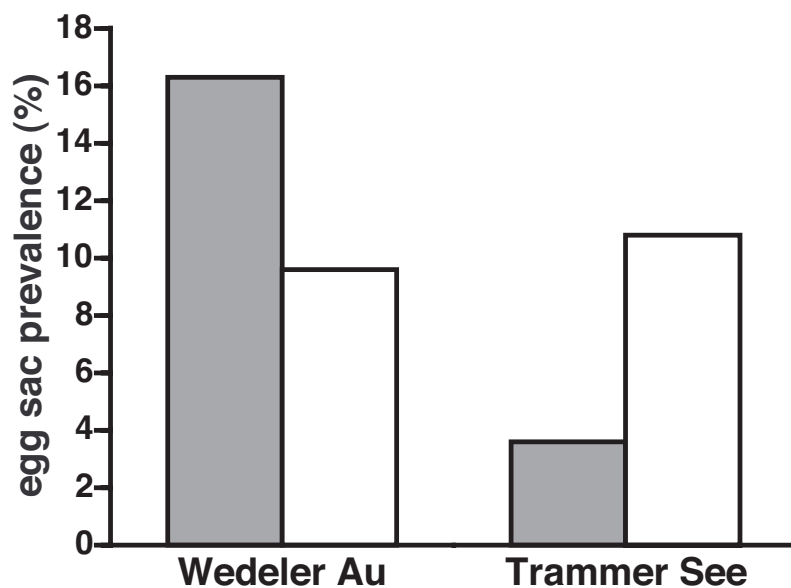

Fig. 6 Percentage of copepods among infected (grey bars) and non-infected (white bars) individuals carrying egg sacs at the two sites: Wedeler Au (nutrient rich) and Trammer See (nutrient poor).

Since the nutritional environment is poorer in Trammer See than in Wedeler Au, it might have been harder for copepods in Trammer See to get enough energy for both coping with the infection and allocating resources to egg production (Price, 1980; Lochmiller & Deerenberg, 2000), resulting in low egg production among infected copepods in Trammer See. On the other hand, in Wedeler Au the environment is richer in nutrients and thus the in-

fected copepods were, besides coping with infection, able to make an investment to egg sacs. This possible explanation for my results led us to test whether infection is costly for females in terms of reproduction and whether females increase their allocation in current reproduction when infected and whether this depends on resource availability (paper V).

Resource allocation and cost of infection in females – paper V

In paper V, I further investigated if copepod females adjust their resource allocation to reproduction in relation to abiotic and biotic factors. I consider it necessary to further investigate this for two reasons. Firstly, I found that the relationship between prevalence of cestodes and the percentage of copepods carrying egg sacs differed between two field sites (paper IV). I would like to test if the differences in egg bearing between the sites could be explained by the differences in resource availability at the two sites. When resource availability is low, infected females might be constrained to produce eggs, whereas, when resource availability is high, it might be possible for infected females to allocate resources to reproduction. Secondly, in paper III, I found that females with low prospects of future reproduction, but with high resource availability, were the earliest to reproduce. Both of these findings could be adaptive adjustments of reproduction by females to an increased risk of mortality. By reproducing earlier, individuals with low residual reproductive value might receive higher fitness gains than if they would invest later into reproduction (Minchella & Loverde, 1981; Thornhill *et al.*, 1986; Hochberg *et al.,* 1992). In paper V, I experimentally investigated the cost of infection and resource allocation patterns to reproduction in copepod sibling females, in response to cestode infection status (control, exposed but non-infected, infected). By using siblings, and thus assuring a similar genetic background, I reduced quality differences between copepods that get infected and copepods that are exposed to the parasite but remain non-infected. Since the cost of infection and resource allocation may be resource dependent, I tested this under two levels of resource availability (high or low). Adaptive adjustments in life-history to reduce the costs of infection might only be possible when enough resources are available (de Lope *et al.*, 1993).

My results clearly show that there were costs related to *S. solidus* infection in *M. albidus* females. Independent of food regime, infected females produced significantly fewer clutches, significantly fewer eggs in their first clutch and significantly fewer eggs in total, compared to both exposed and control females. It is also evident that the costs of infection were higher when resource availability was low. In the low food regime, total egg production was 65% lower in infected females than in control females, whereas

in the high food regime total egg production was only 40% lower in infected females than in control females. This proportional difference in total egg production between infected females in the two food regimes indicates that females in the high food regime could compensate for some of the costs of infection. Firstly, females in the high food regime might have been able to reduce the cost of infection due to their higher resource availability. Secondly, the cost of infection or immune function females pay could be masked by a compensatory resource intake and, thus, the outward sign of infection is reduced (Moret & Schmidt-Hempel, 2000).

