Modelling foraging behaviour in the insect predator *Notonecta maculata* using the individuals approach

Von der Fakultät für Mathematik, Informatik und Naturwissenschaften der RWTH Aachen University zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften genehmigte Dissertation

vorgelegt von

Diplom-Biologe
André Gergs
aus Linnich

Berichter: apl. Professor Dr. Hans Toni Ratte
Universitätsprofessor Dr. Henner Hollert

Tag der mündlichen Prüfung: 7. November 2011

Diese Dissertation ist auf den Internetseiten der Hochschulbibliothek online verfügbar.

Zusammenfassung

Prädation ist in der Lage die Dynamik und Diversität in aquatischen Lebensräumen signifikant zu beeinflussen. Ziel der vorliegenden Arbeit war es daher Mechanismen von Prädationsverhalten, am Beispiel des Rückenschwimmers *Notonecta maculata*, im Kontext von Ökologie, Ethologie und Physiologie zu durchleuchten. Für ökologische und ökotoxikologische Anwendungen wurde anhand von Beobachtungen des Jagdverhaltens individueller Rückenschwimmer ein Prädationsmodell entwickelt, parametrisiert und evaluiert. Hierzu wurden verschiedene wissenschaftliche Fragestellungen in einem iterativen Prozess der Modellentwicklung betrachtet.

Zunächst wurde der ökologischen und ökotoxikologischen Relevanz der Prädation juveniler Rückenschwimmer nachgegangen. In einem Laborversuch wurde die Populationsdynamik von *Daphnia magna* unter Prädationsdruck, unter Exposition eines Xenobiotikums sowie einer Kombination beider Stressoren beobachtet. Im Versuch resultierte das größenselektive Fressverhalten der Rückenschwimmerlarven in einer Veränderung der Daphnien-Populationsstruktur, die wiederum zu einer gesteigerten Sensitivität der Population gegenüber dem Xenobiotikum führte.

Dieser Versuch warf die Frage nach der funktionelle Reaktion und Größenselektivität der Rückenschwimmer und deren Änderung mit dem Larvenstadium der Räuber auf. Ökologische Faktoren welche die Beuteselektion der Rückenschwimmer beeinflussen wurden in Laborversuchen quantifiziert und flossen in die Parameterisierung eines Individuenmodells zur Vorhersage von Prädationsraten ein. Der Vergleich von Modellvorhersage mit unabhängigen Daten aus Laborversuchen legte nahe, dass die Größenselektivität der Rückenschwimmer eher passiver Natur ist und nicht auf der aktiven Auswahl einer bestimmen Beute beruht.

Die Anwendung des Modells offenbarte Unterschiede in den Prädationsraten von Rückenschwimmerlarven zwischen Tag- und Nachtbedingungen. Diese Unterschiede konnten auf Faktoren zurückgeführt werden, die den Beutefang beeinflussen, nicht aber auf einen endogenen zirkadianen Rhythmus. Verhaltungsbeobachtungen ließen den Schluss zu, dass Rückenschwimmer im Dunklen ihre Beute später detektieren als im Hellen und dies

möglicherweise während einer intensiveren Handhabung der Beute kompensieren. Ein Vergleich der Vorhersage des re-parameterisierten Modells mit unabhängigen Daten zur funktionellen Reaktion stütze diese Annahme.

Um der Variabilität von Nahrungsverfügbarkeit gerecht zu werden und damit Langzeitvorhersagen zu ermöglichen, wurde das Prädationsmodell um eine physiologische Komponente erweitert. Hierzu wurden beobachtete Verhaltensmuster im Jagdverhalten der Rückenschwimmerlarven mit der Füllung von Darmkompartimenten korreliert. Es zeigte sich, dass gehungerte Räuber ihre Beute häufiger angreifen und mehr Biomasse aus gefangen Beutetieren extrahieren. Modellanalysen verdeutlichten, dass Rückenschwimmer durch Änderungen im Fressverhalten zu einem gewissen Maße in der Lage sind suboptimale Umweltbedingungen zu kompensieren.

In der vorliegenden Arbeit wurden proximale Faktoren des Beutefangs juveniler Rückenschwimmer identifiziert und in ein Simulationsmodel überführt. Das entwickelte Modell ist geeignet die Größenselektivität und Langzeitprädationsraten der Rückenschwimmer unter Laborbedingungen vorherzusagen. Eine wichtige Aufgabe für die Zukunft ist die Generalisierung der Modellstruktur und der integrierten Mechanismen zur Anwendung auf andere Arten.

Abstract

Predation is considered to significantly alter dynamics and diversity of aquatic communities. The current thesis was therefore aimed at assessing mechanisms behind the predation by the backswimmer *Notonecta maculata* in the context of ecology, ethology and physiology. Moreover, a foraging model was developed, parameterized and evaluated on the basis of individual foraging behaviour, for application in ecology and ecotoxicology. An iterative process of model development thereby provided insights into several research questions.

In a first step the ecological and ecotoxicological relevance of backswimmer predation was examined. Therefore, population dynamics of *Daphnia magna* was observed under predation pressure, xenobiotic stress and a combination of both predation and chemical disturbance.
The experiment revealed that size selective predation of the backswimmers did alter population demography, which in turn led to higher vulnerability of *D. magna* population to toxic stress.

The results mentioned above have raised the question to what extend the functional response and size selectivity of juvenile backswimmers changes with predator instar. Therefore, ecological parameters that were considered influential in prey selection were quantified experimentally and subsequently led to the parameterization of an individuals model to be used for the prediction of predation rates. Testing the model against independent data revealed that prey selection in backswimmer might not be determined by active preference, but by passive selectivity mediated by variations in the components of predation.

Application of the model revealed that predation rates in juvenile backswimmers are reduced under dark conditions compared to light. These differences are accounted for by the presence/absence of light and are not regulated by any endogenous circadian rhythm. Behavioural observations led to the conclusion that in the dark backswimmers probably detect prey items at a shorter distance as compared to light and that the resulting reduction in the encounter rate is compensated by gaining a higher amount of food per item during a lengthier, more thorough handling of the prey. Comparing model output to independent functional response data did support this hypothesis.

In order to account for variations in food availability, and thus allow for long term prediction of predation rates, the model was extended by a physiological component. Therefore, behavioural observations on the components of predations were correlated with gut state of the predator. Moreover, the empirical results showed that food-deprived backswimmers attack their prey more frequently and that they extract more biomass from a single prey item than their well-fed conspecifics do. Model application provided further evidence for compensatory feeding under variable environmental conditions.

In the current study, proximate factors in the foraging behaviour were identified and implemented in a simulation model. The model developed here is able to adequately predict size selectivity and long term predation rates of juvenile backswimmers under laboratory conditions. A major future task will be the generalization of mechanistic rules that will allow predictions for a broad range of species.

Table of content

Chapter 1 ..... **1**

General introduction

1.1 Scope of the thesis **1**

1.2 On the taxonomy and ecology of backswimmers **3**

1.3 Structure and aims of the thesis **4**

Chapter 2 ..... **7**

Size selective predation alters Daphnia magna population response to toxic stress

2.1. Introduction to the topic **7**

2.2 Materials and Methods **9**

2.2.1 Test animals 9

2.2.2 Experimental setup 9

2.2.3 Sampling procedure 10

2.2.4 Nonylphenol exposure 11

2.2.5 Statistical data analysis 11

2.3. Results **11**

2.3.1 Control populations and food resource 11

2. 3.2 Effect of predation stress on abundance and population structure 12

2.3.3 Effect of toxicant stress on abundance and population structure 13

2.3.4 The combined effects in comparison to single stressors 14

2.4. Discussion **16**

2.4.1 Relevance and realism of the study 16

2.4.2 Interaction of size selective predation and intraspecific competition 17

2.4.3 Timing of exposure 19

2.4.4 Basic problem formulation for model development 20

Chapter 3 ..... **21**

Predicting functional response and size selectivity

3.1. Introduction to the topic **21**

3.2 Material and Methods **22**

3.2.1 Video experiments 23

3.2.2 Examination of test vessels, functional response and size selectivity 25

3.2.3 Statistical data analyses 25

3.2.4. Implementation, model evaluation & sensitivity analysis 26

3.3 Results and model description **27**

3.3.1 Purpose of the model 28

3.3.2 State variables and scales 28

3.3.3 Process overview and scheduling 29

3.3.4 Design concepts 29

3.3.5 Initialisation 30

3.3.6 Submodels 30

3.3.6.1 Encounter rate 31

3.3.6.2 Attack rate 34

3.3.6.3 Success rate 35

3.3.6.4 Handling time 35

3.3.7 Sensitivity analysis 36

3.3.8 Predation experiments 39

3.3.9 Model Predictions 41

3.4 Discussion **42**

3.4.1 Parameterisation 42

3.4.2 Sensitivity analysis 44

3.4.3 Model structure 44

3.4.4 Model predictions 46

3.4.5 Limitations of the current modelling approach 47

Chapter 4 ..... **49**

Diurnal and nocturnal functional response considered as a consequence of shifting predation behaviour

4.1 Introduction to the topic **49**

4.2 Material and Methods **50**

4.2.1 Predation experiments 51

4.2.2 Statistical data analysis 52

4.2.3 Model application and analyses 53

4.3 Results **53**

4.4 Discussion **57**

Chapter 5 ..... **61**

Modelling hunger dependent predation behaviour: The role of body size, gut constraints and the interplay between attacking and handling prey

5.1 Introduction to the topic **61**

5.2 Material and Methods **65**

5.2.1 Model description 65

5.2.1.1 Purpose 66

5.2.1.2 State variables and scales 66

5.2.1.3 Process overview and scheduling 68

5.2.1.4 Design concepts 68

5.2.1.5 Initialisation 69

5.2.1.6 Submodels 70

5.2.1.6.1 Encounter 70

5.2.1.6.2 Prey size and extractable food 70

5.2.1.6.3 Gut model 71

5.2.1.6.4 Attack rate 73

5.2.1.6.5 Handling time 73

5.2.1.6.5 Digestive pause 74

5.2.2 Experiments for parameterisation and model testing 74

5.2.2.1 Measurement of Daphnia and Notonecta body weight 75

5.2.2.2 Predation experiments 76

5.2.3 Implementation and statistical analyses 78
5.2.3.1 Data analysis 78
5.2.3.2 Calibration and model testing 78
5.2.3.3 Sensitivity analysis 78

5.3. Results 79
5.3.1 Parameterisation and calibration of the model 80
5.3.2 Model evaluation 85

5.4. Discussion 87
5.4.1 Design concepts and parameterisation 88
5.4.1.1 Attack rate and handling time 88
5.4.1.2 Two compartment gut 90
5.4.1.3 Gut capacity, gut passage rates and satiation 91
5.4.1.4 Plug flow mode of gut passage 92
5.4.1.5 Prey size and predator size 93
5.4.2 Model application 93
5.4.3 Limitations and future challenges 95

Chapter 6 98
General conclusion

References 100
Publications 119
Acknowledgement 120
Curriculum Vitae 121
Appendix 122

Chapter 1

General introduction

1.1 Scope of the thesis

Predation is a major factor controlling dynamics and structure of natural communities. Despite or because of its pervasive role, definitions of predation are subject to diverse discussions. A variety of interactions is usually considered as predation, including true predation, forms of parasitism and herbivory (Begon and Mortimer, 1981). In most, if not all, cases individuals harm or kill organisms in a lower trophic level for food, whereat energy or matter flows from one organism to another (Taylor, 1984). Within the current thesis, the concept of predation is reduced to the most basic definition of one animal foraging on another, concluding with the death and possibly the consumption of the prey. This restriction, to the possibility of consumption, accounts for prey items that might be discarded without being eaten (Curio, 1976), a facet of predation that is touched upon in this thesis.

Predation and its counterpart predator avoidance are clear behavioural acts, and stand thus in contrast to other biological interactions, that passively emerge from their ecological consequences, e.g. competition (Taylor, 1984). Behavioural studies on predator-prey interactions did mainly focus on the prey's risk of predation while treating the predator as a fixed entity (Lima, 1985; Rinke and Petzoldt, 2008). The contribution of predator behaviour to the predator-prey interaction has thereby largely been ignored (Lima, 2002). From a predator's perspective, predator-prey dynamics are traditionally assessed on population level or on the level of individuals, referred to as numerical response and functional response respectively (Solomon, 1949). Regarding this dichotomy, Hassell (1966) argued that some numerical responses by predators are long-term and thus might be termed the intergeneration

response whereas behavioural responses are observable within one generation of the predator. Partly as a consequence of the author's suggestions, in ecology, short-term behavioural responses are often categorized as functional response (Taylor, 1984).
For decades, scientists have attempted to reduce the complexity of predator-prey interactions to mathematical equations in order to analyse or predict numerical and functional responses, of which the formulations of Volterra (1926) and Holling (1959a, 1959b) are probably the most famous ones. These differential equation models often lump individuals together under the assumption that they can be described by a single state variable (Houston et al., 1988). However, differences between individuals as well as complex population interactions cannot be addressed by simple state variable models (Grimm, 1999). Curio (1976) visionary stated that once behavioural mechanisms are successfully assimilated in ecological models, predator-prey models will gain in realism, precision and generality.

Individual-based modelling and ecology has opened the opportunity to account for individual properties and adaptive behaviour in ecological model formulations (Grimm and Railsback, 2005). Individual-based models usually simulate populations on the base of individuals represented by discrete agents that are equipped with a set of specific traits (DeAngelis and Mooij, 2005). Therefore, basically, agents interact with their environment, which includes the habitat and other individuals, and population dynamics emerge from individual properties as well as from interactions.
Kaiser (1983) demonstrated that the interaction of individuals with their environment also has consequences for functional responses of predators and thus individual searching behaviour has to be incorporated in predator-prey models. Accordingly, the individuals approach applied in the current thesis will consider mechanisms behind predation behaviour, variations in individual properties and the unique history of interactions in each individual predator. There will, however, no population dynamics emerge from the presented model framework, since the assessment of numerical responses is beyond the scope of the thesis. The model will therefore be referred to as an individuals model rather than an individual-based one.

In this context, *Notonecta maculata* (Fabricius) specimens foraging on *Daphnia magna* (Strauss) specimens were chosen as the predator-prey interaction to be investigated in the current study. The thesis will mainly focus on the predator's contribution to the interaction, while the daphnid prey is rather passively involved. Predators of the genus *Notonecta* were frequently employed as model organisms for investigating optimal foraging, gut constraints,

functional responses and selective predation or for directly observing components of predation behaviour (Cook and Cockrell, 1978; McArdle and Lawton, 1979; Sih, 1980; Giller, 1980; Scott and Murdoch, 1983; Streams, 1982, 1994); but also their capability of significantly affecting dynamics and diversity of aquatic communities has been demonstrated under field and semi-field conditions (Blaustein et al., 1995; Arner et al., 1998; Hampton et al., 2000; Gilbert and Hampton, 2001; Eitam and Blaustein, 2010).

1.2 On the taxonomy and ecology of backswimmers

Backswimmers swim upside down, hence their vernacular name. The insects belong to the infraorder of Nepomorpha, usually referred to as the true aquatic bugs, and the family of Notonectidae. With about 370 species described for temperate as well as tropical areas of the world, Notonectidae is one of the larger nepomorphan families (Niesser, 2004). The family embraces two subfamilies that are presently recognized in Europe, the Anisopinae and the Notonectinae, representing a single genus respectively. While *Anisops sardeus* (Herrich-Schaeffer), the sole species within its genus in Europe, is described only for Mediterranean countries, species of the genus *Notonecta* are widespread found with the exception of Iceland (Hutchinson, 1933; Visser and Veldhuijzen, 2003).

Backswimmers are abundant predators of ponds, small lakes and backwaters of streams (Visser and Veldhuijzen, 2003). Utilizing a sit-and-wait type of predation, notonectid predators usually attack prey, including aquatic and terrestrial ones trapped on the water surface, from perch sites at the water surface or submerged structures (Martin and López, 2004). As common in Nepomorpha, Notonectidae have life cycles consisting of an egg stage, five larval instars and the adult stage (Savage, 1989). Within the five larval stages of *Notonecta*, early instars usually favour small crustacean prey (Giller, 1986) whereas later juvenile instars and adults were observed to forage on other insects (Giller and McNeill, 1981), on large *Daphnia* and small fish (Dahm, 1972) as well as on conspecifics (Streams, 1994). In a comparative study of backswimmer species, Giller and McNeill (1981) found *Notonecta maculata* specimens preferring open surface waters, showing a large reaction area of predation, a high capture rate and a rapid extraction of prey items, and thus were referred to as opportunistic predators.

Species of the genus *Notonecta* are usually considered univoltine, i.e. they reproduce once per year (Tachet et al., 2002). However, various oviposition strategies were observed in different *Notonecta* species, summarized by Jordan (1960) as follows. Most of the *Notonecta* species studied by the author place their eggs on or in plant tissue, whereas *N. viridis* (Latreille) additionally and *N. maculata* exclusively stick eggs on stones. As a consequence, *N. maculata* shows a strong preference towards aquatic habitats with solid stone substrates and tend to avoid muddy ponds (Briers and Warren, 2000). In all of the native backswimmer species examined by Jordan (1960), the life-cycle usually starts in spring, with the larval development lasting until late summer. Most of the species are overwintering as adults and reproduction is taking place in spring. In contrast, in *N. maculata* adults, oviposition starts in autumn and survivors are able to continue reproduction in spring. In colder regions, *N. maculata* exhibits a single generation per year as e.g. shown for Sweden (Svensson et al. 2000), while in warmer regions, autumn and spring hatchlings develop in distinct generations, and thus can be considered a bivoltine species (Cayrou and Céréghino, 2005).

The ecology of backswimmers, in particular feeding habit and type of reproduction, as described above bears some implications for culturing notonectids in the laboratory as described in the appendix, as well as for the design of experiments and model development.

1.3 Structure and aims of the thesis

The thesis is organized in six chapters: the ongoing general introduction, four chapters dedicated to particular research questions (Chapters 2-5) and a general conclusion. Each of the four research chapters has its own introduction in order to provide background information on the particular topic. To avoid extended repetitions, material and methods are described in detail only once and will be outlined briefly in subsequent chapters when applied. Moreover, results are presented and discussed also separated by chapters. References cited within the six chapters are jointly listed. Data gathered during this study is given in the appendix.

The overall aim of the thesis is to elucidate mechanisms behind the predation of the backswimmer *N. maculata* in the context of ecology, ethology and physiology and to develop, parameterize and evaluate a model that will allow long-term prediction of predation rates on the basis of individual predation behaviour.

The model is build along a general modelling cycle based on three elements, namely development, analysis and application, as suggested e.g. by Schmolke et al. (2010). Model development includes the problem formulation, the model design and implementation as well as the parameterisation and calibration of the model, while sensitivity analysis, verification and testing are essential parts of the model analysis.

The model is developed and analysed in iterations of the modelling cycle, since model applications raised new questions that have to be answered in order to reach the overall aim of the study. Therefore, each of the four topics presented in Chapters 2-5 is dedicated to:

a) specified research questions
b) particular tasks in the development of the model

Chapter 2

a) How will predation by backswimmers affect the dynamics and structure in laboratory populations of *Daphnia magna*? Will size selective predation have an effect on the population response to toxic stress? Which role does the timing of exposure play for the magnitude of the toxic effect?
b) The laboratory study presented in Chapter 2 is dedicated to problem formulation. Moreover, the results of *Daphnia magna* population experiments will provide a dataset for model testing in future ecological and ecotoxicological modelling approaches.

Chapter 3

a) How will patterns of functional response and size selectivity differ across *N. maculata* instars? Do direct observations allow the separation of quantifiable components in the predation behaviour? In which way do these components of predation contribute to differences in observed functional responses and size selectivity? Is size selectivity in backswimmers a consequence of active preference or passively mediated by variations in the components of predation?
b) Based on behavioural observations, an ecological framework is developed in order to predict short-term functional responses and size selective predation in the five larval instars of *N. maculata*.

Chapter 4

a) Are there any differences in the backswimmers' rate of predation under light and dark experimental conditions? If any differences occur, which proximate factors are involved in nocturnal functional responses? How does the absence of light affect components of predation?
b) The ecological framework developed in Chapter 2 is adapted to the dark in order to allow the prediction of functional response under variable light conditions.

Chapter 5

a) How does predation behaviour change with hunger level? Are backswimmers capable of compensatory feeding? What roles do predator body size and gut constraints play in patterns of hunger-dependent predation?
b) The ecological model framework as developed in previous chapters is linked to a physiological model that describes the internal processing of food in order to allow long-term prediction of notonectid predation rates.

Chapter 2

Size selective predation alters *Daphnia magna* population response to toxic stress

2.1. Introduction to the topic

In ecotoxicology an enormous number of laboratory studies were published which were aimed at assessing the effects of pesticides or other toxicants on individual level as reviewed by Stark and Banks (2003). Most of these studies described dose response relationships for acute mortality or sublethal endpoints. In order to reduce variation, test systems were standardized in terms of age, size or weight of the test organism involved and the overall experimental conditions. However, the extrapolation from effects on the individual to higher levels of biological organization, i.e. the population or the community, bears difficulties related to secondary effects and thus might hamper the extrapolation from laboratory to field conditions (Seitz and Ratte, 1991).

In field populations, abundance and demography usually differ in space and time as a consequence of variations in food supply or physical and chemical properties of the habitat as shown for the example of *Daphnia* species (Seitz, 1980 a, b). Processes relevant for the assessment of toxicant effects on population level therefore include e.g. maturation (Reynaldi et al., 2006) or intraspecific competition for food (Liess, 2002). Since individual susceptibility to a toxicant might differ across life stages or body sizes, population structure and the timing of exposure is considered of particular importance for the response of populations to toxic stress (Stark, 1999).

Changes on community level, with regard to species composition and abundance of organisms at different trophic levels, were observed following pesticide exposure in mesocosms (Friberg-Jensen et al., 2003; Wendt-Rasch, 2003) and in natural streams (Liess and von der Ohe, 2005). Community processes that were suggested to alter the magnitude of

toxicant effects include parasitism (Coors and de Meester, 2008; Macrogliese et al. 2009), the presence of predator kairomones (Hanazato and Dodson, 1992; Hanazato et al., 2001) and predation (Schulz and Dabrowski, 2001; Beketov and Liess, 2006). In *Daphnia*, predator conditioned culture medium or the presence of predators did alter egg size (Dodson and Havel, 1988) and resulted in a higher age at maturity (Coors et al., 2004) as well as in smaller clutch sizes (Hanazato and Dodson, 1992). However a rapid juvenile development and a high reproductive output were also observed (Black, 1993). Laboratory studies applying artificial predation by manually removing fixed portions of prey populations observed alterations in prey abundance (Beketov and Liess, 2006) and species composition (Milbrink and Bengtsson, 1991) as well as a delay in the time to recovery after insecticide pulse exposure (Liess and Foit, 2010). Predation and competition were therefore assumed to not be mutually exclusive but to interact in the communities investigated.

Predators tend to specialize on particular sizes or developmental stages in their choice of prey types (Brooks and Dodson, 1965; Campbell 1991). Such size selectivity was frequently found in fish (Zaret and Kerfoot, 1975; Newman and Waters, 1984; Hansson et al., 2007) and invertebrate predators (Pastorok 1981, Murtaugh, 1981; Reynolds and Geddes, 1984; Diguez and Gilbert 2003). Predation on zooplankton has been typically classified corresponding to gape-limited, visual predators (usually vertebrates) which remove the most eye-catching large prey and size-dependent (invertebrate) predators which are unable to handle larger prey and thus extensively feed on smaller species (Greene, 1983). The outcome of predation has also been shown to vary with predator size (Thompson, 1975; Yen, 1983; Paradis et al., 1999; Scharf et al., 2000). Changes in size selectivity and functional response during life history were reported in insect predators of the genus *Notonecta* (Fox and Murdoch, 1978; McArdle and Lawton, 1979; Scott and Murdoch, 1983).

The present study was aimed at assessing single and combined effects of toxicant pulse exposure and predation on the abundance and the size structure of *Daphnia magna* populations. Special attention was drawn to changes in the size selectivity during the predator's life history, the consequences of intraspecific competition within the prey population and the timing of exposure.

2.2 Materials and Methods

Population dynamics in *Daphnia magna* were investigated under pulsed stress of p-353 nonylphenol, under predation pressure and a combination of both, toxic stress and predation by *Notonecta maculata* juveniles.

2.2.1 Test animals

The test was carried out using *Daphnia magna* (clone 5) which had beencultured at the RWTH Aachen University for more than 10 years prior to this experiment. Individually reared *D. magna* received suspensions of the green algae *Desmodesmus subspicatus* ((Chodat) Hegewald & Schmidt) as food source thrice a week (0.1 mg carbon (C)/daphnid) complemented by *Saccharomyces cerevisiae* (Meyen ex Hansen) (0.8 mg C /daphnid) once a week. Algae were derived from log-phase batch cultures grown as described by Kuhl (1962) and were centrifuged and re-suspended in the *Daphnia* culture medium prior to feeding. *Notonecta maculata* specimens were cultured as described in the Appendix.

For culturing and experiments, animals were kept in a constant room set at 20 ± 1°C and a 16h:8h (light:dark) photoperiod. Artificial freshwater M4 was used as a medium (Elendt and Bias, 1990).

2.2.2 Experimental setup

The *Daphnia magna* population experiment was conducted under semistatic conditions using 20 l glass aquaria. Replicate populations (n = 3) were initiated with 5 adults (21-28 days old) as well as 10 third brood neonates (< 24 hours old) and were fed with *D. subspicatus* in a concentration of 6 mg C per day and population until day 10, 15 mg C per day and population until day 21 and 12 mg C per day and population from day 22. Food was provided daily on working days with the amount of algae tripled on Fridays. The development of populations exposed to a control and three disturbance scenarios was observed during a period of 78 days. In all aquaria dead daphnids, carcasses, aborted or ephippial eggs and deposed algae were removed weekly using a suction hose and half of the medium was renewed.

Disturbance triplicates were either exposed to single *N. maculata* juveniles (N), to two pulses of p-353 nonylphenol (Np) or to the combination of a single backswimmer and nonylphenol

(Np-N). Backswimmers were placed in the prepared aquaria at *Daphnia* peak abundance on day 34 of the experiment, one day after hatching and then grew from first to fifth instar (N1-N5) during the remaining period of the test. *N. maculata* juveniles were controlled daily and dead ones were replaced by individuals of the same age. Backup nototectids, which hatched on the same day as the specimens used in the test, were kept individually in 100 ml vessels and were fed *ad libitum* using *D. magna*.

Two two-day nonylphenol pulse exposures were initiated on day 41 and day 69 respectively. For nonylphenol treatment a nominal concentration of 0.1 mg/l was chosen, which is close to the 48 h-EC50 value for *D. magna* neonates (Preuss, 2007).

2.2.3 Sampling procedure

Control and treatment populations of *D. magna* were sampled weekly at the beginning of the experiments and up to three times per week after the introduction of backswimmers. For the quantification of abundances and size distribution of *D. magna* populations, a sample of 2 l was obtained from each aquarium by taking 28-30 subsamples in a predefined pattern. In preliminary tests using different *Daphnia* densities, the pattern chosen was found to provide reliable estimates of the actual population size. For sampling, a plastic tube with a length of 30 cm and a diameter of 2 cm was employed. One end of the tube was sealed, but a small opening allowed air to leave the cylinder when vertically plunge the device into the water column. The removal of enclosed *Daphnia* and water column from the aquaria was possible by closing the upper opening using a finger. The device was replaced after sampling aquaria that were treated with nonylphenol. *Daphnia* samples were sieved (300 µm mesh), transferred to petri dishes and were returned to the aquaria after scanning (Canon CanoScan 8800F, 1200 dpi). Daphnids were counted and body lengths of individuals (excluding spine) were measured using a digital image analyzing program (Preuss, unpublished).

Density of algae cells was measured photometrically (Hitachi 100-40, 720 nm) on eight occasions during the course of the experiment. Therefore, a sample of 50 ml of the test medium was taken from each aquarium prior to feeding with algae. Total organic carbon was estimated from the empirical regression $C = 269.73\ A / (2.76 - A)$ with A being the absorbance.

2.2.4 Nonylphenol exposure

4-(3,5 dimethyl-3 heptyl)phenol (p-353 nonylphenol) was synthesized by Preuss as described previously (Russ et al., 2005), yielding a chemical purity of > 97% (Preuss, 2008). As a carrier solvent acetone (Roth, purity 99.9%, Rotisolv-HPLC) was used. Aliquots of the p353-nonylphenol stock solution (6 mg/l) were added to 200 ml medium and steered before treating full aquaria. The final amount of Acetone in the test systems did not exceed 0.00004% by volume. Nonylphenol exposures were terminated by fully replacing media after carefully cleaning aquaria with ethanol and water. Controls and predation triplicates were treated in the same way.

2.2.5 Statistical data analysis

Total abundances of *Daphnia magna* and abundances within daphnid size classes were compared between control and disturbance scenarios. In accordance with Preuss et al. (2009) daphnids were graded into three size classes; these were neonates (≤ 1.3 mm), juveniles (> 1.3 and ≤ 2.6 mm) and adults (> 2.6 mm). Differences in daphnid abundances and algae density were tested for each sampling date by means of a one-way analysis of variance (ANOVA) with subsequent Tukey-HSD posthoc analysis, since homoscedasticity was proved by Levene's-test for most of the data. Statistical analyses were conducted using PASW Statistics 18 (SPSS Inc., 2009).

2.3. Results

In the current section results of the population experiment were presented in a way that allows the comparison of single treatments to control as well as of combined stressor systems to single stressor triplicates.

2.3.1 Control populations and food resource

Size of *Daphnia magna* populations increased during the first four weeks of the experiment. After reaching maximum abundance at day 34, the total number of daphnids decreased and control triplicates leveled off after reaching environmental capacity at a mean density of 113.4 ± 31.49 (mean ± standard deviation) individuals per liter (Figure 2.1). Similar to total abundance, the number of neonate and juvenile peaked and thereafter leveled off at a mean

density of 8.7 ± 4.89 and 65.4 ± 20.15 individuals per liter respectively. In contrast, the number of adults steadily increased with time (Figure 2.2). The comparison between days 41/46 and days 69/74 revealed that the size structure of control populations had changed during the course of the experiment (Figure 2.3).

Density of algae that were not consumed decreased during the time course and reached a plateau on day 28 at a mean of 0.014 ± 0.0042 mg C per liter. No significant difference was found in the density of algae between control and treatments, with the exception of day 22 (Table 2.1).

Table 2.1: Mean and standard deviation of *Desmodesmus subspicatus* density (n = 3) given as total organic carbon [mg/l], letters indicate differences in one way ANOVA with subsequent Tukey HSD post hoc test. C: control, N: *Notonecta* predation, Np: p353-nonylphenol exposure; Np-N: combined stressor systems

Day	C	N	Np	Np-N	p
8	4.0 ± 0.29^{A}	4.6 ± 0.98^{A}	4.3 ± 1.36^{A}	4.7 ± 1.55^{A}	0.120
15	3.8 ± 1.55^{A}	6.6 ± 1.08^{A}	5.6 ± 0.42^{A}	6.1 ± 3.63^{A}	0.956
22	1.3 ± 0.2^{A}	2.6 ± 0.89^{B}	3.3 ± 1.07^{B}	4.0 ± 0.38^{B}	0.009
28	1.2 ± 0.36^{A}	1.0 ± 0.15^{A}	1.7 ± 0.06^{A}	1.3 ± 0.23^{A}	0.105
39	1.3 ± 0.71^{A}	1.4 ± 0.64^{A}	1.7 ± 0.26^{A}	2.1 ± 0.11^{A}	0.288
50	1.0 ± 0.17^{A}	1.5 ± 0.23^{A}	1.1 ± 0.21^{A}	1.2 ± 0.23^{A}	0.221
60	1.7 ± 0.11^{A}	1.2 ± 0.41^{A}	1.6 ± 0.15^{A}	1.2 ± 0.25^{A}	0.135
70	1.4 ± 0.47^{A}	1.4 ± 0.26^{A}	1.4 ± 0.64^{A}	1.5 ± 0.52^{A}	0.476

2. 3.2 Effect of predation stress on abundance and population structure

The total number of *Daphnia magna* in predation triplicates (N) did not significantly differ from control with the exception of day 43. At this point in time, a significant reduction in abundance was apparent seven days after the introduction of backswimmers into the systems (ANOVA & Tukey HSD, p = 0.036). Thereafter, between day 48 and day 68 of the experiment, total abundances of *Daphnia* slightly increased compared to control, with differences being not significant. This period hereafter is referred to as the recovery phase. Although backswimmer predation did not extensively alter total abundances, differences in the size structure of *D. magna* populations were observed. The comparison of size distribution between control and disturbed populations (Figure 2.3) suggests that small sized *D. magna* were predominantly affected by the predation of 1st instar backswimmers, however, the number of neonates did not significantly differ during the first week after introduction of

backswimmers (Tukey HSD, $p > 0.98$). In contrast, abundance of juvenile daphnids was significantly lower in predation triplicates as compared to control on day 43 (ANOVA & Tukey HSD, $p = 0.01$). Numbers of adult *D. magna* were significantly reduced from day 67 (ANOVA & Tukey HSD, $p \leq 0.001$). The lack of significant differences in total abundance between predation and control can thus be attributed to the significantly higher numbers of neonate *D. magna* from day 71.

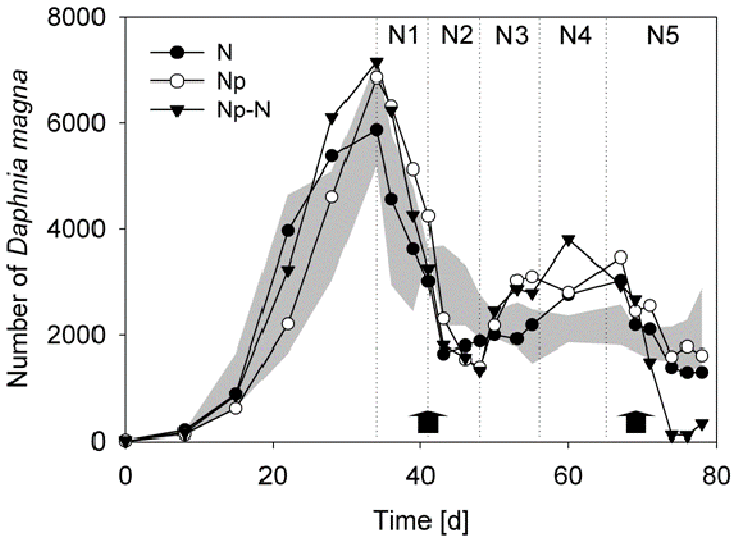

Figure 2.1: Total number of *Daphnia magna* during the course of the experiment run in 20 l aquaria. *Daphnia* populations were exposed to a control as well as to three different disturbance scenarios: pulse exposures of p353-nonylphenol (Np), *Notonecta maculata* predation (N) and a combined disturbance by means of nonylphenol and predation (Np-N). Grey shade symbolizes range of control populations, black arrows mark the initialization of two two-day nonylphenol exposure periods and dotted vertical lines indicate presence of five juvenile instars of *N. maculata* (N1-N5). Dots represent mean of three replicated measurements, standard deviations are not shown for reasons of clarity.

2.3.3 Effect of toxicant stress on abundance and population structure

The first p-353 Nonlyphenol pulse exposure resulted in a significant reduction of the total number of *D. magna* within two days (ANOVA & Tukey HSD, $p = 0.036$). Total abundance again reached control level 7 days after termination of the first Np exposure period. The second nonylphenol treatment did not have a significant effect on the total abundance of daphnids (Tukey HSD, $p \geq 0.158$).

Changes in size structure of the populations indicate that *D. magna* neonates were most severely affected by nonylphenol treatments (Figure 2.3). During the first exposure period, neonates were reduced in numbers by a factor of 12.3 and a significant difference to control was apparent three days after termination of the Np treatment (ANOVA & Tukey HSD, p =

0.002). During the recovery phase, neonate abundance increased and significantly exceeded control level from day 53 to day 60 (ANOVA & Tukey HSD, $p \leq 0.014$). The second nonylphenol treatment reduced the number of neonate *D. magna* by a factor of 5.7 (day 69 compared to day 74); however the difference to control treatment was not significant. Abundances of juvenile and adult daphnids were significantly reduced during the first nonylphenol exposure period by a factor of ~2 (ANOVA & Tukey HSD, $p = 0.01$, $p = 0.028$). Thereafter, the number of juveniles and adults did not significantly differ from control, with the exception of the last day of the experiment where a significant reduction in adult abundance was recorded (ANOVA & Tukey HSD, $p \leq 0.001$).

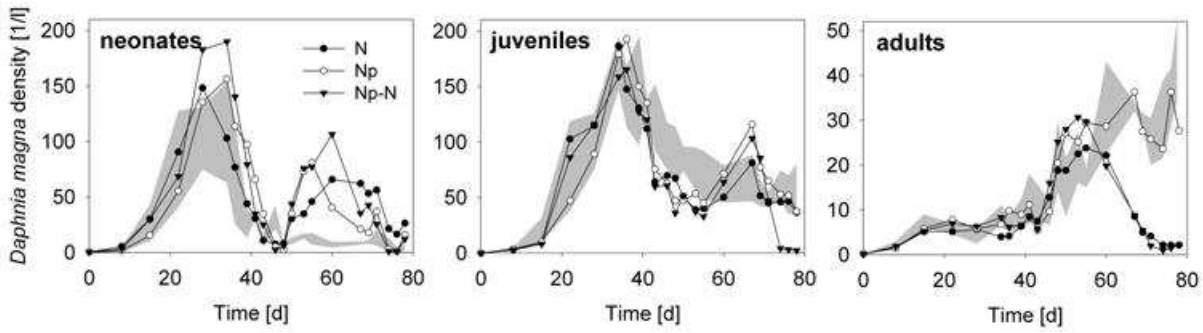

Figure 2.2: Time course of *Daphnia magna* density in populations exposed to p353-nonylphenol (Np), a single predator (N) and combination of nonylphenol and predation (Np-N). *D. magna* were classified as neonates (≤ 1.3 mm), juveniles (> 1.3 and ≤ 2.6 mm) and adults (> 2.6 mm) in order to analyze size structure of populations. For further details see Figure 2.1.

2.3.4 The combined effects in comparison to single stressors

The total abundance of *D. magna* in the triplicates exposed to both, nonylphenol and predator (Np-N) did not significantly differ from single stressors until day 74 of the experiment (Tukey HSD, $p \geq 0.065$). Thereafter the total number of *Daphnia* was significantly reduced compared to predation and nonylphenol treatments (ANOVA & Tukey HSD, $p \leq 0.022$). *Daphnia* populations in Np-N triplicates finally almost became extinct, but started again to increase in abundance in one of the three replicates on the last day of the experiment. At this point, the difference between Np-N and N was not significant possibly due to the high standard deviation (see appendix).

Following the first nonylphenol pulse exposure, the number of neonate *D. magna* in the Np-N triplicates was reduced by a factor of 13.9 (day 41 compared to day 46). The size distributions

of *D. magna* populations suggest that the effect of the first nonylphenol treatment was more pronounced in Np-N systems compared to singe stressors (Figure 2.3) however, abundances of the three size classes did not significantly differ from single stressor scenarios (Tukey HSD, $p \geq 0.06$).

