Prey–predator size-dependent functional response: derivation and rescaling to the real world

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Summary

1. We derived a functional response function that accounted for both predator and prey size. Laboratory experiments were then performed to investigate the size relationships of the functional response of the benthic isopod *Saduria entomon* (L.) feeding on *Monoporeia affinis* (Lindström) amphipods.

2. The *S. entomon* predators, in general, showed sigmoid (type III) functional responses. The attack rate of *S. entomon* was a bent ridge-shaped function of predator and prey size. The maximum attack rates of small predators were found on small prey, and then attack rate declined rapidly as prey size increased. In large predators attack rate increased slowly up to a maximum for large prey. The shape of the attack rate was dependent on the size scaling of predator and prey body mass in the attack rate function. We suggest that the ridge-shaped attack rate function found in our study is likely to be general for predators that feed on prey with a large size range. The handling time of small *S. entomon* increased rapidly as prey size increased. In contrast, we found only small differences in handling time of large predators. The complete functional response may provide size-refuges for very small and large *M. affinis* depending on the size-structure of *S. entomon*.

3. To investigate the realism in our functional response estimates, we incorporated the functional response in a consumption model based on the densities and size-structures of the predator and the prey in the field (Bothnian Sea). We adjusted the attack rate using a correction factor to predict the observed survival of the different age-classes of *M. affinis* from field samples. The field data-based consumption model accounted for 1 year of size-dependent predation by the size-structured population of *S. entomon* on *M. affinis*. In addition, using a growth model for *S. entomon* we checked that the predicted consumption by the predator gave realistic growth curves. We found that the experimentally derived attack rates may have been over-estimated by a factor of 400.

Key-words: attack rate, functional response, handling time, population dynamics, predator size, prey size, Saduria–Monoporeia system, size-refuge, survival.

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Introduction

The functional response of a predator provides important information on mechanisms underlying predator–prey dynamics. In unstructured models, sigmoid (type III) functional responses have the potential to stabilize predator–prey dynamics due to the density-dependent predation mortality. In contrast, a type II functional response destabilizes the dynamics because the predators cause an inverse density-dependent mortality of the prey (e.g. Murdoch & Oaten 1975; Hassell 1978). The shape of the functional response curve is dependent on several characteristics such as encounter rate, capture efficiency and handling time of the predator (Holling 1965; Hassell 1978). These characteristics may differ within a species as a consequence of predator or prey size, interference among predators or presence of alternative prey (Spitze 1985; Chesson 1989; Safina 1990; Tripet & Perrin 1994; Elliott 2003)

Detailed information on size-dependence in the functional response is scarce, as most of the studies performed have incorporated a small variation in predator and prey sizes (Thompson 1975; Moran 1985; Hewett 1988;

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Eggleston 1990). A small prey size range may exclude information concerning presence of maxima or minima in the responses. In systems where the prey population has a large size range, the attack rate as a function of size should have a humped-shaped form (Persson *et al.* 1998). Prey may be too small to be efficiently encountered, or too large to be captured (Hyatt 1979). Persson *et al.* (1998) argued that handling time per prey should have a minimum. For very small prey, handling time decreases with prey size due to difficulties in handling very small prey. Above the minimum, handling time increases as the prey size approaches the predator gape size. In addition, the digestive capacity contributes to an increasing handling time per prey as prey becomes bigger.

The size-dependence in the attack rate may have implications for predator–prey dynamics. In a size-structured consumer-one resource model by Persson *et al.* (1998) the attack rate increased slowly with predator size, and this resulted in unstable recruiter driven predator–prey dynamics. When the attack rate was reduced for the small predators the newborn predators became less dominant, which stabilized the dynamics. Thus, the size scaling of the attack rate and its implication for the functional response provides valuable information for the understanding of dynamics in size-structured populations. In order to perform the corresponding analysis of both predator and prey size on population dynamics we need to know the form of a size-dependent functional response. Kooijman (1993) derived a functional response that accounted explicitly for predator size, but no functional response function has yet been derived to incorporate both predator and prey size.

The aim of this study was to derive a functional response function that included both predator and prey size. In addition, we investigated experimentally the size-dependent functional responses of the benthic isopod *Saduria entomon* feeding on *Monoporeia affinis* amphipods. Both isopods and amphipods had a large variation in body size. The idea of deducing a size-dependent functional response from basic principles is that if it fits well to experimental data, the parameter values give us valuable biological information about the predator and prey behaviour. For modelling purposes it is important that the parameter values are reliable for extrapolation to the real world. For that purpose we performed a reliability analysis of our achieved functional response that allowed rescaling to match survival and growth data from the field.