Females in the low food regime were significantly smaller than females in the high food regime. Thus, food availability had a positive effect on body size and, therefore, there is a possibility that body size and not food availability caused my results. However, since food availability was the factor I manipulated and size was a consequence of food availability I believe I can discuss my results in relation to food availability.

Since infected females have an increased predation risk, which was simulated in this experiment, prospects for future reproduction might be lower after 11 days post infection for the females. This is approximately the minimum time it takes for the parasite to be ready for transmission to the next host, the stickleback. Independent of food regime, infected females produced proportionally more eggs, in the first 11 days of egg production than exposed and control females (Fig. 7a & b). Infected females produced more than half (58%) of their total egg production within 11 days, as compared to control and exposed females who produced about one third (37% and 31%, respectively) of their total egg production within 11 days. Thus, infected females allocated proportionally more resources to egg production, in the first 11 days, than exposed and infected females. There are two possible explanations for this, firstly, this could be an indication that the tapeworm larvae consumes proportionally more resources with increasing age i.e. with increasing body size, which would increase the cost of infection with time (Poulin, 1998). Such a larger energy drain could constrain females to produce eggs with progressing length of infection. Secondly, as suggested before, infected females may have adjusted their resource allocation pattern to the decreased life expectancy they experience when infected (e.g. Minchella & Loverde, 1981; Adamo, 1999; Krist, 2001). By proportionally producing more eggs within the first 11 days, post infection, they might decrease the costs of parasitic infection. When females were constrained by resources only, i.e. control and exposed in the low food regime, they produced a larger proportion of their eggs after 11 days than females with high resource availability. This was in contrast to the allocation pattern of infected females, who produced a lager proportion of their eggs within 11 days (Fig. 7a & b).
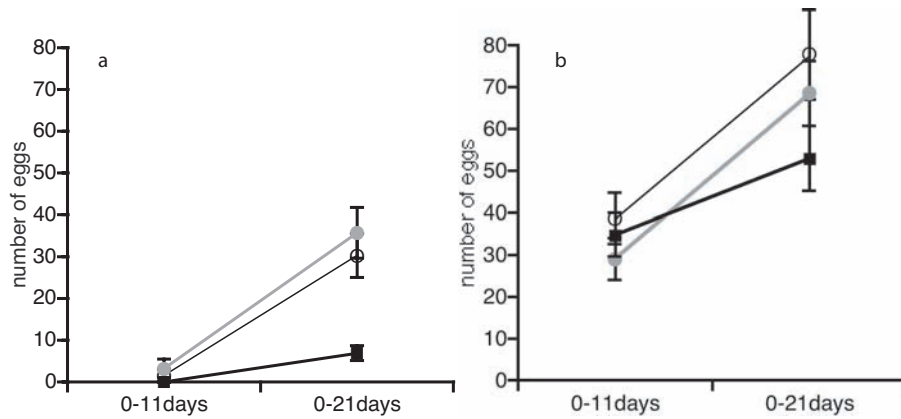
Fig. 7 The effect of infection status (control females open circles ± SE; exposed females grey circles ± SE; infected females black squares ± SE) on number of eggs produced within 11 and 21 days in (a) the low food regime and in (b) the high food regime.

A previous study found no effect of *S. solidus* infection on stored lipids or muscle tissue in *M. albidus* males (Franz & Kurtz, 2002), suggesting that energy depletion by the parasite is not the only factor influencing infected females. This could indicate that not only resource depletion by infection was responsible for the allocation pattern I found in infected females, but also an adaptive pattern of resource allocation, as predicted by life-history theory.

Conclusion

In conclusion, *M. albidus* copepods showed strong phenotypic plasticity in several life-history traits in relation to environmental factors, such as food availability, rearing conditions and infection status. Such phenotypic plasticity is presumably adaptive for copepods as they are likely to reproduce under variable or different environmental conditions.

I have shown that body size is positively related to food availability in both males and females, as are timing of first reproduction and developmental time. When food availability is low, copepods are most likely constrained to grow as large, reproduce and develop as fast as when food availability is high.

I also investigated allocation to current and future reproduction in female and male copepods. In males I investigated the resource allocation to body size and spermatophore size and in females the timing of first reproduction and the egg production pattern over time. The allocation patterns are clearly affected both by constraints and by the relative importance of current and future reproduction. When food availability was low, copepods had to trade-off resources between life-history traits, which was not as evident when resource availability was higher. When current reproduction seemed relatively more important than the chances of future reproduction, female and male copepods consequently allocated more resources to current reproduction, which might be an adaptation to gain higher fitness.