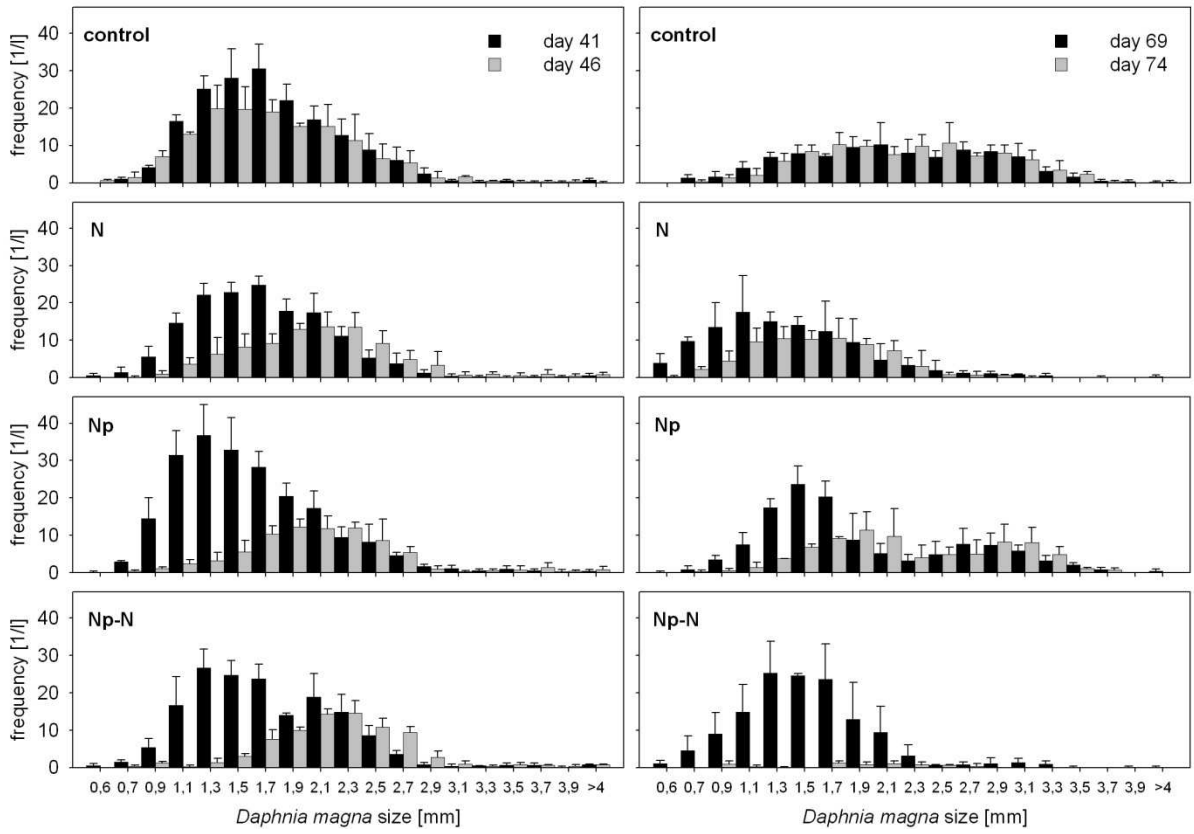

Figure 2.3: Frequency distribution of *Daphnia magna* size in a populations experiment before (black bars) and after (grey bars) the fist (left) and second (right) p353-nonylphenol pulse exposure period; bars represent mean and standard deviation of three replicates in four different treatments: control, exposure to nonylpenol only (Np), predation by *Notonecta maculata* juveniles (N) and a combination of nonylphenol exposure and predation (Np-N).

During the recovery phase, neonate numbers in combined stressor systems increased and significantly exceeded Np-level on day 60 (ANOVA & Tukey HSD, $p = 0.002$), whereas difference to predation was not significant. Following the increase in neonate abundance, in Np-N triplicates a non-significant increase in the number of juveniles was observed from day 60, whereas a reduction in adult abundance was apparent from day 67 (Figure 2.2). This decline can be attributed to the predation of large backswimmers, since significant differences between Np-N and Np (ANOVA & Tukey HSD, $p \leq 0.001$) but no significant differences between Np -N and N were found (Tukey HSD, $p \geq 0.99$).

At the instant of the initialisation of the second nonylphenol pulse exposure size structures of populations that suffered from predation deviated from those populations which were previously exposed to nonylphenol only (Figure 2.3). Neonate and juvenile *D. magna* predominantly contributed to populations under predation of large *N. maculata*, whereas large-sized *Daphnia* were almost missing. Therefore, the number of adults was significantly higher in N-systems compared to Np and Np -N (ANOVA & Tukey HSD, $p \leq 0.001$).
Similar to the first pulse exposure, small sized daphnids were most severely reduced during the second nonylphenol treatment (Figure 2.3). Neonate abundance was significantly lower in combined stressor systems compared to N-systems on day 74 and day 76 (ANOVA & Tukey HSD, $p \leq 0.007$), whereas no difference between disturbance scenarios was found for the number of juveniles. Moreover, post-treatment abundances of *D. magna* adults in Np-N aquaria were significantly lower than Np-level (ANOVA & Tukey HSD, $p < 0.001$), but no significant deviation from Np-systems was found.

2.4. Discussion

Population dynamics of the cladoceran filter feeder *Daphnia magna* were observed for different disturbance scenarios including pulse exposure to p353-nonylphenol, predation of the insect predator *Notonecta maculata* and a combination of both, toxic stress and predation. *D. magna* total abundance was not extensively affected by single stressors, whereas under predation the second nonylphenol pulse exposure did drive daphnid populations to the brink of extinction.

2.4.1 Relevance and realism of the study

Cladocerans provide an important link in aquatic food chains either as grazers on primary producers or as food for many fish species and invertebrate predators (Dodson and Hanazato, 1995; Lampert, 2006). A relatively high sensitivity towards a wide range of xenobiotic compounds was shown for cladocerans in general (Wogram and Liess, 2001) and *Daphnia magna* in particular (Canton and Adema, 1978; Tyagi et al. 2007). Therefore and for practical reasons, *D. magna* is broadly used in acute and chronic toxicity testing (Persoone and Janssen, 1993). As an endpoint of acute bioassays, the EC50 for neonate *D. magna* is frequently applied in environmental risk assessment of pesticides and industrial chemicals (Martins et al., 2007). Nevertheless, protection goals in environmental risk assessment are

formulated in a way that assures sustainability of populations rather than prevention of effects on individual level (Galic et al., 2010; Hommen et al., 2010). Since the effect propagation from individual to population level is largely unclear (Ratte, 1996; Forbes and Calow, 1999), it is assumed here in accordance with Sibley et al. (2005) that population level assessment provides a more realistic measure for responses to toxic stress.

The importance of predation in many natural communities has previously been recognized as reviewed by Jeffries and Lawton (1984) as well as by Sih et al. (1985). In particular, notonectid predators were observed to significantly affect dynamics and diversity of zooplankton communities (Blaustein et al., 1995; Hampton et al., 2000; Eitam and Blaustein, 2010) and were found to be capable of excluding large *Daphnia* species from small water bodies (Murdoch et al. 1984, Arnér et al., 1998). Under semi-field conditions, densities of *Notonecta* populations were observed to stabilize at approximately one individual per 30 l (Bay 1974), and also higher densities up to 80 individuals per m^2 were frequently found in the field (Lang 1975). It is thus assumed that the intensity of predation applied in the current study provides a realistic estimate for prey vulnerability in natural systems.

2.4.2 Interaction of size selective predation and intraspecific competition

Total abundance of *Daphnia magna* was only marginally affected by the predation of backswimmers. Similarly, laboratory populations of *Daphnia pulex* were able to persist when exposed to groups of *Notonecta hoffmani* with daphnid abundances being not significantly different to control systems (Murdoch and Scott, 1984). The authors suggested that an increase of reproductive output and individual survival enables prey populations to maintain densities and to overcome predation. There were, however, alterations in the size distribution of *Daphnia* populations during the time course of the current experiment that might explain the observed patterns by a balance between predation and competitive abilities within prey.

Deviations to the *D. magna* population structure in control systems can partly be assigned to the direct effect of size selective predation in *N. maculata* juveniles. Similar to fish, predators of the genus *Notonecta* are usually considered gape-limited, since they tend to prefer larger zooplankton prey (Milbrink and Bengtsson, 1991). Accordingly, in large backswimmers, intense predation and a preference towards larger prey did reduce the abundance of adult *D. magna* almost to extinction and thereby induced a significant shift in the size structure of

populations towards smaller daphnids. However, predator size may influence prey selection. Small notonectid instars were found to mainly forage on small prey (Scott and Murdoch 1983) and they can thus be considered to be size-dependent predators. The size-dependency in small backswimmers did result in a reduction of neonate and juvenile *D. magna*, although the impact of predation was limited due to lower feeding rates in small instars (McArdle and Lawton, 1979; Gergs and Ratte, 2009).

In addition, alterations in the size structure of *D. magna* populations can be attributed to mechanisms of inter-specific competition. A large number of neonate *D. magna* were produced when total abundance was below the carrying capacity of the experimental systems, i.e. during the initial phase of the experiment and after disturbance. As soon as the carrying capacity was reached, intra-specific competition for food and space presumably exerted a reduction in reproduction, growth and survival. Reductions in the reproductive output and survival on individual level have previously been reported for *D. magna* as a consequence of food shortage (Cox et al., 1992; Glazier, 1992; Preuss et al. 2009) and crowding (Burns, 1995; Preuss et al., 2009). On population level, here, the reduction in food and space did not lead to a rapid but a delayed decrease in *D. magna* population size after reaching peak abundances beyond carrying capacity.

In systems not preyed upon, predominantly, the number of neonate *D. magna* decreased following peak abundances. A considerable portion of neonates grew into juveniles and subsequently into adults, leading to a steadily increasing portion of large individuals. However, shifts in age structure cannot be explained from individual growth alone. A noticeable number of smaller daphnids must have died and a lower number of neonates must have been born after density reached carrying capacity. In predated systems, the removal of daphnids and the emerging surplus environmental capacity allowed a higher reproductive output for the remaining adults. Additionally, growth and survival of large daphnid individuals might have been higher under the presence of small backswimmer instars that mainly reduced the number of small daphnids. In contrast, large backswimmers predominantly reduced the number of large *D. magna* and the emerging gap in population size has been closed by newborns.

Field observations on zooplankton population dynamics similar to those found in the current laboratory study have been mechanistically been explained by size efficiency of individuals or species. According to the size-efficiency hypothesis, first proposed by Brooks and Dodson

(1965) and theoretically worked out by Hall et al. (1976), large bodied zooplankton species will out-compete small ones when predation is of low intensity. In contrast, small zooplankton will become dominant whenever predation is intense and gape-limited predators reduce large individuals. The size-efficiency hypothesis has previously been supported by empirical studies using *Daphnia* species of different sizes (Kreutzer and Lampert, 1999) as well as by physiological modelling approaches (Hülsmann et al. 2005).

2.4.3 Timing of exposure

The toxicant concentration applied in the current experiment was close to the EC50 as determined for neonate *D. magna* from 48 h acute toxicity tests using p353-nonylphenol (Preuss, 2007) or a technical mixture of nonylphenol isomers (Combera et al. 1993). The p353-nonylphenol isomer was found to act in a size depend manner, with the EC50 (48 h) being higher in juvenile and adult *D. magna* as compared to neonates by a factor of ~2.8 and ~4.1 respectively (Preuss, 2007). As a consequence, in the population experiment, predominantly small daphnids were affected by the nonylphenol pulse exposure. However, the response of the *Daphnia* populations to toxic stress differed with the timing of exposure.

The mechanisms behind this observation might be explained as follows. During the initial phase of the experiment there was a predominance of small bodied Daphnia. Therefore, the first nonylphenol pulse exposure did affect a significant portion of the population. In non-predated systems, the contribution of large bodied *D. magna* to total abundance steadily increased during the time course of the experiment. As a consequence, the proportion of small *Daphnia* that might be affected by the toxicant was lower during the second exposure period and thus toxic stress did not result in a significant reduction in population size.

In contrast, after the initialization of predation stress, small backswimmers did reduce the number of small daphnids, and only a small portion of *Daphnia* populations could thus be affected by the toxicant. Consequently, the first nonylphenol exposure did not result in a significant difference between the predated systems and the ones exposed to the combined stressor. Another possible explanation might be that nonylphenol did actually reduce small daphnids and the backswimmers had to disadvantageously switch to large prey in combined stressor systems while in predation systems, backswimmers were able to continuously feed on small prey. Predation of large backswimmers, foraging on larger daphnids, did result in a shift

in population structure towards smaller *Daphnia*. This shift caused a significant reduction of *D. magna* populations by the second nonylphenol pulse exposure.

2.4.4 Basic problem formulation for model development

Size selective predation has a considerable potential to affect *Daphnia magna* population dynamics and thus population response to toxic stress. The effects of toxicants under more complex scenarios can only mechanistically be explained when analyzing population structure. Moreover, multiple effects on population level cannot exclusively be estimated from toxicity tests done on individual level. As predation and competition is present in most natural communities and the timing of exposure is of particular importance, these factors need to be considered in laboratory test designs and whenever extrapolating toxic effects to the field.

The analysis of the combined effects like those described in the current chapter and the prediction of *Daphnia magna* population responses to predation requires a model that simulates size selectivity and long-term predation rates of backswimmers based on a mechanistic understanding of predation behaviour.

Chapter 3

Predicting functional response and size selectivity

3.1. Introduction to the topic

A predator's feeding rate as a decelerating function of food density is known as functional response. Holling (1959a, 1959b) has categorized three types of functional responses of which type II, the so-called disc equation, is the one mostly used. Type II functional responses, equal to Michaelis-Menten equation of enzyme kinetics, are applicable to most organisms which take a certain amount of time to capture and ingest food (Real, 1977). Many modifications of the type II function have been developed for modelling functional responses as reviewed by Jeschke et al. (2002). The classic equations incorporate two coefficients of predation: the rate of attacks and the time spent on handling prey. In practice, a predator-prey interaction might be more complex as the attack rate can be considered, e.g. as a function of distances at which a predator reacts by attacking prey or the proportion of attacks that are successful (Hassell et al., 1976). By separating the components of predation as pioneered by Holling (1966), Gerritsen and Strickler (1977) suggested a general predation cycle based on four conditional events, encounter, attack, capture, and ingestion. Several authors used these components of predation or a modification of the predation cycle for analyzing or modelling foraging in predator-prey interactions (Giller, 1982; Greene, 1983; Jeschke et al., 2002; Jeschke and Hohberg, 2008). Special attention is drawn to the encounter of prey including distances or fields at which a predator detects prey (Gerritsen and Strickler, 1977; Giguere et al., 1982; Rincon and Loboncervia, 1995; Muirhead and Sprules, 2003).

The outcome of predation has been shown to vary with both prey size and/or predator size (Thompson, 1975; Yen, 1983; Paradis et al., 1999; Claessen et al., 2002; Rudolf, 2008).

Selective predation occurs as the difference between relative frequencies of prey types or sizes in a predator's diet and those occurring in the predator's environment (Chesson, 1978; Cock, 1978). In many cases food selection is not determined by active preference, but by passive selectivity mediated by variations in components of predation (Pastorok, 1981; Juanes and Conover, 1994). Components of predation and thus size selectivity and functional response might change through life history of a predator (Hassell et al., 1976; Yen, 1983) and therefore led to the development of stage-structured models (De Roos et al., 2003).

Usually, the rate of attacks and the time spent on handling prey were estimated by fitting the disc equation to measurements of functional response as published for notonectid predators by McArdle and Lawton (1979) as well as Reynolds and Geddes (1984). Although the disc equation provides an adequate fit to the data it is not clear whether the coefficients of predation derived from functional response curves are reliable estimates of actual attack rates and handling times (Streams, 1994; Caldow and Furness, 2001; Tully et al., 2005).
Therefore, in the present study elements of the predation cycle were observed directly by means of video experiments. A simple individuals model was designed that describes the foraging processes by using empirically derived encounter rates, probabilities of attack and capture success as well as time spent on handling prey, without any classic functional response equations included. The results of video experiments led to the parameterisation of the model. Independent data of functional response and size selectivity experiments were used for model testing. The modelling approach presented is aimed at providing a tool for assessing and quantifying the functional response and size selectivity of juvenile backswimmers, considering ontogenic changes of both predator and prey.

3.2 Material and Methods

In the present study, all observations involved five instars of N. maculata (N1–N5) foraging on four size classes of Daphnia magna (D1-D4). For maintenance and experiments backswimmers and daphnids were kept in a 20°C climate chamber with diurnal light rhythm of 16:8 h (day:night). As a medium artificial freshwater M4 was used (Elendt and Bias, 1990). *N. maculata* specimens were bred in the laboratory and raised on daphnids. In tests backswimmer instars were used 2–5 days after moulting. In order to standardize hunger level the individually kept backswimmers were fed with a definite volume of a suspension, containing a mean number of 46 ± 8 daphnids per ml, 16–18 h before experiments were

started. Volumes of daphnid suspension provided were 0.3 ml in N1, 0.6 ml in N2, in 0.8 ml in N3, 1.2 ml in N4 and 1.5 ml in N5.

D. magna is widely employed in laboratory studies, but is also able to establish stable populations in the field. Here *D. magna* is used as a prey organism, because the species provides a wide range of prey size. Daphnids were obtained from a pond in Aachen city area which was cleaned and re-populated twice a year. Prey organisms were held under laboratory conditions for at least 24 h before being used in tests. In accordance to McArdle and Lawton (1979) daphnids were graded into four size classes using non-standard sieves. The mean total body length excluding spine measured under magnification were in ascending order D1: 0.9 ± 0.12mm, D2: 1.4 ± 0.20mm, D3: 2.3 ± 0.29mm, D4: 2.9 ± 0.24mm.

Two independent sets of experiments, video tracking on the one hand and testing of functional response as well as size selectivity on the other, were conducted for the parameterization and the testing of the model respectively. Experiments were run for 3 h and were usually started at midday in order to avoid possible diurnal variations in foraging affecting the results.

3.2.1 Video experiments

To examine whether prey size and density affect foraging of *N. maculata* juveniles, components of predation namely encounter, attack, success, and handling were directly observed and quantified by means of video experiments. A single predator and 20 daphnids were filmed in a cuvette-like aquarium (10:5:2 cm, width:height:depth), replicated three times, using a Sony DCRTRV310E video camera. The relative high number of prey organisms was chosen to initially avoid the encounter rate limiting the number of attacks. For scaling purpose millimetre paper was placed in the background of and beneath the front of the test vessel. The error caused by perspective means is less than 1%. Videos were digitalized before using in further analyses.

Generally prey encounter is equated with prey detection (Streams, 1994), but in many cases a successful attack was not initiated by any visible response of the backswimmer. Therefore, this definition does not provide a useful approach for the determination of encounter rates. Another assumption takes the distance at which a predator was observed to respond apparently to a prey as a basis for an occurring encounter (Pastorok, 1981). In this study, assuming the latter, the random encounter model of Gerritsen and Strickler (1977) was adapted in order to examine encounter rates. Consistently, an encounter is defined here as an

event when prey occurs within the predators encounter radius which is assumed to be constant in any direction.

To establish an encounter model for the predator–prey relationship *N. maculata* and *D. magna* the effect of prey density on the encounter rate was examined in a first step. The number of instances in which a daphnid enters a fixed patch of 1cm×1cm×2 cm was counted for prey densities of 1 up to 20 per 100 ml. Time intervals were chosen from 1 to 10 min at high to low densities. A daphnid may stay in or enter the patch several times due to hop and sink pattern of locomotion within the matter of seconds. In both cases a single entry was treated as one encounter. Counting was done for two next to surface patches, replicated for three consecutive time intervals per film and resulted in a mean encounter rate per prey density and second.

As a sit-and-wait predator the backswimmer in some cases pursues its prey within an encounter distance. Since the actual distance between predator and prey at the moment of attack does not represent a measure for an encounter, the predator-prey distance (d_e) was determined in the instance of a reactive encounter which resulted in a successful attack. A reactive encounter was recorded when the daphnid elicited a visible response of the backswimmer, usually a turn towards the prey. At this occasion the distance between the centre of a prey body and the head of backswimmer was measured using a digital image analysing programme developed by Preuss (unpublished). The programme was also used to measure the body length of *D. magna* in video experiments.

Number and time of successful and ineffective attacks were recorded as well as the time instars of *N. maculata* spent on handling prey. An attack was defined as a rapid acceleration towards a daphnid. A successful attack was noted when the backswimmer grasped a daphnid and held it for several seconds. The time until releasing the prey carcass was recorded as handling time. Thus, total time available for foraging (t) can be defined as the sum of time spent on handling prey (t_h) and cumulative time spent for searching prey or rather the time until the next encounter (t_e). A programme visualising an encounter area as a circle with the backswimmer at its centre allowed counting the number of prey encounter. In video experiments the encounter sphere embraced a volume of the depth of the test vessel multiplied by the circular area based on encounter radius (d_e). The attack rate (A_r), i. e. the probability of attack following an encounter, is calculated as the ratio of number of total attacks (A) and the sum of total encounter (E). To examine the effect of prey density and time the attack rate was additionally calculated per time intervals restricted by successful attacks. The probability of an attack being successful was calculated as ratio of the number of successful attacks and the sum of total attacks.

3.2.2 Examination of test vessels, functional response and size selectivity

Independent experiments were carried out to test the shape of vessels used in experiments (*I*), and to examine functional response (*II*) and size selectivety (*III*) of *N. maculata* juveniles.

(*experiment I*) Since backswimmers preferentially forage at the water surface, the effect of test vessel depth on the outcome of predation was tested in a first experiment. Two sets of 500 ml test vessels, shallow Petri dishes and cylindrical beakers, were applied. The depth of vessels used was 1.7 cm and 11.3 cm in Petri dishes and beakers respectively. Single *N. maculata* were placed in the vessels and given 80 *D. magna* of the third size class (D3). After three hours the number of prey eaten was counted as described below. The experiment was done for each of the five *Notonecta* instars and replicated five times. As no significant difference between the numbers of prey eaten was found for the two types of vessels (see results), beakers of intermediate depth were used in later experiments.

(*experiment II*) In order to examine functional responses, single backswimmers were allowed to forage on five (D1) to six (D2-D4) initial prey densities at 10, 20, 40, 80, 120 and 160 per beaker.

(*experiment III*) In size selectivity experiments the four prey size classes, 30 daphnids per class, were exposed to one juvenile *N. maculata* simultaneously. Both of the experiments were carried out in 500 ml containers with a depth of 6.4 cm and were replicated five times.

As *Notonecta* digest prey externally, the number of prey eaten was obtained by counting, in case of selectivity experiments additionally measuring size of daphnid remains at the end of the tests. Under magnification the remains could easily be distinguished from exuviae or naturally died *D. magna*. Control mortality was less than 1%, and the error due to miss-counting was higher at small *Daphnia* but less than 3%.

3.2.3 Statistical data analyses

For encounter rates differences between *Daphnia* size classes were evaluated by means of a one-way ANOVA using the daphnid density as a co-variable (ANCOVA). For analyses and model fitting the time spent on handling prey was logarithmically transformed on the base of 10. Differences in handling time across *Notonecta* instars were evaluated by means of an ANCOVA with daphnid body length as co-variable. Differences between prey size classes in attack rate and success rate as well as log transformed handling time were calculated separately for instars 1-5 using a one-way ANOVA. As the number of *Daphnia* was reduced during video experiments, the correlation between prey density and foraging components can

be analysed. With respect to the lack of variance homogeneity within single instars, experimental runs with comparable rates were clustered for analysing density effects on attack and success using a one-way ANOVA. Density related differences in time spent on handling prey were evaluated by means of an ANCOVA (co-variable: daphnid body length). The difference in the number of daphnids eaten, as examined for the two different sets of test vessels, was evaluated using a Student t-Test.

3.2.4. Implementation, model evaluation & sensitivity analysis

The source code was implemented in Delphi® using Borland Delphi® 2007 for Win32® Professional Edition. Equations of submodels were fitted by linear and non-linear regressions using SigmaPlot 8.0 (SPSS Inc. 2002). Statistical analyses were performed using the statistical package SPSS 15.0 (SPSS Inc. 2006).

The coefficient of determination (r^2) was used to assess the proportion of variance explained in non-linear regression models of attack rates and success rates. Due to its dependency on the slope of the curve the r^2 value might be small for flat increasing patterns, irrespective of low variance. Thus the X^2-test was used as a tool to assess the linear regression of log transformed handling time as recommended by FOCUS (2006). In order to evaluate the predictions of the model, regressions of observed vs. predicted data were plotted. As proposed by Piñeiro (2008)**,** additionally the r^2 value and the root mean squared deviation (RMSD) was calculated and the hypothesis that the regressions slope is equal to 1 and the intercept equals 0 was tested.

In order to identify a subset of parameters that will significantly affect the output of the model, a screening design method was used, which varies one factor per simulation run to observe the variation in the output - a so called one-factor-at-a-time (OAT) technique. Morris (1991) suggested an OAT technique for sensitivity analyses, based on the computation of each input parameter with a number of incremental ratios, called elementary effects, which are averaged to assess the overall importance of the input. As an output, the approach provides qualitative ranks of parameter importance for the model evaluated. This technique is referred to as the Morris method hereafter.

The principle of the Morris method is to evaluate which parameters may be considered important or negligible, linear and additive or nonlinear and those that may interact with other

parameters (Morris, 1991; Campolongo et al, 2007). For each of the input parameters two sensitivity measures are computed: μ estimates the overall influence and σ estimates the higher order effects of the given parameter, i.e. interactions with other parameters and/or its non-linear behaviour. Details described in Morris (1991). The experimental design of the Morris method includes randomized OAT experiments which were run using the Simulation Environment for Uncertainty and Sensitivity Analysis, version 2.2 (SIMLAB, 2010). In the experiments the impact of changing the value of each factor is evaluated. The number of model executions (n) is calculated from the product of the number of trajectories (r) and the number of model input factors (k) as: $n = r (k + 1)$. For each of the model input factors, the Morris method operates on selected levels, which correspond to different quantiles of the factor distribution. Regarding computational costs of the analysis, the lower number of input variables allowed for the application of a relative high number of levels. Therefore, the sensitivity analysis was done using 8 random levels chosen from 13 parameters, generating 70 sample experiments.

Further sensitivity analyses were carried out in four ecological parameters, these were the encounter distance (d_e), the attack rate (a_r), the success rate (s_r) and the handling time (t_h), by gradually changing values to test their effect on the output of interest in the models.

3.3 Results and model description

As a result, the development of the foraging model is described in six sections according to the ODD procedure proposed by Grimm et al. (2006). In a first step, the outcome of the video tracking experiments led to a two-dimensional encounter model and the parameterisation of individual properties of the backswimmers, both described as submodels. In a second step, results of functional response and size selectivity experiments were compared to the model predictions. The effects of prey size, density and time upon predation elements as well as the model itself were evaluated.

3.3.1 Purpose of the model

The model was developed to predict functional responses and to assess whether the combination of foraging elements chosen account for the size selectivity of juvenile backswimmers. At a later stage, this model might be integrated into an individual-based model, which is designed to appraise the effect of food limitation on the larval development of *Notonecta maculata*.

3.3.2 State variables and scales

The model is arranged in three hierarchical levels: ecosystem, population, and individuals as proposed by Preuss et al. (2009). The ecosystem level features the volume of the test vessel in laboratory scale. Further properties like temperature and light are assumed to be constant and are not considered yet. The state of the daphnid population is defined as the abundance of *Daphnia* which is not allowed to change by natural means but fed on by backswimmers. In the current state of the model the *Notonecta* population is restricted to a single backswimmer.

Table 3.1: State variables ecological parameters of the model

State variable	Abbreviation	Unit	Dependency
Ecosystem			
Total volume	v	ml	test vessel
Population			
Number of *Daphnia*	n_d	number	
Number of *Notonecta*	n_n	1	
Individual Daphnid			
Identification number	ID_d	number	initial number of daphnids
body length	s	mm	
Size class	sc	1, 2, 3, 4	
Alive	al	yes/no	
Individual Notonecta			
Identification number	ID_n	number	Monte-Carlo simulations
Instar	I	1, 2, 3, 4, 5	
Encounter distance	d_e	cm	I
Attack rate	a_r	0,….1	I, s
Success rate	s_r	0,….1	I, s
Handling time	t_h	sec	I, s

The interaction between individual backswimmers and daphnids is feeding. All individuals of both backswimmers and daphnids are characterized by a number of state variables at the start of the simulation. *Daphnia* properties are the identification number, the body length, and the corresponding size class. The instar, encounter distance, and handling time are fixed parameters while attack- and success-coefficients are individual variables of backswimmers. The probability of attack and success as well as the time spent on handling depend on the body length of the encountered daphnid. An overview of state variables and units are given in Table 3.1.

3.3.3 Process overview and scheduling

The model proceeds in discrete time steps on the base of seconds following a general predation cycle divided into four stages (Figure 3.1). (1) A daphnid is randomly chosen from the population and the time until an encounter occurs, is being calculated on the base of the volume of the test vessel and the population size of *Daphnia*. (2) The probability of attacking the selected daphnid is being calculated. In case of a successful attack (3) a certain time for handling prey is being calculated and the daphnid eaten is being removed from the population (4). In functional response simulations the predation cycle is run for a number of Monte-Carlo simulations before increasing the density of prey.

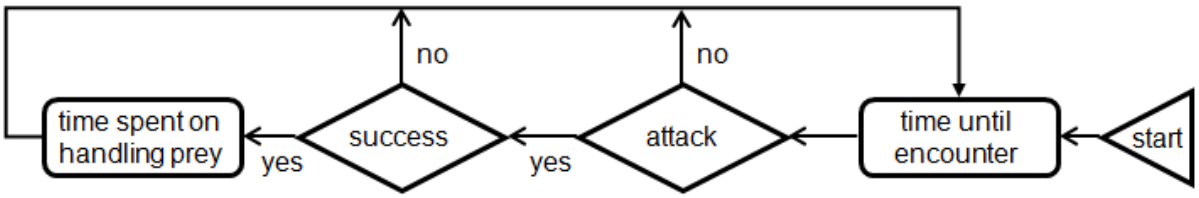

Figure 3.1: Conceptual diagram of the model on the base of a general predation cycle divided into four stages. The rectangles indicate the partition of time available for foraging whereas rhombi illustrate individual level queries.

3.3.4 Design concepts

Although abundance of *Daphnia* depends on individual foraging of backswimmers, population dynamics do not emerge from any individual properties at this stage of the model. An adaption or fitness seeking is not explicitly modelled, but is included in the empirical submodels. Environmental and population level factors sensed by *Notonecta* are the number

of prey available per volume, included as the actual concentration of *Daphnia* in the encounter submodel. Individual state variables influencing the response of the backswimmers are their instar and the body length of the daphnids encountered. Except for the predator-prey relationship no direct interactions between individuals are taken into consideration.

Each daphnid owns an individual body length which is stochastically selected from a normal distribution. Variations in attack rates and success rates of *N. maculata* individuals are generated by a normal distribution with the mean of 1 and the coefficient of variation resulting in an individual parameter multiplied with the mean rate calculated from submodels. The decision whether an encounter provokes an attack, or whether the attack is successful, is based on two random numbers between 0 and 1 selected at every encounter. The attack or the success is rejected in case of the calculated rate exceeding the random number. The time spent on handling prey is calculated for every daphnid grasped, using a normal distribution. The stochastic approach considers the natural variability in individual handling time, attack and success observed in video tracking experiments.

Per scenario, 100 Monte-Carlo simulations were run in order to examine individual variability. For model analysis the number of prey eaten or rather the number of prey removed from population were recorded as arithmetic mean, minimum, and maximum in every simulation run. In case of size selectivity simulations the size classes of *Daphnia* eaten were recorded additionally.

3.3.5 Initialisation

Each simulation was evaluated for prey densities tested in laboratory experiments. The initialisation of settings comprises the notonectid instar and daphnid size class, the volume of the vessel, prey abundances tested, simulation time and the number of Monte-Carlo runs. No additional input is necessary during the simulation.

3.3.6 Submodels

Equations of submodels described as follows were derived empirically from video experiments as shown in Figure 3.2 and 3.3. Parameters of equations and variability coefficients used in modelling individual foraging of backswimmers are listed in Table 3.2.

Table 3.2: Ecological and mathematical parameters of individual *Notonecta* including coefficients of variability (CV) used in modelling processes.

Process	Parameter					
	N1	N2	N3	N4	N5	CV
Attack rate						
A_a	7	11.2	5.4	8.2	9.7	
A_b	0.4	0.16	0.165	0.23	0.21	
A_{x0}	0.7	1.58	1.93	2.04	2.06	
A_{y0}	3.2	1.2	1.6	1.2	0.4	
Equation	(4)	(4)	(4)	(4)	(4)	0.54
Success Rate						
S_a	38.3	54.5	116.54	58	85	
S_b	-0.1	-0.437	0.705	0.42	0.275	
S_{x0}	2.05	2.212	1.736	2.3	1.38	
S_{yo}	2.8	1	-48.52	21	-1.5	
Equation	(3.6)	(3.6)	(3.5)	(3.5)	(3.6)	0.34
Handling time						
H_a	0.082	0.034	0.178	0.278	0.22	
H_b	2.22	2.151	1.863	1.548	1.661	
CoV	102	90	120	156	96	
Equation	(3.7)	(3.7)	(3.7)	(3.7)	(3.7)	
Encounter						
d_e	0.77	1.32	1.37	1.64	2.02	

3.3.6.1 Encounter rate

The encounter rate can be calculated by various formulae mostly including the movement of predator and/or prey (Gerritsen and Strickler, 1977; Paradis, 1999; Muirhead, 2003). For reasons of simplicity, here, the encounter rate is computed in a more statical way as time until next encounter. The calculation of the time until encounter is based on the predators encounter volume and an encounter probability depending on the prey size and density.

The predators' encounter volume may include e.g. a spherical or cylindrical shape with the predator located at its centre (Gerritsen and Strickler, 1977; Giguere, 1982) or a certain perceptive area (Caparroy 2000, Muirhead 2003). In the absence of underwater attachment points, *Notonecta* are usually searching for prey underneath the water-surface.

Thus, the encounter volume (v_n) was assumed to be a hemisphere where the radius equals the encounter distance (d_e):

$$v_n = 0.667\ \pi\ d_e^3 \qquad (3.1)$$

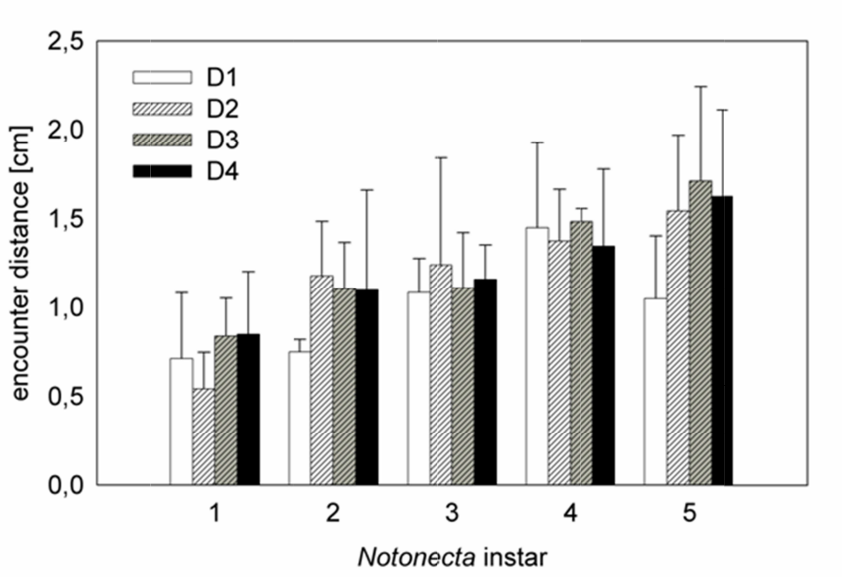

Figure 3.2: Mean and standard deviation of encounter distances measured in video tracking experiments for each combination of *Notonecta* instar and *Daphnia* size class (n = 153).

The arithmetic mean and the standard deviations of encounter distances per instar are shown in Figure 3.2. Although, in video experiments slight differences occurred between reactive encounter distances of *Notonecta* instars in terms of prey size classes, the results were not significant (Table 3.3). The outer quartile of encounter distances were integrated into the model, since the arithmetic mean of the distance may ignore that the individual predator is basically able to detect prey any farther, and considering the error that may be caused by optical distortion in experiments.

The number of encounter per ml and second observed in video experiments is quadratically correlated with prey density (Figure 3.3). Encounter rates were significantly different between the four daphnid size classes used in experiments (Ancova, p = 0,003). As expected from random encounter models, the largest prey occurred within the observed patch most frequently. Since the measured encounter rates in D2 and D3 showed higher variations, these size classes were clustered for regression analysis. A linear correlation between the

coefficients of the encounter curves slope (λ) and the mean body length (s) of the three *Daphnia* size classes was observed (Figure 3.3). Thus, the number of encounters (e) per volume (v_n) and time interval (t_e) can be calculated as:

$$e/t_e\, v_n = \lambda(0.006\, n_d{}^2 + 0.12 n_d)/v \qquad (3.2)$$

Substituting equation (3.1) into equation (3.2) with $\lambda = 0.35\, s + 0.34$ derived from linear regression the time until the next encounter (e = 1) is given by:

$$t_e = (2.095\, d_e{}^3\, v)/((0.35\, s + 0.34)\,(0.006\, n_d{}^2 + 0.12\, n_d)) \qquad (3.3)$$

The encounter submodel assumes that the animals are randomly distributed, the predators encounter radius depends on their instar, and the encounter rate is positively correlated with prey size.

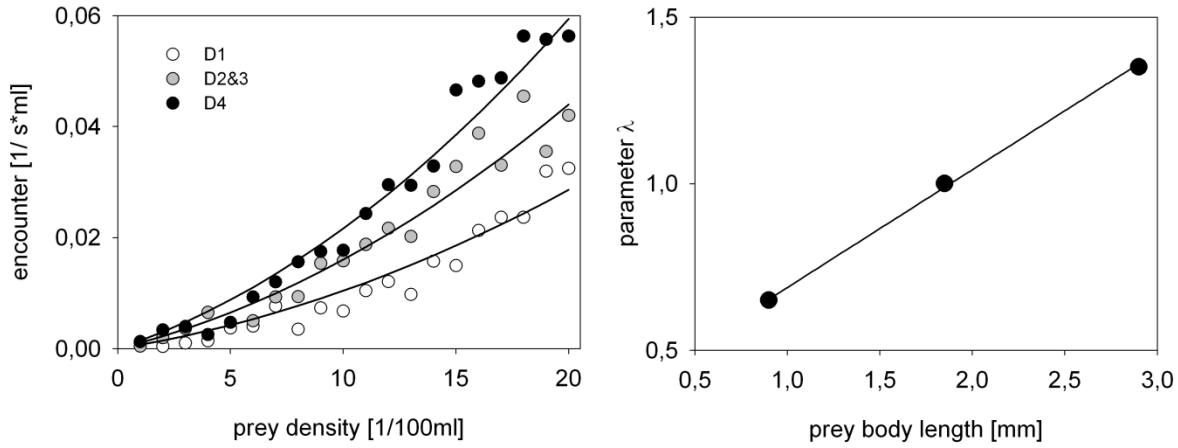

Figure 3.3: Encounter rates and quadratic regressions (left) of three daphnid size classes, D1 (r^2 = 0,905)), D4 (r^2 = 0,955) and coupled D2 and D3 (r^2 = 0,933). Each data point represents a mean of six (D1, D4) or twelve (D2 & D3) replicated measurements (n = 480). Coefficient of the regression curve's slope λ plotted against mean body length of the three size classes (right, r^2 = 0,999).