DERIVATION OF A SIZE-DEPENDENT ATTACK RATE

To derive a mathematical function for a size-dependent attack rate we divided the function into two components; encounter rate and capture efficiency. The sequence of prey capture could be described briefly by the following. A predator encounters and detects a prey, there is then some probability of attacking it, and when the predator attacks the prey there will be a capture efficiency, a probability of capturing the prey. The encounter rate arises from encounters within the predator's search area due to movements of predators and (or) prey. The velocity, ν, of aquatic animals generally scales with body mass to the power 1/3 (Peters 1983). Following Skellam (1958), Werner & Anholt (1993) and Crowley & Hopper (1994) we approximated the encounter rate per prey by:

$$
\begin{aligned}
\lambda &= g(W_N, W_P) \sqrt{\nu_P^2 + \nu_N^2} \\
&= g(W_N, W_P) \sqrt{\vartheta_P W_P^{2/3} + \vartheta_N W_N^{2/3}},
\end{aligned} \qquad \text{eqn 1}
$$

where $g(W_N, W_P)$ is the search area of a predator as a function of prey and predator size and the proportion of time they are active, ν is the velocity of the prey and the predator, indexed by N, P, respectively, W_N and W_P and is the body mass of the prey and the predator, respectively, and ϑ_N and ϑ_P are constants. The search area is given by the reactive distance of the predator and this distance often changes with prey size (Pastorok 1981; Crowl 1989; Parker 1993; Streams 1994). The size scaling of the search area is likely to change with the predator's foraging mode and with variations in prey size availability. Thus, the reactive distance for visually hunting predators is expected to be proportional to the prey area (silhouette), i.e. it scales to $W_N^{2/3}$. This would imply the search area to be proportional to $W_N^{4/3}$ when the search area is proportional to the squared reactive distance. In general, the search area should be proportional to W^{2s}, when the allometric scaling of the stimulus is given by s. For tactile hunters, reacting to vibrations of the prey, $s = 1$. In contrast, for filter feeders prey size may be less important, $s = 0$, and search area should rather scale with predator size as $W_P^{2/3}$ as indicated in the functional response given by Kooijman (1993). Because we expect the size scaling of the search area to vary between species, we made the mathematical function general and included a prey size-scaling constant (γ) in the function for the search area. To complete the function $g(W_N, W_P)$, information on the size-dependence of the predator and prey activity patterns was required. It was difficult to define a general expression for such a size-dependence. Here we included the prey size-dependence into the constant γ, while for the predator size-dependence we entered a new size-scaling constant α, W_P^α. Thus, the search area was defined as: $g(W_N, W_P) = dW_N^\gamma, W_P^\alpha$, where d is a combined constant for the two allometric relationships.

For the attack probability and capture efficiency, we assumed that it could be expressed as a hump-shaped function of the prey/predator mass ratio (cf. Munk 1992). The decrease towards a low ratio, implying small prey, is due to reduced prey detectability, catchability. In contrast, the decrease towards a large ratio should be due to difficulties to handle large prey, and for some predator species an upper ratio may be set by gape

limitation. A mathematical function that satisfies these conditions is:

$$f(x) = c\,x\,e^{-kx}, \qquad \text{eqn 2}$$

where c is a scaling constant, e is the natural base for the exponential function, k is the rate at which the combined attack probability and capture efficiency declines with increasing size ratio, $x = W_N^{-1}W_P$.

The complete attack rate function, eqn 1 × eqn 2 yields a hump-shaped response, both in relation to prey and predator size, producing a ridge in a three-dimensional space. This ridge, i.e. the maximum attack rate, becomes a linear function in the prey–predator mass plane when the species are completely isometric. To allow for possible nonlinearity in this maximum attack rate, we let the ratio x be defined by $W_N^{-1}W_P^{\beta}$, where β is a size-scaling constant. Then the maximum attack rate scales with predator mass as $W_N = z\,W_P^{\beta}$, where z is a constant, when either the predator or prey velocity is zero. The complete function for the attack rate becomes:

$$a(W_N, W_P) = C\,W_N^{\gamma+1}W_P^{\alpha-\beta}\,e^{\frac{-kW_N}{W_P^{\beta}}}\sqrt{\vartheta_P W_P^{2/3} + \vartheta_N W_N^{2/3}}. \qquad \text{eqn 3}$$

This attack rate is density independent. For the density-dependent case, as in the sigmoid functional response, the attack rate in eqn 3 needs to be multiplied by the prey density.

DERIVATION OF A SIZE-DEPENDENT HANDLING TIME

The functional response accounting for predator size given by Kooijman (1993) had a size scaling of the handling time expressed as $W_P^{-2/3}$. Thus, handling time for a fixed prey size should decrease with predator size. The handling time results from physical handling time which involves capture and eating, and the time to digest the prey (Jeschke, Kopp & Tollrian 2002). A complicating fact is that these two components may overlap. That is, while physically handling one prey, the predator may digest another prey. A reasonable assumption for the physical handling is that it is proportional to the ratio of prey size to predator size. An extra term is necessary to allow the handling time to increase for very small prey in relation to predator size. Multiplying each of the two terms with separate constants adjusts the levels and allows the result to be expressed in correct units. The digestion time should be proportional to prey mass when the predator consumes the prey in pieces, as in *S. entomon*. However, it is difficult to deduce a complete handling time function based on the current knowledge. We therefore prefer to keep the function short and flexible to capture most of the variation in the observed data. The digestion and the physical handling time will therefore be confounded in our handling time function. The function we chose to describe the size-dependence in the handling time is therefore partly phenomenological:

$$t_h(W_N, W_P) = h_h W_N^{\eta_N} W_P^{\eta_P} + h_d W_N W_P^{-1}, \qquad \text{eqn 4}$$

where h_h, and h_d are constants, η_N and η_P are the size-scaling constants with indices N and P corresponding to the prey and the predator, respectively.