Copepods in two water bodies in northern Germany were found to have relatively low levels of cestode infections, between 0-3% depending on water body, temperature and part of the season. Infected females carried more often egg sacs in the more nutritious stream than in the less nutritious lake. I suggest this to be an adaptation for infected females to get higher fitness, which might only be possible if resources are abundant. Consequently, copepods experimentally infected with a cestode (*S. solidus*) paid a higher cost of infection in terms of reproduction when food availability was low than when food availability was high.

I found that many of the life-history traits of *M. albidus* under study were phenotypically plastic. The differences in allocation patterns I found with varying resource availability, infection status and rearing conditions can be explained by constraints as well as by adaptations. An individual that adaptively allocates its resources differently in different environments in such a way that it maximizes its fitness in each of the environments will be fa-

voured by natural selection. However, individuals can be constrained to allocate their resources in the most beneficial pattern, for example, by low resource availability. The knowledge about resource allocation, as an adaptation or a constraint, will improve our evolutionary understanding. With the help of detailed knowledge of the interactions between adaptations and constraints in allocation patterns and life-history trade-offs, it will be possible to predict what will happen in a population when environmental conditions, such as food availability or parasite prevalence, change.

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Sammanfattning

Det är lätt att tänka sig ett super-djur, en s.k. darwinistisk demon, som kan växa sig enormt stor och producera massor med avkommor hela tiden, samtidigt som det försvarar sig mot alla tänkbara faror, som parasiter och rovdjur. Men varför finns inte super-djuren i naturen? För att växa sig stor, producera avkommor och försvara sig mot fiender krävs resurser, till exempel i form av föda, men ingen organism har tillgång till obegränsade mängder med resurser. Ingen organism har heller obegränsat med tid, när all tid går åt till att födosöka och äta finns det ingen tid kvar att söka efter en partner och att producera avkommor. Den här resursbristen leder till att resurser inte kan spenderas på en livs-historiekaraktär (t.ex. reproduktion, tillväxt, underhåll av kroppsfunktioner), utan att samtidigt påverka en annan livs-historiekaraktär. För att lyckas i livet måste resurserna allokeras så bra som möjligt mellan tillväxt, underhåll och reproduktion. Konsekvensen blir att om mer resurser avsätts till det ena blir det mindre kvar till något annat. Därför förväntas en avvägning (ett negativt samband) mellan olika livs-historiekaraktärer. Varje allokering måste noga avvägas mot kostnader och fördelar. Vissa individer har mer resurser att spendera än andra och kan satsa på både tillväxt och reproduktion, vilket genererar ett positivt samband när en grupp individer studeras. (Precis som i vårt samhälle där en del människor har råd med både dyr bil och dyrt hus, och andra varken eller). De som gör de mest fördelaktiga avvägningarna är också de som producerar mest avkomma och därigenom selekteras de fördelaktiga allokeringsmönstren vidare till nästa generation. Men ett allokeringsmönster som är fördelaktigt i en miljö behöver inte nödvändigtvis vara fördelaktigt i en annan. Till exempel, i en miljö kan stor kroppstorlek vara fördelaktigt, medan i en annan miljö där predatorer lättare ser stora individer kan det vara bra att vara liten. Resursallokeringsmönstren kan också påverkas av om framtida fortplantning är osäker, till exempel om det finns en risk att bli sjuk av ett parasitangrepp eller uppäten. Då kan fördelarna vara stora med att allokera alla tillgängliga resurser till reproduktion så fort som möjligt, d.v.s. hinna fortplanta sig innan man blir sjuk eller uppäten. Konsekvensen av att avvakta och allokera sina resurser, som om i en parasitfri-miljö, kan vara fatala i den mer riskabla miljön. Trots potentiella fördelar med ett flexibelt allokeringsmönster kan det vara kostsamt för individen att tidigarelägga sin fortplantning, då det kan leda till förkortad livslängd, färre eller mindre avkommor.