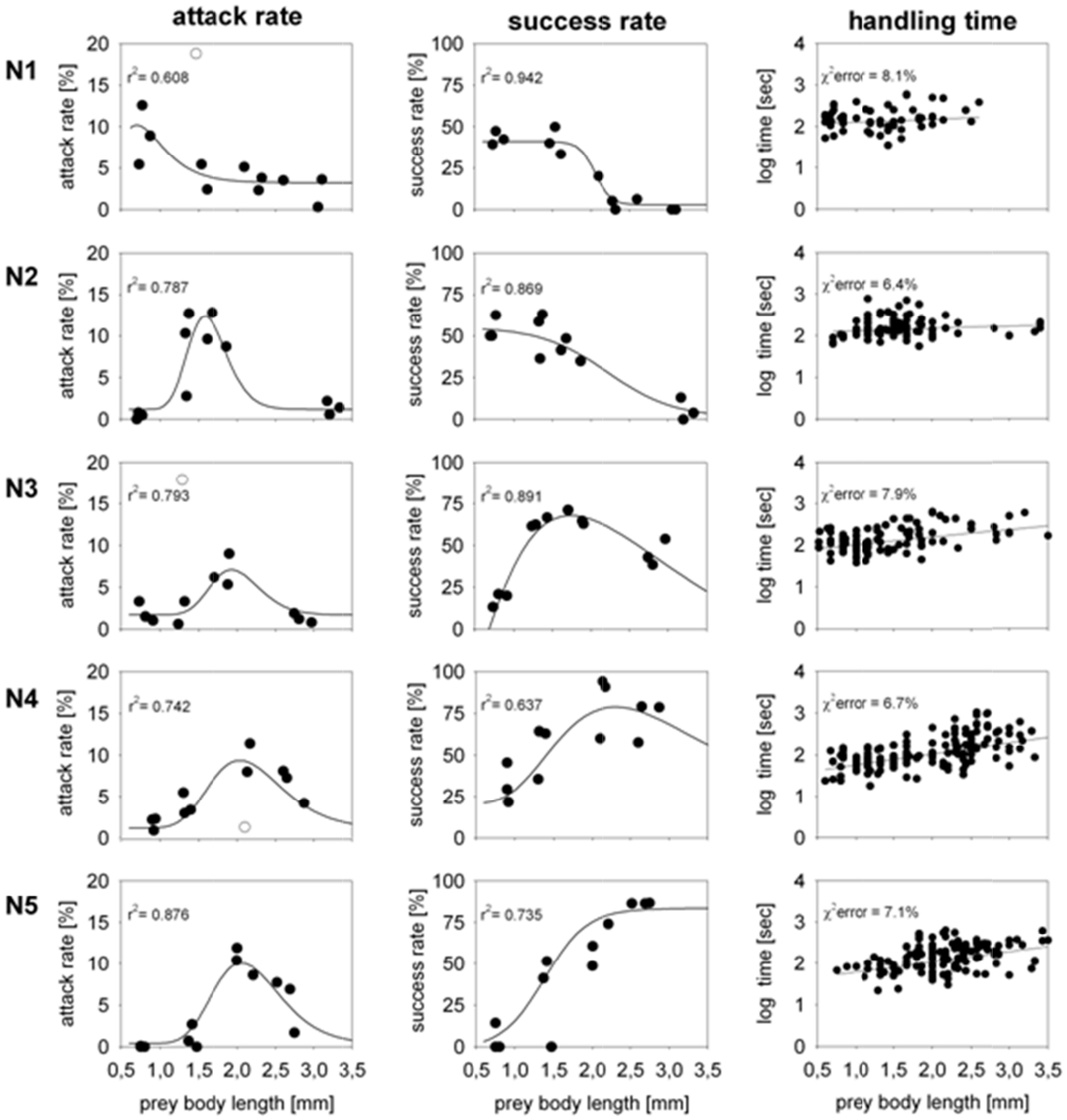

Figure 3.4: Effect of prey size on components of predation in five instars of *Notonecta maculata* (N1-N5). Dots show measured data, while lines indicate parameterization gathered from fitting either log normal or sigmoid functions in attack and success rates and linear regression in log transformed handling time. Data marked as white dots were treated as outliers.

3.3.6.2 Attack rate

Attack rates as functions of mean daphnid body length, determined from video experiments, are shown in Figure 3.2. There were significant correlations between the attack rate (a_r) and *Daphnia* size classes in all *Notonecta* instars but N1 (Table 3.3). The proportion of prey that was attacked when encountered can be described best by means of a lognormal function where A_a, A_b, A_{x0} and A_{yo} are instar specific parameters listed in Table 3.2:

$$a_r = \left(A_{y0} + A_a \, e^{-0.5 \ln\left(\frac{s \, A_{x0}}{A_b}\right)^2} \right) / 100 \qquad (3.4)$$

The body length of most attacked *Daphnia* specimens increased with the *Notonecta* instar indicating that larger predator preferentially attack larger prey. No significant correlation between attack rate and prey density was observed (ANOVA, p = 0.152), thus the attack rate per prey size was assumed to be constant.

3.3.6.3 Success rate

The success rate (s_r) is significantly correlated with *Daphnia* size classes in all *Notonecta* instars (Table 3.3). Attacks of small backswimmers were more successful in small prey while larger prey was not caught when attacked or was able to escape after capture in most cases. Large *Notonecta* instars often failed to grasp small prey but were successful in attacking larger daphnids (Figure 3.2). Therefore, the success rate of instars N1, N2 and N5 is determined by a sigmoid regression:

$$s_r = \left(S_{y0} + S_a \; / (1 + e^{-\frac{s - S_{x0}}{S_b}}) \right) / 100 \qquad (3.5)$$

Because instars N3 and N4 were most successful in attacking intermediate sized *Daphnia*, D2 and D3 respectively, the success rate is described by means of a lognormal function:

$$s_r = \left(S_{y0} + S_a \, e^{-0{,}5 \ln\left(\frac{\ln(s \, / S_{x0})}{S_b}\right)^2} \right) / 100 \qquad (3.6)$$

The parameters S_a, S_b, S_{x0} and S_{yo} are listed in Table 3.2. There was no correlation between success rate and prey density (ANOVA, p = 0.117).

3.3.6.4 Handling time

Occasional pursuing daphnids within the encounter distance did last for a split second. In comparison to the time spent on handling prey the cost of pursuing prey is negligible. Thus, the handling time is recorded from the actual attack until the release of daphnid remains.

Linear regressions are able to describe the correlation between the log transformed handling time and *Daphnia* body length, parameters H_a and H_b shown in Table 3.2:

$$t_h = 10^{H_a s + H_b} \quad (3.7)$$

Time spent on manipulating and exhausting prey varied significantly between *Notonecta* instars (Ancova, $p < 0.001$). Handling small daphnids took a substantial amount of time in small instars and decreased with increasing instar as indicated by the axis intercept (H_b). Decreasing slopes (H_a) suggested that the time spent on handling larger prey decreased from N4 to N5 (Table 3.2). Handling time significantly differs between *Daphnia* size classes in later instars (Table 3.3). As no significant correlation between handling time and prey density was found (Table 3.3) the submodel does not take density effects into account.

Table 3.3: P-Values as results of one-way analyses of variance and t-test

Analysis	N1	N2	N3	N4	N5
Encounter distance x prey size class	0.109	0.823	0.887	0.912	0.360
Attack rate x prey size class	0.056	0.005	0.008	0.006	0.001
Success rate x prey size class	< 0.001	0.001	< 0.001	0.018	0.001
Handling time x prey size class	0.086	0.003	< 0.001	< 0.001	< 0.001
Handling time x prey density	0.977	0.254	0.884	0.553	0.969
Petri dish x beaker	0.749	0.826	0.759	0.215	0.520

3.3.7 Sensitivity analysis

Relative sensitivity of parameters was calculated using the two different equations for capture success (Equations 3.5 & 3.6). Results are shown in Figure 3.5. Within the two analyses, the parameters A_a and A_{x0} as well as H_a and S_b were detected to have relatively strong effects on the fluctuation in the number of prey eaten compared to other parameters and thus considered to be the most important parameters. The parameters Aa and Ax0 are used to calculate the probability of attacking a particular prey item: The parameter Aa is a proportionality factor determining the maximum attack rate, whereas Ax0 is the prey size corresponding to the maximum attack rate, i.e. the prey size which is preferentially attacked. H_a and S_b turned out

to be the most important parameters when running the analysis for the sigmoid function of the success rate. The parameter H_a is the intercept of the handling time linear regression, i.e. the minimum mean handling time. The parameter S_b is proportional to the range of prey sizes which are most successfully attacked.

Furthermore, a number of parameters were found to have an intermediate influence on the model output as compared to others. These were the parameters S_a (proportional to maximum success), A_b, (proportional to the range of prey sizes mostly attacked), the size and number of prey items initially available (s and n_d), the slope of handling time linear regression (H_b) and the predators encounter distance (d_e). The minimum attack rate (A_{y0}) and the minimum success rate (S_{y0}) appeared to be parameters of low importance in both analyses. Furthermore the parameter S_{x0} was found to be less sensitive. This parameter marks the inflexion point in the sigmoid function of the success rate and the prey size most successfully attacked when using the logistic function.

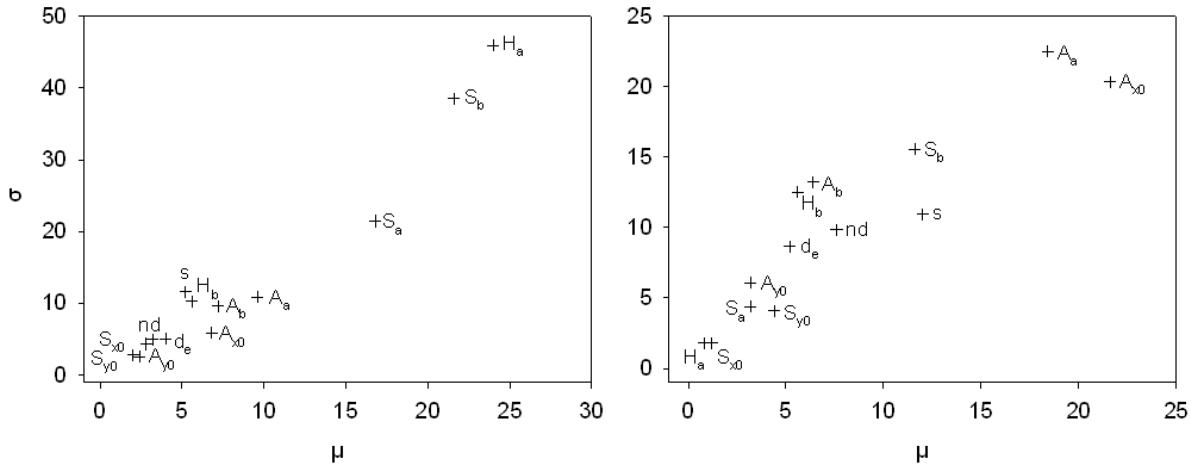

Figure 3.5: Relative importance of parameters, based on μ and δ, calculated for simulations using the two different equations for capture success: Equation 5 (left) and Equation 6 (right). Capital letters indicate the parameters of model equations for calculating attack rates and success rates and handling times. Small letters indicate ecological parameters.

When analyzing components of predation, gradually increasing parameter values did result in decelerating responses of the model output as shown for the example of the 4th instar in Figure 3.6. The number of prey eaten increased with increasing encounter distance, attack rate and success rate, whereas increasing handling times did result in decreasing numbers of prey eaten. Variations in encounter distance and handling time caused the biggest changes in the number of prey eaten whereas the output of the model did respond less sensitive to variations

in the attack rate and in the success rate. The highest alteration in the number of prey eaten was found for daphnid size classes which are most (successfully) attacked by *Notonecta* instars in video experiments.

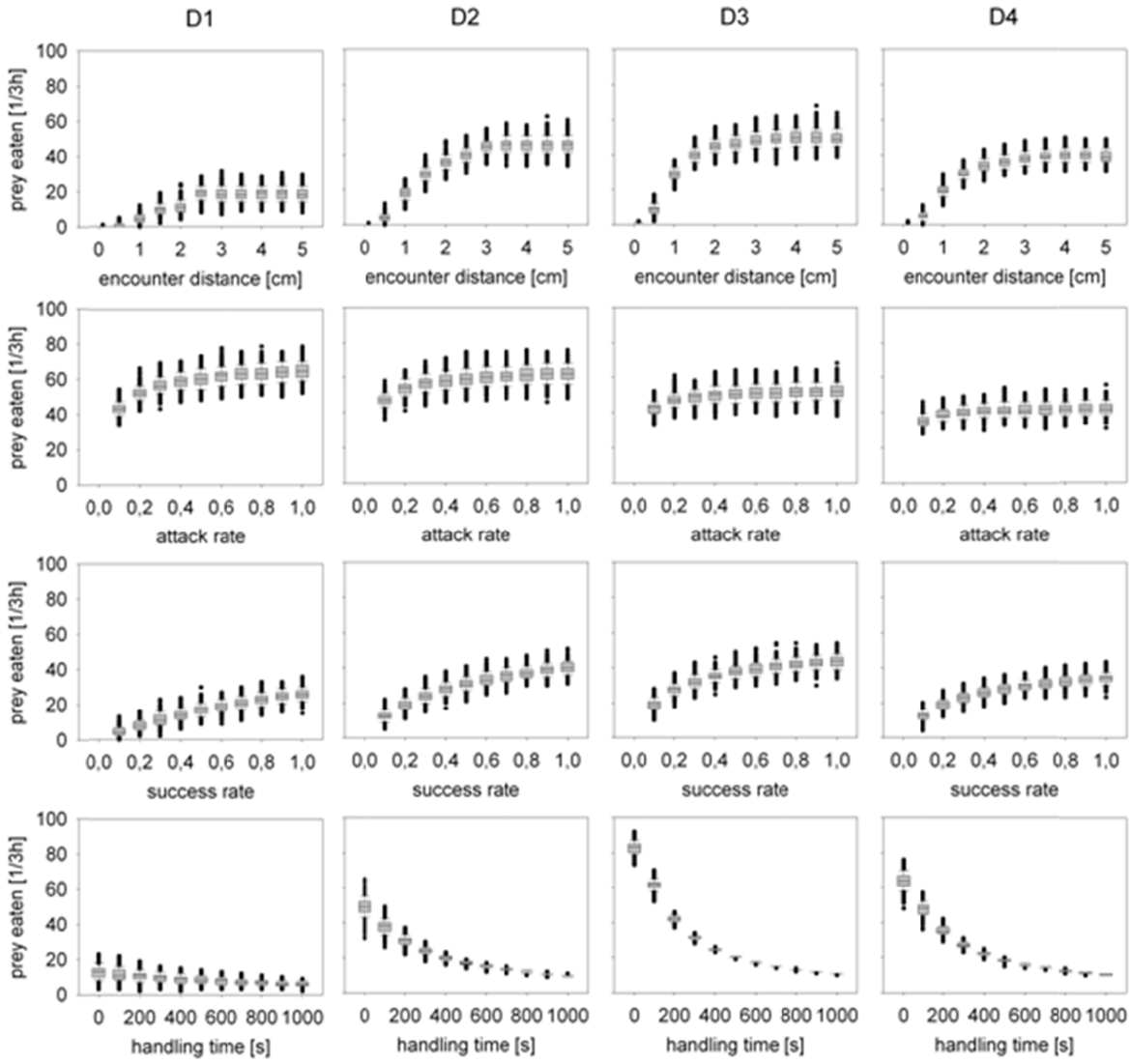

Figure 3.6: Variation in the number of *D. magna* (D1-D4) eaten by backswimmers derived from gradually increasing parameter values of foraging components. Simulations were done for the example of the 4th instar using an initial prey density of 100/l. Boxplots show median, quartiles and outliers of 1000 Monte-Carlo simulations.

3.3.8 Predation experiments

The number of daphnids eaten in test vessel experiments increased with backswimmer instars (Figure 3.7). However, no significant difference in the outcome of predation was found between the shallow and deeper test vessels (Table 3.3).

As expected from video experiments, the number of eaten prey increased with *Notonecta* instars in large *Daphnia* prey, while the number of the first daphnid size class appeared to be reduced more extensively by small instars (Figure 3.8).

The number of daphnids eaten per size class apparently differed from the number of prey composition offered in size selectivity experiments across *N. maculata* instars (Figure 3.9). Generally speaking, the prey size preferred increases with predator size, but large predator instars favoured prey size class D3 over D4.

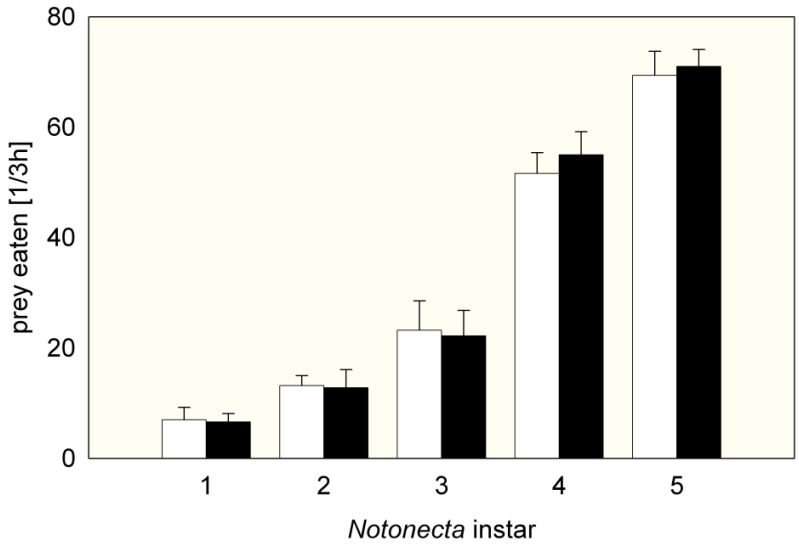

Figure 3.7: Mean number of *Daphnia magna* (D3) eaten by backswimmers of instars 1-5. 80 daphnids were initially given to single backswimmers using shallow Petri dishes (white bars) and deep beakers (black bars). Error bars indicate standard deviation experimental results (n = 5). No significant differences were found in t-Tests.

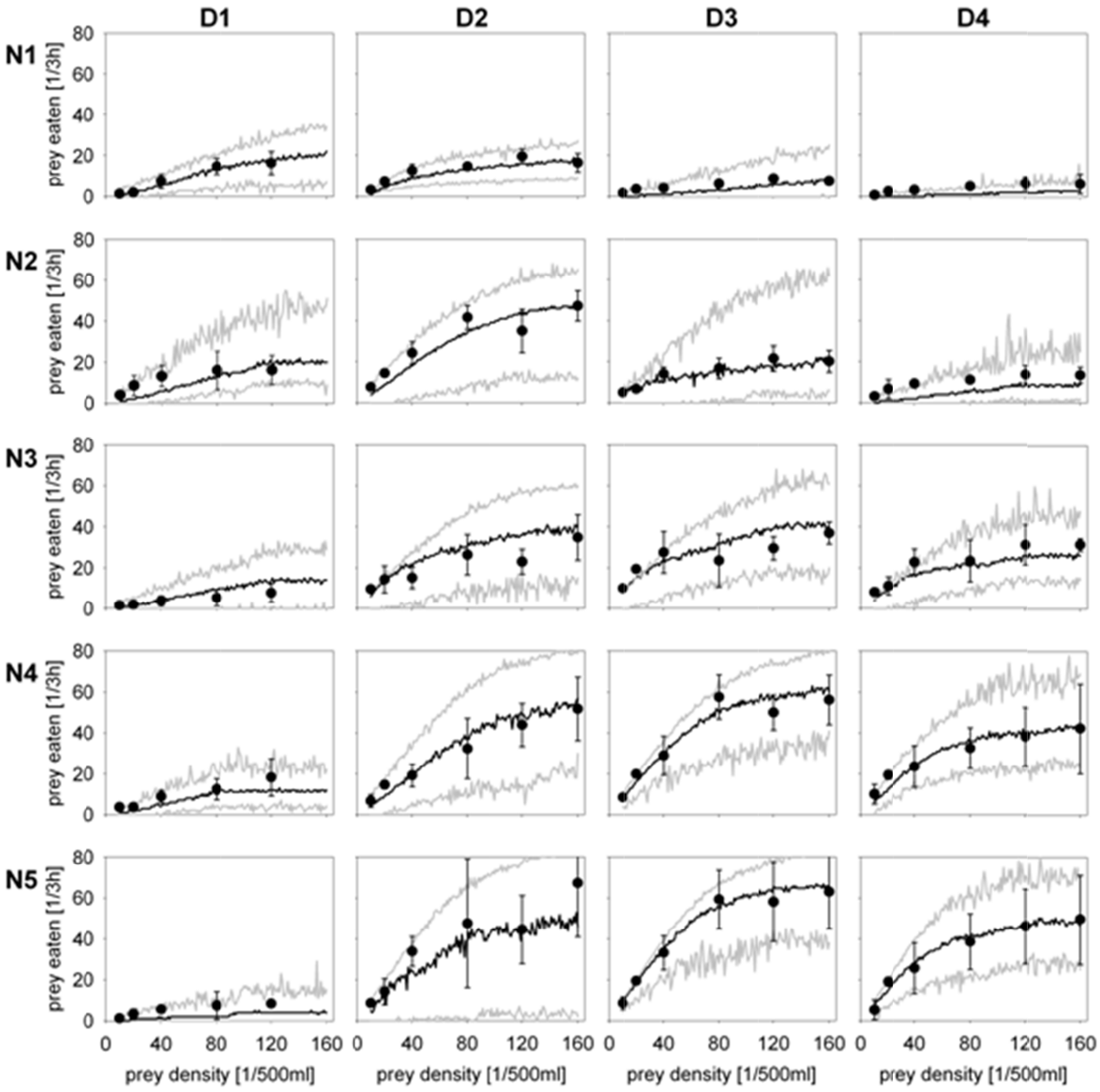

Figure 3.8: Results of functional response experiments compared to model prediction in combinations of *Notonecta* instar (N1-N5) and *Daphnia* size class (D1-D4). Black lines represent mean and grey lines minimum and maximum values of the 100 Monte-Carlo simulations. Dots show mean and standard deviation of 5 replicated measurements.

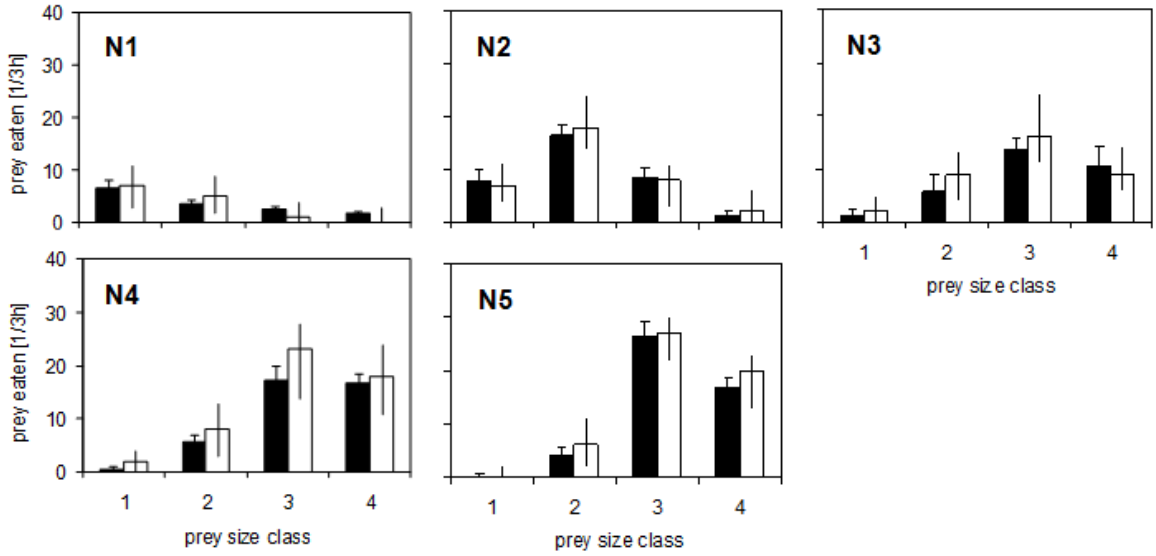

Figure 3.9: Mean number of prey eaten per size class in size selectivity experiments (black bars) and model predictions (white bars). 30 daphnids were exposed to single backswimmer (N1-N5) simultaneously. Error bars indicate standard deviation of experiments (n=5) and minimum/maximum of 100 Monte-Carlo simulation respectively.

3.3.9 Model Predictions

The presented individuals model can be run in order to predict either functional response or size selectivity of juvenile *N. maculata*. The model was tested using the results of functional response and size selectivity experiments (Figure 3.8 & 3.9). The evaluation of the model was performed on the base of the submodels described above and the set of parameter shown in Table 3.2. No further calibration of the model was done.

Good correlations between observed mean number of eaten *D. magna* in functional response experiments and the model prediction were found as indicated by scatter plots including the estimation of r^2 and the RMSD (Figure 3.10). The parameters of the observed vs. predicted regression did not significantly differ from one and zero in slope ($p = 0.216$) and intercept ($p = 0.452$) respectively. Furthermore, the standard deviation of experimental data can be reproduced by predictions of minimum and maximum values derived from Monte-Carlo simulations in most cases.

The correlation between observed and predicted number of eaten *Daphnia* per size class is fairly high (Figure 3.10). As before, the hypotheses of the regressions slope equals one ($p = 0.128$) and the intercept is equal to zero ($p = 0.962$) are accepted.

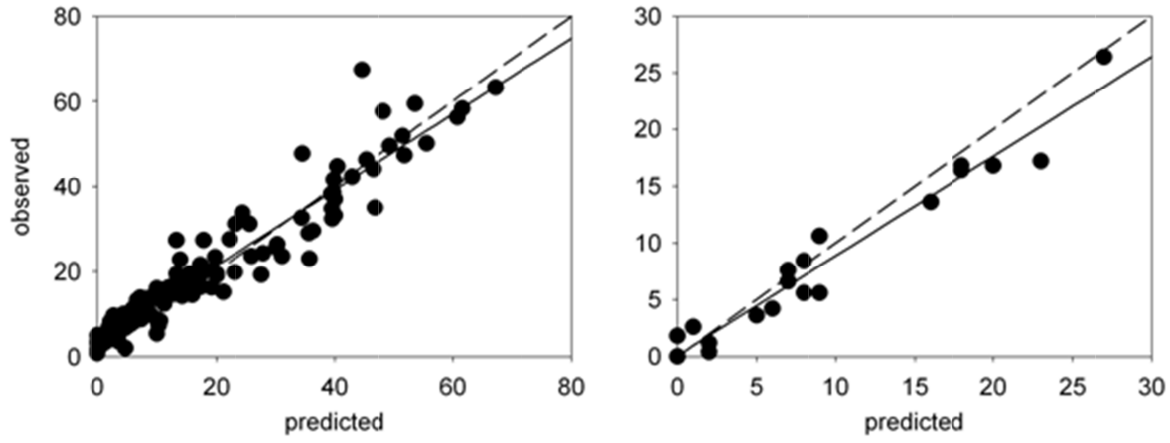

Figure 3.10: Observed mean number vs. predicted mean number of eaten prey in functional response (left; r^2 = 0.913; y = 0.891x + 3.562, RMSD = 5.3) and size selectivity experiments (right; r^2 = 0.953; y = 0.877x + 0,087, RMSD = 2.2). Dots represent data, solid line linear regression and dashed line 1:1 reference.

3.4 Discussion

A model incorporating directly observed encounter, attack and success rates as well as time spent on handling prey was developed for predicting functional responses and size selectivity of *Notonecta maculata* instars foraging on *Daphnia magna*.

3.4.1 Parameterisation

Generally, the rate of encounter is based on the movement of both prey and predator. Observations in video experiments suggest that backswimmers do not search for daphnia extensively. The number of predator movements is relative small compared to movements of prey. As shown by Gerritsen and Strickler (1977) the greater of two speeds has the stronger effect on the encounter rate. Thus, the locomotion of *Notonecta* can be neglected similarly to observations done for *Chaoborus* larvae (Giguère, 1982). Giller (1982) reported that backswimmers orientate towards and pursue prey when detected until reaching attack distance. The encounter submodel presented in this study accounts for these short term movements by incorporating encounter rather than attack distances. Movements of differently sized *Daphnia magna* were included by empirically derived encounter rates. Encounter rates depending on either prey or predator size were reported previously (Pastorok, 1981; Streams,

1994; Rincon, 1995; Paradis, 1999; Jeschke and Hohberg, 2008). In the present study the encounter rates estimated from video experiments exhibited a quadratic function of prey density. Similarly, a quadratic correlation of prey encounters and level of density was found by Tully (2005) for a mite-springtail system.

The attack rate of *Notonecta maculata* instars appeared to be a hump shaped function of daphnia body length. In contrast, Thompson (1975) found monotonical relationships between predator and prey size when estimating attack rates from functional response experiments. Furthermore, Reynolds and Geddes (1984) observed a preference towards smaller prey of notonectid predator *Anisops deanei* (Brooks), whereas Scott and Murdoch (1983) found a strong tendency for *Notonecta* instars to choose the largest zooplankton available.
The contrasting findings may result from small ranges of prey size included in these studies. More complex functions of attack rates can be expected when incorporating a wide range of prey size (McArdle and Lawton, 1979; Aljetlawi et al., 2004). The rate of successful attacks as a coefficient of functional response is generally estimated from Holling's (1959a) disc equation or Roger's (1972) random predator equation by non-linear regression. Thus, only few studies distinguish between attack and success rates when analysing foraging strategies (Streams, 1994; Juanes and Conover, 1994; Jeschke et al., 2002) as the classic equations do not include unsuccessful attacks. The present study recommends taking both attack and success into account since, the prey size highly provoking an attack may differ from the prey size highly generating attack success within a predator instar.

Being a sensitive parameter of functional response, handling time has frequently been examined in predator-prey studies. Handling time increasing with prey size was reported (Pastorok, 1981; Reynolds and Geddes, 1984) as well as the opposite case (Juanes and Conover, 1994). Here, a more complex relationship between prey size and handling time was found when incorporating predator instar, similar to handling time surfaces published previously (Thompson, 1975; McArdle and Lawton, 1979; Aljetlawi et al., 2004).

Numerous studies using pre-starved predators have shown some evidence that handling time tends to increase with decreasing prey density or number of prey consumed (Cook and Cockrell, 1978; Kruse, 1983; Bailey, 1986). For starved predators the time spent on handling prey decreases in a catch sequence. At low densities, only the first prey captured results in a high mean handling time (Giller, 1980). Adopting a gut-filling model (Cook and Cockrell,

1978), one explanation might be that low prey densities and high inter-catch intervals lead to slow satiation. Correspondingly, high densities result in fast satiation and low mean handling time. By feeding backswimmers prior to experiments, density related differences in handling time seem to be less pronounced in this study. The same applies to attack and success rates, being independent of prey density or number of prey consumed.

3.4.2 Sensitivity analysis

As revealed by the Morris method, parameters influencing the maximum rate of attack and success, the range of prey sizes (successfully) attacked and the minimum handling times are significantly affecting the output of the model, and thus considered the most sensitive parameters. This finding back the implication that a broad range of prey sizes have to be taken into account when investigating predator prey relationships. In contrast one parameter related to prey sizes, namely S_{x0}, was found to be of low importance. This finding might be due to the small range of parameter values used in the analysis as derived from experimental data. The relative small range of values is a consequence of using two different equations for calculating the probability of attack on the base of prey sizes. Moreover the parameter is lacking a consistent ecological meaning for the same reason.

Analyzing components of predation revealed the sensitivity of encounter distance and handling time. In simulations, the number of prey consumed increased with increasing encounter distance as a consequence of higher numbers of encounters. However, similar to functional response curves the number of eaten prey is limited by handling times. In turn, the number of eaten prey decreased with increasing handling times in a decelerating manner. When gradually changing the handling time, the highest variation for the model output was observed in prey sizes which are frequently attacked whereas in prey sizes which are hardly attacked handling times can be neglected compared to the large inter-catch intervals. As a consequence in further studies more pronounced effects of factors tested can be expected when using the most preferentially attacked prey size in *Notonecta* instars.

3.4.3 Model structure

Many approaches to assess functional response or selectivity have been published during the last decades. Either these approaches discussed aspects of foraging in a more theoretical way or aimed at estimating foraging components from the disc equation or the random predator model. Only few attempts have been made to quantify attack rates, attack success or handling

times directly and it is not clear whether the coefficients derived from equations match those determined from direct behavioural observations (Giller, 1982; Juanes and Conover, 1994; Streams, 1994; Jeschke and Hohberg 2008). Similar to previous modelling approaches the model presented here is based on the predation cycle divided into four components as introduced by Gerritsen and Strickler (1977). However, parameterisation of the model by directly measuring components of predation allowed comparing model predictions to independently obtained data of functional response and size selectivity.

The underlying mechanism of foraging is implemented in the model as a series of stochastic events. Although the model procedure allows encounters occurring in a strict sequence only, encounter events might be given within a matter of seconds in high prey densities. The hump shaped distribution of attack probability as a function of prey size followed by a probability of success in the model procedure provides an appropriate decision tree for modelling the foraging of juvenile backswimmers. The model takes into account ontogenic changes in both predator and prey characteristics. Encounter, attack rates, and success rates as well as handling time as functions of prey size are calculated by means of linear and non-linear regressions. Computing rates in a continuous manner rather than using definite size classes meets the assumptions of recently published, individual-based *Daphnia* models (Preuss et al., 2008; Rinke and Petzold, 2008). Here, daphnid size classes were used for statistical analyses and for displaying results only.

The model structure is open to modifications and inclusion of further processes. For example modelling the probabilities of attack and success explicitly allows replacing the stochasticity by a steering element of attack e.g. the predator's hunger level and satiation (Jeschke et al., 2002; Jeschke and Hohberg, 2008) which might become important in low prey densities and long simulation time.

Here, individual *Notonecta* and individual daphnids were modelled explicitly. The process-based modelling approach was chosen in order to quantify and analyse the uptake of food during larval development of single *Notonecta* in later stages of the model. This approach will allow assessing the effect of prey size available and prey density on the individual life history of backswimmers.

3.4.4 Model predictions

The model is suitable to predict both, the mean number of *Daphnia* eaten in functional response experiments and the size selectivity of backswimmer instars, as indicated by observed vs. predicted scatter plots including the estimation of r^2 and the RMSD.

Most patterns derived from functional response experiments can be described as type II functional response as formulated by Holling (1959a). McArdle and Lawton (1979) as well as Reynolds and Geddes (1984) similarly found decelerating type II responses in backswimmer-daphnid systems. Although, the type of functional response was not analysed explicitly and to discriminate different types of responses might be difficult in some cases (Trexler, 1988; Pervez and Omkar, 2005), visual assessment of observed data and model predictions indicates that the functional response of *N. maculata* foraging on small prey tends to exhibit a sigmoid type III functional response. Switching types of functional responses have been observed previously. Prey density related responses of *Notonecta glauca* (Linnaeus) to small *Asellus aquaticus* (Linnaeus) was found to be type III whereas response to large water louse was type II (Hassell, 1977). The presence of alternative prey, have also been shown to alter the type of functional response (Akre and Johnson, 1979). On the base of similar results, Streams (1994) argued that low attack rates or low attack success coupled with increasing density dependence of these rates might produce sigmoid responses. The model presented here produced type III-like responses without any density dependency of attack parameters included. Thus, low feeding efficiency when prey density is low might be due to prey size related differences in encounter rates. Nevertheless, in few cases the model tends to underestimate the number of prey eaten in low prey densities. This might be due to increasing rates of attack with high inter-catch intervals, which is not included in the model yet.

The results from size-selectivity experiments demonstrate strong selectivity of backswimmers when fed with a choice of *Daphnia* size classes. The patterns of preference differed across *Notonecta* instars. When comparing patterns of prey size ingested and prey size available in the laboratory, it is not clear whether selectivity is a result of active preference or passive selection (Juanes and Conover, 1994). The model presented here was able to predict size selectivity on the base of foraging parameters derived from video experiments using single prey size classes. Prediction of size selectivity was achieved without any additional factor of active preference included. Thus, the modelling approach clearly indicates a passive process in the selective predation of *Notonecta*. This finding is in accordance with previous studies

suggesting that preference might be a function of probability of encounter or the probability of size-based capture success (Chesson, 1978; Juanes and Conover, 1994). In case of simultaneous encounters with prey types, a predator has to determine the prey that should be attacked (Sherratt and Harvey, 1993), therefore the probability of attacking the one or the other prey type has also to be considered as a major factor of selectivity. Especially in predators faced with high densities of prey resulting in high encounter rates, size-selective predation might be predominantly mediated by probabilities of attack and attack success based on prey size.

3.4.5 Limitations of the current modelling approach

In the current state the model is applicable to *Notonecta maculata* kept at 20°C only as the temperature is known to affect foraging components (Thompson, 1978). Since an equal distribution of prey is assumed, the encounter submodel is restricted to laboratory scale. More realistic approaches have to consider spatial aggregations of *Daphnia* swarms, e.g. as a result of phototactism, or defence mechanisms that reduce encounter rates like predator avoidance (Jeschke and Tollrian, 2000).

Empirically estimated parameters of encounter and foraging might be applicable to *Daphnia magna* only, but also to species of similar locomotion and morphology. Morphological changes in prey characteristics are known to decrease capture success of the predator. For instance, the development of crests in *Daphnia* allowed to evade successful attacks of notonectid predators (O'Brien and Vinyard, 1978; Grant and Bayly, 1981). Defence mechanisms aimed at the reduction of the predator's success will have the largest impact at low prey density (Jeschke et al., 2002).

The presence of alternative prey types may also effect the foraging of notonectid predators. Scott and Murdoch (1983) found *N. hoffmanni* (Hungerford) specimens preferring *Daphnia* prey over same sized *Ceriodaphnia* specimens. By offering alternative food sources, Chesson (1989) observed that the presence of daphnids did not result in a decreased number of eaten mosquito larvae in functional response experiments but that of *Drosophila* flies did, even though *N. hoffmanni* specimens showed a significant preference for daphnids relative to mosquitoes. The effect of alternative prey types is not included in the model, but probably has to be considered in modelling field populations.

In its current state the model is validated on the base of short term experiments using backswimmers with comparable satiation levels. As the satiation of individual *Notonecta* in

long term experiments might change depending on the number and size of prey available, foraging parameters included in the model possibly have to be adopted for predicting long term data. For predicting the impact of notonectid predation on *Daphnia magna* populations under field conditions the model has to take the effect of temperature and light regime on foraging parameters into account.

Chapter 4

Diurnal and nocturnal functional response considered as a consequence of shifting predation behaviour

4.1 Introduction to the topic

Light is considered to have a significant impact on spatial distribution and predation within freshwater communities. In relation to light intensity, the avoidance of visual predators was found to be a major ultimate factor for the diel vertical migration of zooplankton in lakes (Zaret and Suffern 1976; Stich and Lampert, 1981; Ringelberg, 1991; Dini and Carpenter, 1992). Recently, a model based scenario analysis revealed the adaptive value of diel vertical migration in case of intensive fish predation (Rinke and Petzold, 2008). In the absence of fish, an avoidance-response cascade of plankton organisms in a shallow pond was suggested to be possibly induced by the notonectid predator *Buenoa macrotibialis* (Hungerford) (Gilbert and Hampton, 2001).

Like many predatory insects, backswimmers of the genera *Anisops*, *Buenoa* and *Notonecta* detect prey using both visual and tactile mechanisms. Mechanoreceptors provide accurate information of prey location via wave detection and enable backswimmers to distinguish between prey and non-prey organisms (Lang, 1980). However, information available on the efficiency of backswimmers to feed under light and dark conditions is contradictory, owing to the different propensities found in several notonectid species (O'Brien and Vinyard, 1978; Zalom, 1978; Giller and McNeil, 1981; Scott and Murdoch, 1983).

When observing predation behaviour functional responses usually serve as indicators. According to their shape Holling (1959a) classified three types of functional responses, of which the decelerating type II and the sigmoid type III are the ones mostly used (Jeschke et al., 2004). Type II functional responses have frequently been fitted to empirical data by using

either Hollings disc equation or the random predator equation (Royama, 1971; Rogers, 1972). For decades the type II equations were subject to many modifications for modelling functional responses as reviewed by Jeschke et al. (2002). The classic equations incorporate two coefficients of predation usually termed the attack rate and the handling time. However, coefficients obtained by fitting empirical functional responses cannot necessarily be biologically interpreted (Jeschke and Tollrian, 2005). Furthermore, the predator-prey interaction might be more complex e.g. attack rates can be considered as a function of reactive distances between predator and prey or as the proportion of successful attacks (Hassell et al., 1979). Consequently, several authors used a more complex predation cycle based on four conditional events, namely encounter, attack, capture and ingestion, for analysis or modelling of foraging processes (Gerritsen and Strickler, 1977; Giller, 1982; Greene, 1983; Jeschke et al., 2002; Jeschke and Hohberg, 2008).