THE FUNCTIONAL RESPONSE FOR ONE PREY SIZE

Previous functional response experiments with *S. entomon* and *M. affinis* indicate that the functional response is sigmoid (Leonardsson 1994). We therefore focus on the type III functional response:

$$f = \frac{aN^2}{1 + a\,t_h N^2}, \qquad \text{eqn 5}$$

where f is number of prey of a given size consumed by one predator. We used this function to estimate attack rate and handling time in the experiments where we offered only one prey size at a time.

FUNCTIONAL RESPONSE EXPERIMENTS

Species description

In the sublittoral zone below 50 m depth in the Bothnian Sea only two species are common in the benthic invertebrate macrofauna (Kuparinen *et al.* 1996). These species are the omnivorous isopod *Saduria entomon* and its main prey the amphipod *Monoporeia affinis*. *S. entomon* has a large size range from 3 mm as newborn up to 90 mm as adult (Haahtela 1990; Leonardsson 1991). The size of newborn and adult *M. affinis* amphipods is 2 and 11 mm, respectively (Leonardsson, Sörlin & Samberg 1988). In the *Saduria–Monoporeia* system, *S. entomon* may either hunt actively on non-moving *M. affinis* in the sediment, or adopt a sit-and-wait strategy to forage on moving prey. Alternatively, *S. entomon* may capture moving prey while using the first strategy (Green 1957). *S. entomon* use either tactile sensory organs or chemoreceptors on the antennae to detect prey as it has poor visual ability (Pynnönen 1985).

Experiment

We performed the functional response experiments in plastic aquaria (height 0·3 m, bottom area 0·2 m²) with 3-cm soft muddy clay as substrate. The water content of the substrate (following Dybern, Ackefors & Elmgren 1976) was 73·2 ± 0·6% (mean ± 1 SD in the following text, $n = 3$ for both water content and organic content). The organic content was 6·7 ± 0·3%. The aquaria were supplied with seawater with a salinity of 4·5‰ at 5·7 ± 0·2 °C. The *S. entomon* predators were captured by dredging at 20–80 m depth in the northern Bothnian Sea, 40 km South of Umeå, northern Sweden. In total we placed five predators from the same size class in each aquarium from four size classes; 10–15, 25–30, 40–45

and 55–70 mm (total length from the tip of rostrum to the end of telson). The length intervals corresponded to a wet weight range of: 0·06–0·10, 0·39–0·64, 1·36–1·85 and 3·15–5·95 g, respectively. During the experiment, the predators from different size classes were not mixed in the same aquarium. The predators were kept at most for 10 days in large aquaria (height 0·5 m and bottom area 4 m^2) and fed continuously with *M. affinis* prey before the start of each experiment. We collected the *M. affinis* prey by dredging at 20 m depth, in the same sea area where we collected the *S. entomon* predators. The prey densities were 60, 160, 260, 360 and 460 individuals per aquarium corresponding to 300–2300 ind. m^{-2}. We used different size categories of *M. affinis* specimens from three age cohorts; young-of-the-year (0+, size range 0·04–0·28 mg, 60 °C, dry weight), 1-year-old (1+, 0·58–0·93 mg) and 2-year-old (2+, 1·93–2·72 mg). During the experiment, different size categories of amphipods were not mixed in the same aquarium. We performed the experiment in darkness for 24 h, and consumed prey were not replaced. At the end of the experiment the sediment and water were sieved through a 0·3-mm mesh net, and the remaining amphipods, alive or dead, were counted as non-consumed.

Estimations of attack rate and handling time

The estimation of the attack rate and the handling time from the functional response of *S. entomon* was performed using eqns 6 and 7.

$$N_E = N_0 - \frac{\sqrt{\frac{4t_h}{a} + \left(Pt - \frac{at_h N_0^2 - 1}{aN_0}\right)^2} - \left(Pt - \frac{at_h N_0^2 - 1}{aN_0}\right)}{2t_h}$$

$$\text{(6)}$$

$$m = \frac{N_E}{N_0} \qquad \text{(7)}$$

where N_E is the number of prey eaten, N_0 is the initial number of prey available, a is attack rate, t_h is handling time, P is number of predators, t is the duration of the experiment and m is the mortality of the prey. Equation 6 gives the number of prey eaten by all predators per unit of time (here per day) when prey density decreases due to prey consumption. For derivation of eqn 6, see Appendix I. A non-linear least-squares analysis was used for the parameter estimation of eqns 6 and 7 simultaneously for each predator and prey size. We used simultaneous estimation of both equations to obtain more reliable estimates of attack rate and handling time. The estimations of a and t_h were performed separately for each predator size-replicate. The size-dependencies were found by assigning both a and t_h, respectively, to the predator and prey sizes. Non-linear regression was used to fit the attack rate (eqn 3) and handling time (eqn 4) functions to the estimated values of the attack rates and the handling times, respectively.