Hoppkräftor (Copepoda) är små vattenlevande kräftdjur och jag har studerat sötvattensarten *Macrocyclops albidus* som är vanligt förekommande i norra Europa. I jämförelse med andra hoppkräftor är denna art förhållandevis stor och honorna är större än hanarna, 2.5 respektive 1.3 mm. Första larvstadierna är frisimmande nauplius som efter skalömsningar och metamorfos övergår i copepoditstadier. Efter ytterligare skalömsningar är copepoden vuxen och könsmogen. Jag har studerat hoppkräftornas resursallokering till olika livs-historiekaraktärer vid olika resurstillgång och i relation till parasitinfektion. Fortplantning och tillväxt är kostsamma livs-historiekaraktärer som är viktiga för en individs fitness. För att kunna växa sig stor och kunna producera många avkommor krävs resurser, men hoppkräftor har precis som alla andra organismer begränsade resurser.

I artikel I studerade jag utvecklingen hos hoppkräftslarver. Hos hoppkräftor är kroppsstorleken viktig, större individer kan producera fler och större ägg vilket höjer individens fitness. Men större kroppsstorlek betyder oftast längre utvecklingstid, vilket i sin tur kan sänka fitness, eftersom en längre utvecklingstid kan innebära en ökad risk att bli uppäten eller angripen av parasiter. Ett parasit- eller rovdjursangrepp kan resultera i att individen inte kan reproducera sig alls. Mina resultat visade att hoppkräftor med riklig födotillgång utvecklades både snabbare och till större individer än hoppkräftor med mer begränsad födotillgång. De med riklig födotillgång allokerade mer resurser till båda livs-historiekaraktärerna, än individerna med begränsad födotillgång vilka antagligen var förhindrade att allokera likaledes. Dessutom fann jag att när kroppsstorlek och utvecklingstid standardiserades för både hanar och honor, satsade båda könen företrädesvis på en större kroppsstorlek framför en kortare utvecklingstid. Den här effekten var starkare hos honorna, vilket teoretiskt stämmer med att hoppkräftor av arten *Macrocyclops albidus* är starkt storleksdimorfa, d.v.s. honan är mycket större än hanen.

Kroppsstorlek är viktigt även hos hanar, eftersom det är möjligt att större hanar lättare kan konkurrera om honor, och har större motståndskraft mot parasiter. Honor parar sig bara en gång och lagrar sedan spermier från hanens spermatofor inuti kroppen till kommande reproduktionstillfällen. Hanen däremot kan para sig många gånger med olika honor, och det innebär att det antagligen är svårare för en hane att hitta en parningsvillig hona, än för en hona att hitta en parningsvillig hane. Honan föredrar kanske hanar med stora spermatoforer, vilka skulle kunna innehålla fler spermier som kan befrukta fler ägg än spermierna i en liten spermatofor. I artikel II, undersökte jag hanars allokering av resurser till kroppsstorlek och spermatoforstorlek. Jag fann att om resurstillgången var riklig hade större hanar också större spermatoforer. När resurstillgången var begränsad visade det sig att mindre hoppkräftshanar hade, i förhållande till sin kroppsstorlek, större spermatoforer. Resursallokering till spermatoforstorlek kan betyda att hanen satsar allt på ett kort; den första (och kanske enda) parningen. Medan resursallokering till

kroppsstorlek indikerar en fördelad satsning mellan nutida och framtida reproduktion. Mina resultat visar att hanar som parat sig en gång, producerade en mindre spermatofor till nästföljande parning, vilket indikerar att det är kostsamt för hanar att para sig. Hos andra arter har kostnader av reproduktion oftare påvisats hos honor än hos hanar.

Honors fortplantning påverkades också av resurstillgången, honor med mindre mat producerade sin första kull senare och dessutom färre antal kullar (artikel III). Däremot påverkades honornas livslängd inte av resurstillgången. Om honorna däremot hade lite tuffare uppväxtförhållanden påverkades livslängden negativt. De blev också mindre som vuxna och producerade färre kullar, vilket givetvis är negativt för fitness. Man kan förutsäga att honor som vuxit upp under tuffa förhållanden har lägre förväntningar på framtida reproduktionstillfällen just för att deras korta livslängd gör det omöjligt. Därför förutsade jag, att när resurstillgången är riklig, borde honor med tuffare uppväxtförhållanden ändra resursallokeringen och producera sin första kull snabbare än honor som förväntar sig mer av framtiden. Det var precis vad jag fann, vid riklig resurstillgång producerade honor med tuffa uppväxtförhållanden sin första kull snabbare än honor som vuxit upp under goda förhållanden. Mönstret var omvänt när resurstillgången var begränsad, då var honorna med tuffa uppväxtförhållanden bakom sig långsammast att reproducera sig. Vilket troligen beror på att honorna var förhindrade av resursbrist att tidigarelägga sin fortplantning. Honor som hade växt upp under goda förhållanden, och som därför hade goda framtidsutsikter, producerade sin första kull medelsnabbt. För de honorna var det antagligen bättre att avvakta med fortplantningen då en tidig fortplantning kan vara mycket kostsamt för individen t.ex. genom mindre eller färre avkommor totalt sett.