The purpose of the present chapter is to examine proximate factors affecting the diurnal and nocturnal predation behaviour of juvenile *Notonecta maculata* by directly observing and quantifying components of predation. In order to appraise the findings of the observations, an individuals model was employed that describes the foraging process empirically on the basis of a general predation cycle. The model includes four conditional events (encounter, attack, capture success and handling of prey) and was designed to predict daytime functional responses. Within the current study the model is re-parameterized based on the results of light/dark observations. The dark-adapted model is tested by comparing actually observed functional responses with the independent model outcome. If the fit is found to be accurate, it can be concluded that the crucial differences between diurnal and nocturnal predation behaviour of *Notonecta maculata* juveniles were considered in the approach.

4.2 Material and Methods

Experiments were carried out in a constant room set at 20 ± 1°C and a diurnal light rhythm of 16:8h (day:night). Artificial freshwater M4 (Elendt and Bias, 1990) was used as a medium. All observations were made with the five instars of *Notonecta maculata* (N1-N5) foraging on *Daphnia magna*.

Notonectid specimens were bred in the laboratory and raised separately on daphnids. In the experiments, backswimmers were used only 2 to 5 days after moulting. *N. maculata* specimens were fed 16-18 hours prior to the experiments. Feeding quantities provided were

0.3 ml in N1, 0.6 ml in N2, in 0.8 ml in N3, 1.2 ml in N4 and 1.5 ml in N5 of a suspension, containing a mean number of 46 ± 8 *D. magna* items per ml.

Daphnids were gathered from a nearby pond and maintained under laboratory conditions for at least 24 h before being used in experiments. Prey sizes were applied in the present experiments which were consumed by instars of *N. maculata* to a high amount as observed in previous functional response experiments (Chapter 3). The prey was classified into two groups and graded using non-standard sieves. The smaller *D. magna* prey was used in N1-N2 and the larger in N3-N5. The body lengths were 1.4 ± 0.20 mm in smaller daphnids and 2.3 ± 0.29 mm in larger daphnids (mean ± standard deviation, n = 100 each), measured under magnification excluding the spine.

4.2.1 Predation experiments

Independent screening (*I*), video (*II*) and functional response (*III*) experiments were conducted in order to examine whether the predation rates in light and dark conditions are a matter of light or of an endogenous circadian rhythm, to identify parameters of foraging affected by dark conditions and to verify findings of video experiments respectively. To ensure darkness in dark experiments, sets were covered with paper boxes. Light intensity was in the range of 400-900 lx and 0.01-0.03 lx in light and dark conditions respectively. Details of video experiments have been previously described in Chapter 3, and therefore only briefly outlined below.

(*experiment I*) Screening experiments were carried out under light and dark conditions with ten replicates. Light experiments were conducted in the morning immediately after ‘sunrise’ (light/morning) and at midday (light/noon). Dark experiments were run at midday (dark/noon) and at midnight (dark/night). The dark assays during noon were carried out with two sets of backswimmers. Below one box a camera of the type Sony DCR-TRV 310E was installed and the night shot turned on, in order to verify any influences of infrared (IR) function on foraging in video experiments (dark/noon/IR). Each backswimmer was placed in a 200 ml beaker and given 30 daphnids. After one hour the notonectids were taken out of the test vessels. As notonectids digest prey externally, dead as well as live prey was counted as a control of the given amount. Within the dead prey, only daphnids that had been sucked out were considered eaten. Remains could easily be distinguished from exuviae or naturally dead *D. magna* items. The error due to miss-counting was less than 3%.

(*experiment II*) To examine whether attack rates, capture success and handling times of *N. maculata* juveniles were affected by the absence of light, parameters were directly observed by means of video experiments. A cuvette-like aquarium (10:5:2 cm, width:height:depth) was filled with 100 ml medium and 20 *Daphnia magna* specimens. A single backswimmer was placed into the prepared aquarium and filmed for 60 minutes. The experiments were conducted at midday under light as well as dark conditions and replicated three times. The IR function of the camera was turned on while filming in dark conditions. Films were digitalized to allow the quantification of encounter rates, attack rates, capture success, and handling times as described in detail in Chapter 3. The number of instances per time interval in which a daphnid appeared within the backswimmers encounter distance, visualised as a circle with the predator at its centre was noted as encounter rate. An attack was defined in terms of a rapid acceleration toward the prey. A successful attack was noted when the backswimmer grasped the prey and held it for several seconds. In case of successful attacks, the time between the attack and the release of daphnid remains was recorded as handling time. Additionally, the number of reactive encounters was compared between light and dark sets. An encounter was assumed reactive in case an attack was initiated by a visible response of the backswimmer, usually a turn towards the prey. During a reactive encounter the distance between the centre of a daphnid body and the head of the backswimmer was measured. In case of capture success the distance between prey and predator was measured at the moment the attack started. Scale paper served as a benchmark and distances were measured using a digital image processing program (Preuss unpublished).

(*experiment III*) In order to examine functional responses under dark conditions, single backswimmers were allowed to forage on six initial prey densities of 10, 20, 40, 80, 120 and 160 daphnids per beaker for three hours. The experiments were carried out at midday using 500 ml beakers and were replicated five times. The number of eaten prey items was counted in a way similar to the screening experiments.

4.2.2 Statistical data analysis

Statistical analyses were performed using the statistical package SPSS 15.0 (SPSS Inc., 2006). As eating quantities differ and patterns of foraging are similar across *Notonecta* instars, data was transformed before being used in a combined analysis as follows: First, the mean numbers of daphnids eaten (derived from screening experiments) and mean values of attack rates, success rates, handling times and distances (quantified in video experiments) were

calculated separately for all instars. Thereafter relative eating quantities and relative parameter values were determined as the ratio between replicate and mean. Differences in the normalised number of daphnids eaten in screening experiments were analysed by means of a one-way analysis of variance (ANOVA) with subsequent Tukey-HSD posthoc analysis, since data passed Levene's-Test. Light dependent differences in normalised attack rates, success rates, handling times and measured distances derived from video experiments did not pass Kolmogorov-Smirnov Test and thus were examined using a Mann-Whitney U-Test.

4.2.3 Model application and analyses

To test whether differences in foraging parameters as observed in video experiments could explain the patterns derived from functional response experiments, the individuals model, introduced in Chapter 3, was employed. The model describes the foraging process empirically, based on a general predation cycle including four conditional events: encounter, attack, capture success and handling of prey. Each of the events was modelled separately in order to predict the functional response of *N. maculata* juveniles. Since the model is validated under light conditions, parameters were adapted to darkness. The predictions of the model when adapted to dark conditions were compared to the observed number of daphnids consumed in functional response experiments. To evaluate the performance of the model, regressions of observed vs. predicted data were plotted including the calculation of the coefficient of determination (r^2) and the root mean squared deviation (RMSD). As proposed by Pineiro et al. (2008), the hypothesis that the slope of the regression is equal to one and the intercept equals zero was tested using a t-Test.

4.3 Results

All juvenile instars of *Notonecta maculata* consumed more daphnids during light periods than during dark periods. The results of screening experiments showed significant differences (ANOVA, $p < 0{,}001$) in the foraging of juvenile backswimmers under different light regimes (Figure 4.1). The number of prey consumed was ~2-fold higher in light experiments as compared to the dark experimental conditions. The posthoc analysis clarified that there were no significant differences in the diurnal eating quantities under light conditions (Tukey-HSD, $p = 0.245$). Furthermore, the analysis did not reveal any difference in eating quantities within

the dark experiments (Tukey-HSD, p = 0.771). Neither the time of the day nor the IR function of the camera had a significant effect on the number of prey consumed in the dark.

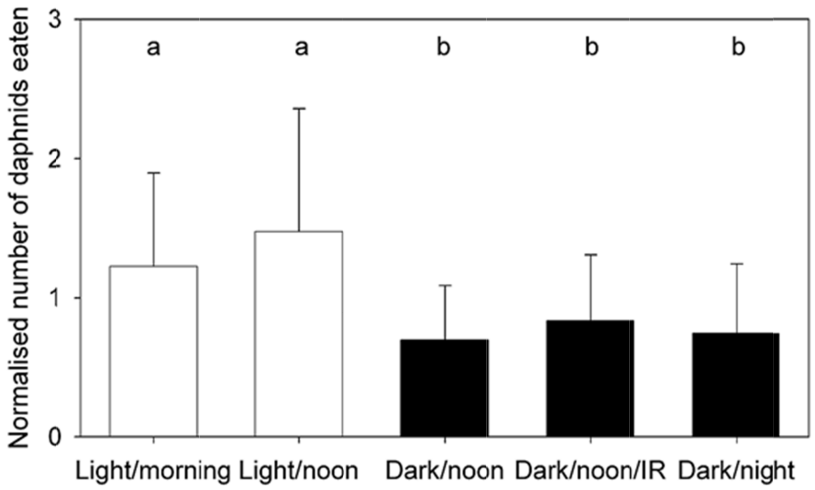

Figure 4.1: Number of prey eaten in one hour experiments (mean and standard deviation), normalized at the mean number per *Notonecta* instar for combined analysis (n = 50); experiments were carried out under light conditions in the morning (light/morning) and at midday (light/noon) and under different dark conditions at midday (dark/noon) and midnight (dark/night) and the additional use of the IR camera function at midday (dark/noon/IR); letters indicate significant differences in one-way ANOVA with subsequent post-hoc analysis

Normalised mean attack rates, success rates and handling times derived from video experiments are shown in Figure 4.2. There were significant differences in the rate of attacks (U-Test, p = 0.014) and time spent on handling prey (U-Test, p < 0.001) under light and dark conditions. The attack rate was found to be 2.4 times lower and handling time was 1.7 times higher in the dark as compared to the light experiments. However, capture success was not affected by the absence of light (U-Test, p = 0.455). Of the successful attacks, 16% and 18% were initiated by a reactive encounter in light and dark periods respectively. Encounter distances significantly differed between light and dark conditions (U-Test, p = 0.001), whereas no difference was found in the distances from which prey was attacked (U-Test, p = 0.21). The encounter distance was reduced by an average of 34%. For the demonstration of actual differences in encounter distances and attack distances, results are shown for the example of the 4th instar in Figure 4.3.

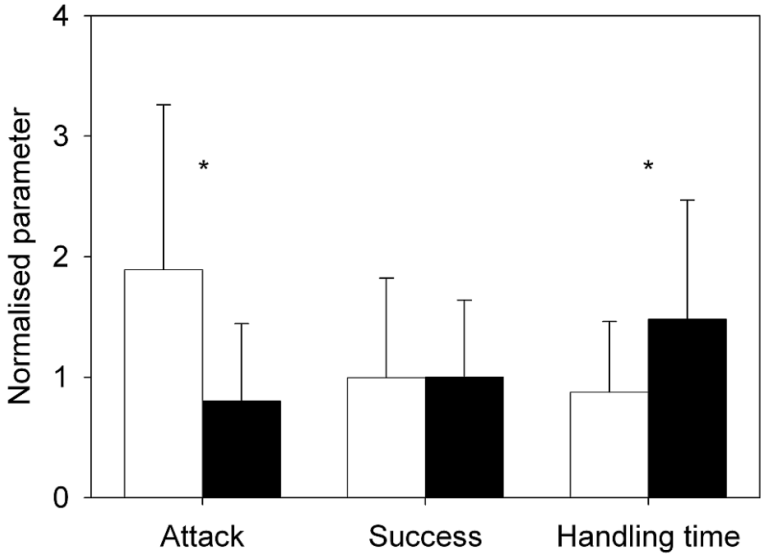

Figure 4.2: Components of predation as measured in video experiments (mean and standard deviation) under light (white bars) and dark (black bars) conditions. Attack rates (n = 15), success rates (n_{light} = 14; n_{dark} = 11) and handling times (n_{light} = 169; n_{dark} = 44) were normalized at their mean parameter per notonectid instar for combined analysis; asterisks indicate significant differences in U-Tests

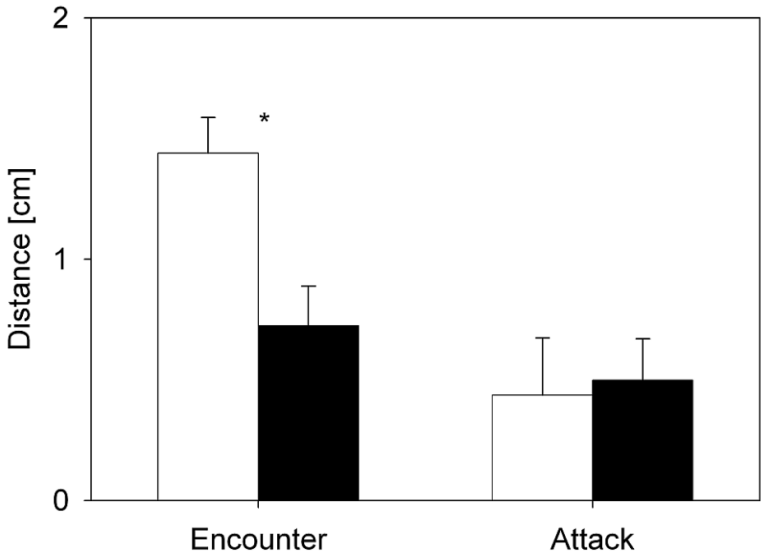

Figure 4.3: Mean distances and standard deviation between predator and prey at the occasion of reactive encounters (n_{light} = 4; n_{dark} = 4) and attacks (n_{light} = 39; n_{dark} = 19) under light (white bars) and dark (black bars) conditions shown for the example of the 4th instar; asterisk indicates a significant difference in U-Test

The predation model introduced in Chapter 3 was used to test the findings of the video experiments. In order to predict functional responses under dark conditions, parameters of the original model, namely the encounter distance and the handling time were multiplied by a factor of 0.66 and 1.7 respectively based on the results reported above. No further calibration of the model was done. For evaluation purposes, the outcome of the model was compared to the results of the functional response experiments (Figure 4.4). As expected from model predictions, the number of prey eaten per size class in experiments increased with *Notonecta* instars. A good correlation between observed and predicted mean number of daphnids consumed was found (Figure 4.5). Parameters of the observed vs. predicted regression did not significantly differ from one and zero in slope (t-Test, $p = 0.912$) and intercept (t-Test, $p = 0.812$) respectively. The comparison of simulated functional responses under light and dark conditions as shown in Figure 4.4 clarified that the foraging of juvenile backswimmers is affected by the light regime.

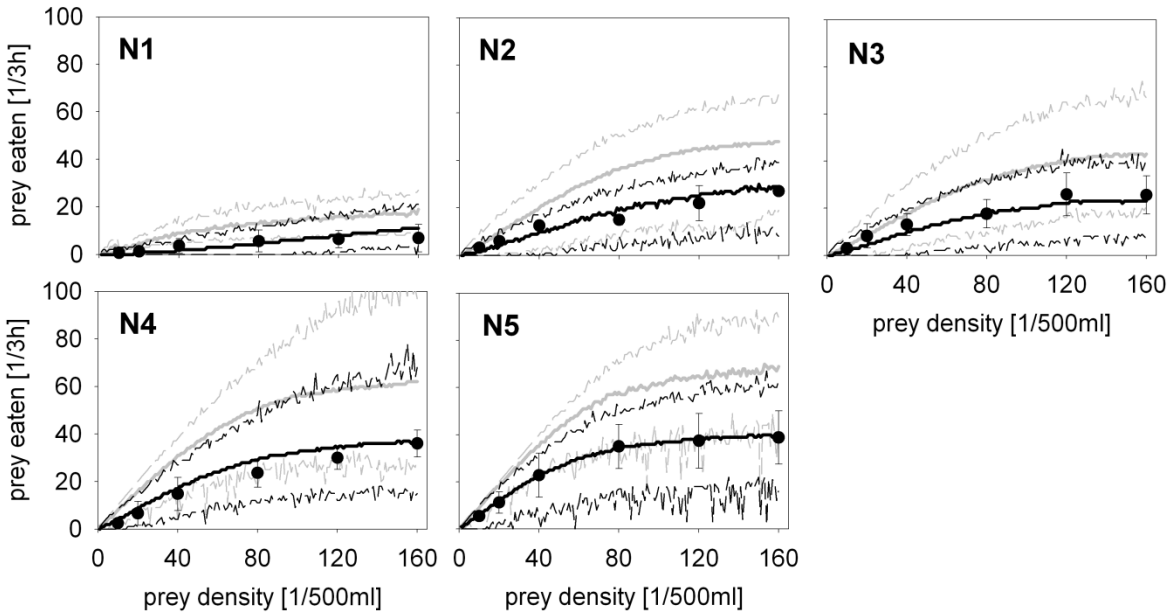

Fig. 4.4 Results of functional response experiments run in the dark (dots: mean and standard deviation, n = 5) compared to independent model predictions; lines represent mean (solid) minimum and maximum (dotted) of 1000 Monte-Carlo simulations under light (grey) and dark (black) conditions

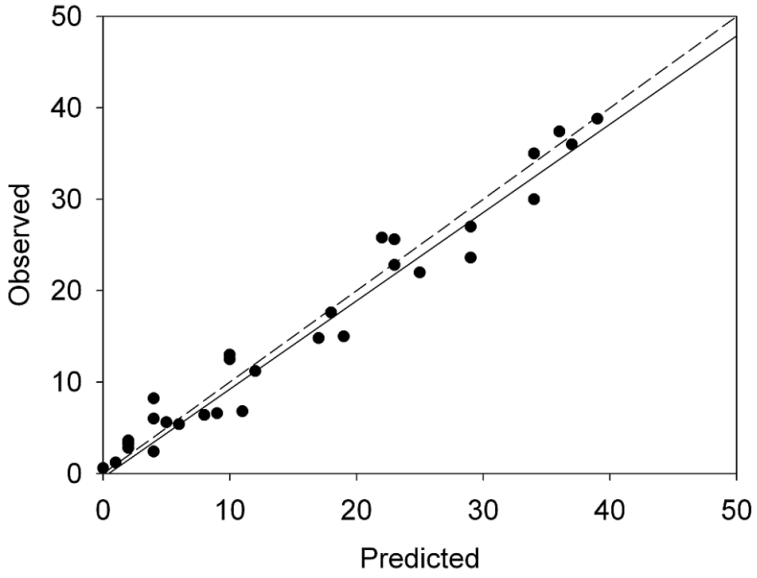

Figure 4.5: Observed mean number versus predicted mean number of prey eaten in functional response experiments under dark conditions; dots represent data, dashed line 1:1 reference and solid line the linear regression ($y = 0.945x + 0.606$, $r^2 = 0.962$, RMSD = 2.42)

4.4 Discussion

The use of vision for prey detection has been considered to play a minor role in backswimmers (Murphey and Mendenhall, 1973; Zalom, 1978); however, the opposite was also suggested (O´Brien and Vinyard, 1973; Scott and Murdoch, 1983; Diéguez and Gilbert, 2003). Giller and McNeil (1981) observed patterns of light/dark predation differing across *Notonecta* species. In their study, adults of *Notonecta maculata* showed a statistically non-significant trend to increased feeding in light conditions. Streams (1982) found *Notonecta undulata* (Say) specimens to forage more effectively in light than in the dark, with differences being more pronounced in larvae.

In the present study foraging of *N. maculata* juveniles was significantly affected by the absence of light. Furthermore, the analysis of the dark data indicates that there were no differences in foraging in case the dark conditions were natural or artificially re-created in the afternoon. Thus, lower foraging in the dark can rather be linked to the absence of light than to a circadian rhythm. Similarly, Streams (1982) concluded that day/night differences in the feeding behaviour of *N. undulata* are due to the presence or absence of light rather than due to an endogenous circadian rhythm of the predator. He suggested that the backswimmers when foraging on aquatic prey heavily depend on vision for prey location and capture.

To analyse effects on components of predation, two coefficients, i.e. attack rates and handling times, were usually estimated by fitting the disc equation or the random predator equation to measurements of functional response as published for notonectids by McArdle and Lawton (1979) as well as Reynolds and Geddes (1984). However, it remains unclear whether the coefficients derived from equations match those determined from direct behavioural observations (Giller, 1982; Juanes and Conover, 1994; Streams, 1994; Jeschke and Tollrian, 2005; Jeschke and Hohberg, 2008). Therefore, in the present study the foraging behaviour of juvenile *N. maculata* was observed directly with video experiments in order to examine whether light/dark differences of predation are a matter of detection and attack, capture success or handling of prey. Directly measuring differences in the components of predation under light and dark conditions for model parameterisation allowed the comparison of model predictions to independently obtained data which proved the model outcome to be consistent with the observations.

All stages of *N. maculata* showed visible pre-attack responses to prey encounter, such as turning towards and occasionally pursuing the prey independent of the light regime. However, distances at which prey was detected were significantly reduced under dark conditions. In the experiments, constant encounter distances per instar were employed in order to quantify the number of encounters in light and dark and subsequently to compare attack rates, i.e. the ratio between number of attacks and the sum of encounters. Shorter distances, as observed in the dark, would lead to a smaller encounter area and thus to a lower number of encounters. In turn, a lower rate of attacks, as quantified in video experiments, can be expected when assuming constant numbers of attack and applying longer distances. In model applications, similar results for the functional response of the backswimmers were obtained by either reducing the rate of attacks or the distance of encounter.

As the distance between predator and prey might give important clues to the sensory information most likely used by a predator (Pohlmann et al., 2001), the results reveal that backswimmers of the species *N. maculata* rely on vision to locate *D. magna* prey items from a distance, while in the absence of light only nearby daphnids of the size used in experiments can be detected via mechanoreception. Correspondingly, the concordance of attack distances under light and dark conditions back the assumption that capture success is independent of sight.

Mechanoreception is thought to be a major mechanism driving nocturnal foraging in backswimmers. Vibration receptors on the 1st and 2nd pair of legs as well as tactile hairs on the

abdomen enable *Notonecta* specimens to detect prey dropped at the water surface and likewise allow detecting prey in the dark (Murphey1973; Murphey and Mendenhall, 1973; Wiese, 1974). Thresholds of mechanoreceptive prey detection and localization were observed to depend on frequency and amplitude of the waves (Markl and Wiese, 1969). As different prey types produce turbulences of different intensity (Lang, 1980), patterns in light/dark predation may be a matter of prey species or size. Diéguez and Gilbert (2003) found that the notonectid *Buenoa macrotibialis* shows periodic foraging on smaller prey due to the absence of light and no differences in predation rates within larger prey types. It is suggested that *Buenoa* predators are only dependent on sight and therefore on light to detect small prey. As the sensitivity of prey location additionally depends on the distance between backswimmers and their prey (Markl and Wiese, 1969), relative weakly swimming prey in general, might be detected from a shorter distance only.

Time spent on handling prey was found to increase under dark conditions. Thus, it might be suggested that visual mechanisms also play a role in the handling of the prey. A possible explanation might be that vision is helpful to the backswimmers to find a proper spot to penetrate the prey. Another explanation for longer handling times in the dark accounts for the satiation of the backswimmer, independent of sight. The amount of food ingested was shown to increase to a certain extent with the increase in time spent on feeding (Cook and Cockrell, 1978; Giller, 1980; Bailey, 1986). A reduced number of attacks, as found in video experiments, leads to higher inter-catch intervals, i.e. the time from dropping one prey item to catching the next, and thus to a reduced satiation of the backswimmer when assuming a constant quantity of food extracted from a single prey item. Adopting a satiation model (Jeschke and Tollrian, 2005), the consumption rate increases with the hunger level of a predator. As a consequence, nocturnal fasting would lead to increasing feeding activity during the night and in the morning, but the opposite was found. There were no significant differences in the number of prey items consumed in the morning compared to those consumed at noon. Therefore it is likely that longer handling times in the dark allow the backswimmer to compensate the reduced number of prey consumed by extracting a higher amount of food per prey item.

In conclusion, the present study demonstrates that the predation behaviour of *Notonecta maculata* juveniles differ during light and dark periods, resulting in a significant reduction of nocturnal predation. Differences in the rate of predation were attributed to the detection and

handling of prey. The detection of daphnid prey from a distance rather than attacking the prey was suggested to depend on vision. In the dark, juvenile *N. maculata* were able to locate only nearby daphnid prey as encounter distances were found to be reduced. Increasing handling time was suggested to be a compensatory response to the reduced number of encounters in the dark. There is a good match between the measured functional response data and the output of the individuals model, which was empirically parameterized under dark conditions, indicating that the crucial light/dark differences in the foraging of *Notonecta maculata* are considered in the model approach.

The behavioural mechanisms outlined above should have consequences on both predator and prey. When foraging on daphnid prey, juvenile *Notonecta* specimens probably obtain most of their food during daylight. The adaptive value of diurnal feeding is supported while also considering higher daytime temperatures to which backswimmers are usually exposed under field conditions. In general, increasing temperatures lead to increased feeding activity and higher growth rates. In *Daphnia*, the risk of predation is higher during light periods when exposed to backswimmers. Despite the cost of defence mechanisms, the avoidance of predators might appear as an adaptive strategy in case of intense backswimmer predation. Defence mechanisms aimed at the reduction of the predator's success, e.g. swarming, will have the largest impact at low prey density whereas strategies to avoid encounters, e.g. diel vertical migration, might maximize individual survival at high zooplankton densities.

Chapter 5

Modelling hunger dependent predation behaviour: The role of body size, gut constraints and the interplay between attacking and handling prey

5.1. Introduction to the topic

Ultimately, feeding is an exercise to acquire nutrients needed for growth, development and reproduction (Behmer, 2009). Many animals are able to regulate food intake using a repertoire of feeding behaviours. Since most consumers feed in discrete bouts rather than continuously, the timing of meals and the cessation of feeding is a matter of particular interest (Strubbe and Woods, 2004). In predators, individual queries include the decision of when to attempt catching prey and in case of capture success how much to feed from a single item, when not engulfing entire prey. However, a predators feeding rate will also depend on ecological aspects like the rate of prey encounter (Whelan and Brown, 2005) or the avoidance of predation risk (Pastorok, 1981).

The motivation for meal onset depends on a number of endogenous factors probably related to the imbalance of nutrients and metabolites or to peptide level (Nagata et al. 2010). Furthermore, the probability of attacking prey depends on various exogenous factors like light conditions, prey density or the sensory input e.g. triggered by prey size or movement and that affect prey detectability (Streams, 1982, 1994; see also Chapter 4).
Regarding the offset of food intake, many predators were found to consume only a portion of their prey, referred to as partial consumption or wasteful killing (Cook and Cockrell, 1978; Giller, 1980; Formanowicz, 1984; Lucas and Grafen, 1985; Samu, 1993). A number of models were developed and parameterized for different predator-prey systems to address partial consumption. Each of these models can be classified either as optimal foraging model

(Sih, 1980; Hohberg and Traunspurger, 2009) or as model of proximate mechanisms referring to physiological constraints on foraging (Holling, 1966; Johnson et al 1975; Griffith, 1982).

According to the optimal foraging theory a predator tends to maximize energy uptake (sensu McArthur and Pianka, 1966). While foraging, the predator has to find a compromise between energy acquisition and costs. Therefore, an individual should make its foraging decisions on the basis of prey quality, e.g. size, handling time, nutrition constraints and perceptibility, as well as on the base of environmental conditions (Pyke, 1984). Many optimal foraging models are related the marginal value theorem as developed by Charnov (1976) to predict patch use. Cook and Cockrell (1978) as well as Sih (1980) suggested that a single prey type can be treated as a patch, rendering the marginal value theorem applicable to describe optimal prey exploitation. In terms of partial prey consumption, an optimal foraging model predicts that a predator will drop a prey item in case the investment for further exploitation is higher than that for searching new prey.

Proximate models concerning physiological constraints on feeding have mainly focused on the rate of food ingestion and gut size of a predator. Griffith (1982) for example suggested that in predators externally digesting prey, feeding is limited by the rate of digestive enzyme production. A more general model describing the regulation of food intake was first proposed by Holling (1966). The author suggested that hunger, determined by the amount of food in the gut, is the internal drive of different types of feeding behaviours. Predation behaviour can be thought of as a number of conditional events, namely search, capture and ingestion, each of which is controlled by the hunger level. Therefore, food intake is approaching a maximum value which is determined by the capacity of the gut. Reaching the capacity, the hunger level drops to zero and feeding ceases. Based on the observations that the process of satiation is stimulated by ingested food and inhibits food intake, physiological studies confirm the concept of satiation being a negative-feedback process (Smith, 1998). Modified from Holling's model, Johnson et al. (1975) suggested that in insects two levels of hunger independently affect some component of the predation behaviour. The first level of hunger is related to foregut filling, which affects the rate of attacks and the ingestion of food, whereas the second level involves the filling of the midgut, which affects the attack rate only. In mammals, it was also believed that factors determining the onset of food ingestion are different from those controlling the offset of feeding (Strubbe and Woods, 2004). Gut limitation models predict that partial consumption occurs when a predator does not have enough space in the gut to consume an entire prey item.

There is growing evidence that many animals tend to regulate nutrient intake rather than maximizing energy intake (Simpson et al., 2004; Skorupa et al, 2008; Hengeveld et al., 2009). In general, the need for maximizing food intake should be higher in organisms that are primarily limited by their partition of time than in those animals predominantly digestion limited. As reviewed by Jeschke et al. (2002), most predators can be considered as digestion limited, i.e. they internally digest prey items slower than they externally handle them. In contrast to external handling of prey, digestion can be considered as a background process which does not prevent the predator from searching for or handling new prey (Jeschke et al., 2002). Digestive physiology determines how efficiently and quickly food is processed and therefore considerably affects foraging behaviour (Karasov and Diamond, 1988; Levey and Martínez del Rio, 1999). A number of physiological models were developed for simulating the digestive performance of guts, in a manner analogous to engineered chemical reactors, and were subsequently applied to deduce ecological implications (Penry and Jumars, 1986, 1987; Martínez del Rio and Karasov, 1990; Horn and Messer, 1992). Other models combining ecological and physiological aspects of foraging have incorporated digestion constraints into formulations of functional response (Hirakawa 1997; Jeschke et al., 2002; Whelan and Brown, 2005; Jeschke and Hohberg, 2008).

The quality and quantity of ingested food may vary with a consumer's life stage as found e.g. in holometabolous insects, whereas hemimetabolous insects often employ the same food resource throughout their lives (Boggs, 2009). Even in those species foraging on the same type of prey during their life history, the preference towards certain prey sizes may change since the outcome of predation has been shown to vary with both, prey size and/or predator size (Thompson, 1975; Yen, 1983; Warren and Lawton, 1987; Paradis et al., 1999; Scharf et al., 2000, 2002; Claessen et al., 2002; Rudolf, 2008). In particular, prey characteristics like body size or bulkiness are influencing both external characteristics and internal state of the predator (Whelan and Brown, 2005).

Facing physiological and ecological constraints associated with finding and processing food, insects are capable of diet selection and to some extent of compensatory feeding (Lee et al., 2008; Maklakov et al., 2008; Boggs, 2009). For example, locusts were found to adjust food intake with respect to protein and carbohydrate content of their diet by adjusting their intermeal interval rather than the size of individual meals (Simpson and Abisgold, 1985). Moreover, the example of partial prey consumption illustrates that predators also commonly

regulate meal size. Under variable environmental conditions individual predators might either adjust meal frequency or prey exploitation in order to control the amount of food to be ingested, here referred to as the interplay between attacking and handling prey.

In ecological models, searching for and handling food are usually considered mutually exclusive events. Searching rates or attack rates as well as handling times usually have fixed values only depending on the type of food (Whelan and Brown 2005). Moreover, basic expressions of functional responses, of which the disc equation pioneered by Holling (1959b) is probably the most frequently applied, are based on the assumption that satiation aspects will not significantly influence short term consumption rates (Jeschke and Hohberg, 2008).
Similarly, a the basic foraging model (Chapter 3) was parameterized by means of experiments using backswimmers which were fed to a certain fixed extend and thus were assumed to have a constant level of satiation. However, this will probably not hold true under more realistic conditions since a predator's environment might vary in space and time. For example light conditions may affect prey detectability, and habitat patchiness or fluctuations in prey population dynamics may lead to different levels of hunger or satiation especially when prey is scarce.

In the current study a model is developed, parameterized and tested that realistically incorporates proximate factors referring to ecological and physiological constraints on predation. The digestion based foraging model presented here exceeds the earlier model framework presented in Chapter 3 by linking attack responses and handling of prey to the gut state of the predator, and is thus expected to allow for long term predictions of *N. maculata* predation rates. In contrast to model approaches that combine digestion constraints and mathematical formulations of functional response, this study applies a two compartment model to capture patterns of predation behaviour as observed in experiments. Therefore, attacking and handling of prey are considered mutually dependent processes.
The presented model framework is based on a general predation cycle including conditional events, as previously applied for quantifying or analyzing foraging behaviour (Gerritsen and Strickler, 1977; Greene, 1983; Riessen et al., 1984; Scharf et al., 2002; Nilsson et al, 2007; see also Chapter 3). Each of the components, formulated in submodels, was parameterized by means of behavioural observations and quantitative predation experiments. For the purpose of parameterization, backswimmers and environments were manipulated in terms of hunger level, prey size and density as well as light conditions. Animals were allowed to foraging

more self-determinedly in larger environments and over a longer period in experiments that were independently used for model testing.

The study was aimed at analyzing mechanisms behind the compensatory feeding behaviour of backswimmers with a special emphasis on the role of prey size and prey density. In an exemplary model application, differences in light/dark predation of *N. maculata* juveniles were investigated.

5.2. Material and Methods

In the following paragraphs, the foraging model and the experiments done for parameterization and model testing are described. Both modelling and experiments involved different instars of *Notonecta maculata* and a number of size classes of *Daphnia magna*; corresponding body weights or body length are given in Table 5.1.

5.2.1 Model description

Within the model, the foraging process is described on the basis of a general predation cycle including five conditional events, these being prey encounter, attack, capture success, handling of prey and digestive pause (Figure 5.1). The basic model was developed using data derived from direct observations of backswimmer predation and was tested on the base of functional response and size selectivity experiments. Model testing proved that the model is able to quantitatively predict patterns of short-term predation of juvenile *N. maculata* (see Chapter 3 and Chapter 4). However, the model failed to reproduce long term consumption (see results section). In order to enable long term predictions, the model was adapted to dark conditions in a first step as notonectid predation was found to be affected by the absence of light (Chapter 4). The current study aims to incorporating gut constrains into the model to assess the regulation of feeding behaviour in a third step.

Processes and submodels that exceed the basic model are described below, following the ODD protocol as proposed by Grimm et al. (2006).

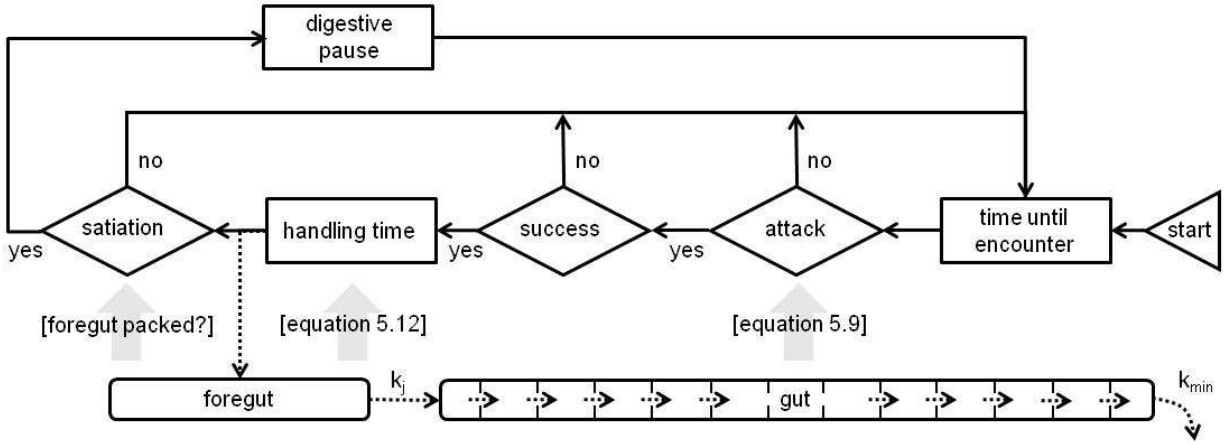

Figure 5.1: Conceptual diagram of the model on the basis of a general predation cycle. The rectangles illustrate the partition of time available to forage, rhombi indicate individual level queries and rounded rectangles demonstrate partitioning of the gut. Solid lines mark the decision tree whereas dotted lines indicate the passage of food extracted from prey items modelled as background process. Within the model, gut content is assumed to affect the attack rate whereas the state of the foregut determines handling time and satiation of the predator.

5.2.1.1 Purpose

The current model was developed to assess ontogenic changes in the predation of *Notonecta maculata* specimens foraging on *Daphnia magna* prey items and to provide a framework for the quantification of long term feeding rates under laboratory conditions, including differences in population structure and density of the prey species. The model is expected to allow reliable estimates for food intake of the five juvenile backswimmer instars and for the impact of backswimmer predation on prey populations.

5.2.1.2 State variables and scales

The model is arranged in three hierarchical levels, these being ecosystem, populations and individuals. Within the ecosystem, experimental conditions are simulated, i.e. the light regime (on/off) is allowed to change with time of the day whereas further properties like temperature and volume are considered constant. The sizes of *Daphnia* and *Notonecta* populations are given by the experimental setups, however, sizes of daphnid populations were allowed to change due to predation. Individuals of both notonectids and daphnids are equipped with a number of state variables at the start of the simulation. An overview on state variables, units and dependencies is given in Table 5.2.

Table 5.2: State variables of the model

Abbreviation	Description	Unit	Dependency
Ecosystem			
v	total volume	ml	experimental setup
l	light regime	on/of	time of the day
Population			
n_d	number of *Daphnia*	number	experimental setup
n_n	number of *Notonecta*	1	experimental setup
Individual Daphnia			
Al	alive	yes/no	
D_{dw}	body dry weight	mg	D_L
D_{ex}	maximum extractable food	mg	D_{dw}
D_s	body length	mm	experimental setup
ID_d	identification number	Number	experimental setup
Individual Notonecta			
A_r	attack rate	0,…, 1	$G2_{content}$, $G2_{max}$, A_x
d_e	encounter distance	mm	i, l
$G1_{content}$	actual foregut content	mg	ε, k_j
$G1_{max}$	foregut capacity	mg	N_{bw}
$G2_{content}$	actual gut content	mg	ε, k_j
Gs_n	number of gut segments	20	-
$G2_{max}$	gut capacity	mg	N_{bw}
$Gs_{content}$	content of gut segment	mg	ε, k_j
Gs_{max}	capacity of gut segment	mg	$G2_{max}$, $G2_{length}$
i	instar	1, 2, 3, 4, 5	experimental setup
ID_n	identification number	Number	Monte-Carlo simulations
k_j	actual passage rate	mg/s	$gs_{content}$, gs_{max}, k_{max}
k_{max}	maximum gut passage rate	mg/s	N_L
k_{min}	minimum gut passage rate	mg/s	N_L
N_{dw}	body dry weight	mg	i
N_L	structural body length	mm	N_{dw}
N_V	structural body volume	mm	N_{dw}
S_r	success rate	0,…, 1	i, D_L
t_{dp}	digestive pause	s	N_V
t_h	handling time	s	$G1_{content}$, $G1_{max}$, t_x

Since the development of individuals involves an increase in body size, within the model framework a number of variables related to the internal state of both predator and prey were assumed as measures proportional to body length or weight. Therefore, presumptions on scaling relationships were applied as suggested by Kooijman (2010) in a dynamic energy budget (DEB) approach. In isomorphs, i.e. animals conserving shape during growth, body

volume is assumed proportional to body length to the power of three. Isomorphism applies to the majority of species (Kooijman 2010) and also will hold true for *N. maculata* and *D. magna*. Body weight can be described as a function of body volume multiplied by a factor of mass density. In *Daphnia*, density of body dry weight is empirical derived from laboratory data, whereas, for reasons of simplicity, mass density is assumed to be 1 mg/mm^3 in *Notonecta*. Accordingly, *Notonecta* dry weight scales with *Notonecta* size, hereafter referred to as structural length. Further DEB related assumptions used in the model include the gut volume as a function of body volume (the cubed structural length) and the proportionality of ingestion rate and animal structural surface area (the squared structural length).