Check for bias in the attack rate

Our estimates may be biased because of small aquarium size, activity changes due to handling conditions, etc. In order to check for such bias, we used the parameters in a population dynamic model to predict the survival of *M. affinis* in the field. The densities and the size-distributions of predators and prey were obtained from field data from two consecutive years.

Field samples

We collected the field samples from an open-sea area (63°22′18″ N, 19°55′54″ E) in the northern Bothnian Sea (see Leonardsson 1991). The radius of the sampling area was 4·3 km, and the depth range was 58–63 m. In total 108 van Veen grabs (0·1 m^2) were taken each year during October in 1995 and September in 1996. The samples were sieved through a 0·5-mm mesh net and preserved in 4% formalin.

After counting the *M. affinis* and *S. entomon* specimens we measured the wet weight and length of all *Saduria entomon*. We also measured the size (mm^2 wet area) of the *M. affinis* specimens to separate the age classes and estimate sizes and number of individuals in each class. For the area measurements we used a digital camera (Nikon CoolPix 990, and image analysing software; Scion Image, Release Beta 3, 1998). We separated the size-distributions into age-classes in a three-step procedure. First we transformed the wet areas to obtain normally distributed wet areas for each age-class. Secondly, we fitted one normal distribution curve to each of the age-classes' wet area distribution simultaneously and calculated the sum of the three normal curves for each wet area-class. The best fit was found using least-squares minimization based on residuals given by the difference between the observed size-distribution and the sum-curve. The proportion of individuals in each age-class was then calculated using each of the normal curves, respectively. Thirdly, we used the average wet areas, the associated standard deviations and the estimated proportions from step 2 as initial conditions in a maximum likelihood (ML) estimation. While the previous analysis and results relies on grouping of individuals into size-classes, the third step avoids this problem because each individual's wet area was included in the analysis. We maximized the log-likelihood function (*LLF*);

$$LLF = \sum_{i=1}^{n} (-\ln(p_1 pdf(A_i, \mu_1, \sigma_1) + p_2 pdf(A_i, \mu_2, \sigma_2) + (1 - p_1 - p_2)pdf(A_i, \mu_3, \sigma_3)))$$

by adjusting the probabilities p_1 and p_2 within the constraints $0 < p_j < 1$ and $\text{Sum}(p_j) = 1$, and by adjusting the average wet areas, μ, and the associated standard deviation, σ, for each age class, j. An individual's wet area is denoted by A_i, where i is the individual index from 1 to n. Pdf is short for probability density function,

Table 1. Predator (*Saduria entomon*), and prey (*Monoporeia affinis*) sizes and densities from the field data that was used in the consumption model and in the predator growth model. In 1995 the samples were collected in October; in 1996 the samples were collected in September

Saduria entomon			*Monoporeia affinis*				
				Dry weight (mg)		Density (ind. m^{-2})	
Length class (mm)	Wet weight (g)	Density (ind. m^{-2})	Age class	1995	1996	1995	1996
10–15	0·038	3·1	0+	0·24	0·12	2450	6500
15–20	0·106	5·9	1+	0·71	0·56	2000	1340
20–25	0·197	5·7	2+	1·28	1·24	1300	1640
25–30	0·351	3·1					
30–35	0·559	2·8					
35–40	0·867	2·4					
40–45	1·198	0·7					
45–52	1·779	0·4					
53–60	2·764	0·3					
> 60	4·937	0·1					

based on the normal distribution. After the ML estimation we noted the estimated proportion of individuals in each age-class, and the age classes' estimated median wet areas. The proportions were then used to calculate the density of each age-class in 1995 and 1996, respectively. From these data we estimated the survival of each age-class. The median wet areas were transformed to dry weights to be used in the model.

In *S. entomon*, the specimens were separated into size-classes, and the average number per size class was calculated. We used the size-distribution of the predator population and the median sizes of each age-class of the prey population in the consumption model (Table 1).

MODELS

In contrast to the experiments, the predators in the model had access to all three age-classes of *M. affinis* simultaneously, and we used the median mass for each of these. The total number of consumed prey of one age-class, *j*, per day of all predators belonging to size-class *k* was formulated as:

$$f_{m,j} = \sum_k \left\{ \frac{a_{j,k} N_j^2 P_k q}{1 + \sum_i (a_{i,k} h_{i,k} N_i^2 q)} \right\}. \qquad \text{eqn 8}$$

Here *a* is attack rate, *h* is handling time, *N* is prey density, *P* is predator density, and the indices denote size-class of predator and prey, respectively. The subscripts *m*, *j* denote that prey mortality of size-class *j* is given by the function. A constant *q* was introduced as a correction factor to adjust for potential bias in the attack rate estimates. The total daily prey consumption in terms of prey biomass per predator was estimated from:

$$f_{g,k} = \frac{\sum_i (a_{i,k} N_i^2 W_i)}{1 + \sum_i (a_{i,k} h_{i,k} N_i^2)}. \qquad \text{eqn 9}$$

Here the subscripts *g*, *k* denote that the function is used to calculate growth of a predator belonging to size-class *k*, W_i is the individual prey mass of age class *i*.