I fältstudien (artikel IV) har hoppkräftor från en sjö och en å i norra Tyskland studerats, under en vår och sommar säsong, för att få en uppfattning om hur ofta hoppkräftor är parasiterade av bandmask. Denna kunskap är värdefull för att förstå infektionsrisken i naturliga populationer av hoppkräftor, vilket kan visa hur viktigt det skulle kunna vara för hoppkräftor att utveckla ett försvar mot parasitering. Om en parasitinfektion är mycket ovanlig kanske det inte finns några fördelar med ett kostsamt försvar. Dessutom kan parasiteringen i fält ge oss en inblick i hur studier i laboratoriet ska utföras. Till exempel, om de flesta infekterade hoppkräftorna enbart bär en bandmask i fält bör experimentella studier, som vill påvisa effekter av parasiter, följa liknande infektionsmönster. I fältstudien, fann jag att förhållandevis få hoppkräftor var parasiterade (mellan 0-3% av populationen). Jag fann också att parasiterade hoppkräftor oftare hade ägg i den näringsrika ån jämfört med i den näringsfattiga sjön. Vilket skulle kunna betyda att infekterade hoppkräftor producerar ägg så fort som möjligt, när de har tillräckligt med resurser, innan parasiten eventuellt gör det omöjligt att undvara resurser för reproduktion. Genom att ändra sitt allokeringsmönster och satsa mer på fortplantning i ett tidigt stadium så ökar de sin fitness.

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I den sista artikeln (artikel V) infekterade jag hoppkräftshonor med en bandmask för att studera kostnader av en infektion och om infekterade honor allokerar sina resurser annorlunda jämfört med icke-infekterade honor. Hoppkräftor är det första värddjuret i bandmasken *Schistocephalus solidus* livscykel. Hoppkräftan äter parasitlarverna vilka tar energi från sin värd och tillväxer i hoppkräftans kroppshåla. Infekterade hoppkräftor förändrar sitt beteende och blir på så sätt ett lättare byte för rovdjur, vilket gör att framtiden inte ser hoppfull ut för en infekterad hoppkräfta. För att parasitens livscykel ska fortföljas, och för att parasiten ska tillväxa ytterligare, måste en storspigg äta upp en infekterad hoppkräfta. Parasiterade fiskar blir även de mindre försiktiga och är på så sätt ett lätt byte för den tredje och sista värden, en fiskätande fågel. I fågelns mage fortplantar sig parasiten, antingen sexuellt med en partner eller asexuellt genom självbefruktning. Parasitäggen förs sedan ut i vattnet, med fågelns avföring, där de kläcks och cirkeln är sluten. Jag visade att det finns en tydlig kostnad för hoppkräftor av att få en bandmasksinfektion. Infekterade honor producerade färre kullar, färre ägg i första kullen och färre ägg totalt sett jämfört med icke-infekterade honor. Dessutom, om resurstillgången för honorna var lägre, blev kostnaden av infektionen högre. Honor med begränsade resurser hade förmodligen inte tillräckligt med resurser för att klara av en resurskrävande parasit i kroppen och samtidigt producera avkommor. Jag visade också att när resurstillgången är riklig producerade infekterade honor en stor andel av sin totala äggproduktion tidigare än icke-infekterade honor. Det skulle kunna vara en anpassning för infekterade honor att maximera fitness. Infekterade honor som spar sina resurser till ett senare tillfälle blir i värsta fall uppätna av parasitens nästa värd innan de hunnit få några avkommor. På så sätt skulle honor som i olika miljöer kan ändra sitt resursallokeringsmönster och tidigarelägga sin reproduktion gynnas av det naturliga urvalet.

Omgivningsfaktorer, som födotillgång, uppväxtförhållanden och parasitinfektioner, har betydande effekt på hur en organism, i det här fallet hoppkräftor, avsätter resurser till olika livs-historie karaktärer. I vissa fall är organismen förhindrad att allokera resurserna på bästa sätt, i andra situationer kan organismen anpassa resursallokeringen på ett adaptivt sätt eller vid god resurstillgång kan resurser allokeras till fler egenskaper samtidigt. I ett evolutionärt perspektiv är det viktigt att förstå växelverkan mellan omgivningsfaktorer och livs-historie egenskaper.

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