5.2.1.3 Process overview and scheduling

Model processes are adapted from a general predation cycle which is divided in into four consecutive events (Figure 5.1): An encounter between predator and prey might evoke an attack, followed by manipulation and exhaustion of the prey item, referred to as handling of prey, in case the attack is successful. Within the model, time proceeds on the base of seconds and is spent on searching for prey (empirically calculated as time until encounter) as well as on prey handling and digestion. Modified from Jeschke et al. (2002), digestion is modeled as a background process influencing the states of foregut and gut, which in turn determine the time spent on handling prey as well as the length of the digestive pause and the probability of attack respectively.

5.2.1.4 Design concepts

The general design concepts of the model are described below following the checklist of questions given by the ODD procedure. A more detailed description of foraging components is provided in the submodel section.

Emergence: Abundance of daphnids as well as the size distribution of the prey population depends on foraging of individual *Notonecta*. The number of prey items consumed is expected to emerge from environmental conditions, more precisely from the light regime. However, population dynamics do not emerge from any individual properties at this stage of the model, neither in *N. maculata* nor in *D. magna*.

Adaptation and fitness: Within the model an adaptation or fitness seeking of backswimmers is implicated in empirical submodels. Ontogenic changes in foraging strategies are explicitly considered since parameters of the submodels are changing with instars.
Sensing: Environmental and population level factors that are sensed by backswimmers are the light regime and the daphnids available as prey in the environment. Responses of individual backswimmers are assumed to depend on their instar, the corresponding structural length, the size of the daphnid encountered and the amount of food in the gut.
Interaction: The predator prey interaction between individual *D. magna* and *N. maculata* is explicitly modeled. Beyond that no direct interspecies or intraspecies interactions are taken into consideration.
Stochasticity: Size measures of individual *Daphnia* (D_s) and individual *Notonecta* (N_{dw}) are stochastically selected from a normal distribution and assigned at the start of each simulation. Variations in attack rates (A_r) and success rates (S_r) are generated at birth by a normal distribution ($\mu = 1$, σ = coefficient of variation) resulting in an individual parameter multiplied with the calculated rate. The decision whether to attack a prey item, or whether the attack is successful, is based on random numbers between 0 and 1 selected at every encounter. If the calculated rate exceeds the random number, the attack or the success is rejected. In case of successful attacks, the reference handling time (t_x) is calculated using a normal distribution. The stochastic approach is chosen in order to consider the natural variability in the components of predation as observed in video experiments.
Observations: For model analysis in each scenario or time step, the number of prey eaten was saved as an arithmetic mean, minimum, and maximum of 1000 Monte-Carlo simulations.

5.2.1.5 Initialisation

Model initialization is based on experimental setups to be simulated either for calibration or testing of the model. Initial settings involved the volume of the test vessel, simulation time and specification of the chosen predator-prey interaction. On the one hand the number and size class of daphnids were chosen. While on the other hand the instar and deprivation time of the single backswimmers were defined. At the beginning of a simulation body length is randomly assigned to each backswimmer and each daphnid, corresponding to instar and size class respectively.

5.2.1.6 Submodels

The submodels described below are based on empirically derived equations used for modelling the time until encounter, the attack rate, the capture success and the time spent on handling prey as given in Chapter 3. In order to consider the internal handling of prey, the intake and the gut passage of food is explicitly modeled. Further extensions of the basic model involved the encounter as a function of light regime and the formulation of the attack rate and the handling time as a function of gut state and foregut state respectively. The capture success is assumed to be independent of the predators hunger level and is thus not considered in the following description.

5.2.1.6.1 Encounter

In accordance with other modelling approaches (Gerritsen and Strickler, 1977; Pastorok, 1981) an encounter refers to the occurrence of a prey item within the predators' encounter radius. The time spent on waiting until a next encounter (t_e) is calculated on the basis of the encounter radius (d_e) and an encounter probability which depends on prey density (n_d/v) and size (D_s). The encounter radius equals the distance between predator and prey at the instance of a visible response of the predator. In order to account for the light regime affecting foraging of backswimmers the encounter distance is multiplied by a factor of 0.66 for modelling dark conditions as described in Chapter 4. The time until next encounter can be described by the following empirical equation, for derivation see Chapter 3:

$$t_e = (2.095\ d_e^3\ v)\ /\ ((0.35\ D_s + 0.34)\ (0.006\ n_d^2 + 0.12\ n_d)) \qquad (5.1)$$

5.2.1.6.2 Prey size and extractable food

Encounter rate, attack rate, capture success and handling time are described as functions of the prey body length, whereas the predator's intake of food is considered a function of the body weight of the prey. In accordance with Kooijman (2010), *D. magna* dry weight (D_{dw}) is assumed to scale with daphnid body length (D_s) to the power of three, where d_{vd} is a proportionality factor derived from experimental data:

$$D_{dw} = d_{vd} * D_s^3 \qquad (5.2)$$

In the case of a predator which completely engulfs prey, the amount of food taken up equals the body weight of the prey item. Since notonectids manipulate and exhaust prey externally, only a portion of each caught prey item is ingested. The food extracted therefore can be assumed as a proportion of the prey biomass. With e being the empirically estimated maximum extraction efficiency, the maximum extractable food (D_{ex}) per prey item can be described by

$$D_{ex} = e * D_{dw} \quad (5.3)$$

5.2.1.6.3 Gut model

The concept of a two-compartment gut is applied to model the backswimmers' intake and internal handling of food. The first compartment, referred to as foregut, fills at a faster rate than it empties into the second compartment, i.e. the gut. Since notonectids feed by way of meals rather than continuously, the foregut is assumed to serve as a storage having a maximum capacity. While externally handling prey and during the inter-catch interval, i.e. the time from releasing prey carcass until capture of next prey item, food leaves the foregut and enters the gut. Correspondingly, the actual content of the foregut ($G1_{content}$) is calculated from the intake of food and the passage rate. The foregut capacity ($G1_{max}$) is assumed to increase with the backswimmer structural volume (N_V), with *g1* being a proportionality factor of the foregut:

$$G1_{max} = g1 * N_V \quad (5.4.1)$$

Gut clearance is likewise processing: The gut receives food from the foregut and after passing the gut the food is finally discharged. The gut content ($G2_{content}$) is assumed to be limited by a maximum capacity ($G2_{max}$) which is also proportional to N_V:

$$G2_{max} = g2 * N_V \quad (5.4.2)$$

While the foregut is considered a single compartment, the gut is modeled in the sense of a plug-flow reactor (Penry and Jumars; 1986, 1987). For computing the sequence of food passage the gut is divided into segments (Figure 5.1). Each gut segment (Gs) has a uniform size and the content is assumed to be well mixed, while the composition of the segments

might differ in the axial direction of the gut. However, any digestive activity is not included in a first approximation. The calculation of gut segment depletion is based on a maximum and a minimum clearance rate, k_{max} and k_{min} respectively. According to Kooijman (2010) the change of gut content is assumed proportional to *Notonecta* structural surface area (N_L^2):

$$k_{min} = \kappa_{min} * N_L^2 \quad (5.5.1)$$

$$k_{max} = \kappa_{max} * N_L^2 \quad (5.5.2)$$

The number of segments (Gs_n) is herein set to maximum gut residence time [h], independent of the real number of body segments. Accordingly, the capacity of each segment (Gs_{max}) is given by the ratio of $G2_{max}$ and $G2_n$. Starting at the posterior segment, the clearance rate of the foregut and the actual gut passage rate (k_j), i.e. the amount of food moving from $Gs_{(j)}$ to $Gs_{(j-1)}$, is calculated as follows:

$$k_j = \min [\min [Gs_{content(j)}, k_{max}], (Gs_{max(i-1)} - Gs_{content(i-1)})] \quad (5.6.1)$$

Within the model, the most posterior gut segment (j = 1) is assumed to release digested food with the minimum gut clearance rate. Hence, k_{min} is limiting the process of gut passage in the case of a full gut:

$$k_1 = \min [Gs_{content(1)}, k_{min}] \quad (5.6.2)$$

The content of each gut segment after a certain period of time (Δt) is given by:

$$\Delta Gs_{content(j)} / \Delta t = - k_j$$

and $$\Delta Gs_{content(j-1)} / \Delta t = k_j \quad (5.7)$$

Where Δt represents either the time until next encounter, the handling time or the length of the digestive pause. Since the model proceeds on the base of seconds, changes in gut content are calculated for $\Delta t = 1$ [s]. Based on the time until encounter and the actual passage rates, the actual gut content ($G2_{content} = \sum Gs_{content}$) is calculated, which is in turn used to determine the attack rate. The length of the inter-catch interval and the actual passage rate also determine

how empty the foregut is at the beginning of the next meal. This will control the amount of food that can be ingested and thus regulate the handling time. These processes are described in more detail below.

5.2.1.6.4 Attack rate

The attack rate is defined here as the ratio of the number of attacks and the number of encounters between predator and prey. Within the basic model, the attack rate of *Notonecta* instars was implemented as a hump-shaped function of *Daphnia* body length (Chapter 3). Since hunger was assumed to be constant in the previous approach, the basic attack rate (A_x) is herein multiplied by a variable (α) related to gut state:

$$A_r = \alpha * A_x \tag{5.8}$$

The attack rate is assumed to be an exponentially decreasing function of the actual gut content, relative to the maximum capacity of the gut:

$$\alpha = A_{min} + A_{max} * \exp\left(- g2_{area} * N_L^2 * (G2_{content} / G2_{max}\right) \tag{5.9}$$

The parameter A_{min} is considered the mean attack rate at full gut, whereas A_{max} is the mean attack rate at empty gut. The slope of the exponential equation is supposed to depend on a certain area of the gut that might be responsible for feelings of satiation or hunger and thus evoking attacks. This area is assumed to be proportional to *Notonecta* squared structural length (N_L^2).

5.2.1.6.5 Handling time

The time between grasping a prey item and releasing the prey carcass is calculated as handling time. In the basic model handling time is included as a function of *Daphnia* body length and *Notonecta* instar. Within the current model, the calculation of handling times is based on the filling of the foregut. In order to account for differences in handling times observed in different prey sizes and backswimmer instars, the handling time as calculated from the basic model is used herein as a reference time (t_x).

The cumulative weight of food extracted during the time spent on feeding by *Notonecta* can be described by means of a decelerating exponential function depending on prey size (Cook

and Cockrell, 1978). Here the amount of food extracted (ε) during a certain time interval spent on handling a daphnid (t_h) is calculated relative to t_x, where the parameter *h* allows for a maximum handling time only:

$$\varepsilon = h * D_{ex} * (1 - \exp (- t_h / t_x)) \quad (5.10)$$

To calculate the handling time, it is assumed that the time a backswimmer spends on handling a single daphnid will be determined either by the amount of space in the foregut at the start of feeding or by the maximum extractable food (D_{ex}) per prey item:

$$\varepsilon = \min [(G1_{max} - G1_{content}), D_{ex}] \quad (5.11)$$

Hence, considering equation (3) the manipulation of equation (10) leads to:

$$t_h = - \ln (1 - ((\min [(G1_{max} - G1_{content}), (e * D_{dw})]) / (h * e * D_{dw})) * t_x \quad (5.12)$$

5.2.1.6.5 Digestive pause

In accordance to the conceptual model of Riessen et al. (1984), a digestive pause is calculated in case the backswimmer's foregut becomes packed ($G1_{content} = G1_{max}$). In general it can be expected that digestion time decreases with animal body mass (Jeschke & Tollrian 2005). Therefore, it is assumed here that the length of digestive pauses (t_{dp}) is negatively correlated with *Notonecta* structural volume (N_V) :

$$t_{dp} = P_{max} * \exp (-p * N_V) \quad (5.13)$$

The frequency of digestive pauses depends on gut content and thus will emerge from the aforementioned submodels.

5.2.2 Experiments for parameterisation and model testing

In a first set of experiments (*A*) state variables related to prey and predator biomass were estimated, whereas foraging parameters and data used for model testing were derived from a second set of predation experiments (*B*). An overview on model parameters and corresponding experiments is given in Table 5.3.

Observations involved five instars of *Notonecta maculata* (N1-N5) foraging on four size classes of *Daphnia magna* (D1-D4). For maintenance and experiments backswimmers and daphnids were kept in a constant room set at 20 ± 1 °C under a diurnal light rhythm of 16:8 (day:night). Artificial freshwater M4 (Elend and Bias, 1990) was used as a medium. Notonectids were bred in the laboratory and raised separately on daphnids. Backswimmer instars were used in tests within 2-5 days after moulting only. For interrupt-feeding experiments, specimens of *N. maculata* were fed *ad libitum* before being deprived of food for a certain time period prior to experiments as specified below.

Daphnia magna specimens used in experiments were derived from laboratory cultures. Daphnid prey was classified into four groups and graded using non standard sieves (Chapter 3). In predation experiments, relative high prey densities (specified below) were employed in order to initially avoid attacks being limited by the number of encounters between predator and prey. Unless otherwise stated, experiments were run at midday.

5.2.2.1 Measurement of Daphnia and Notonecta body weight

In different experiments (*AI - AIII*), the biomass of individual *Daphnia magna* and *Notonecta maculata* was determined by drying (75°C for 48 h) and measuring entire specimens, carcasses and guts using a Mettler Toledo UMX5 (d=0,1 µg).

(*experiment AI*) In order to model the backswimmers' intake of food during the foraging process, the corresponding ration of dry weight to the body length of prey (entire daphnids and carcasses) was determined. For calculating the length-to-biomass ratio, *Daphnia magna* body length (excluding spine) was measured using a digital image analysis program (Preuss, unpublished). Therefore a total of 50 daphnids per size class and an additional of 25 larger daphnids were scanned (Canon CanoScan 8800F, 1200 dpi) and their dry masses were measured subsequently. As backswimmers digest prey externally, in a second step the biomass extracted from a single prey item was calculated from the balance of total dry weight and carcass dry weight per daphnid size class. A total of 20 *ad libitum* fed *N. maculata* specimens were placed individually in 100 ml beakers and each was given a single daphnid. After consumption, the dry weights of the carcasses and an additional of 20 complete daphnids that were derived from the same sieving were recorded. The procedure was repeated for all combinations of N1-N5 and D2-D4 supplemented by N1 foraging on D1. In a third

step, prey biomasses extracted by deprived and *ad libitum* fed backswimmers were compared. Again, 20 daphnids were given to backswimmers already fed and additionally to backswimmers deprived of food for 24 h respectively. As no significant difference was found within the amount of food extracted by *Notonecta* instars (see results section), daphnids of each size class (D1-D4) were randomly given to backswimmers of different instars. Biomass measurements of prey carcasses were processed as described above.

(*experiment AII*) Since hunger is assumed to correlate with gut state, the capacity of the foregut and the gut as a daphnid biomass equivalent was determined as follows. Two sets of *N. maculata* juveniles were used for the measurements; the first set was fed *ad libitum* whereas the second set was deprived of food for 48 h to allow complete depletion of guts. Animals were killed in ethanol and guts, including the foregut, midgut and hindgut, were immediately removed under magnification. Thereafter dry weight of bodies and guts were quantified separately and dry weights of empty guts were added to body weights. Gut capacity was calculated from the balance of full and empty guts. Measurements were done for N2-N5 with a total of 80 backswimmers involved. The proportion of the foregut to total gut dry weight was thereafter calibrated on the base of the predation experiments described below.

5.2.2.2 Predation experiments

Four independent sets of predation experiments (*BI - BIV*) were carried out for parameterization, additional calibration and testing of the model. In experiments, prey sizes, which were found to be consumed to a high extend by *Notonecta* instars, were applied (see Chapter 3): D2 in N1-N2 and D3 in N3-N5.

(*experiment BI*) Steady-state feeding was observed in experiments using deprived (48 h) and non-deprived backswimmers which were allowed to forage individually on 20 daphnids in 100 ml vessels during 5 h. Experiments were done for the five instars of *N. maculata* replicated five times. To estimate biomass intake per daphnid, the body length of prey was measured digitally (as described above) prior to the experiments. During each observation the time of successful attacks was noted and prey was replaced after consumption. The resulting steady-state feeding rate [mg/s] was calculated from the ratio of cumulative consumption and the timing of attacks. Based on the assumption of Jeschke et al. (2002) that digestion time per

prey item can be estimated from long term consumption, steady-state feeding rates of deprived and well-fed *N. maculata* were utilized as gut passage rates (k_{max}, k_{min}). In deprived backswimmers, the foregut and gut are supposed to be empty, allowing food to pass unobstructed with k_{max}. In turn, when the foregut and gut are believed to be full, the intake of food can only be as fast as its release after passage in the guts of backswimmers that were fed *ad libitum*. Thus, k_{min} was estimated from long term feeding rates using non-deprived *N. maculata* individuals.

(*experiment BII*) Patterns of predation behaviour were derived and parameters were estimated by directly observing foraging of juvenile backswimmers in video experiments. Observations were conducted using a cuvette-like aquarium (10:5:2 cm) filled with 100 ml media and 20 daphnids. Single *Notonecta* juveniles which were deprived for 0, 4 and 48 h prior to experiments were placed into the prepared aquarium. Filming was done during 1 h using a camera of the type Sony DCR-TRV 310E. Video experiments were replicated three times. Attack rates, capture success and handling times, were quantified as described in detail in Chapter 3.

(*experiment BIII*) For additional calibration of model parameters, predation of the five notonectid instars was quantified in interrupt-feeding experiments. In order to create different hunger levels, backswimmers were deprived for 0, 2, 4, 6, 24 and 48 h prior to observations, each of the experiments replicated 10 times. To achieve a slightly different prey density, single backswimmers were placed in 200 ml beakers and allowed to forage on 30 *D. magna*. After 1 h, notonectids were taken out of the test vessel and dead as well as live prey was counted, and compared to the initially introduced numbers taken as control. Within the dead prey, only *D. magna* items that had been sucked out were considered eaten. Daphnid carcasses could be easily distinguished from naturally dead prey items or exuviae.

(*experiment BIV*) For testing the model, foraging of *N. maculata* juveniles was observed during 48 h. Experiments were started 2 h after ‘sunrise’ and involved two 8 h dark periods. Observations were carried out using 5 l aquaria and initial prey densities of 300 in N1, 400 in N2-N4 and 800 in N5, replicated five times. The number of daphnids eaten was obtained in a manner similar to the experiments described above. Dead prey was counted after 3, 6, 9, 12, 24, 36 and 48 h. In order to check the prey density initially given, live prey was additionally counted after 48 h. The error due to miss counting was less than 3 %. Control experiments where no backswimmers were involved verified that mortality due to natural causes was less than 1 %.

5.2.3 Implementation and statistical analyses

The source code of the model was implemented in Delphi® using Borland Delphi® 2007 for Win32® Professional Edition. Equations of submodels were fitted to data by means of SigmaPlot 8.0 (SPSS Inc. 2002). Statistical analyses were carried out using the statistical package PASW Statistics 18 (SPSS Inc. 2009).

5.2.3.1 Data analysis

Differences in *Daphnia* dry weight consumed by the instars of *Notonecta* were evaluated by means of a one-way ANOVA using the dry weight of entire daphnids as a co-variable (ANCOVA) since the data passed Levene's-Test. Differences in attack rates, success rates and handling times quantified in video experiments were analyzed using a Kruskal-Wallis-Test. Although parameter values differed, patterns of foraging were similar across *Notonecta* instars, thus data was transformed before being used in a combined analysis as follows: First, mean values of attack rates, success rates and handling times were calculated separately for all instars. Thereafter relative parameter values were determined as the ratio between replicate and mean.

5.2.3.2 Calibration and model testing

A number of model variables could not be directly measured in the laboratory and therefore were estimated by fitting the model to the outcome of predation experiments. Fitting was done by minimizing the residual sum of squares using the downhill simplex technique (Nelder & Mead 1965) which is implemented in the mathematical library tpmath, version 0.70 (Debord 2008). Model efficiency (EF, Loague and Green 1991) was used to evaluate the performance of the model.

For the evaluation of the model predictions, regressions of observed vs. predicted data were plotted. In doing so, the coefficient of determination (r^2) as well as the root mean squared deviation (RMSD) were calculated and the hypothesis that the slope of regressions is equal to 1 and the intercept equals 0 was tested as proposed by Piñeiro (2008) using a t-Test.

5.2.3.3 Sensitivity analysis

In order to identify a subset of parameters that significantly affects the output of the model, the screening design method suggested by Morris (1991). The technique provides qualitative

ranks of parameter importance for the evaluated model. For each of the variables two sensitivity measures are computed: μ estimates the overall influence and σ estimates the higher order effects of the given parameter. The experimental design of the method includes randomized OAT experiments which were run using the Simulation Environment for Uncertainty and Sensitivity Analysis, version 2.2 (SIMLAB, 2010). Further details were described in Chapter 3. The sensitivity analysis was done using 8 random levels chosen from 18 variables, generating a 76-sample experiment. Each of the experiments was run for 1000 Monte-Carlo simulations.

5.3. Results

In the results section, the parameterization and calibration of the model is described as a result of dry weight measurements and predation experiments in a first step. In a second step, the relative sensitivity of parameters is evaluated and the results of the independent predation experiment are compared to the model output.

Table 5.3: Parameterisation of individuals within the model

	value	description	values derived from
A_{max}	2.35	maximum attack rate	*experiment B II*
A_{min}	0.12	minimum attack rate	*experiment B II*
A_x	$f(i, D_s)$	reference attack rate	Chapter 3
d_{vd}	0.0082	density of dry weight in *Daphnia*	*experiment A I*
d_{vn}	1	density of dry weight in *Notonecta*	assumed
g1	0.021	proportionality factor of foregut capacity	calibrated (*experiment B III*)
g2	0.123	proportionality factor of gut capacity	*experiment A II*
$g2_{area}$	3.43	proportionality factor of the part of the gut that is responsible for feelings of hunger or satiation	calibrated (*experiment B III*)
h	1.08	limiting factor of handling time	calibrated (*experiment B II*)
p	0.195	proportionality factor of digestive pause	calibrated (*experiment B III*)
P_{max}	210.01	factor of maximum digestive pause	calibrated (*experiment B III*)
t_x	$f(i, D_s)$	reference handling time	Chapter 3
e	0.5	maximum extraction efficiency	*experiment B II*
κ_{max}	0.000011	proportionality factor of maximum gut passage rate	*experiment B I*
κ_{min}	0.000007	proportionality factor of minimum gut passage rate	*experiment B I*

5.3.1 Parameterisation and calibration of the model

Parameter values that were empirically derived from experiments or those that were calibrated to the results of predation experiments are given in Table 5.3. In the modelling process, a number of parameters and state variables are scaled to prey body weight. *D. magna* dry weight was found to correlate with body length to the power of three as shown in 5.2. The amount of food extracted from a single prey item increased with daphnid dry weight (Figure 5.3). When comparing the dry weight of *Daphnia* carcasses to the dry weight of similar sized whole *Daphnia*, it appeared that 31% of the prey item was consumed by *N. maculata* specimens which were fed *ad libitum* prior to experiments. No significant difference was thereby found in the amount of food extracted by the different notonectid instars (Ancova, p=0.582). Furthermore, the experiment revealed that the amount of food extracted by backswimmers which were deprived for 48 h prior to experiments increased by 19% compared to the food consumed by backswimmers fed *ad libitum*, thus, in total, 50 % of *D. magna* individuals is available for extraction by backswimmers.

Dry weights of guts were observed to increase with the structural volume of backswimmers (Figure 5.4). From the balance of full and empty guts, the fraction of the gut capacity, measured as daphnid dry weight equivalents was determined as 14.4% of *Notonecta* structural volume.

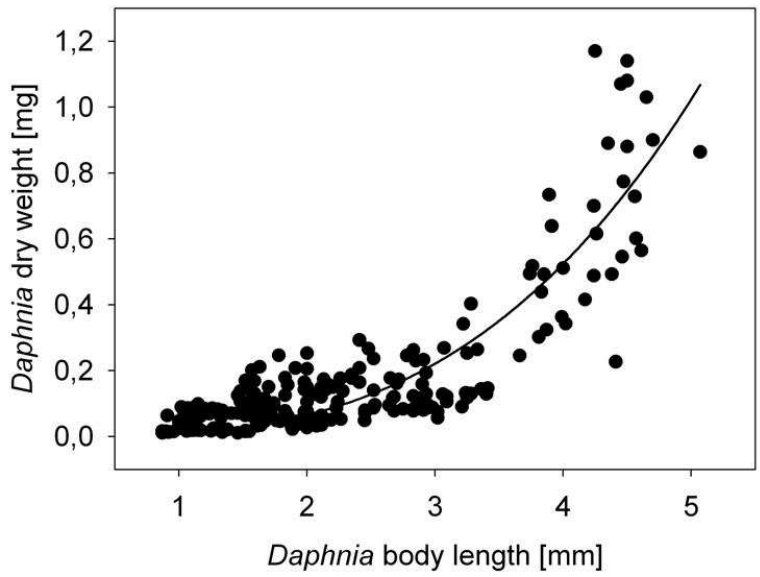

Figure 5.2: Dry weight of *Daphnia magna* as a function of body length ($y = 0.0082x^3$, $r^2 = 0.766$, n = 225).

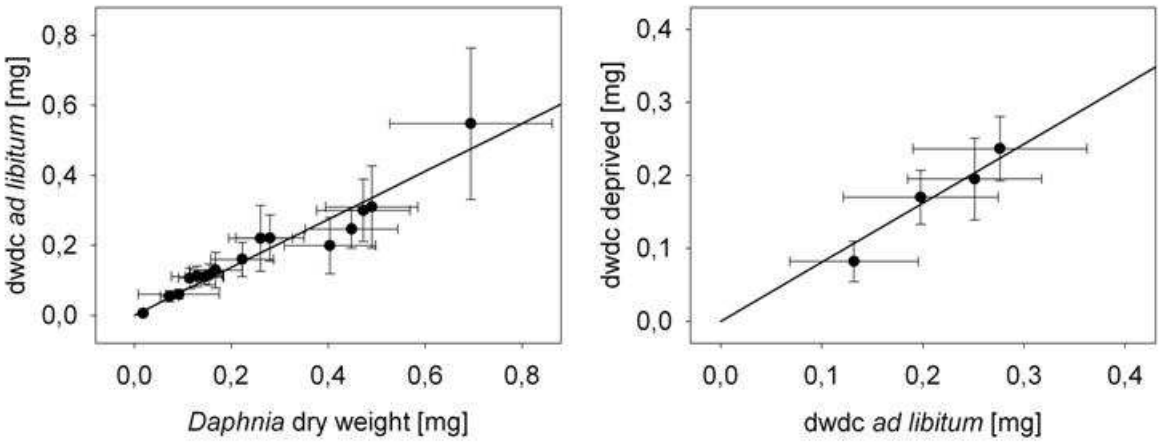

Figure 5.3: Dry weight of *Daphnia magna* carcasses (dwdc) after being consumed by backswimmers fed *ad libitum* prior to experiments as a function of *D. magna* dry weight (left, y = 0.69x, r2 = 0.921), and dry weight of daphnid carcasses after being consumed by backswimmers deprived for 48 h as a function of daphnid carcasses previously consumed by backswimmers fed *ad libitum* (right, y = 0.81x, r2 = 0.926). Dots represent mean and standard deviation of 20 replicated measurements each (40 daphnids involved).

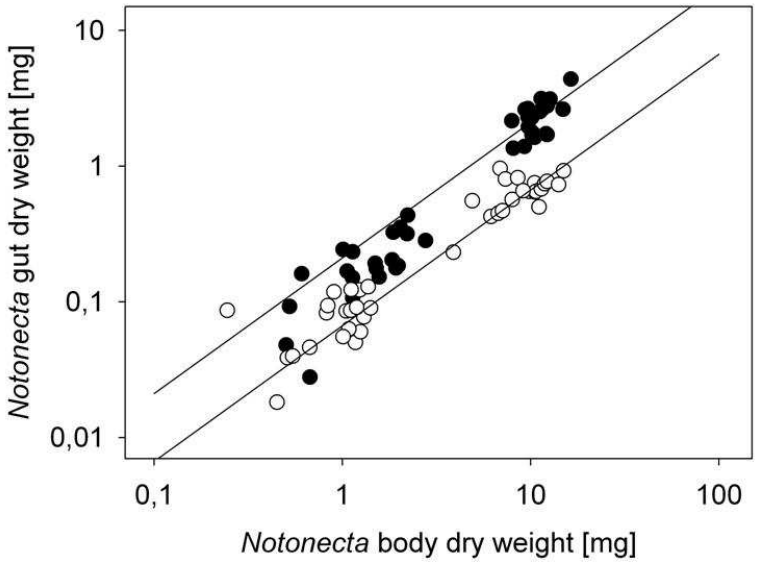

Figure 5.4: Dry weight of guts as a function of *Notonecta* body dry weight (n = 80). Black dots represent measurements of backswimmers fed *ad libitum* prior to experiments (y = 0.211x, r^2 = 0.891) and white dots represent measurements of backswimmers deprived for 48 h (y = 0.067x, r^2 = 0.777).

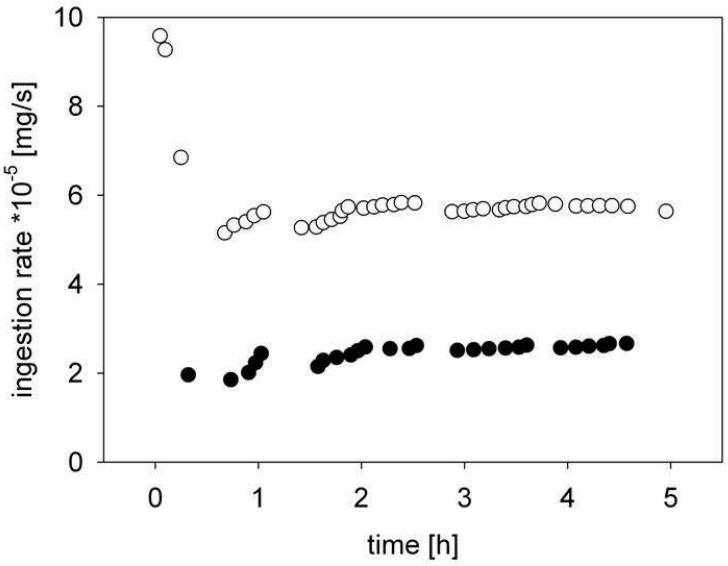

Figure 5.5: Ingestion rate during the course of a steady-state feeding experiment. Results are shown for the example of single backswimmers of the 4th instar which were fed *ad libitum* (black dots) and deprived of food for 48 h prior to experiments (white dots) respectively.

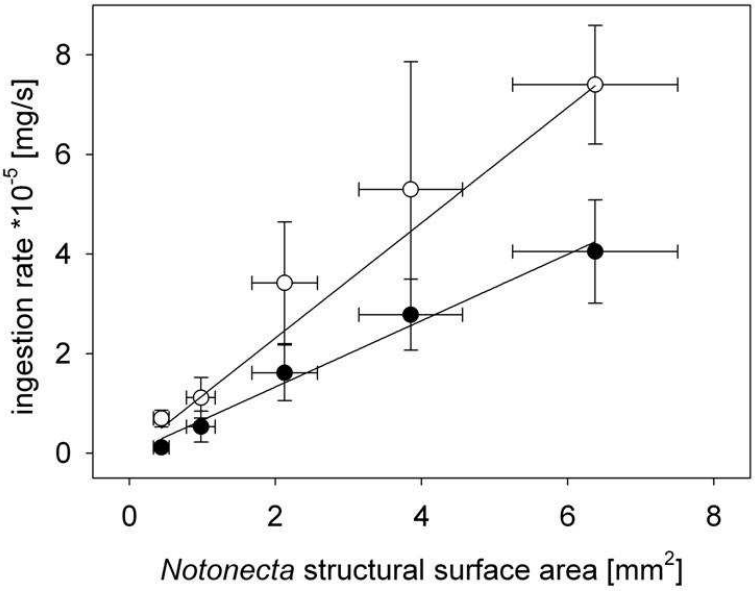

Figure 5.6: Steady-state ingestion rate as a function of structural surface area in *N. maculata* specimens deprived for 48 h (white dots, $y = 1.1 * 10^{-5}x$, $r^2 = 0.933$) and in *N. maculata* fed *ad libitum* (black dots, $y = 0.7 * 10^{-5}x$, $r^2 = 0.987$) prior to experiments (n = 5 each). Within the model, ingestion rates of pre-fed and pre-deprived backswimmers were utilized as minimum and maximum gut passage rates (k_{min}, k_{max}) respectively.

In deprived backswimmers, ingestion rate sharply decreased until reaching a steady-state following the consumption of the first daphnids as exemplified in Figure 5.5. In *Notonecta* fed *ad libitum* prior to experiments, feeding was directly in a steady-state. Since the ingestion rate did not further decrease in deprived backswimmers, no satiation effects were observed during the 5 h experiments. Steady-state ingestion rates of both deprived and well-fed animals were found to be proportional to the squared structural length of backswimmers (Figure 5.6).

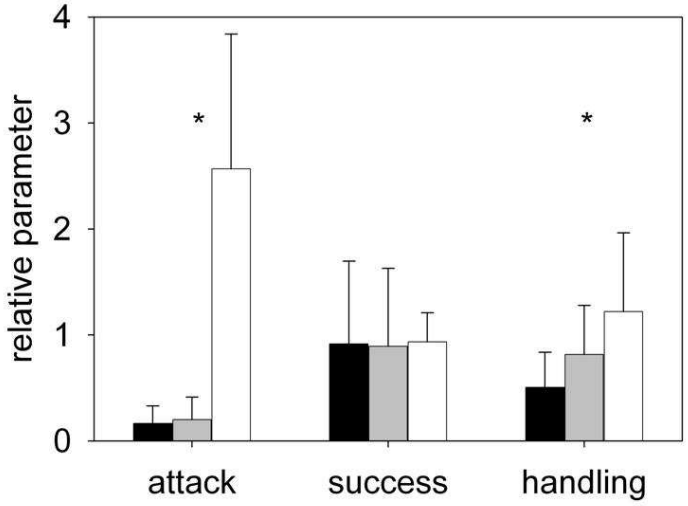

Figure 5.7: Components of predation as measured in video experiments (mean and standard deviation) for backswimmers fed *ad libitum* (black bars) and deprived for 4 h (grey bars) and 48 h (white bars) prior to experiments. Attack rates (n = 45), success rates (n = 41) and handling times (n = 180) were normalized at their mean parameter value per backswimmer instar for combined analysis. Asterisks indicate significant differences in Kruskal-Wallis-Test.

Normalized mean attack rates, success rates and handling times derived from video experiments are shown in Figure 5.7. There were significant differences in the rate of attacks (Kruskal-Wallis-Test, $p < 0.001$) and the time spent on handling prey (Kruskal-Wallis-Test, $p < 0.001$) between different levels of deprivation. However, capture success was not significantly affected (Kruskal-Wallis-Test, $p = 0.904$). The attack rate was found to increase by a factor of 14 in backswimmers which were deprived for 48 h compared to those fed *ad libitum* prior to experiments or those which were pre-deprived for 4 h only. Handling time gradually increased with the level of deprivation. The mean handling time was 2.4 times higher in backswimmers which were deprived for 48 h compared to individuals which were fed *ad libitum* until the beginning of experiments. The examination of handling times in a sequence of catches as done for the example of the 4th instar reveals that the time spent on

handling prey declines with the number of items consumed in backswimmers pre-deprived for 48 h (Figure 5.8). When calibrating the parameter *d* to the data, the model is able to adequately describe the pattern observed in video experiments (EF = 0.75).

Results of interrupt-feeding experiments are shown in Figure 5.9. All juvenile instars of *N. maculata* consumed more daphnids when being deprived for more than 24 h compared to those backswimmers deprived for shorter periods or fed *ad libitum* prior to experiments. Moreover, a decrease in the number of prey eaten is apparent for short deprivation periods compared to *ad libitum* fed animals, with the decline being more pronounced in larger instars. After reaching an inflexion point, the number of consumed prey items increases and levels off at a maximum value. The pre-deprivation time corresponding to the inflexion point was found to increase with the backswimmer instar. The fitted model is able to catch the essential patterns of the observations but fails to reproduce details (EF = 0.57), e.g. the number of prey eaten after long deprivation periods is overestimated in N3 and N4.

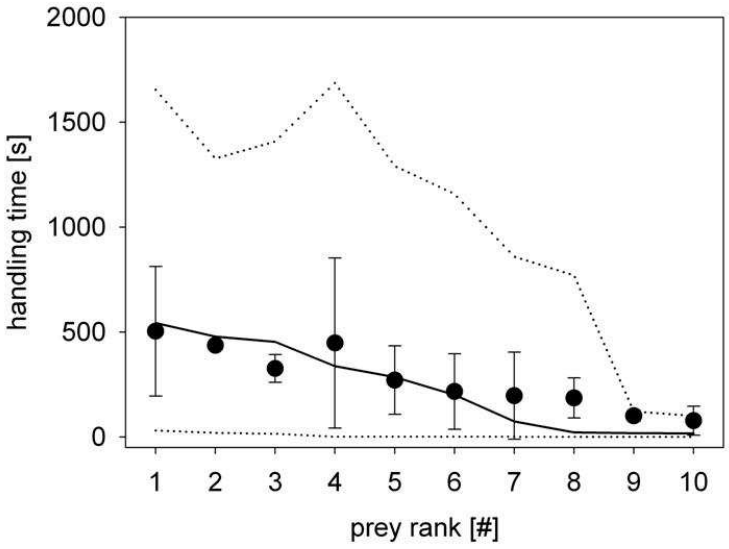

Figure 5.8: Calibration of the parameter *h* to the decay in mean handling time through the prey catch sequence. Dots represent mean and standard deviation as observed in video experiments for *Notonecta maculata* specimens of the 4th instar deprived for 48 h prior to experiments (n = 3 each). Lines mark mean (solid), minimum and maximum values (dashed) of 1000 Monte-Carlo simulations.

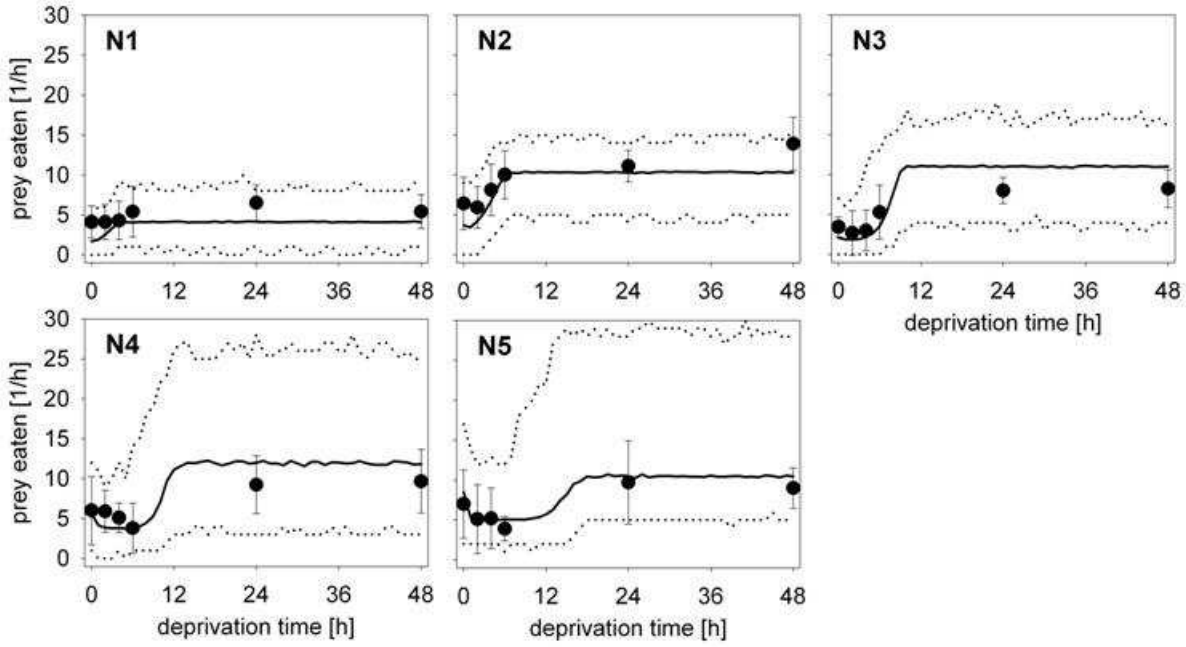

Figure 5.9: Calibration of the parameters *g1*, $g2_{area}$, *p* and P_{max} to the number of daphnids eaten in interrupt-feeding experiments during 1 h. Dots represent mean and standard deviation as observed in predation experiments for *Notonecta maculata* instars (N1-N5) deprived for certain periods prior to experiments (n = 10 each). Lines illustrate mean (solid), minimum and maximum values (dotted) of 1000 Monte-Carlo simulations.