The prey consumption of the predator was modelled as a continuous process, using daily rates. For *M. affinis* with a fecundity of about 30 eggs and a 3-year semelparous life cycle there is little room for mortality. We therefore assumed that the mortality of *M. affinis* due to other factors than predation by *S. entomon* was negligible. Our model handled the change in the actual size-structure of the prey throughout the year, accounting for spawning with male death (mid-November), female death after release of her offspring (1 March) and growth (March–September). Growth of *M. affinis* is concentrated to the spring–early summer period following the spring bloom (Elmgren 1978; Sarvala 1986).

The field data available indicate that the spawning of the predator is distributed all over the year. Moreover, the size-distributions from 1995 and 1996 in our field data indicated that growth compensated for mortality, leading to a stable size-distribution. For this reason we chose to keep the predator size-distribution constant in the model. Collecting information on prey biomass consumption by each predator size-class in the model allowed us to construct growth curves for the predators. These growth curves were one part of the check for realism in our results.

A modelling schedule with more detailed description of the events throughout the year is as follows. The consumption simulation starts with the initial prey and predator size distributions in October and covers 340 days. At day 40, 2+ males (40% of the age-class, estimated from samples collected in 1996) mate and die. At day 160, the offspring are released and the spent females die. Until now winter prevails and no growth has taken place. The remaining 180 days of the simulation covered the growing season. The growth rate of the prey was defined using a log-normal distribution (*LND*) to mimic the seasonal growth and reach the observed sizes in September. The growth rate was given by;

Table 2. Description of parameters and their numerical values used in the consumption model, and in the predator growth model

Symbol	Value	Unit	Description
Prey parameters			
x	1–340		Day number, starting mid-October
μ	210		Day number when maximum growth occurs
σ	0·3		Parameter in the lognormal distribution
G_0	0·002		Basic growth for 0+. G_0 is zero for 1+ and 2+
z_0	0·0125		Constant, scaled for 0+ to reach correct final size
z_1	0·00486		Constant, scaled for 1+ to reach correct final size
z_2	0·00322		Constant, scaled for 2+ to reach correct final size
f	30/20		Fecundity, eggs per female. Two scenarios
m	0·01	mg	Newborn dry weight
Predator parameters			
$\hat{c}$	0·7/a	dim. less	Conversion coefficient, where a = 180 converts prey mass from mg dry weight to g wet weight
m_1	0·00005		Size-independent metabolic cost
m_2	0·85		Allometric scaling of metabolic cost
W_P		g	Predator mass, wet weight

$G_0 + z_i * exp(x) * pdf(LND, x = \ln(\text{day number}), \mu, \sigma)$, where G_0 also provides growth of 0+ during late summer, z_i is a scaling constant for each age-class (*i*) to reach the correct final size, x is day number, pdf is short for probability density function, μ and s are parameters in the lognormal distribution. The parameters for the growth function are given in Table 2 together with the other parameters used in the model. We performed several simulations by varying the correction factor, q, to obtain an estimate of the sensitivity of the predicted results in relation to the experimentally derived attack rate estimate. After each simulation, we compared the predicted number of surviving prey of each age-class with that observed from the field samples.

The second part of the model concerned the growth rate of the predator, which needed to be realistic to rely on the correction for possible bias in the experimentally derived attack rate. The growth model for the predator followed:

$$\frac{dW_P}{dt} = \hat{c}f_g - m_1 W_P^{m_2}, \qquad \text{eqn 10}$$

where $\hat{c}$ is a conversion coefficient, m_1 is the size-independent metabolic cost and m_2 is the allometric scaling of metabolic cost. These parameters were estimated from Sparrevik & Leonardsson (1999); see Table 2. We obtained the predator growth curves by integrating eqn 10 over time, using prey densities and prey sizes from the consumption model (extended to cover 365 days). The smallest predators, i.e. less than 10 mm, are probably not efficient consumers of *M. affinis* due to these predators' soft exoskeleton. For this reason extrapolations for the first year of growth would be too uncertain. Also the size at 1 year of age is not clear from the literature or from our data. Because of lack of knowledge of how large 1-year-old *S. entomon* are at these deep bottoms we chose to use two different 1-year-old predator sizes (9 mm and 15 mm) as starting points for

the growth curves. Using these sizes at year 1 we predicted the size at year 1 by integrating eqn 10, and then repeatedly predicted the size at next year using W_t of previous year as a new starting point.

Results

FUNCTIONAL RESPONSE

The number of *M. affinis* prey consumed in the experiment varied with prey size and density and size of *S. entomon* predators. In general, the functional response curves showed a sigmoid (type III) form (Fig. 1). The per capita mortality risk of *M. affinis* was hump-shaped in relation to prey density due to the sigmoid functional responses. The most distinct density-dependent prey mortality patterns were found in amphipods from the 0+ and 1+ cohorts in the presence of predators from the two intermediate size classes (Fig. 1).