5.3.2 Model evaluation

The examination of sensitivity using the OAT method revealed the relative importance of variables which are indirectly or directly related to the attack rate (Figure 5.10): Whereas the initial number of prey available (n_d) and the *Notonecta* encounter distance (d_e) influence the number of encounters between predator and prey, the reference attack rate (A_x) and the initial content of the gut ($G2_{content}$) contribute to the number of attacks. Furthermore, a number of variables were identified as having an intermediate influence on the number of consumed prey as compared to others. These were the size of both, predator and prey (D_s, N_V), the proportionality factor of the absorptive gut area ($g2_{area}$), the proportion of the foregut capacity to *Notonecta* structural volume (*g1*) and the handling time limiting factor (*h*). Other parameters like those related to gut passage rates or digestive pause were found to be less sensitive.

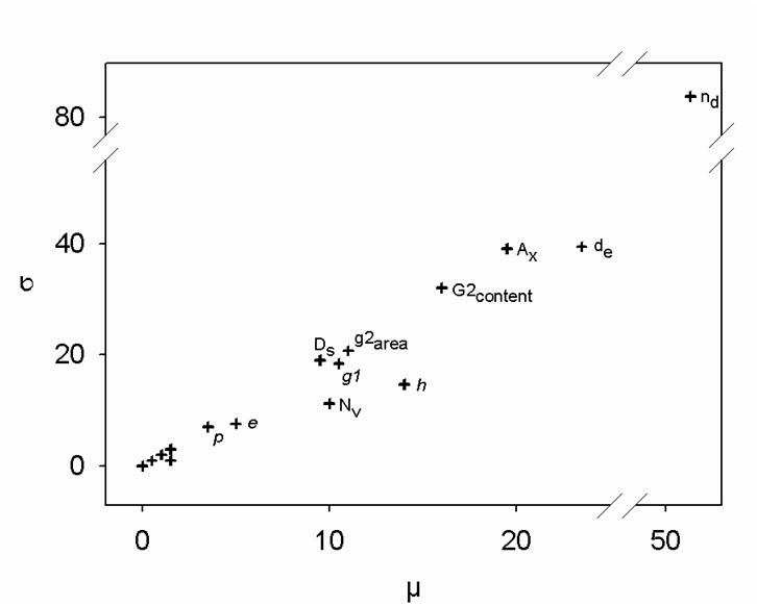

Figure 5.10: Relative importance of model parameters and variables as derived from the OAT sensitivity analysis. For each of the variables, μ estimates the overall influence and σ appraises higher order effects. For reasons of clarity, labels of the seven, less sensitive parameters were omitted.

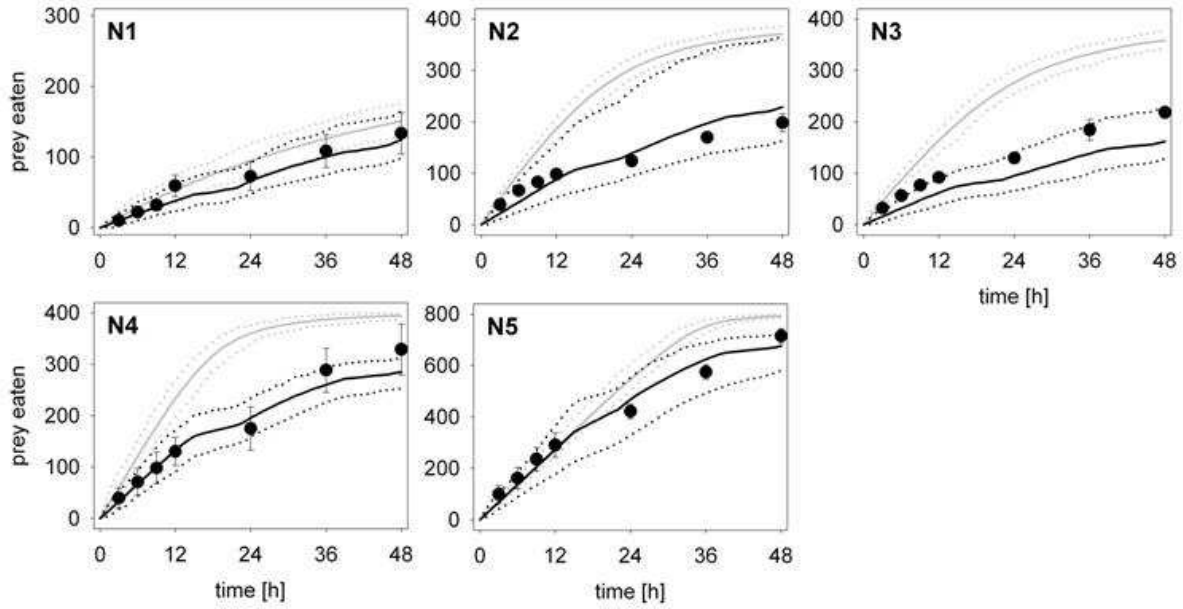

Figure 5.11: Model testing based on 48 h predation experiments done for the five *Notonecta maculata* instars (N1-N5). Y-Axes are set to the number of daphnids initially given to single backswimmers. The experiments involve two 8 h-dark periods (after 14 h and 38 h). Dots represent mean and standard deviation of five replicated measurements, lines indicate mean (solid), minimum and maximum values (dotted) of 1000 Monte-Carlo simulations using the basic model (grey lines, Chapter 3) and the digestion based foraging model (black lines).

For model testing, the output of the model was compared to the results of the 48 h predation experiments (Figure 5.11). This revealed that the basic model, which does not consider any satiation aspects (see Chapter 3), overestimates the number of prey items eaten in most of the notonectid instars, whereas the digestion base foraging model is able to adequately predict the observations for the chosen foraging scenarios. For the latter, a good correlation between observed and predicted mean numbers of eaten daphnids was found for the experiments (Figure 5.12). Parameters of the observed versus predicted regression did not significantly differ from one and zero in slope (t-Test, p = 0.791) and intercept (t-Test, p = 0.924), respectively.

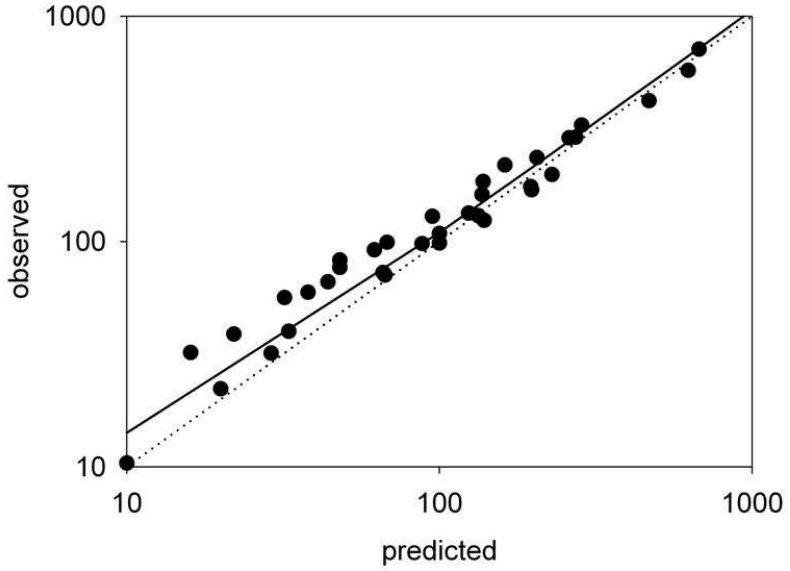

Figure 5.12: Observed mean number versus predicted mean number of prey eaten during 48 h predation experiments. Dots represent data, dashed line 1:1 reference and solid line the linear regression (y = 3.56x + 1.06, r^2 = 0.966, RMSD = 27.3).

5.4. Discussion

The rate of food intake depends on both, the external conditions and the internal state of an animal (Doucet and van Straalen, 1980). However, ecological and physiological characteristics of consumers are usually viewed in isolation (Whelan and Brown, 2005). By incorporating encounter rates, attack rates and capture success as well as external and internal handling of prey, the model presented here adds physiological characteristics to an ecological framework. Therefore, changing predator satiation over time was implemented in a mechanistic manner. The filling of the gut and the foregut were assumed to determine the

probability of attack in case of a prey encounter and the time spent on handling prey items following successful attacks, respectively. Based on empirical observations, the model considers onthogenic changes during juvenile development of the insect predator *Notonecta maculata* and was shown to adequately predict the results of independent predation experiments.

5.4.1 Design concepts and parameterisation

The design of the presented model is largely based on patterns of predation behaviour as observed in experiments. Relating components of the predation cycle to gut content allowed conclusions on mechanisms behind the observed patterns to be drawn. In the current section, the derivation of the model structure and the parameterisation of submodels are discussed.

5.4.1.1 Attack rate and handling time

In their study on damselfly naiads, Johnson et al. (1975) hypothesized that the filling of the foregut affects the attack response to prey encounters, via digestive pauses, and eating while the (mid-)gut affects attack responses only. In a more recent review Strubbe and Woods (2004) stated that the factors that control the onset of feeding might be different from those that cease food intake. In the current study, empirical observations back the hypothesis that distinct mechanisms may control attacks and handling of prey items.
In video experiments, the sets of backswimmers used were either fed *ad libitum* or deprived for 4 h and 48 h prior to observations. Observations of removed guts from backswimmers specimens demonstrated that both, the foregut and gut were full in well-fed animals whereas the gut was empty in backswimmers deprived for 48 h. By calculating the content of the foregut and the gut from gut capacity data and passage rates and assuming that the calibrated foregut capacity is close to the natural size of the foregut, it appears that in all notonectid instars the foregut was empty after 4 h of food deprivation and that the gut was full or only partly cleared at the beginning of experiments.

The attack rate was observed to increase in backswimmers which were deprived for 48 h prior to experiments. However, no significant difference was found in the attack rate of well-fed individuals and those deprived for a short period only (foregut assumed empty), indicating that the attack rate might depend on the emptiness of the gut. Since several empirical studies found a hyperbolic relationship between deprivation time and hunger level as reviewed by

Jeschke et al. (2002), consumption rate increases with hunger level (Jeschke and Hohberg, 2008) and gut state is correlated to deprivation time, here the assumption of the attack rate being an exponential function of gut filling (equation 5.9) is not too unlikely. The slope of the exponential attack rate curve was found to be steep, indicating that only a part of the gut might be responsible for translating digestive activity into attack responses of backswimmers. The relative size of this part will differ across instars (Tillyard, 1917). Given that the surface area of the gut scales with animal surface area (Kooijman, 2010), the assumption that the slope scales with structural surface area of juvenile *N. maculata* appears to be a realistic one.

In deprived *N. maculata* specimens, handling time per prey item decreased during a catch sequence. This finding is in agreement with results previously reported for aquatic insect predators (Cook and Cockrell, 1978; Giller, 1980; Kruse, 1985, Bailey 1986). Moreover, video experiments revealed that mean handling time increased with increasing time of food deprivation in all juvenile instars of *N. maculata*. From a gut-limiting perspective, higher mean handling times after 4 h of deprivation are a result of empty foreguts allowing for a more thorough extraction of prey. Higher handling times in backswimmers depleted for 48 h, as compared to those deprived for a short period only cannot be explained from the limiting foregut capacity alone. Within the model, the foregut empties with a minimum gut passage rate in case of a full gut. Consequently, the foregut is always close to full in high prey densities leading to relative low handling times. An empty gut allows the foregut to empty in a much faster rate resulting in higher handling times. These processes emerging from the model structure might provide an explanation for the pattern observed in the video experiments: In short-term deprived animals, only the firstly captured prey items led to higher handling times as compared to well-fed *N. maculata* specimens until foregut reaches capacity. In contrast, it is suggested here that in long-term deprived backswimmers, handling time per prey item decreases only gradually due to faster emptying of the foregut during handling and inter-catch intervals, overall leading to higher mean handling times.

Several empirical studies have shown that the total amount of food extracted from an individual prey item increases in a decelerating manner with time, implying that the rate of food extraction from an single item decreases as consumption proceeds (Cook and Cockrell, 1978; Giller, 1980; Kruse, 1985, Hohberg and Traunspurger 2009). In animals digesting prey externally, a considerable part of the handling time might be spent on the injection of enzymes, leading to an initially lower consumption rate (Griffith, 1982; Samu, 1992). This delay in the extraction of food becomes apparent as an increase in prey wet weight after

enzyme injection (Bailey, 1986). Griffith (1982) suggested that the rate of enzyme injection is limiting feeding time. However, when considering a delay in prey extraction as a fixed proportion of handling time within the current model framework, values of the parameter derived from calibration to handling time data were close to zero. This finding is in line with empirical studies reporting a rapid extraction of food in *Notonecta* (Giller and McNeill, 1981), starting immediately after prey capture (Cook and Cockrell, 1978). Therefore, here a decelerating exponential function was used to model prey extraction over time as suggested by Cook and Cockrell (1978).

A consequence to the concept of gut controlled feeding behaviour is that attack rate and handling time are not independent. High attack rates, when followed by capture success, will lead to frequent prey captures and thus to guts which are filled close to capacity. Assuming that foregut capacity is the major factor controlling the exploration of a prey item of a particular size, this will lead to low handling times. In turn, intense prey exploitation during long handling time will result in an increase of gut content and thus will affect the attack rate.

5.4.1.2 Two compartment gut

The concept of a two-compartment gut was applied for modelling satiation aspects in the foraging of backswimmers, in accordance to the conceptual model of Johnson et al. (1975). Other empirical studies described a similar compartmentalization of insect guts (Tillyard, 1917; Giller, 1980, 1984, Sangpradub and Giller, 1998). In contrast, previous studies also successfully applied models to describe feeding behaviour using a single internal state variable (Holling, 1966; Doucet and van Straalen, 1980; Dam et al., 1991; Jeschke and Hohberg, 2008). This single state variable might include gut content or reserves of the animal and helps limiting the number of initial model assumptions (Doucet and van Straalen, 1980). Since parameters related to the attack rate were found to be most sensitive within the current model framework, it could be argued that a single internal state variable influencing the attack rate might also lead to reasonable predictions for the feeding rate of backswimmers.
A model using a single internal state variable related to hunger will predict an increase in the number of prey items consumed with increasing hunger level. Here, the opposite was found for backswimmers which were deprived for a short period prior to experiments. As revealed by the analysis of the model output, the lower number of daphnids consumed by individuals deprived for a short period as compared to those which were well fed might be a result of

longer handling times. An increase in the number of eaten prey was observed after long periods of food depletion only. A model based on a single internal state variable will probably not be able to capture the mechanism behind this kind of feeding behaviour. Consequently, in the current study the concept of a two-compartment system was applied in order to model satiation aspects in notonectid predation.

5.4.1.3 Gut capacity, gut passage rates and satiation

Within a physiological framework, feeding ceases when the gut reaches its maximum capacity and starts again after the food is sufficiently processed (Whelan and Brown, 2005). However, a physical limit to the capacity of the gut in a volumetric sense is not the sole constraint since gastric stimuli related to digestion might also have a significant contribution to satiation effects of the ingested food (Smith, 1998). The latter aspect might be important when considering more than one food source and different food qualities. Whelan and Brown (2005) suggested that even when the gut is full, a consumer will accept additional prey items provided they are of sufficient nutritional richness. However, the concept of gut maximum capacity controlling satiation appeared to be a reasonable first approximation for modelling digestion constraints when including only a single type of food source.

Gut passage rates were derived from steady-state feeding experiments assuming that food passes the gut with the same rate as the animal ingests prey. The foregut is therefore considered a storage continuously discharging into the gut. In order to derive minimum and maximum gut passage rates, well-fed and deprived *N. maculata* individuals were employed. As described above, the gut was full in well-fed backswimmers, whereas foregut and gut were found to be empty in individuals deprived for 48 h. Faeces remaining in posterior parts of the hindgut were observed in some long term deprived individuals only, whereas e.g. *Daphnia pulex* (Linnaeus) tend to keep their guts full at low food densities (Evers and Kooijman, 1989), and the complete evacuation of guts as observed for *N. maculata* juveniles is in line with observations done e.g. for copepods (Christoffersen and Jespersen 1986) and fish (Jobling 1981).

In steady-state feeding experiments, daphnid prey was observed to be consumed to a higher extent by backswimmers deprived for 48 h as compared to those fed *ad libitum*. Following the aforementioned assumptions, one conclusion of this observation is that food passes through

the foregut in a faster rate in case the gut is empty as compared to a filled gut. In case of a full gut, food passage is as slow as the process of food leaving the gut. Linear and exponential models were proposed to describe evacuation of guts (Christoffersen and Jespersen, 1986). Due to the lack of detailed data and for the sake of simplicity here, linear evacuation was assumed.

The steady-state ingestion rate was found to remain stable in deprived backswimmers indicating a lack of satiation effects for a period of at least 5 h. Therefore, the experiment provides some evidence that food also passes through an empty gut faster than a full one and that the process limiting the gut passage might be located in a more posterior region of the gut and/or the feeling of satiation is being delayed e.g. due to absorption processes.
Absorptive activity was previously suggested to be predominantly located in the midgut or hindgut compartments depending on the investigated species (Giller; 1984; Thor and Wendt, 2010). The region that is responsible for feeling of satiation possibly differs across taxonomic groups and cannot be located using the present data. Waterhouse (1957) suggested that the peritrophic membrane, a part of the midgut, influences feeding in insects. The peritrophic membrane was found to compartmentalize digestive processes and to be involved in nutrient acquisition and the reuse of enzymes (Hegedus et al., 2009). Gut capacity and passage rate might be particularly determined by the process of peritrophic membrane regeneration (Johnson 1975; Griffith 1982).

5.4.1.4 Plug flow mode of gut passage

For computing the passage of food and gut evacuation, the gut was compartmentalized in the sense of a plug flow reactor. Analogous to engineered chemical reactors, plug flow reactors are the most frequently applied models for simulating food passage and digestive activity of animal guts (Jumars, 2000). Plug flow reactor models are fast and easy to use while still catching the most important flow features (Gresch et al., 2009). The reason for compartmentalizing the gut, instead of using a single compartment only, is the possibility of immediate food excretion. In case of an empty gut, food that is discharged by the foregut will be directly available for further release when applying a single compartment gut model. In contrast, dividing the gut into compartments prevents food from being immediately excreted and thus indirectly affects attack rate and handling time. However, the number of gut compartments was found to be of low importance for the output of the model.

5.4.1.5 Prey size and predator size

Prey size and predator size were among the parameters observed as having an intermediate importance for the output of the present model. The model accounts for different prey sizes by incorporating the probability of attack and capture success as functions of prey body length as discussed in detail in Chapter 3 and by additionally considering the amount of food that is potentially available to the forager for extraction. The amount of food extracted from a single *D. magna* was found to increase with *Daphnia* body weight. Similar results were described by Cook and Cockrell (1978) and Griffith (1982) for backswimmers and ant-lions respectively. In accordance with the study of Griffith (1982), here the extraction efficiency, measured as the percentage of prey weight extracted, was independent of the predator instar. This finding allows for extrapolation across different *Notonecta* sizes in the handling time submodel (equation 12). A mean of 50% of the D. magna dry weight was observed to be available for extraction to notonectid juveniles. This value is in range with other predator prey systems with predators digesting prey externally (Fox and Murdoch, 1978; Bailey 1986; Ranta and Espo, 1989; Van Zyl 1997).

In accordance with previous studies (Thompson, 1975; McArdle and Lawton, 1979; Yen, 1983; Spitze 1985; Hirvonen and Ranta, 1996; Woodward and Hildrew, 2002; Latham and Mills, 2009, Gustafsson et al., 2010), consumption was found to increase with predator size. Moreover, Fox and Murdoch (1978) observed that small instars of *Notonecta undulata* became satiated with fewer prey items than did large backswimmer and suggested that increasing predation rates are an effect of gut size increasing with predator instars.

5.4.2 Model application

Submodels for each of the components of the predation cycle were fitted using behavioural observations of *N. maculata* juveniles deprived for distinct periods prior to experiments. Modelling the food intake and the subsequent gut passage in a dynamic manner allows for the interpolation between different hunger levels of the predator. By additionally considering variable encounter rates depending on prey density and light regime, the model enables predictions of predation rates under laboratory conditions that extend the possibilities of experimental setups. Furthermore, in using body size scaling relationships it is possible to extrapolate across different sizes of daphnid prey and notonectid predators, respectively, thus allowing for long term predictions during larval development of *N. maculata* including population dynamics of the prey species.

The model was able to quantitatively predict the predation of the five juvenile instars of *N. maculata* as observed in 48 h experiments. Thereby, also the decline in consumption rates during dark periods recorded in the experiments is adequately reproduced by the model (Fig. 10). A number of studies previously reported lower predation efficiency of backswimmer species in the dark as compared to light periods (Giller and Mcneill, 1981; Scott and Murdoch, 1983; Streams, 1982; Dieguez and Gilbert, 2003; Chapter 4). The decline in the rate of predation during dark periods was considered a consequence of reduced encounter distances resulting in lower attack rates. Moreover, it was suggested that the lower number of consumed daphnid prey might be compensated by a longer and more thorough handling of prey (Chapter 4).

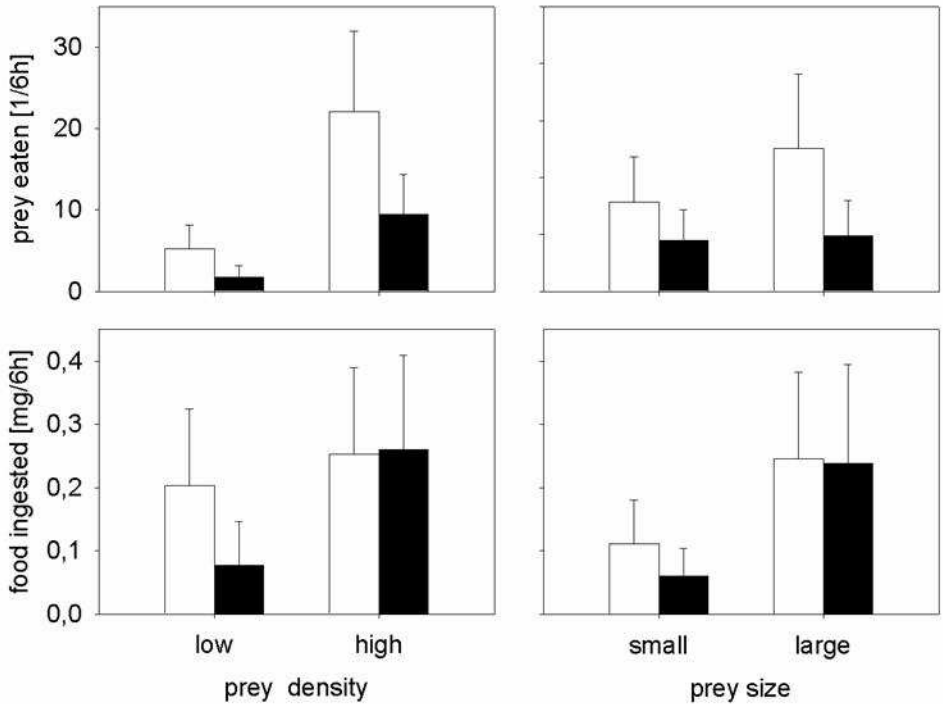

Figure 5.13: Simulated number of prey items eaten and total food ingested under light (white columns) and dark environmental conditions (black columns). Simulations were run for the 4th instar of backswimmers foraging on daphnids during 6 hours applying different scenarios. Left: Different initial prey densities, low (30/l) and high (90/l) were used to simulate foraging on a single daphnid size class (D3). Right: Different daphnid size classes, small (D2) and large (D4), were offered to single backswimmer at high initial prey density (90/l). Columns indicate mean and standard deviation of 1000 Monte-Carlo simulations.

Figure 5.13 illustrates light/dark differences in the number of prey eaten and the food ingested as simulated for the example of the 4th instar of *N. maculata*. Irrespective of prey density and prey size, the simulated number of consumed prey items is lower under dark conditions. Furthermore, the model application reveals that the total amount of food ingested during dark periods is also reduced in backswimmers foraging on low prey density and small prey, whereas food ingested in the dark is as high as during light conditions in backswimmers foraging in environments supplying high prey densities and larger prey. The model application provides further evidence for the interplay between attack rate and prey handling as a possibility of compensatory predation behaviour in *N. maculata* juveniles during dark periods. However, under non-optimal environmental conditions backswimmer instars probably obtain most of their food during daylight.

5.4.3 Limitations and future challenges

The presented model is applicable to *Notonecta maculata* juveniles foraging on *Daphnia magna* prey under constant temperature conditions. However, the model faces a number of limitations, partly because predation is not exclusively satiation driven (van Rijn et al. 2005).

Temperature was found to significantly alter consumption rates (Burns, 1969; Thompson, 1978; Hofer et al, 1982; McCoull et al., 1998). From a gut-limiting perspective this might be a consequence of changing digestive activity since temperature is known to affect e.g. gut passage rate (Hofer et al, 1982; Sangpradub and Giller, 1994; Irigoien 1998). Moreover, e.g. in studies using translucent zooplankton species, gut transit time was found to vary with food quality (Mayzaud et al. 1998, DeMott et al., 2010), time of the day (Irigoien 1998) and food densitiy (Evers and Kooijman, 1989). Variations in food quality and quantity will affect gut transit time as well assimilation efficiency, and thus feeding and finally growth of a consumer (Mitra and Flynn, 2007). However, these aspects are not considered in the presented model.

Prey density was also observed to affect capture success due to predator confusion (Jeschke and Tollrian, 2005). A reduction in capture success leads to a lower number of consumed prey items, which might be compensated by backswimmers via a more thorough extraction of prey during longer handling times. Lower capture success here presumably accompanied by longer handling times contribute to dome-shaped functional response curves as previously observed in different predator prey systems (Young et al., 1994; Jeschke and Tollrian, 2005). The

present model therefore will overestimate the number of consumed prey items at high prey densities and thus will not consider spatial aggregations of daphnid prey, e.g. swarming as a result of phototactism. Other defence mechanisms of prey like predator avoidance via vertical migration or morphological changes (Grant and Bayly, 1981; Tollrian, 1995; Jeschke and Tollrian 2000) are also not included in the model.

In addition, prey utilization might depend on prey density. For example Kruse (1983) showed that in diving beetle larvae, handling time was longer when offering a single prey item at a time compared to higher prey densities. Because this difference could not be ascribed to differences in inter-catch intervals and prey size, gut limitation appeared to be an inadequate explanation. Similar to the observations of Kruse (1983), here, later instars of backswimmers were sometimes observed in video experiments to untimely drop a partially consumed daphnid and then immediately capture another prey item as it passes by. In animals externally digesting prey, extraction efficiency declines as handling of a prey item proceeds. Therefore, one explanation might be that at one point it appears more profitable to a predator to catch an encountered prey item instead of proceeding in the exploitation of the captured one. Since density dependence in prey utilization is not included, the model will underestimate the number of prey captures especially at low prey density where usually longer handling times occur.

Prey type is known to affect predation in notonectid predators (Scott and Murdoch, 1983; Chesson, 1989; Saha et al., 2010). From an ecological point of view, selective predation might be a matter of prey detectability. Like many predatory insects, backswimmers use both visual and tactile mechanisms for prey detection. Mechanoreceptors provide information on prey location and enable backswimmers to distinguish between prey and non-prey organisms (Lang, 1980). Since performance of mechanoreceptors depends on the frequency and amplitude of waves (Markl and Wiese, 1969), turbulences of different intensities allow *Notonecta* to differentiate between prey types (Lang, 1980). Moreover, optimal foraging theory predicts that predators tend to select profitable over unprofitable food (Pulliam, 1974; Sih, 1987) to balance food intake when foraging on several prey types (Hengeveld et al., 2009). However, the mechanisms behind optimization of feeding behaviour are largely unknown.

From a physiological perspective, changes in mechanical and chemical stimuli following food uptake affect digestive capacity and therefore meal size (Smith, 1998; Jensen, 2001). Receptors allow for communication between gut and central nervous systems. Whereas

mechanoreceptors detect deformation or the stretching of mucosal surface, chemical receptors respond to e.g. osmolarity, glucose or lipids (Raybould, 1998). Besides bulkiness, nutritional value, digestibility and prey utilization, e.g. in terms of energy acquisition, differ across prey species (Lawton, 1970, 1971; Pandian and Delvi, 1973; Van Zyl et al., 1997, Thor and Wendt, 2010) and also intraspecific variations in prey quality were reported (Wilder et al., 2010). Since the gut can detect food quantity as well as quality, different prey types might differ in their contribution to satiation and the costs related to consuming one or another food item.

Both, ecological and the physiological aspects have to be considered for successfully modelling predation under field conditions. In order to overcome limitations, the present modellling framework is open to modifications which might include the effect of temperature regimes and digestive activity related to prey densities and multi species systems. Regarding the latter, the probability of attack for example can be considered as a function of absorptive activity in the gut, including differences in the gut passage rate. Moreover, prey utilization might take into account that some parts of a prey are easier to consume than others and thresholds of ingestion rates might allow for optimization of prey exploitation.

Chapter 6

General conclusion

Kaiser (1979) emphasized the importance of individual properties on population level processes, whereas population dynamics might affect the individual life history of organisms (de Roos et al., 2003). Accordingly, an individual predator is able to affect populations of their prey and, in turn, the composition of prey populations might affect the individual predator. The magnitude of the particular effect will depend on environmental conditions, on prey characteristics and on the life history of an individual predator, which is characterized by size selective foraging and food-dependent growth (De Roos and Persson, 2002). Therefore, the current thesis aimed at analysing and quantifying the impact of prey characteristics, heterogeneous environmental conditions and predator physiology on the outcome of notonectid predation.

As most populations are size-structured, size selective predation has a considerable potential to alter population dynamics as shown in Chapter 2. Moreover, in Chapter 3 it was demonstrated that the size selectivity as well as the rate of predation, and thus the top down effect, might change with the ontogenensis of a predator. However, the actual impact of selectivity in freshwater systems is largely unexplored (Aljetlawi et al., 2004) probably due to the complexity of interactions, as e.g. the bottom up effect on an individual predator might change with ontogenic alterations in life history traits of both predator and prey as well.
For optimizing the intake of food in environments that vary in time and space, a predator has to decide when and which prey item to attack and after prey capture how much time to spend on exploitation. In doing so, an individual faces a number of ecological and physical limitations which have to be taken into account when studying the mechanisms behind foraging behaviour. In Chapter 4, the analysis of mechanisms behind the shifting foraging behaviour under different light conditions revealed that the investigated species conceivably

compensates reduced attack capability by a more thorough exploitation of prey items. Moreover, depending on prey availability, heterogeneous environments will create different hunger levels of a predator. Studies that artificially create different levels of hunger provide the possibility of investigating physiological mechanisms behind predation behaviour as demonstrated in Chapter 5.

Mechanisms that played a role in forming foraging behaviours during evolution might include processes on the molecular level, physical constraints of the organisms as well as interactions of individuals on population or ecosystem level. The current thesis illustrated that modelling individuals in a mechanistic manner provides an adequate tool for integrating different levels of biological organization and for testing assumptions and hypotheses.
The presented modelling framework might be useful for physiologists, ecologists and ecotoxicologists. Since the model allows for the quantification of food intake during *Notonecta maculata* larval development, this provides physiologists with the possibility to assess how much food actually enters the gut of predators living in variable environments. The model might also be useful to ecologists in assessing the long term impact of notonectid predation on prey population dynamics by applying the model framework presented to stage based or individual-based *Daphnia* population models as published recently by Rinke and Vijverberg, (2005) or Preuss et al. (2009). In turn, a combined modelling approach will allow the numerical response of backswimmers to be assessed based on behavioural properties of the individual predator, or more specifically the consequences of e.g. un-appropriate food in *Notonecta* larval development. For ecotoxicologists, coupling an individual-based *Daphnia magna* model and the predation model presented in the current thesis will enable predictions of toxic effects under more realistic conditions by taking into account both intraspecific competition and size selective predation.

A major future task that remains is, based on ethology, physiology and ecology, the derivation of general mechanistic rules in predator-prey interaction that provide a basis for the development of a model framework that is applicable to a broader range of species.

References

Akre, B.G. and Johnson, D.M., 1979. Switching and sigmoid functional-response curves by damselfly naiads with alternative prey available. Journal of Animal Ecology, 48: 703-720.

Aljetlawi, A.A., Sparrevik, E. and Leonardsson, K., 2004. Prey-predator size-dependent functional response: derivation and rescaling to the real world. Journal of Animal Ecology, 73: 239-252.

Arner, M., Koivisto, S., Norberg, J., Kautsky, N., 1998. Trophic interactions in rockpool food webs: regulation of zooplankton and phytoplankton by *Notonecta* and *Daphnia*. Freshwater Biology 39, 79-90.

Bailey, P.C.E., 1986. The feeding-behavior of a sit-and-wait-predator *Ranatra dispar* (Heteroptera, Nepidae) - optimal foraging and feeding dynamics. Oecologia, 68: 291-297.

Bay, E.C., 1974. Predator-prey relationships among aquatic insects. Annual Review of Entomology 19, 441-453.

Begon, M., Mortimer, M., 1981. Population ecology: A unified study of animals and plants. Blackwell Scientific Publications, Oxford, 256 p.

Behmer, S.T., 2009. Insect herbivore nutrient regulation. Annual Review of Entomology 54, 165-187.

Beketov, M.A., Liess, M., 2006. The influence of predation on the chronic response of *Artemia sp* populations to a toxicant. Journal of Applied Ecology 43, 1069-1074.

Black, A.R., 1993. Predator-induced phenotypic plasticity in *Daphnia pulex* - life-history and morphological responses to *Notonecta* and *Chaoborus*. Limnology and Oceanography 38, 986-996.

Blaustein, L., Kotler, B.P. and Ward, D., 1995. Direct and indirect effects of a predatory backswimmer (*Notonecta maculata*) on community structure of desert temporary pools. Ecological Entomology, 20: 311-318.

Boggs, C.L., 2009. Understanding insect life histories and senescence through a resource allocation lens. Functional Ecology 23, 27-37.

Briers, R.A., Warren, P.H., 2000. Population turnover and habitat dynamics in *Notonecta* (Hemiptera: Notonectidae) metapopulations. Oecologia, 123, 216–222

Brooks, J.L., Dodson, S.I., 1965. Predation body size and composition of plankton. Science 150, 28-35.

Burns, C.W., 1969. Relation between filtering rate, temperature, and body size in four species of *Daphnia*. Limnology and Oceanography 14, 693-700.

Burns, C.W., 1995. Effects of crowding and different food levels on growth and reproductive investment of *Daphnia*. Oecologia 101, 234-244.

Caldow, R.W.G. and Furness, R.W., 2001. Does Holling's disc equation explain the functional response of a kleptoparasite? Journal of Animal Ecology, 70: 650-662.

Campbell, C.E., 1991. Prey selectivities of threespine sticklebacks (*Gasterosteus aculeatus*) and phantom midge larvae (*Chaoborus spp*) in Newfoundland lakes. Freshwater Biology 25, 155-167.

Campolongo, F., Cariboni, J., Saltelli, A., 2007. An effective screening design for sensitivity analysis of large models. Environmental Modelling and Software, 22: 1509–1518.

Canton, J.H., Adema, D.M.M., 1978. Reproducibility of short-term and reproduction toxicity experiments with *Daphnia magna* and comparison of sensitivity of *Daphnia magna* with *Daphnia pulex* and *Daphnia cucullata* in short-term experiments. Hydrobiologia 59, 135-140.

Cayrou, J., Céréghino R., 2005. Life-cycle phenology of some aquatic insects: implications for pond conservation. Aquatic conservation: Marine and freshwater ecosystems, 15, 559–571

Charnov, E.L., 1976. Optimal foraging: The marginal value theorem. Theoretical Population Biology 9, 129-136.

Chesson, J., 1978. Measuring preference in selective predation. Ecology, 59: 211-215.

Chesson, J., 1989. The effect of alternative prey on the functional response of *Notonecta hoffmani*. Ecology 70, 1227-1235.

Christoffersen, K., Jespersen, A.M., 1986. Gut evacuation rates and ingestion rates of eudiaptomus-graciloides measured by means of the gut fluorescence method. Journal of Plankton Research 8, 973-983.

Claessen, D., Van Oss, C., de Roos, A.M. and Persson, L., 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology, 83: 1660-1675.

Cleuvers, M., Goser, B., Ratte, H.T., 1997. Life-strategy shift by intraspecific interaction in *Daphnia magna*: Change in reproduction from quantity to quality. Oecologia 110, 337-345.

Cock, M.J.W., 1978. Assessment of preference. Journal of Animal Ecology, 47: 805-816.

Comber, M.H.I., Williams, T.D., Stewart, K.M., 1993. The effects of nonylphenol on *Daphnia magna*. Water Research 27, 273-276.

Cook, R.M. and Cockrell, B.J., 1978. Predator ingestion rate and its bearing on feeding time and theory of optimal diets. Journal of Animal Ecology, 47: 529-547.

Coors, A., De Meester, L., 2008. Synergistic, antagonistic and additive effects of multiple stressors: predation threat, parasitism and pesticide exposure in *Daphnia magna*. Journal of Applied Ecology 45, 1820-1828.

Cox, E.J., Naylor, C., Bradley, M.C., Calow, P., 1992. Effect of differing maternal ration on adult fecundity and offspring size in laboratory cultures of *Daphnia magna* Straus for ecotoxicological testing. Aquatic Toxicology 24, 63-74.

Curio, E.; 1976. The ethology of predation. Springer, Berlin, 250 p.

Dahm, E., 1972. On the biology of *Notonecta glauca* (Insecta, Hemiptera) with special reference to its damage to fisheries. International Review of Hydrobiology, 57, 429-461

Dam, H.G., Peterson, W.T., Okubo, A., 1991. A simple mathematical-analysis of the limitations to inferring feeding-behavior of zooplankton from gut content. Marine Ecology-Progress Series 69, 41-45.

De Roos, A.M. and Persson, L., 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. Proceedings of the National Academy of Sciences of the United States of America, 99: 12907-12912.

De Roos, A.M., Persson, L. and McCauley, E., 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters, 6: 473-487.

DeAngelis, D.L.,Wolf M. Mooij, W.M., 2005. Individual-based modeling of ecological and evolutionary processes. Annual Review of Ecology, Evolution, and Systematics, 36,147-68

Debord, Jean, (2008): TPmath- mathematical library for Pascal compilers Version 0.70. http://www.unilim.fr/pages_perso/jean.debord/tpmath/tpmath.htm, downloaded in March 2010

DeMott, W.R., McKinney, E.N., Tessier, A.J., 2010. Ontogeny of digestion in *Daphnia*: implications for the effectiveness of algal defenses. Ecology 91, 540-548.

Dieguez, M.C. and Gilbert, J.J., 2003. Predation by *Buenoa macrotibialis* (Insecta, Hemiptera) on zooplankton: effect of light on selection and consumption of prey. Journal of Plankton Research, 25: 759-769.

Dini, M.L. & Carpenter, S.R., 1992. Fish predators, food availability and diel vertical migration in *Daphnia*. Journal of Plankton Research, 14: 359-377.

Dodson, S.I., Hanazato, T., 1995. Commentary on effects of anthropogenic and natural organic-chemicals on development, swimming behavior, and reproduction of *Daphnia*, a key member of aquatic ecosystems. Environmental Health Perspectives 103, 7-11.

Dodson, S.I., Havel, J.E., 1988. Indirect prey effects - some morphological and life-history responses of *Daphnia pulex* exposed to *Notonecta undulata*. Limnology and Oceanography 33, 1274-1285.

Doucet, P.G., Vanstraalen, N.M., 1980. Analysis of hunger from feeding rate observations. Animal Behaviour 28, 913-921.

Eitam, A., Blaustein, L., 2010. Effects of predator density and duration of predator occupancy on crustacean abundance and diversity in experimental pools. Hydrobiologia 652, 269-276.

Elendt, B.P. and Bias, W.R., 1990. Trace nutrient deficiency in daphnia-magna cultured in standard medium for toxicity testing - effects of the optimization of culture conditions on life-history parameters of *Daphnia magna*. Water Research, 24: 1157-1167.

Evers, E.G., Kooijman, S., 1989. Feeding, digestion and oxygen-consumption in daphnia-magna - a study in energy budgets. Netherlands Journal of Zoology 39, 56-78.

FOCUS, 2006. Guidance Document on Estimating Persistence and Degradation Kinetics from Environmental Fate Studies on Pesticides in EU Registration.

Forbes, V.E., Calow, P., 1999. Is the per capita rate of increase a good measure of population-level effects in ecotoxicology? Environmental Toxicology and Chemistry 18, 1544-1556.

Formanowicz, D.R., 1984. Foraging tactics of an aquatic insect - Partial consumption of prey. Animal Behaviour 32, 774-781.

Fox, L.R., Murdoch, W.W., 1978. Effects of feeding history on short-term and long-term functional responses in *Notonecta hoffmanni*. Journal of Animal Ecology 47, 945-959.

Friberg-Jensen, U., Wendt-Rasch, L., Woin, P., Christoffersen, K., 2003. Effects of the pyrethroid insecticide, Cypermethrin, on a freshwater community studied under field conditions. I. Direct and indirect effects on abundance measures of organisms at different trophic levels. Aquatic Toxicology 63, 357-371.

Galic, N., Hommen, U., Boveco, J.M., van den Brink, P.J., 2010. Potential Application of Population Models in the European Ecological Risk Assessment of Chemicals II: Review of Models and Their Potential to Address Environmental Protection Aims. Integrated Environmental Assessment and Management 6.

Gelperin, A., 1971. Regulation of feeding. Annual Review of Entomology 16, 365- 378.

Gerritsen, J. and Strickler, J.R., 1977. Encounter probabilities and community structure in zooplankton - mathematical-model. Journal of the Fisheries Research Board of Canada, 34: 73-82.

Giguere, L.A., Delage, A., Dill, L.M. and Gerritsen, J., 1982. Predicting encounter rates for zooplankton - a model assuming a cylindrical encounter field. Canadian Journal of Fisheries and Aquatic Sciences, 39: 237-242.

Gilbert, J.J. and Hampton, S.E., 2001. Diel vertical migrations of zooplankton in a shallow, fishless pond: a possible avoidance-response cascade induced by notonectids. Freshwater Biology, 46: 611-621.

Giller, P.S. and McNeill, S., 1981. Predation strategies, resource partitioning and habitat selection in *Notonecta* (Hemiptera, Heteroptera). Journal of Animal Ecology, 50: 789-808.

Giller, P.S., 1980. The control of handling time and its effects on the foraging strategy of a heteropteran predator, *Notonecta*. Journal of Animal Ecology, 49: 699-712.

Giller, P.S., 1982. Locomotory efficiency in the predation strategies of the British Notonecta (Hempitera, Heteroptera). Oecologia, 52: 273-277.

Giller, P.S., 1984. Predator gut state and prey detectability using electrophoretic analysis of gut contents. Ecological Entomology 9, 157-162.

Giller, P.S., 1986. The natural diet of the Notonectidae - field trials using electrophoresis. Ecological Entomology, 11: 163-172.

Giller, P.S., McNeill, S., 1981. Predation strategies, resource partitioning and habitat selection in *Notonecta* (Hemiptera, Heteroptera). Journal of Animal Ecology 50, 789-808.

Glazier, D.S., 1992. Effects of food, genotype, and maternal size and age on offspring investment in *Daphnia magna*. Ecology 73, 910-926.

Grant, J.W.G. and Bayly, I.A.E., 1981. Predator induction of crests in morphs of the daphnia-carinata king complex. Limnology and Oceanography, 26: 201-218.

Greene, C.H., 1983. Selective predation in fresh-water zooplankton communities. Internationale Revue Der Gesamten Hydrobiologie, 68: 297-315.

Gresch, M., Brugger, R., Meyer, A., Gujer, W., 2009. Compartmental models for continuous flow reactors derived from CDF simulations. Environmental Science & Technology 43, 2381-2387.

Griffiths, D., 1982. Tests of alternative models of prey consumption by predators, using ant-lion larvae. Journal of Animal Ecology 51, 363-373.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecological Modelling, 115, 129-148

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U., Jorgensen, C., Mooij, W.M., Muller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R.A., Vabo, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecological Modelling 198, 115-126.

Grimm, V., Railback, S.F., 2005. Individual-based modeling and ecology. Princeton University Press, New Jersey, 428 p.

Gustafsson, P., Bergman, E., Greenberg, L.A., 2010. Functional response and size-dependent foraging on aquatic and terrestrial prey by brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish 19, 170-177.

Hampton, S.E., Gilbert, J.J. and Burns, C.W., 2000. Direct and indirect effects of juvenile *Buenoa macrotibialis* (Hemiptera : Notonectidae) on the zooplankton of a shallow pond. Limnology and Oceanography, 45: 1006-1012.

Hanazato, T., Dodson, S.I., 1992. Complex effects of a kairomone of *Chaoborus* and an insecticide on *Daphnia pulex*. Journal of Plankton Research 14, 1743-1755.

Hanazato, T., Fueki, K., Yoshimoto, M., 2001. Fish-induced life-history shifts in the cladocerans *Daphnia* and *Simocephalus*: are they positive or negative responses? Journal of Plankton Research 23, 945-951.

Hansson, L.A., Nicolle, A., Brodersen, J., Romare, P., Nilsson, P.A., Bronmark, C., Skov, C., 2007. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. Limnology and Oceanography 52, 696-706.

Hassell, M.P., 1966. Evaluation of parasite or predator responses. Journal of Animal Ecology, 35, 65-75

Hassell, M.P., Lawton, J.H. and Beddington, J.R., 1976. Components of arthropod predation. 1. prey death-rate. Journal of Animal Ecology, 45: 135-164.

Hassell, M.P., Lawton, J.H. and Beddington, J.R., 1977. Sigmoid functional responses by invertebrate predators and parasitoids. Journal of Animal Ecology, 46: 249-262.

Hegedus, D., Erlandson, M., Gillott, C., Toprak, U., 2009. New Insights into peritrophic matrix synthesis, architecture, and function. Annual Review of Entomology 54, 285-302.

Hengeveld, G.M., van Langevelde, F., Groen, T.A., de Knegt, H.J., 2009. Optimal Foraging for Multiple Resources in Several Food Species. American Naturalist 174, 102-110.

Hirakawa, H., 1997. Digestion-constrained optimal foraging in generalist mammalian herbivores. Oikos 78, 37-47.

Hirvonen, H., Ranta, E., 1996. Prey to predator size ratio influences foraging efficiency of larval *Aeshna juncea* dragonflies. Oecologia 106, 407-415.

Hofer, R., Forstner, H., Rettenwander, R., 1982. Duration of gut passage and its dependence on temperature and food-consumption in roach, *Rutilus rutilus*. l - laboratory and field experiments. Journal of Fish Biology 20, 289-299.

Hohberg, K., Traunspurger, W., 2009. Foraging theory and partial consumption in a tardigrade-nematode system. Behavioral Ecology 20, 884-890.

Holling, C.S., 1959a. The components of predation revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist, 91: 293-320.

Holling, C.S., 1959b. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91, 385-398.

Holling, C.S., 1966. The functional response of invertebrate predators to prey density. Memoirs of the Entomological Society of Canada, 48: 1-86.

Hommen, U., Baveco, J.M., Galic, N., van den Brink, P.J., 2010. Potential Application of Ecological Models in the European Environmental Risk Assessment of Chemicals I: Review of Protection Goals in EU Directives and Regulations. Integrated Environmental Assessment and Management 6.

Horn, M.H., Messer, K.S., 1992. Fish guts as chemical reactors - a model of the alimentary canals of marine herbivorous fishes. Marine Biology 113, 527-535.

Hülsmann, S., Rinke, K., Mooij, W.M., 2005. A quantitative test of the size efficiency hypothesis by means of a physiologically structured model. Oikos 110, 43-54.

Huston, M., DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. BioScience. 38, 682-691.

Hutchinson, E.G., 1933. The zoo-geography of the African aquatic Hemiptera in relation to past climatic change. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 28, 436-468

Irigoien, X., 1998. Gut clearance rate constant, temperature and initial gut contents: a review. Journal of Plankton Research 20, 997-1003.

Jeffries, M.J., Lawton, J.H., 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23, 269-286.

Jensen, J., 2001. Regulatory peptides and control of food intake in non-mammalian vertebrates. Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology 128, 471-479.

Jeschke, J.M. and Hohberg, K., 2008. Predicting and testing functional responses: An example from a tardigrade-nematode system. Basic and Applied Ecology, 9: 145-151.

Jeschke, J.M. and Tollrian, R., 2000. Density-dependent effects of prey defences. Oecologia, 123: 391-396.

Jeschke, J.M. and Tollrian, R., 2005. Effects of predator confusion on functional responses. Oikos, 111, 547-555.

Jeschke, J.M., Kopp, M. and Tollrian R., 2004. Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews, 79, 337-349

Jeschke, J.M., Kopp, M. and Tollrian, R., 2002. Predator functional responses: Discriminating between handling and digesting prey. Ecological Monographs, 72: 95-112.

Jeschke, J.M., Tollrian, R., 2005. Predicting herbivore feeding times. Ethology 111, 187-206.

Jobling, M., 1981. Mathematical-models of gastric-emptying and the estimation of daily rates of food-consumption for fish. Journal of Fish Biology 19, 245-257.

Johnson, D.M., Akre, B.G., Crowley, P.H., 1975. Modeling arthropod predation - wasteful killing by damselfly naiads. Ecology 56, 1081-1093.

Jordan, K.H.C., 1960. Wasserwanzen. A Ziemsen Verlag, Wittenberg, 38 p.

Juanes, F. and Conover, D.O., 1994. Piscivory and prey size selection in young-of-the-year bluefish - predator preference or size-dependent capture success. Marine Ecology-Progress Series, 114: 59-69.

Jumars, P.A., 2000. Animal guts as nonideal chemical reactors: Partial mixing and axial variation in absorption kinetics. American Naturalist 155, 544-555.

Kaiser, H., 1979. Dynamics of populations as result of the properties of individual animals. Fortschritte Der Zoologie, 25: 109-136.

Kaiser, H., 1983. Small scale spatial heterogeneity influences predation success in an unexpected way: Model experiments on the functional response of predatory mites (Acarina). Oecologia, 56, 249-256

Karasov, W.H., Diamond, J.M., 1988. Interplay between physiology and ecology in digestion. Bioscience 38, 602-611.

Kooijman, S.A.L.M., 2010. Dynamic energy budget theory for metabolic organization. Camebridge University Press, Camebridge 514 pp.

Kreutzer, C., Lampert, W., 1999. Exploitative competition in differently sized Daphnia species: A mechanistic explanation. Ecology 80, 2348-2357.

Kruse, K.C., 1983. Optimal foraging by predaceous diving beetle larvae on toad tadpoles. Oecologia, 58: 383-388.

Kuhl, A., 1962. The physiology of the accumulation of condensed inorganic phosphate in *Chlorella* - Contribution to the physiology and morphology of the algae. Vort Gesamtgebier Bot 1, 157-166.

Lampert, W., 2006. *Daphnia*: Model herbivore, predator and prey. Polish Journal of Ecology 54, 607-620.

Lang, H.H., 1975. Die Analyse des Dispersionsmusters und seine Bedeutung für eine Population räuberischer Wasserwanzen (*Notonecta glauca* L.). Oecologia, 20, 311-320

Lang, H.H., 1980. Surface wave discrimination between prey and nonprey by the backswimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). Behavioral Ecology and Sociobiology, 6: 233-246.

Latham, D.R., Mills, N.J., 2009. Quantifying insect predation: A comparison of three methods for estimating daily per capita consumption of two aphidophagous predators. Environmental Entomology 38, 1117-1125.

Lawton, J.H., 1970. Feeding and food energy assimilation in larvae of damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata - Zygoptera). Journal of Animal Ecology 39, 669- 689.

Lawton, J.H., 1971. Ecological energetics studies on larvae of damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata-Zygoptera). Journal of Animal Ecology 40, 385- 423.

Lee, K.P., Simpson, S.J., Clissold, F.J., Brooks, R., Ballard, J.W.O., Taylor, P.W., Soran, N., Raubenheimer, D., 2008. Lifespan and reproduction in *Drosophil*a: New insights from nutritional geometry. Proceedings of the National Academy of Sciences of the United States of America 105, 2498-2503.

Levey, D.J., del Rio, C.M., 1999. Test, rejection, and reformulation of a chemical reactor-based model of gut function in a fruit-eating bird. Physiological and Biochemical Zoology 72, 369-383.

Liess, M., 2002. Population response to toxicants is altered by intraspecific interaction. Environmental Toxicology and Chemistry 21, 138-142.

Liess, M., Foit, K., 2010. Intraspecific competition delays recovery of population structure. Aquatic Toxicology 97, 15-22.

Lima, S.L., 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia, 66, 60-67

Lima, S.L., 2002. Putting predators back into behavioural predator-prey interactions. Trends in Ecology and Evolution, 17, 70-75.

Loague, K. and Green, R., 1991. Statistical and graphical methods for evaluating solute transport models: Overview and application. Journal of Contaminant Hydrology, 7: 51-73.

Lucas, J.R., Grafen, A., 1985. Partial prey consumption by ambush predators. Journal of Theoretical Biology 113, 455-473.

Macarthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. American Naturalist 100, 603-609.

Maklakov, A.A., Simpson, S.J., Zajitschek, F., Hall, M.D., Dessmann, J., Clissold, F., Raubenheimer, D., Bonduriansky, R., Brooks, R.C., 2008. Sex-specific fitness effects of nutrient intake on reproduction and lifespan. Current Biology 18, 1062-1066.

Marcogliese, D.J., King, K.C., Salo, H.M., Fournier, M., Brousseau, P., Spear, P., Champoux, L., McLaughlin, J.D., Boily, M., 2009. Combined effects of agricultural activity and parasites on biomarkers in the bullfrog, *Rana catasbeiana*. Aquatic Toxicology 91, 126-134.

Markl, H. and Wiese, K., 1969. Die Empfindlichkeit des Rückenschwimmers *Notonecta glauca* L. für Oberflächenwellen des Wassers. Zeitschrift für vergleichende Physiologie, 62: 413-420

Martín, J. and López, P., 2004. Balancing predation risk, social interference, and foraging opportunities in backswimmers, *Notonecta maculata*. Acta Ethologica, 6: 59–63

Martinez Del Rio, C., Karasov, W.H., 1990. Digestion strategies in nectar-eating and fruit-eating birds and the sugar composition of plant rewards. American Naturalist 136, 618-637.

Martins, J., Teles, L.O., Vasconcelos, V., 2007. Assays with *Daphnia magna* and *Danio rerio* as alert systems in aquatic toxicology. Environment International 33, 414-425.

Mayzaud, P., Tirelli, V., Bernard, J.M., Roche-Mayzaud, O., 1998. The influence of food quality on the nutritional acclimation of the copepod *Acartia clausi*. Journal of Marine Systems 15, 483-493.

McArdle, B.H. and Lawton, J.H., 1979. Effects of prey-size and predator-instar on the predation of *Daphnia* by *Notonecta*. Ecological Entomology, 4: 267-275.

McCoull, C., Swain, R., Barnes, R.W., 1998. Effect of temperature on the functional response and components of attack rate in *Naucoris congrex* Stal (Hemiptera : Naucoridae). Australian Journal of Entomology 37, 323-327.

Mitra, A., Flynn, K.J., 2007. Importance of interactions between food quality, quantity, and gut transit time on consumer feeding, growth, and trophic dynamics. American Naturalist 169, 632-646.

Morris, M. D., 1991. Factorial sampling plans for preliminary computational experiments. Technometrics, 33: 161-174.

Muirhead, J. and Sprules, W.G., 2003. Reaction distance of *Bythotrephes longimanus*, encounter rate and index of prey risk for Harp Lake, Ontario. Freshwater Biology, 48: 135-146.

Murdoch, W.W., Scott, M.A., 1984. Stability and extinction of laboratory populations of zooplankton preyed on by the backswimmer *Notonecta*. Ecology 65, 1231-1248.

Murdoch, W.W., Scott, M.A., Ebsworth, P., 1984. Effects of the general predator, *Notonecta* (Hemiptera) upon a fresh-water community. Journal of Animal Ecology 53, 791-808.

Murphey, R.K. and Mendenhall, B, 1973. Localization of receptors controlling orientation to prey by backswimmer *Notonecta undulata*. Journal of Comparative Physiology, 84: 19-30.

Murphey, R.K., 1973. Mutual inhibition and organization of a non-visual orientation in Notonecta. Journal of Comparative Physiology, 84: 31-40.

Murtaugh, P.A., 1981. Size-selective predation on daphnia by *Neomysis mercedis*. Ecology 62, 894-900.

Nagata, S., Morooka, N., Asaoka, K., Nagasawa, H., 2011. Identification of a novel hemolymph peptide that modulates silkworm feeding motivation. Journal of Biological Chemistry 286, 7161-7170.

Nelder, J.A., Mead, R., 1965. A simplex-method for function minimization. Computer Journal 7, 308-313.

Newman, R.M., Waters, T.F., 1984. Size-selective predation on *Gammarus pseudolimnaeus* by trout and sculpins. Ecology 65, 1535-1545.

Nieser, N., 2004. Guide to aquatic Heteroptera of Singapore and peninsular Malaysia III. Pleidae and Notonectidae. The Raffles Bulletin of Zoology, 52, 79-96

Nilsson, P.A., Lundberg, P., Bronmark, C., Persson, A., Turesson, H., 2007. Behavioral interference and facilitation in the foraging cycle shape the functional response. Behavioral Ecology 18, 354-357.

O'Brien, W.J. and Vinyard, G.L., 1978. Polymorphism and predation - effect of invertebrate predation on distribution of 2 varieties of *Daphnia carinata* in South-India ponds. Limnology and Oceanography, 23: 452-477.

Pandian, T.J., Delvi, M.R., 1973. Energy extraction efficiency in some chosen insects. Oecologia 13, 397-401.

Paradis, A.R., Pepin, M. and Pepin, P., 1999. Disentangling the effects of size-dependent encounter and susceptibility to predation with an individual-based model for fish larvae. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1562-1575.

Pastorok, R.A., 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology, 62: 1311-1324.

Penry, D.L., Jumars, P.A., 1986. Chemical reactor analysis and optimal digestion. Bioscience 36, 310-313.

Penry, D.L., Jumars, P.A., 1987. Modeling animal guts as chemical reactors. American Naturalist 129, 69-96.

Persoone, G., Janssen, C.R., 1993. Freshwater invertebrate toxicity tests. In: Calow, P. (ed.), Handbook of Ecotoxicology, Blackwell Scientific Publications, Cambridge, 51–65

Pervez, A. and Omkar, 2005. Functional responses of coccinellid predators: An illustration of a logistic approach. Journal of Insect Science, 5.

Pineiro, G., Perelman, S., Guerschman, J.P. and Paruelo, J.M., 2008. How to evaluate models: Observed vs. predicted or predicted vs. observed? Ecological Modelling, 216: 316-322.

Pohlmann, K., Grasso, F.W. and Breithaupt, T., 2001. Tracking wakes: The nocturnal predatory strategy of piscivorous catfish. Proceedings of the National Academy of Sciences of the United States of America, 98: 7371-7374.

Preuss, T.G., 2007. Ökotoxikologische Charakterisierung von Nonylphenol Isomeren, Shaker, Aachen, 212 p.

Preuss, T.G., Hammers-Wirtz, M., Hommen, U., Rubach, M.N. and Ratte, H.T., 2009. Development and validation of an individual based *Daphnia magna* population model: The influence of crowding on population dynamics. Ecological Modelling, 220: 310-329.

Preuss, T.G., Telscher, M., Ratte, H.T., 2008. Life stage- dependent bioconcentration of a nonylphenol isomer in *Daphnia magna*. Environmental Pollution 156, 1211-1217.

Pulliam, H.R., 1974. Theory of optimal diets. American Naturalist 108, 59-74.

Ranta, E., Espo, J., 1989. Predation by the rock-pool insects *Arctocorisa carinata carinata*, *Callicorixa producta* (Het. Ccorixidae) and *Potamonectes griseostriatus* (Col. Dytiscidae). Annales Zoologici Fennici 26, 53-60.

Ratte, H.T., 1996. Statistical implications of end-point selection and inspection interval in the *Daphnia* reproduction test - A simulation study. Environmental Toxicology and Chemistry 15, 1831-1843.

Raybould, H.E., 1998. Does your gut taste? Sensory transduction in the gastrointestinal tract. News in Physiological Sciences 13, 275-280.

Real, L.A., 1977. Kinetics of functional response. American Naturalist, 111: 289-300.

Reynaldi, S., Duquesne, S., Jung, K., Liess, M., 2006. Linking feeding activity and maturation of *Daphnia magna* following short-term exposure to Fenvalerate. Environmental Toxicology and Chemistry 25, 1826-1830.

Reynolds, J.G. and Geddes, M.C., 1984. Functional response analysis of size-selective predation by the notonectid predator *Anisops deanei* (Brooks) on *Daphnia thomsoni* (Sars). Australian Journal of Marine and Freshwater Research, 35: 725-733.

Riessen, H.P., Obrien, W.J., Loveless, B., 1984. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. Ecology 65, 514-522.

Rincon, P.A. and Loboncervia, J., 1995. Use of an encounter model to predict size-selective predation by a stream-dwelling cyprinid. Freshwater Biology, 33: 181-191.

Ringelberg, J., 1991. A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. Journal of Plankton Research, 13: 83-89.

Rinke, K. and Petzoldt, T., 2008. Individual-based simulation of diel vertical migration of Daphnia: A synthesis of proximate and ultimate factors. Limnologica, 38: 269-285.

Rinke, K. and Vijverberg, J., 2005. A model approach to evaluate the effect of temperature and food concentration on individual life-history and population dynamics of *Daphnia*. Ecological Modelling, 186: 326-344.

Rogers, D., 1972. Random search and insect population models. Journal of Animal Ecology, 41: 369-383.

Royama, T., 1971. A comparative study of models for predation and parasitism. Researches on Population Ecology, S1: 1-90.

Rudolf, V.H.W., 2008. Consequences of size structure in the prey for predator-prey dynamics: the composite functional response. Journal of Animal Ecology, 77: 520-528.

Russ, A.S., Vinken, R., Schuphan, I., Schmidt, B., 2005. Synthesis of branched para-nonylphenol isomers: Occurrence and quantification in two commercial mixtures. Chemosphere 60, 1624-1635.

Saha, N., Aditya, G., Saha, G.K., Hampton, S.E., 2010. Opportunistic foraging by heteropteran mosquito predators. Aquatic Ecology 44, 167-176.

Samu, F., 1993. Wolf spider feeding strategies - optimality of prey consumption in Pardosa hortensis. Oecologia 94, 139-145.

Sangpradub, N., Giller, P.S., 1994. Gut morphology, feeding rate and gut clearance in 5 species of caddis larvae. Hydrobiologia 287, 215-223.

Savage, A.A., 1989. Adults of the British aquatic Hemiptera Heteroptera: A key with ecological notes. Freshwater Biological Association, 173 p.

Scharf, F.S., Buckel, J.A., Juanes, F., 2002. Size-dependent vulnerability of juvenile bay anchovy *Anchoa mitchilli* to bluefish predation: Does large body size always provide a refuge? Marine Ecology-Progress Series 233, 241-252.

Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Marine Ecology-Progress Series 208, 229-248.

Schmolke, A., Thorbek, P., DeAngelis, D.L., Grimm, V., 2010. Ecological models supporting environmental decision making: a strategy for the future. Trends in Ecology and Evolution, 25, 479-486

Schulz, R., Dabrowski, J.M., 2001. Combined effects of predatory fish and sublethal pesticide contamination on the behavior and mortality of mayfly nymphs. Environmental Toxicology and Chemistry 20, 2537-2543.

Scott, M.A. and Murdoch, W.W., 1983. Selective predation by the backswimmer, *Notonecta*. Limnology and Oceanography, 28: 352-366.

Seitz, A., 1980a. The coexistence of three species of *Daphnia* in the Klostersee. I. Field studies on the dynamics of reproduction. Oecologia, 45, 117.-130.

Seitz, A., 1980b. The coexistence of three species of *Daphnia* in the Klostersee. II. The stabilizing effect of selective mortality and conclusions for the stability of the system. Oecologia, 47, 333-339.

Sherratt, T.N. and Harvey, I.F., 1993. Frequency-dependent food selection by arthropods - a review. Biological Journal of the Linnean Society, 48: 167-186.

Sibly, R.M., Akcakaya, H.R., Topping, C.J., O'Connor, R.J., 2005. Population-level assessment of risks of pesticides to birds and mammals in the UK. Ecotoxicology 14, 863-876.

Sih, A., 1980. Optimal foraging - partial consumption of prey. American Naturalist 116, 281-290.

Sih, A., 1987. Nutritional ecology of aquatic insect predators, in: Slansky, F., Jr., Rodriguez, J.G. (eds.), Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, pp. 579-607.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities - a review of field experiments. Annual Review of Ecology and Systematics 16, 269-311.

SIMLAB, version 2.2, free software for uncertainty and sensitivity analysis. Joint Research Centre of the European Commission. http://simlab.jrc.ec.europa.eu. Downloaded in May 2010.

Simpson, S.J., Abisgold, J.D., 1985. Compensation by locusts for changes in dietary nutrients - behavioral mechanisms. Physiological Entomology 10, 443-452.

Simpson, S.J., Sibly, R.M., Lee, K.P., Behmer, S.T., Raubenheimer, D., 2004. Optimal foraging when regulating intake of multiple nutrients. Animal Behaviour 68, 1299-1311.

Skorupa, D.A., Dervisefendic, A., Zwiener, J., Pletcher, S.D., 2008. Dietary composition specifies consumption, obesity, and lifespan in *Drosophila melanogaster*. Aging Cell 7, 478-490.

Smith, G.P., 1998. Pregastric and gastric satiety, in: Smith, G.P. (ed.), Satiation: from gut to brain. University press, Oxford, pp. 10-39.

Solomon, M.E., 1949. The natural control of animal populations. Journal of Animal Ecology, 19, 1-35

Spitze, K., 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66, 938-949.

Stark, J.D., Banken, J.A.O., 1999. Importance of population structure at the time of toxicant exposure. Ecotoxicology and Environmental Safety 42, 282-287.

Stark, J.D., Banks, J.E., 2003. Population-level effects of pesticides and other toxicants on arthropods. Annual Review of Entomology 48, 505-519.

Stich, H.B. and Lampert, W., 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature, 293: 396-398.

Streams, F.A., 1982. Diel foraging and reproductive periodicity in *Notonecta undulata* Say (Heteroptera). Aquatic Insects, 4: 111-119.

Streams, F.A., 1994. Effect of prey size on attack components of the functional response by *Notonecta undulata*. Oecologia, 98: 57-63.

Strubbe, J.H., Woods, S.C., 2004. The timing of meals. Psychological Review 111, 128-141.

Svensson, B.G., Tallmark, B., Petersson, E., 2000. Habitat heterogeneity, coexistence and habitat utilization in five backswimmer species (*Notonecta spp*.; Hemiptera, Notonectidae). Aquatic Insects, 22, 81–98.

Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2002. Invertébrés d'eau douce: systématique, biologie, écologie. CNRS, Paris, 587 p.

Taylor, R.J., 1984. Predation. Chapman and Hall, New York, 166 p.

Thompson, D.J., 1975. Towards a predator-prey model incorporating age structure - effects of *Daphnia magna* by *Ischnura elegans*. Journal of Animal Ecology, 44: 907-916.

Thompson, D.J., 1978. Towards a realistic predator-prey model - effect of temperature on functional response and life-history of larvae of damselfly, *Ischnura elegans*. Journal of Animal Ecology, 47: 757-767.

Thor, P., Wendt, I., 2010. Functional response of carbon absorption efficiency in the pelagic calanoid copepod *Acartia tonsa* Dana. Limnology and Oceanography 55, 1779-1789.

Tillyard, R.J., 1917. The biology of dragnonflies (Odonata or Paraneuroptera). Cambridge University Press, Cambridge 396 pp.

Tollrian, R., 1995. *Chaoborus crystallinus* predation on *Daphnia pulex*: can induced morphological-changes balance effects of body-size on vulnerability. Oecologia, 101, 151-155.

Trexler, J.C., McCulloch, C.E. and Travis, J., 1988. How can the functional response best be determined. Oecologia, 76: 206-214.

Tully, T., Cassey, P. and Ferriere, R., 2005. Functional response: rigorous estimation and sensitivity to genetic variation in prey. Oikos, 111: 479-487.

Tyagi, V.K., Chopra, A.K., Durgapal, N.C., Kumar, A., 2007. Evaluation of *Daphnia magna* as an indicator of toxicity and treatment efficacy of municipal sewage treatment plant. Journal of Applied Sciences and Environmental Management, 11, 61 - 67

van Rijn, P.C.J., Bakker, F.M., van der Hoeven, W.A.D., Sabelis, M.W., 2005. Is arthropod predation exclusively satiation-driven? Oikos 109, 101-116.

VanZyl, A., VanderWesthuizen, M.C., VanderLinde, T.C.D., 1997. Utilisation of prey by antlion larvae (Neuroptera: Myrmeleontidae) in terms of energy and nutrients. Journal of Insect Physiology 43, 605-613.

Visser, H., Veldhuijzen van Zanten, H.H., 2003. European Limnofauna. http://nlbif.eti.uva.nl/bis/limno.php

Volterra, V., 1926 Variations and fluctuations of the numbers of individuals in animal species living together. ICES Journal of Marine Science (J. Cons. int. Explor. Mer), 3, 3-51

Warren, P.H., Lawton, J.H., 1987. Invertebrate predator-prey body size relationships - an explanation for upper-triangular food webs and patterns in food web structure. Oecologia 74, 231-235.

Waterhouse, D.F., 1957. Digestion in insects. Annual Review of Entomology 2, 1-18.

Wendt-Rasch, L., Friberg-Jensen, U., Woin, P., Christoffersen, K., 2003. Effects of the pyrethroid insecticide Cypermethrin on a freshwater community studied under field conditions. II. Direct and indirect effects on the species composition. Aquatic Toxicology 63, 373-389.

Whelan, C.J., Brown, J.S., 2005. Optimal foraging and gut constraints: reconciling two schools of thought. Oikos 110, 481-496.

Wiese, K., 1972. Das mechanorezeptorische Beuteortungssystem yon *Notonecta*: 1. Die Funktion des tarsalen Scolopidialorgans. Journal of Comparative Physiology, 78: 83-102.

Wilder, S.M., Mayntz, D., Toft, S., Rypstra, A.L., Pilati, A., Vanni, M.J., 2010. Intraspecific variation in prey quality: a comparison of nutrient presence in prey and nutrient extraction by predators. Oikos 119, 350-358.

Wogram, J., Liess, M., 2001. Rank ordering of macroinvertebrate species sensitivity to toxic compounds by comparison with that of *Daphnia magna*. Bulletin of Environmental Contamination and Toxicology 67, 360-367.

Woodward, G., Hildrew, A.G., 2002. Differential vulnerability of prey to an invading top predator: integrating field surveys and laboratory experiments. Ecological Entomology 27, 732-744.

Yen, J., 1983. Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata*. Marine Biology, 75: 69-77.

Young, S., Watt, P.J., Grover, J.P., Thomas, D., 1994. The unselfish swarm. Journal of Animal Ecology 63, 611-618.

Zalom, F.G., 1978. Comparison of predation rates and prey handling times of adult *Notonecta* and *Buenoa* (Hemiptera, Notonectidae). Annals of the Entomological Society of America, 71, 143-148.

Zaret, T.M., Kerfoot, W.C., 1975. Fish predation on *Bosmina longirostris* - body-size selection versus visibility selection. Ecology 56, 232-237.

Zaret, T.M., Suffern, J.S., 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnology and Oceanography, 21, 804-813.

Publications

Peer reviewed journal articles

Gergs, A., Ratte, H.T., 2009. Predicting functional response and size selectivity of juvenile Notonecta maculata foraging on Daphnia magna. Ecological Modelling 220, 3331-3341

Gergs, A., Hoeltzenbein, N.I., Ratte, H.T., 2010. Diurnal and nocturnal functional response of juvenile *Notonecta maculata* considered as a consequence of shifting predation behaviour. Behavioural Processes, 85, 151-156

Imron, M.A., Gergs, A., Berger, U., in press. Structure and sensitivity analysis of individual-based predator-prey models - Reliability Engineering & System Safety

Conference contributions

Gergs, A., Riehm, S., Preuss, T.G., 2011. Sensitivity shift in *Daphnia magna* population response caused by size selective predation - Platform presentation SETAC Europe 21th Annual Meeting (Milan, Italy)

Imron, M.A., Gergs, A, Berger, U., 2010. What do tigers and backswimmers have in common? An analysis of structure and sensitivity in individual-based models - Procedia Social and Behavioral Sciences 2, 7680-7681

Gergs, A., Ratte, H.T., 2009. Der Einfluss von Beutedichte und -größe auf die Larvalentwicklung des Rückenschwimmers *Notonecta maculata* - Platform presentation German Limnological Society Annual Meeting (Oldenburg, Germany)

Luther, S., Ratte, H.T., Gergs, A., 2009. Der Einfluss von Hunger auf das Fraßverhalten des Rückenschwimmers *Notonecta maculata* - Poster presentation German Limnological Society Annual Meeting (Oldenburg, Germany)

Gergs, A., Ratte, H.T., 2009. Parameterisation and validation of a mechanistic model for the growth of *Notonecta maculata* - Platform presentation 4th Workshop of the Young Modellers in Ecology (Neunzehnhain, Germany)

Gergs, A., Ratte, H.T., 2008. Größenselektives Jagdverhalten juveniler Rückenschwimmer - Platform presentation German Limnological Society Annual Meeting (Konstanz, Germany)

Acknowledgements

First and foremost I would like to thank my supervisor Prof. Dr. Hans Toni Ratte for giving me the opportunity and freedom to work on such a fascinating aspect of ecology like foraging behaviour. Dr. Thomas Preuss provided valuable advices on model development and implementation as well as fruitful discussions on the topic, not only during coffee breaks, and I am grateful for this.

Special thanks are also given to the group of Aquatic Ecology and Ecotoxicology at RWTH Aachen University, in alphabetical order to Birgitta Goffart, Hanna Maes, Dr. Richard Ottermanns, Silvana Siehoff and Helga von Lochow, for discussions on practical issues in the laboratory and/or for their comments on parts of the manuscripts. I also thank Dr. Monika Hammers-Wirtz and Dr. Tido Strauss, Research Institute for Ecosystem Analysis (gaiac), for providing the initial stock of backswimmers and discussions on ecological issues.

Thanks are given to Nora Hoeltzenbein, Svenja Luther, Stefan Rhiem and Kerstin Szonn for their courage to work under my supervision. Stefan Rhiem helped maintaining the laboratory systems used for the Daphnia magna population experiments (Chapter 2) and has sampled populations as well as measured the size of the daphnids. Parts of the experiments run under dark experimental conditions as described in Chapter 4 were done by Nora Hoeltzenbein during a practical course. In preparation of Chapter 5, parts of the experiments were done by Svenja Luther during her work for Bachelor graduation. The analyses Kerstin Szonn has done during her practical course gave first insights in the sensitivity of model parameters.
I thank Muhamad Ali Imron for sharing his knowledge on sensitivity analysis and Lara Ibrahim, Devdutt Kulkarni and Pia Liedtjens for proofreading parts of the present thesis respectively.

Furthermore, I would like to thank my brother René Gergs for comments on the thesis and for inspiring discussions on various ecological topics.

Katrin Liedtjens never lost confidence in me during the course of my PhD and helped keep me sane. She occasionally provided assistance in the preparation of functional response experiments and we discussed nearly everything I have written in this thesis. I would like to thank her for that.

Curriculum Vitae

Name	André Gergs
Date of birth	17th of September, 1972
Place of Birth	Linnich, Germany
Nationality	German

2011 - ongoing	Post Doc, Department of Environmental, Social and Spatial Change, Roskilde University, Denmark
2008 - 2011	Research Associate, Institute for Environmental Research, RWTH Aachen University, Germany
2005 - 2008	Research Associate, Forum Environmental Science, RWTH Aachen University, Germany
2005 - 2011	PhD student, RWTH Aachen University, Germany
2005	Diploma in Biology
1999 - 2005	Studies in Biology, RWTH Aachen University, Germany
1999	Social Pedagogue, District Craft Trades Association, Heinsberg, Germany
1997 - 1998	Social Pedagogue, instruction year, Youth Welfare Office, Mönchengladbach, Germany
1997	Diploma (FH) in Social Pedagogy
1993 - 1997	Studies in Social Pedagogy, University of Applied Sciences, Cologne, Germany
1992 - 1993	Community service
1992	Graduation from secondary school (Abitur)

Appendix

Culture conditions of *Notonecta maculata*

Both juveniles and adults of *Notonecta maculata* were kept in a constant room set at 20 ± 1°C. As a medium artificial freshwater M4 (Elendt and Bias, 1990) was used. *Daphnia magna* items were provided as a food source that was either derived from laboratory cultures or collected in the field, i.e. in outdoor mesocosms or a pond in Aachen city area. Daphnids were sieved and aliquots of *D. magna* suspension were given to the backswimmers. Numbers of *D. magna* in the suspensions are given in Figure A1.1. Although the composition of *Daphnia* size classes in the suspension varied during the course of time, the amount of biomass available for extraction by backswimmers as calculated by means of equation 5.2 and 5.3, which was based on measurements of *D. magna* cultured in the laboratory, was relatively stable (Figure A1.2). *D. magna* size classes were in ascending order D1: 0.9 ± 0.12mm, D2: 1.4 ± 0.20mm, D3: 2.3 ± 0.29mm, D4: 2.9 ± 0.24mm (mean and standard deviation of total body length excluding spine measured under magnification).

Collection and maintenance of adults

Backswimmer adults were originally collected at a nearby outdoor mesocosm site and determined to species level using the key of Savage (1989). Adult *N. maculata* were maintained in 100 l aquaria in mixed gender groups of up to 20 individuals. *D. magna* ≥ D2 were given as a food source three times per week. Number of *D. magna* provided was > 80 per individual *N. maculata*. A third of the medium was replaced weekly and *Daphnia* carcasses were removed using a suction hose. Full replacement of the medium and cleaning of the aquaria was done every other month.

Oviposition and storage of eggs

For oviposition stones, 5-10 cm in diameter, were placed into the aquaria, but notonectids were also observed to stick eggs to the glass walls. However, stones facilitated the removal of eggs. Eggs were collected on the occasion of aquaria cleaning. Stones and eggs that were taken from the aquaria walls were transferred to 500 ml vessels filled with M4 media. Eggs were stored at 5 ± 2°C for periods up to 6 month.