ATTACK RATE

In large *S. entomon* the attack rate increased slowly to a maximum on the largest *M. affinis* prey. In contrast, in small *S. entomon* the attack rate had a maximum on small prey (Fig. 2a,b). This decline in attack rate on large prey was due probably to difficulties for small predators attempting to capture large prey. The prey movement term was not significant, i.e. $\vartheta_N = 0$, when using eqn 3 in a non-linear regression analysis to estimate attack rate. This indicated that the most common foraging mode of *S. entomon* is on non-moving *M. affinis* buried into the sediment. Furthermore, the size-dependence in the predator activity was not significantly different from zero, i.e. $\alpha = 0$, which reduced the attack rate function to:

$$a(W_N, W_P) = \hat{C} W_N^{\gamma+1} W_P^{1/3-\beta} e^{\frac{-kW_N}{W_P^{\beta}}}, \qquad \text{eqn 11}$$
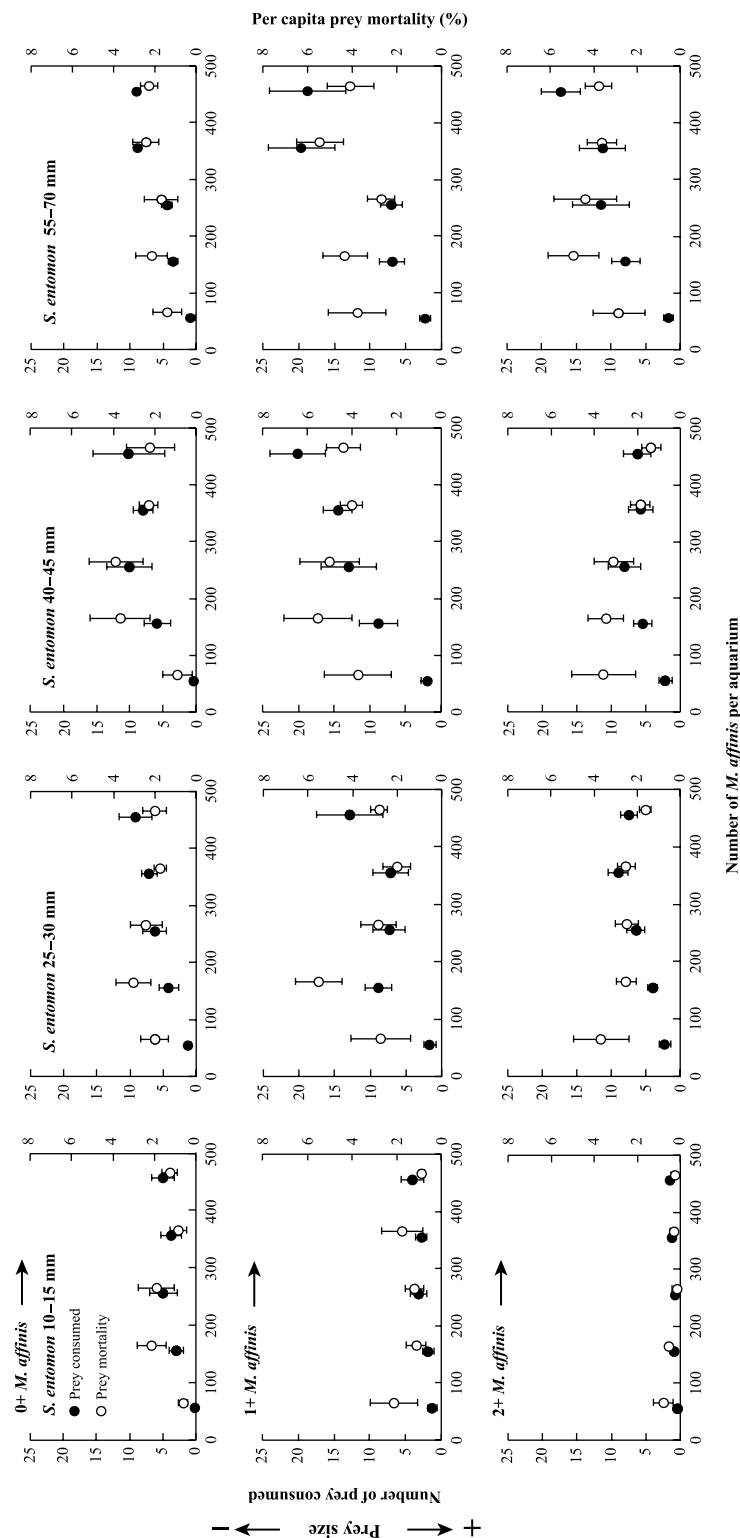
Fig. 1. Number of prey consumed (filled circles) and percentage prey mortality (open circles) at four size classes (10–15, 25–30, 40–45 and 55–70 mm) of *Saduria entomon* predators preying on young-of-the-year (0+), 1-year (1+) and 2-year (2+)-old *Monoporeia affinis* prey cohorts. Vertical lines show SE, and $n = 6$ for each prey density in each age-cohort.
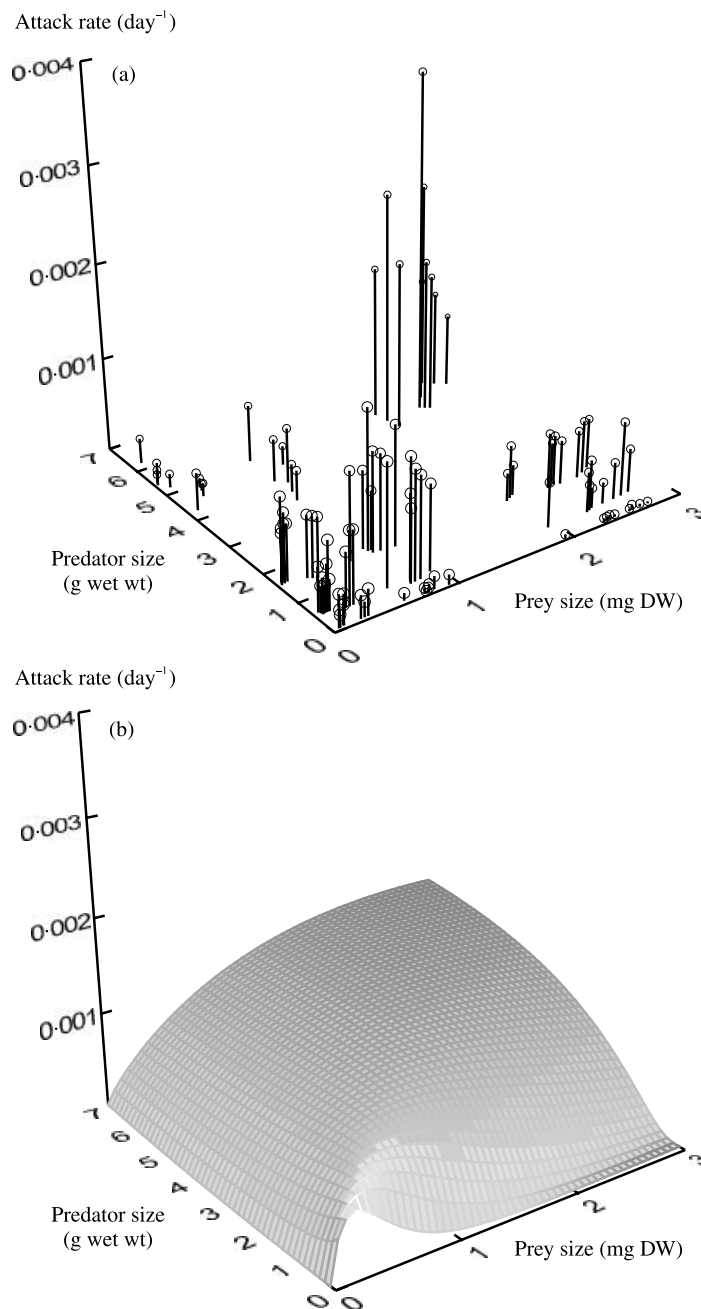
A. A. Aljetlawi,
E. Sparrevik &
K. Leonardsson