Hatching and maintenance of larvae

Prior to experiments, eggs were stored at 20 ± 1°C. Larvae did start hatching from day 7 after increasing temperature. From the day after hatching, *N. maculata* larvae were reared individually in 100 ml vessels and fed with daphnids. Aliquots of *D. magna* suspensions given to each of the five larval instars of *N. maculata* are summarized in Table A1.1. Daphnid carcasses were removed from culture vessels and half of the medium was renewed before feeding. Backswimmers specimens that were used in experiments were treated in a way specified in the materials and methods sections of Chapter 2-5.

Table A1.1: Summary of daphnid food provided to the five larval instars of *N. maculata* (N1-N5).

Instar	*D. magna* suspension [ml]	Size classes of *D. magna*	Feeding interval
N1	0.2	≤ D2	3 x per week
N2	0.3	≤ D2	3 x per week
N3	1.5	≥ D2	3 x per week
N4	2	≥ D2	daily
N5	2.5	≥ D2	daily

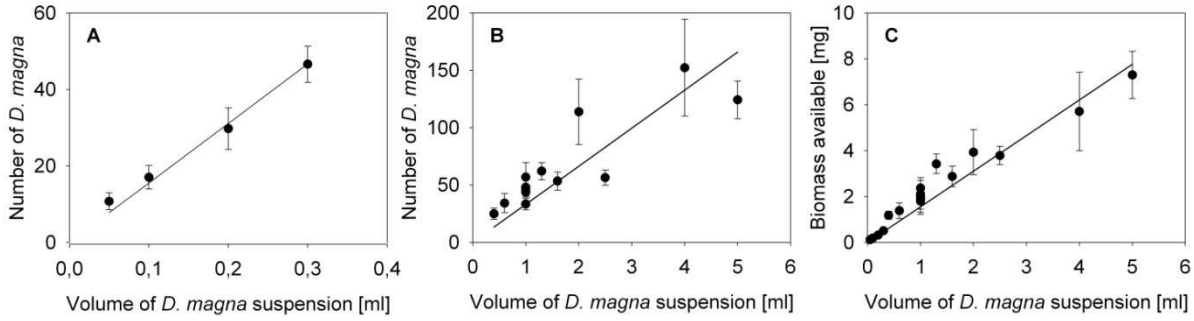

Figure A1.1: Number of daphnids ≤ D2 (A, y = 155.6x, r2 = 982), number of daphnids ≥ D2 (B, y = 33.17x, r2 = 0.628) and *D. magna* biomass (dry weight) available to consumption by backswimmers (C, y = 1.55x, r2 = 0.937) as functions of daphnid suspension volume. Dots represent mean and standard deviation of 20 replicated measurements.

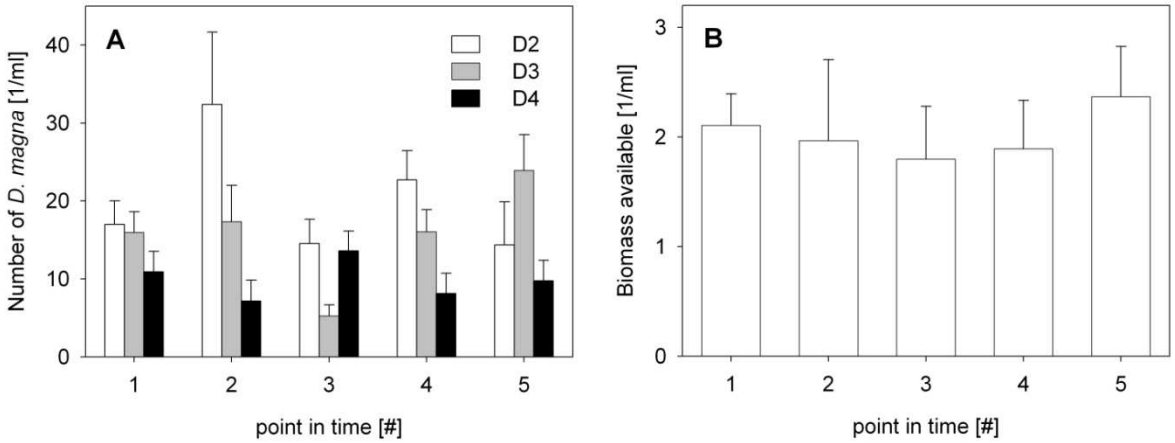

Figure A.1.2: Number of *D. magna* of three different size classes (D2-D4, A) and *D. magna* biomass (dry weight) available to extraction by backswimmers (B) in one ml of daphnid suspension as used for feeding of backswimmers at five different instants of time during the study.

Chapter 2

Table A2.1: Mean and standard deviation of *Daphnia magna* total abundance (n = 3), letters indicate differences in one way ANOVA with subsequent Tukey HSD post hoc test. C: control, N: *Notonecta* predation, NP: p353-nonylphenol exposure; Np-N: combined stressor

Day	C	N	Np	Np-N	p
8	163,3±63,51^{A}	210,0±79,37^{A}	140,0±51,96^{A}	160,0±60,83^{A}	0,616
15	1133,3±510,82^{A}	896,7±126,62^{A}	623,3±374,48^{A}	870,0±452,99^{A}	0,510
22	3476,7±1595,44^{A}	3970,0±762,10^{A}	2213,3±861,18^{A}	3236,7±860,72^{A}	0,305
28	4273,3±1088,55^{A}	5376,7±167,73^{A}	4613,3±2000,13^{A}	6106,7±654,55^{A}	0,436
34	5883,3±1132,31^{A}	5870,0±487,54^{A}	6853,3±1140,19^{A}	7143,3±863,96^{A}	0,185
36	4390,0±1410,96^{A}	4570,0±317,65^{A}	6326,7±2957,94^{A}	6236,7±279,70^{A}	0,077
39	3636,7±1180,06^{A}	3620,0±359,30^{A}	5130,0±1416,30^{A}	4263,3±341,22^{A}	0,251
41	3553,3±75,06^{AB}	3023,3±469,29^{B}	4246,7±635,09^{A}	3266,7±378,46^{AB}	0,043
43	3063,3±784,75^{A}	1653,3±291,43^{B}	2316,7±64,29A^{B}	1813,3±571,78^{AB}	0,036
46	2773,3±571,43^{A}	1806,7±193,48^{AB}	1553,3±356,98^{B}	1583,3±536,69^{AB}	0,029
48	2386,7±418,61^{A}	1886,7±287,29^{A}	1406,7±583,98^{A}	1343,3±505,60^{A}	0,078
50	2150,0±257,10^{A}	2006,7±201,08^{A}	2190,0±160,93^{A}	2463,3±492,17^{A}	0,381
53	2120,0±446,77^{A}	1930,0±426,73^{A}	3040,0±579,40^{A}	2876,7±395,26^{A}	0,070
55	1970,0±510,29^{A}	2196,7±537,99^{A}	3110,0±510,29^{A}	2796,7±543,08^{A}	0,095
60	2150,0±262,11^{A}	2766,7±800,40^{A}	2813,3±735,82^{A}	3803,3±686,25^{A}	0,081
67	2073,3±438,90^{A}	3040,0±675,06^{A}	3470,0±705,48^{A}	2953,3±470,57^{A}	0,094
69	1866,7±210,79^{A}	2200,0±417,61^{A}	2456,7±309,25^{A}	2676,7±600,11^{A}	0,171
71	1790,0±310,00^{AB}	2116,7±192,96^{AB}	2560,0±271,85^{B}	1496,7±482,11^{A}	0,022
74	1870,0±330,61^{A}	1396,7±191,40^{A}	1596,7±718,15^{A}	123,3±66,58^{B}	0,003
76	1893,3±523,48^{A}	1303,3±106,93^{A}	1786,7±558,24^{A}	116,7±96,09^{B}	0,002
78	2096,7±724,73^{A}	1306,7±90,74^{AB}	1623,3±132,04^{A}	333,3±330,2^{B}	0,004

Table A2.2: Mean and standard deviation of *Daphnia magna* neonates (n = 3), letters indicate differences in one way ANOVA with subsequent Tukey HSD post hoc test. C: control, N: *Notonecta* predation, NP: p353-nonylphenol exposure; Np-N: combined stressor

Day	C	N	Np	Np-N	p
8	40,0±40,00^{A}	110,0±70,00^{A}	36,7±20,82^{A}	63,3±51,32^{A}	0,303
15	600,0±345,98^{A}	603,3±136,50^{A}	310,0±245,56^{A}	600,0±337,79^{A}	0,522
22	1663,3±870,48^{A}	1810,0±311,77^{A}	1106,7±486,04^{A}	1373,3±287,29^{A}	0,442
28	2196,7±617,20^{A}	2966,7±171,56^{A}	2710,0±1788,55^{A}	3656,7±313,42^{A}	0,372
34	2183,3±910,29^{A}	2060,0±492,75^{A}	3126,7±1111,95^{A}	3800,0±628,65^{A}	0,094
36	1390,0±890,17^{A}	1533,3±751,82^{A}	2273,3±1662,12^{A}	2806,7±325,32^{A}	0,356
39	536,7±254,23^{A}	880,0±132,29^{A}	1946,7±1146,05^{A}	1586,7±213,85^{A}	0,072
41	623,3±30,55^{A}	616,7±182,3^{A}	1316,7±416,33^{B}	696,7±180,09^{AB}	0,022
43	236,7±127,41^{A}	220,0±120,00^{A}	693,3±289,19^{A}	500,0±314,32^{A}	0,102
46	600,0±213,78^{A}	153,3±100,17^{B}	106,7±66,58^{B}	50,0±36,06^{B}	0,002
48	140,0±30,00^{A}	163,3±50,33^{A}	50,0±36,06^{A}	120,0±95,39^{A}	0,182
50	200,0±62,45^{A}	610,0±363,46^{A}	703,3±541,51^{A}	876,7±481,8^{A}	0,288
53	300,0±45,83^{A}	696,7±449,59^{AB}	1460,0±617,33^{B}	1516,7±195,02^{B}	0,014
55	230,0±108,17^{A}	916,7±376,08^{AB}	1620,0±135,28^{B}	1543,3±591,81^{B}	0,005
60	133,3±51,32^{A}	1316,7±342,69^{BC}	810,0±363,87^{AB}	2130,0±599,08^{C}	0,002
67	170,0±30,00^{A}	1243,3±892,26^{A}	420,0±155,24^{A}	706,7±251,06^{A}	0,103
69	190±30^{A}	1066,7±505,21^{A}	360,0±105,83^{A}	853,3±537,25^{A}	0,064
71	270,0±155,24^{A}	1126,7±376,87^{B}	743,3±241,32^{AB}	510,0±405,96^{AB}	0,049
74	126,7±122,2^{A}	430,0±177,76^{B}	63,3±32,15^{A}	20,0±10,00^{A}	0,007
76	63,3±35,12^{A}	330,0±70^{B}	23,3±23,09^{A}	23,3±32,15^{A}	0,000
78	80,0±85,44^{A}	530,0±124,90^{B}	320,0±105,36^{AB}	243,3±240,28^{AB}	0,038

Table A2.3: Mean and standard deviation of *Daphnia magna* juveniles (n = 3), letters indicate differences in one way ANOVA with subsequent Tukey HSD post hoc test. C: control, N: *Notonecta* predation, NP: p353-nonylphenol exposure; Np-N: combined stressor

Day	C	N	Np	Np-N	p
8	73,3±37,86^{A}	66,7±15,28^{A}	73,3±25,17^{A}	60,0±10,00^{A}	0,891
15	380,0±223,38^{A}	190,0±26,46^{A}	196,7±60,28^{A}	163,3±56,86^{A}	0,184
22	1700,0±840,71^{A}	2056,7±430,16^{A}	950,0±339,56^{A}	1723,3±581,58^{A}	0,200
28	1980,0±506,85^{A}	2296,7±262,74^{A}	1786,7±243,79^{A}	2323,3±325,93^{A}	0,257
34	3513,3±512,28^{A}	3730,0±380,00^{A}	3590,0±43,59^{A}	3176,7±485,01^{A}	0,430
36	2873,3±557,70^{A}	2953,3±434,66^{A}	3856,7±1228,06^{A}	3306,7±244,4^{A}	0,382
39	2926,7±980,07^{A}	2613,3±481,28^{A}	3003,3±240,28^{A}	2543,3±244,4^{A}	0,709
41	2683,3±142,24^{A}	2236,7±257,75^{A}	2706,7±382,14^{A}	2403,3±368,28^{A}	0,247
43	2586,7±652,87^{A}	1283,3±176,16^{B}	1513,3±337,10^{B}	1200,0±281,6^{B}	0,010
46	1976,7±427,71^{A}	1396,7±180,37^{A}	1253,3±355,01^{A}	1213,3±417,89^{A}	0,101
48	1840,0±538,14^{A}	1346,7±217,33^{A}	946,7±578,13^{A}	720,0±365,92^{A}	0,065
50	1666,7±227,45^{A}	1020,0±306,43^{A}	943,3±597,69^{A}	1026,7±250,27^{A}	0,142
53	1403,3±431,55^{A}	783,3±200,33^{A}	1076,7±170,10^{A}	746,7±219,39^{A}	0,062
55	1393,3±445,01^{A}	803,3±55,08^{A}	900,0±330,45^{A}	660,0±91,65^{A}	0,058
60	1353,3±383,97^{A}	1006,7±223,01^{A}	1430,0±431,39^{A}	1276,7±360,19^{A}	0,531
67	1246,7±456,54^{A}	1626,7±304,36^{A}	2323,3±765,01^{A}	2070,0±674,46^{A}	0,188
69	1073,3±240,28^{A}	1033,3±205,99^{A}	1546,7±374,21^{A}	1713,3±271,54^{A}	0,110
71	986,7±140,12^{A}	906,7±220,08^{A}	1300,0±495,18^{A}	946,7±90,74^{A}	0,368
74	1180,0±284,78^{A}	923,3±87,37^{AB}	1060,0±780,83^{AB}	83,3±57,74^{B}	0,046
76	1126,7±374,34^{A}	930,0±183,58^{AB}	1036,7±669,35^{AB}	63,3±56,86^{B}	0,037
78	1116,7±449,59^{A}	733,3±51,32^{A}	750,0±245,56^{A}	46,7±56,86^{B}	0,006

Table A2.4: Mean and standard deviation of *Daphnia magna* adults (n = 3), letters indicate differences in one way ANOVA with subsequent Tukey HSD post hoc test. C: control, N: *Notonecta* predation, NP: p353-nonylphenol exposure; Np-N: combined stressor

Day	C	N	Np	Np-N	p
8	50,0±17,32^{A}	33,3±15,28^{A}	30±17,32^{A}	36,7±5,77^{A}	0,417
15	153,3±30,55^{A}	103,3±11,55^{A}	116,7±70,95^{A}	106,7±60,28^{A}	0,606
22	113,3±25,17^{A}	103,3±20,82^{A}	156,7±60,28^{A}	140,0±10,00^{A}	0,289
28	96,7±40,41^{A}	113,3±20,82^{A}	116,7±37,86^{A}	126,7±30,55^{A}	0,743
34	186,7±49,33^{A}	80,0±30,00^{A}	136,7±65,06^{A}	166,7±30,55^{A}	0,092
36	126,7±37,86^{A}	83,3±32,15^{A}	196,7±89,63^{A}	123,3±47,26^{A}	0,180
39	173,3±68,07^{A}	126,7±37,86^{A}	180,0±30,00^{A}	133,3±5,77^{A}	0,348
41	246,7±110,15^{A}	170,0±122,88^{A}	223,3±109,70^{A}	166,7±40,41^{A}	0,717
43	240,0±75,5^{A}	150,0±26,46^{B}	110,0±26,46^{B}	113,3±37,86^{B}	0,028
46	196,7±58,59^{A}	256,7±37,86^{A}	193,3±47,26^{A}	320,0±86,6^{A}	0,099
48	406,7±162,58^{A}	376,7±112,4^{A}	410,0±10,00^{A}	503,3±155,03^{A}	0,649
50	283,3±133,17^{A}	376,7±83,86^{A}	543,3±125,03^{A}	560,0±113,58^{A}	0,051
53	416,7±119,3^{A}	450,0±141,07^{A}	503,3±115,90^{A}	613,3±101,16^{A}	0,278
55	346,7±41,63^{A}	476,7±170,1^{A}	590,0±51,96^{A}	593,3±142,95^{A}	0,093
60	663,3±205,51^{A}	443,3±248,46^{A}	573,3±50,33^{A}	396,7±274,29^{A}	0,449
67	656,7±20,82^{A}	170,0±91,65^{B}	726,7±215,48^{A}	176,7±120,97^{B}	0,001
69	603,3±37,86^{A}	100,0±60,00^{B}	550,0±196,72^{A}	110,0±85,44^{B}	0,001
71	533,3±115,9^{A}	83,3±37,86^{B}	516,7±135,77^{A}	40,0±26,46^{B}	0,000
74	563,3±189,3^{A}	43,3±32,15^{B}	473,3±100,17^{A}	20,0±17,32^{B}	0,000
76	703,3±130,13^{A}	43,3±23,09^{B}	726,7±189,03^{A}	30,0±17,32^{B}	0,000
78	900,0±190,79^{A}	43,3±15,28^{C}	553,3±156,31^{B}	43,3±37,86^{C}	0,000

Chapter 3

Table A3.1 Mean and standard deviation of encounter distances [cm] measured in video experiments for each combination of *Notonecta* instar (N1-N5) and *Daphnia* size class (D1-D4).

	D1	D2	D3	D4
N1	0.71 ± 0.37	0.54 ± 0.21	0.84 ± 0.21	0.85 ± 0.35
N2	0.75 ± 0.07	1.18 ± 0.31	1.11 ± 0.26	1.1 ± 0.56
N3	1.09 ± 0.19	1.24 ± 0.6	1.11 ± 0.31	1.16 ± 0.19
N4	1.45 ± 0.48	1.38 ± 0.29	1.48 ± 0.07	1.35 ± 0.43
N5	1.05 ± 0.35	1.54 ± 0.43	1.71 ± 0.53	1.62 ± 0.49

Table A3.2: Mean and standard deviation of encounter rates [1/(s*ml)] in four daphnid size classes (D1-D4) over a range of densities, as derived from video experiments.

Prey density [1/200ml]	D1	D2 & D3	D4
1	0.0010 ± 0.0025	0.0004 ± 0.0007	0.0013 ± 0.0013
2	0.0004 ± 0.0018	0.0019 ± 0.0023	0.0033 ± 0.001
3	0.0010 ± 0.0007	0.0036 ± 0.0013	0.0040 ± 0.0006
4	0.0014 ± 0.0013	0.0065 ± 0.0016	0.0025 ± 0.0013
5	0.0037 ± 0.0024	0.0047 ± 0.0007	0.0047 ± 0.0005
6	0.0040 ± 0.0037	0.0050 ± 0.0014	0.0093 ± 0.0007
7	0.0076 ± 0.0029	0.0093 ± 0.0057	0.0120 ± 0.0012
8	0.0035 ± 0.0036	0.0094 ± 0.0063	0.0156 ± 0.0021
9	0.0073 ± 0.0024	0.0154 ± 0.0094	0.0175 ± 0.0055
10	0.0068 ± 0.0016	0.0158 ± 0.0035	0.0177 ± 0.001
11	0.0104 ± 0.0007	0.0188 ± 0.0072	0.0243 ± 0.0007
12	0.0120 ± 0.0076	0.0217 ± 0.014	0.0295 ± 0.0024
13	0.0097 ± 0.0011	0.0202 ± 0.0077	0.0294 ± 0.0061
14	0.0157 ± 0.0069	0.0283 ± 0.0139	0.0329 ± 0.0029
15	0.0149 ± 0.0045	0.0328 ± 0.0092	0.0465 ± 0.0026
16	0.0213 ± 0.0017	0.0388 ± 0.0176	0.0481 ± 0.0085
17	0.0236 ± 0.0042	0.033 ± 0.0037	0.0488 ± 0.0057
18	0.0236 ± 0.0041	0.0454 ± 0.0096	0.0563 ± 0.0021
19	0.0319 ± 0.0082	0.0355 ± 0.002	0.0557 ± 0.0082
20	0.0324 ± 0.0017	0.0420 ± 0.0042	0.0563 ± 0.0063

Table A3.4: Mean and standard deviation of components of predation in five instars of *N. maculata* (N1-N5) foraging on four size classes of *Daphnia magna* (D1-D4) as observed in video experiments.

	D1	D2	D3	D4
Attack rate				
N1	9.0 ± 3.6	3.9 ± 2.1	3.7 ± 1.4	2.5 ± 1.9
N2	0.4 ± 0.4	8.6 ± 5.2	10.4 ± 2.2	1.4 ± 0.8
N3	1.9 ± 1.2	2.0 ± 1.9	6.8 ± 1.9	1.3 ± 0.6
N4	1.8 ± 0.8	4.0 ± 1.3	9.7 ± 2.4	6.5 ± 2.1
N5	1.8 ± 0.8	4.0 ± 1.3	9.7 ± 2.4	6.5 ± 2.1
Success rate				
N1	43.1 ± 4.0	41.7 ± 11.8	8.3 ± 10.4	2.1 ± 3.6
N2	54.2 ± 7.2	52.6 ± 14.3	41.6 ± 6.8	5.6 ± 6.7
N3	18.0 ± 4.2	62.0 ± 0.7	66.3 ± 4.3	45.1 ± 7.9
N4	32.3 ± 12.1	54.3 ± 16.1	92.5 ± 2.3	71.8 ± 12.3
N5	32.3 ± 12.1	54.3 ± 16.1	92.5 ± 2.3	71.8 ± 12.3
Handling time [s]				
N1	169.2 ± 75.8	174.7 ± 142.6	262.3 ± 149.5	244.0
N2	95.2 ± 25.3	193.3 ± 125.9	229.8 ± 196.9	142.5 ± 50.5
N3	134.5 ± 59.6	114.7 ± 57.5	233.3 ± 170.6	291.9 ± 145.2
N4	71.2 ± 38.7	95.7 ± 61.6	150.8 ± 142.3	322.1 ± 260.4
N5	67.0	85.9 ± 42.8	177.6 ± 128.9	228.9 ± 132.7

Table A3.5: Results of sensitivity analyses using the two different equations for the calculation of the success rate. Parameters were ranked by their relative importance based on μ and δ. Capital letters indicate the parameters mathematical equations. Small letters indicate ecological parameters.

	equation 3.5			equation 3.6		
Parameter	μ	σ	rank	μ	σ	rank
A_a	9.60	10.90	4	21.60	20.37	1
A_b	7.20	9.65	5	6.40	13.22	6
A_{x0}	6.80	5.93	6	18.40	22.51	2
A_{y0}	2.80	4.38	11	3.20	6.10	10
d_e	4.00	5.10	9	5.20	8.67	8
H_a	24.00	45.93	1	0.80	1.79	13
H_b	5.60	10.33	7	5.60	12.52	7
n_d	3.20	5.02	10	7.60	9.84	5
s	5.20	11.63	8	12.00	10.95	3
S_a	16.80	21.48	3	3.20	4.38	11
S_b	21.60	38.56	2	11.60	15.58	4
S_{x0}	2.40	2.61	12	1.20	1.79	12
S_{y0}	2.00	2.83	13	4.40	4.10	9

Table A3.5: Mean number and standard deviation of *Daphnia magna* (D3) eaten by *Notonecta* instars (N1-N5) in experiments using shallow Petri dishes and deep beakers.

	N1	N2	N3	N4	N5
Petri dish	7.0 ± 2.2	14.2 ± 4.8	23.2 ± 5.3	56.2 ± 7.5	62.8 ± 7.5
beaker	6.6 ± 1.5	15.0 ± 6.4	22.2 ± 4.6	55.0 ± 4.2	66.8 ± 4.2

Table A3.6: Mean number and standard deviation of prey eaten in functional response experiments: *Notonecta* instars (N1-N5) were fed with four *Daphnia* size class (D1-D4) of 5-6 initial prey densities.

Initial prey density [1/500ml]		D1	D2	D3	D4
N1	10	1.4 ± 1.1	3.3 ± 1.1	1.8 ± 1.3	0.8 ± 0.4
	20	2.0 ± 1.6	7.3 ± 1.3	3.6 ± 1.1	2.6 ± 1.5
	40	7.4 ± 3.3	12.5 ± 3.1	4.2 ± 1.1	3.2 ± 1.3
	80	14.6 ± 3.8	14.6 ± 1.6	6.2 ± 0.8	5 ± 1.6
	120	16.2 ± 5.6	19.5 ± 3.5	8.6 ± 1.1	6.4 ± 3.0
	160	-	16.4 ± 4.5	7.6 ± 1.1	6.3 ± 4.6
N2	10	4 ± 1.6	7.8 ± 1.5	5.0 ± 1.9	3.2 ± 1.3
	20	8.6 ± 4.9	14.5 ± 1.9	6.8 ± 1.3	6.8 ± 4.6
	40	13.2 ± 5.1	24.3 ± 5.5	14 ± 3.4	9.4 ± 1.3
	80	16 ± 9.2	41.5 ± 5.8	16.8 ± 5	11.2 ± 1.8
	120	16.2 ± 7.0	35.0 ± 10.7	21.6 ± 6.2	13.8 ± 4.3
	160	-	47.3 ± 7.4	20.2 ± 5.4	13.6 ± 3.9
N3					
	0	1.6 ± 1.9	9.6 ± 0.9	10 ± 0	8.2 ± 2.0
	20	2.0 ± 1.3	14.4 ± 6.6	19.4 ± 0.9	11.2 ± 4.4
	40	3.8 ± 2.4	15.2 ± 5.2	27.6 ± 10.2	22.8 ± 6.4
	80	5.4 ± 4.0	26.4 ± 9.8	23.6 ± 13.0	23.4 ± 10.2
	120	7.8 ± 4.7	23.0 ± 6.1	29.6 ± 5.7	31.2 ± 9.8
	160	-	34.8 ± 11.1	37.0 ± 5.4	31.2 ± 3.1
N4	10	3.6 ± 1.5	6.7 ± 3.1	8.4 ± 1.8	10.0 ± 4.8
	20	3.6 ± 1.9	14.6 ± 2.1	19.8 ± 0.4	19.4 ± 2.2
	40	8.8 ± 3.0	19.2 ± 5.6	29.0 ± 9.6	23.6 ± 10.2
	80	12.4 ± 5.2	32.4 ± 14.7	57.6 ± 10.7	32.6 ± 10.0
	120	18.2 ± 9.1	44.0 ± 10.6	50.0 ± 8.6	38.2 ± 14.3
	160	-	51.8 ± 15.5	56.2 ± 12.1	42.2 ± 21.9
N5	10	1.2 ± 1.3	8.6 ± 1.7	8.6 ± 3.1	5.4 ± 4.8
	20	3.2 ± 2.6	14.2 ± 6.4	19.4 ± 0.9	19.0 ± 2.2
	40	5.6 ± 1.5	33.8 ± 7.3	33.2 ± 8.3	25.6 ± 12.5
	80	7.4 ± 6.7	47.6 ± 31.4	59.4 ± 14.4	38.6 ± 13.7
	120	8.4 ± 1.7	44.6 ± 16.8	58.2 ± 19.3	46.2 ± 18.2
	10	-	67.4 ± 26.4	63.2 ± 18.2	49.4 ± 21.9

Table A3.7: Mean number and standard deviation of prey eaten in size selectivity experiments. Four size classes of *D. magna* (D1-D4) were simultaneously exposed to single backswimmers (N1-N5).

	D1	D2	D3	D4
N1	6.6 ± 1.7	3.6 ± 0.9	2.6 ± 0.5	1.8 ± 0.4
N2	7.6 ± 2.3	16.4 ± 2.1	8.4 ± 1.8	1.2 ± 1.1
N3	1.2 ± 1.1	5.6 ± 3.2	13.6 ± 2.3	10.6 ± 3.5
N4	0.4 ± 0.7	5.6 ± 1.5	17.2 ± 2.9	16.8 ± 1.8
N5	0	4.2 ± 1.0	26.4 ± 6.5	16.8 ± 1.6

Chapter 4

Table A4.1: Number of prey eaten by *N. maculata* (N1-N5) in one hour experiments (mean and standard deviation), experiments were carried out under light conditions in the morning (light/morning) and at midday (light/noon) and under different dark conditions at midday (dark/noon) and midnight (dark/night) and the additional use of the IR camera function at midday (dark/noon/IR).

	light/morning	ligth/noon	dark/noon	dark/noon/IR	dark/night
N1	6.7 ± 2.26	7.33 ± 3.16	2.7 ± 1.06	3.1 ± 1.73	3.6 ± 1.78
N2	4.6 ± 2.63	6.4 ± 3.27	4.2 ± 1.93	4.2 ± 2.15	4.5 ± 2.72
N3	4.1 ± 2.23	4.2 ± 2.66	2.2 ± 1.62	3 ± 1.7	1.2 ± 1.32
N4	7.5 ± 3.44	11.4 ± 5.83	3.9 ± 1.73	4.5 ± 2.37	3.1 ± 1.79
N5	4.8 ± 4.05	5.8 ± 4.78	3.3 ± 2.54	3.7 ± 2.58	4.7 ± 2.31

Table A4.2: Components of predation as measured in video experiments (mean and standard deviation) under light and dark experimental conditions.

	Attack rate		Success rate		Handling time	
	light	dark	light	dark	light	dark
N1	0.047 ± 0.045	0.071 ± 0.018	0.41 ± 0.084	0.56 ± 0.268	236.7 ± 96.98	174.1 ± 136.99
N2	0.153 ± 0.089	0.019 ± 0.017	0.53 ± 0.143	0.75 ± 0.354	410.0 ± 136.46	175.7± 82.87
N3	0.062 ± 0.030	0.002 ± 0.004	0.66 ± 0.043	0.75 ± 0.250	433	226.6 ± 181.71
N4	0.063 ± 0.054	0.060 ± 0.010	0.82 ± 0.188	0.92 ± 0.144	194.6 ± 185.56	118.6 ± 81.59
N5	0.090 ± 0.026	0.030 ± 0.018	0.61 ± 0.128	0.83 ± 0.289	252.8 ± 99.59	137.9 ± 86.58

Table A4.3: Mean distances and standard deviation between predator and prey at the occasion of reactive encounters and attacks under light and dark conditions

	Encounter distance [cm]		Attack distance [cm]	
	light	dark	light	dark
N1	0.54 ± 0.10	0.38 ± 0.19	0.29 ± 0.13	0.38 ± 0.18
N2	1.18 ± 0	0.96 ± 0.29	0.38 ± 0.14	0.43 ± 0.24
N3	1.13 ± 0.24	1.13 ± 0.24	0.37 ± 0.17	0.44 ± 0.09
N4	1.44 ± 0.14	0.73 ± 0.12	0.44 ± 0.23	0.50 ± 0.17
N5	1.68 ± 0.02	0.98 ± 0.51	0.63 ± 0.35	0.49 ± 0.17

Table A4.4: Mean number and standard deviation of prey eaten by *N. maculata* (instars N1-N5) in functional response experiments carried out under dark conditions using six initial prey densities.

Initial prey density [1/500ml]	N1	N2	N3	N4	N5
10	0.6 ± 0.89	3.25 ± 0.50	2.8 ± 2.59	2.4 ± 1.14	5.4 ± 1.95
20	1.2 ± 1.10	6.0 ± 1.15	8.2 ± 5.12	6.6 ± 5.08	11.2 ± 4.55
40	3.6 ± 3.05	12.5 ± 1.73	13.0 ± 4.69	14.8 ± 6.98	22.8 ± 9.31
80	5.6 ± 4.62	15.0 ± 2.16	17.6 ± 6.07	23.6 ± 5.94	35.0 ± 9.35
120	6.4 ± 3.65	22.0 ± 7.39	25.8 ± 9.09	30.0 ± 4.95	37.4 ± 11.63
160	6.8 ± 5.76	27.0 ± 1.41	25.6 ± 8.08	36.0 ± 5.70	38.8 ± 11.30

Chapter 5

Table A5.1: Mean and standard deviation of dry weight of whole *Daphnia magna* (size classes D1-D4) and of *D. magna* carcasses after being consumed by *Notonecta maculata* instars (N1-N5)

Instar	*Daphnia* size class	*Daphnia* [mg]	Carcass [mg]
N1	D1	0.02 ± 0.004	0.01 ± 0.004
N1	D2	0.07 ± 0.019	0.05 ± 0.016
N1	D3	0.14 ± 0.040	0.11 ± 0.021
N1	D4	0.40 ± 0.094	0.20 ± 0.081
N2	D2	0.12 ± 0.024	0.11 ± 0.029
N2	D3	0.22 ± 0.065	0.16 ± 0.048
N2	D4	0.45 ± 0.095	0.25 ± 0.055
N3	D2	0.09 ± 0.084	0.06 ± 0.014
N3	D3	0.26 ± 0.066	0.22 ± 0.094
N3	D4	0.47 ± 0.096	0.30 ± 0.089
N4	D2	0.16 ± 0.027	0.12 ± 0.03
N4	D3	0.28 ± 0.070	0.22 ± 0.066
N4	D4	0.49 ± 0.095	0.31 ± 0.117
N5	D2	0.13 ± 0.053	0.11 ± 0.029
N5	D3	0.17 ± 0.054	0.13 ± 0.051
N5	D4	0.69 ± 0.168	0.55 ± 0.216

Table A5.2: Mean and standard deviation of dry weight of *Daphnia magna* carcasses (size classes D1-D4) after being consumed by *Notonecta maculata* that were fed *ad libitum* or starved for 48 h prior to experiments respectively; instars were randomly chosen.

Daphnia size class	Carcass [mg] fed	Carcass [mg] deprived
D1	0.08 ± 0.064	0.064 ± 0.027
D2	0.17 ± 0.076	0.076 ± 0.037
D3	0.19 ± 0.066	0.066 ± 0.056
D4	0.24 ± 0.086	0.086 ± 0.044

Table A5.3: Mean and standard deviation of dry weight of *Notonecta maculata* bodies (gut removed), and dry weight of guts from backswimmers that were fed *ad libitum* (gut full) and from backswimmers that were deprived for 48 h (gut empty) prior to experiments respectively.

Instar	body weight - gut [mg]	gut full [mg]	gut empty [mg]
N2	0.82 ± 0.308	0.14 ± 0.072	0.07 ± 0.036
N3	1.43 ± 0.541	0.26 ± 0.123	0.14 ± 0.025
N4	7.66 ± 1.873	2.18 ± 0.542	0.59 ± 0.220
N5	11.25 ± 1.729	2.46 ± 0.880	0.70 ± 0.110

Table A5.4: Mean and standard deviation of steady-state ingestion rates (SS-IR) in *Notonecta maculata* instars (N1-N5) as recorded during 5 h predation experiments for individuals that were fed *ad libitum* and deprived prior to experiments respectively.

Instar	SS-IR fed [mg/s]	SS-IR deprived [mg/s]
N1	0.000008 ± 0.0000026	0.0000320 ± 0.0000077
N2	0.000018 ± 0.0000105	0.0000105 ± 0.000051
N3	0.000028 ± 0.0000098	0.0000098 ± 0.000058
N4	0.000046 ± 0.0000117	0.0000117 ± 0.000087
N5	0.000055 ± 0.0000142	0.0000142 ± 0.000108

Table A5.5: Components of predation as measured in video experiments (mean and standard deviation). Notonecta maculata juveniles (N1-N5) were for deprived different time intervals prior to experiments.

	Deprivation time [h] prior to experiments		
	0	4	48
Attack rate			
N1	0.019 ± 0.0099	0.006 ± 0.0050	0.273 ± 0.1196
N2	0.009 ± 0.0083	0.013 ± 0.0124	0.119 ± 0.0830
N3	0.002 ± 0.0021	0.004 ± 0.0056	0.127 ± 0.0478
N4	0.011 ± 0.0041	0.043 ± 0.0188	0.206 ± 0.1488
N5	0.020 ± 0.0185	0.007 ± 0.0103	0.168 ± 0.1084
Success rate			
N1	0.611 ± 0.3469	0.333 ± 0.5774	0.323 ± 0.1596
N2	0.875 ± 0.1768	0.719 ± 0.2448	0.483 ± 0.2075
N3	0.500 ± 0.7071	0.333 ± 0.2887	0.561 ± 0.0536
N4	0.833 ± 0.2357	0.467 ± 0.4163	0.827 ± 0.1573
N5	0.729 ± 0.2062	0.744 ± 0.3097	0.679 ± 0.1646
Handling time			
N1	262.9 ± 181	295.7 ± 172.9	662.5 ± 354.5
N2	146.8 ± 77.1	333.6 ± 156.4	297.6 ± 216.4
N3	545 ± 0	204.3 ± 90.5	385.8 ± 222.4
N4	77.9 ± 62.8	211.1 ± 111.7	318.5 ± 202
N5	123.2 ± 54.3	112.4 ± 37.4	331.7 ± 181.6

Table A5.6: Number of *Daphnia magna* (mean and standard deviation) eaten during 1h by *Notonecta maculata* instars (N1-N5) that were deprived for different time intervals prior to experiments

	Deprivation time [h] prior to experiments					
Instar	0	2	4	6	24	48
N1	4.1 ± 2.02	4.1 ± 2.18	3.7 ± 2.41	5.4 ± 3.17	6.5 ± 2.22	5.4 ± 2.12
N2	6.4 ± 3.27	5.9 ± 2.6	8.1 ± 3.21	10.0 ± 3.02	11.1 ± 1.97	13.9 ± 3.31
N3	3.3 ± 1.25	2.7 ± 2.79	3.0 ± 2.55	5.5 ± 3.14	8.0 ± 1.63	7.9 ± 2.77
N4	6.0 ± 4.27	5.9 ± 2.64	5.1 ± 1.85	3.8 ± 3.16	9.2 ± 3.63	9.7 ± 4
N5	7.0 ± 4.27	5.1 ± 4.31	5.2 ± 3.79	3.9 ± 1.52	9.7 ± 5.21	9 .0 ± 2.54

Table A5.7: Results of the one-factor-at-a-time sensitivity analysis. Parameters were ranked by their relative importance based on μ and δ.

Parameter	μ	σ	rank
A_{max}	0,0	0,0	19,0
A_{min}	1,5	3,0	12,0
A_x	19,5	39,0	3,0
d_e	23,5	39,4	2,0
D_s	10,5	18,4	7,0
e	5,0	7,6	10,0
g1	9,5	19,0	9,0
$G1_{content}$	16,0	32,0	4,0
$G1_{content}$	0,5	1,0	15,0
g2	0,5	1,0	15,0
$g2_{area}$	11,0	20,7	6,0
Gs_n	0,5	1,0	15,0
h	14,0	14,7	5,0
k_{max}	0,0	0,0	20,0
k_{min}	0,5	1,0	15,0
n_d	54,0	85,7	1,0
N_V	10,0	11,2	8,0
p	3,5	7,0	11,0
P_{max}	1,0	2,0	14,0
t_x	1,5	1,0	13,0

Table A5.8: Cumulative number of eaten Daphnia magna (mean and standard deviation) recorded after different time intervals during the course of a 48 h predation experiment. D. magna size classes offered to Notonecta instars were D in N1 and N2 and D3 in N3-N5.

	Sampling during the time course of the experiment [h]						
Instar	3	6	9	12	24	36	48
N1	10.4 ± 3.29	22.2 ± 5.4	32.0 ± 4.30	59.6 ± 14.83	72.8 ± 20.03	108.6 ± 23.09	133.6 ± 29.33
N2	38.8 ± 6.10	66.2 ± 5.85	82.8 ± 9.04	98.0 ± 8.03	124.2 ± 8.81	169.8 ± 5.45	198.4 ± 17.31
N3	32.2 ± 4.87	56.4 ± 6.99	76.8 ± 5.50	91.8 ± 7.98	129.6 ± 10.83	184.6 ± 20.28	218.6 ± 11.37
N4	40.0 ± 19.43	71.0 ± 26.39	98.4 ± 30.97	130.4 ± 27.25	175.0 ± 41.97	288.4 ± 42.87	329.0 ± 49.38
N5	99.2 ± 35.37	161.8 ± 41.92	236 ± 46.01	290.4 ± 47.83	421.6 ± 28.52	574.4 ± 27.84	715.0 ± 29.33