Fig. 2. (a) Attack rate of the predator *Saduria entomon* estimated from experiments with different predator and *Monoporeia affinis* prey sizes. (b) Three-dimensional shape of the attack rate function of the predator *Saduria entomon* at different predator and *Monoporeia affinis* prey size. The attack rate function and its parameter values are given in Table 3.

here $\hat{C}$ includes $C\sqrt{\vartheta_P}$. The fit of this model yielded a raw $r^2 = 0.81$, and a corrected $r^2 = 0.56$. We found the prey size-scaling constant γ for the search area and the activity to be -0.16 (Table 3), indicating that small prey were encountered more frequently than large ones. The maximum attack rate showed a non-linear relationship with respect to prey and predator sizes, $W_N = zW_P^{2/3}$.

HANDLING TIME

The handling time increased rapidly in the smallest *S. entomon* predators when the size of *M. affinis* prey increased. In the large predators the handling time was

Table 3. Parameter estimates of coefficients in the attack rate function of *Saduria entomon* feeding on *Monoporeia affinis*. SE of coefficients, lower and upper (95%) Wald confidence intervals are given. The attack rate function was: attack rate = $\hat{C}W_N^{\gamma+1}W_P^{1/3-\beta}e^{\frac{-kW_N}{W_P^{\beta}}}$, where W_N is *M. affinis* size, W_P is *S. entomon* size, and e is the natural base in the exponential function

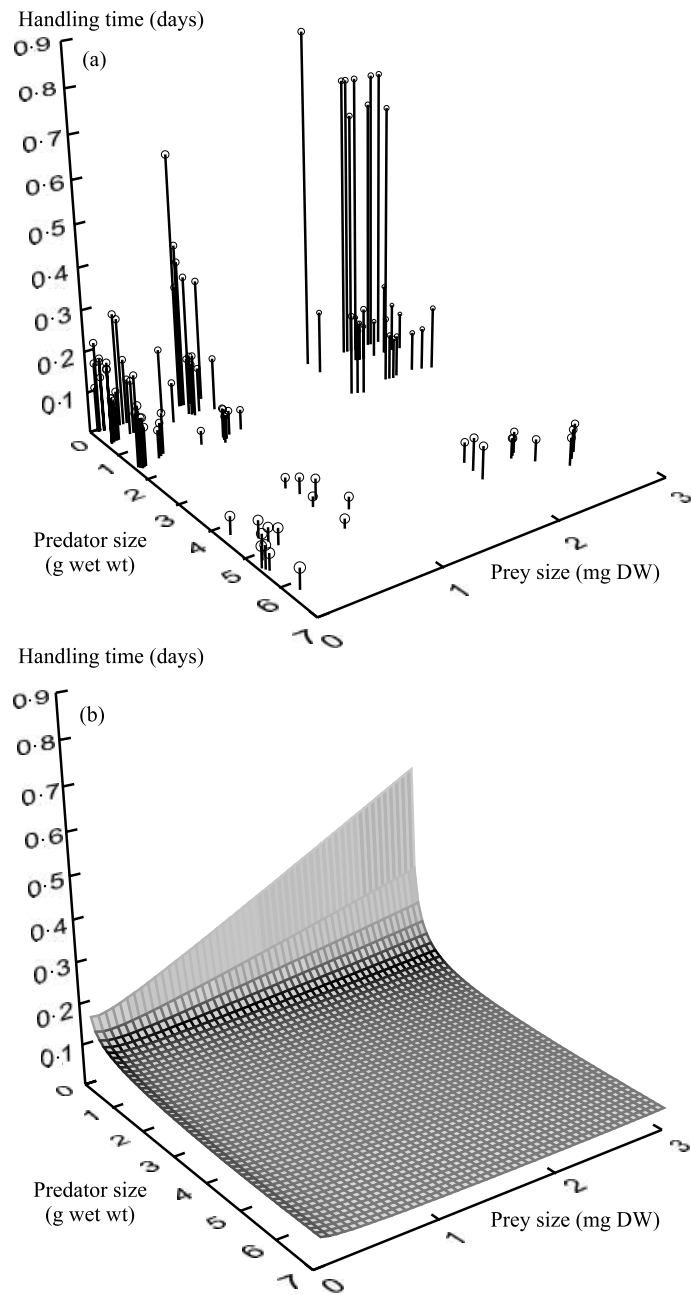| Parameter	Estimate	SE Coeff	Wald lower	Wald upper
$\hat{C}$	0·003	0·00004	0·002	0·004
γ	−0·158	0·062	−0·281	−0·034
β	0·692	0·118	0·458	0·926
k	1·134	0·123	0·889	1·378

Fig. 3. (a) Handling time of the predator *Saduria entomon* calculated from experiments with different predator and *Monoporeia affinis* prey size. (b) Three dimensional shape of the handling time function of the predator *Saduria entomon* at different predator and *Monoporeia affinis* prey sizes. The handling time function and its parameter values are given in Table 4.

short both for small and large prey (Fig. 3a,b). The results of the non-linear regression analysis using eqn 4 to estimate the handling time gave a high degree of explanation, raw $r^2 = 0.95$, and corrected $r^2 = 0.91$. The size scaling with respect to the predator size was expected to be $\eta_P = -2/3$ according to Kooijman (1993). Our estimate was $\eta_P = -0.23$, with the lower confidence limit reaching -0.33 (Table 4).

EVALUATION OF EXPERIMENTAL BIAS

The predicted survival of all *M. affinis* size-classes was much lower than the observed ones when using the

Table 4. Parameter estimates of coefficients in the handling time function of *Saduria entomon* feeding on *Monoporeia affinis*. SE of coefficients, lower and upper (95%) Wald confidence intervals are given. The handling time function was: $t_h(W_N, W_P) = h_h W_N^{\eta_N} W_P^{\eta_P} + h_d W_N W_P^{-1}$, where W_N is *M. affinis* size, W_P is *S. entomon* size

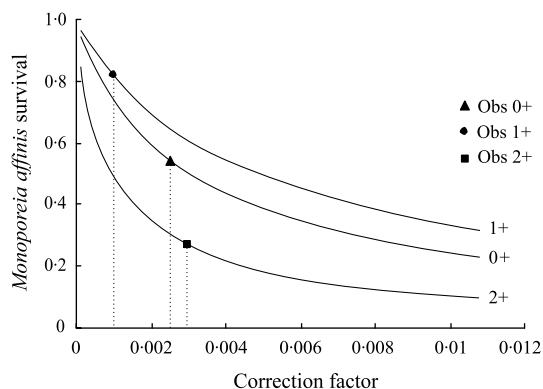| Parameter	Estimate	SE Coeff	Wald lower	Wald upper
h_h	0·022	0·001	0·019	0·024
h_d	0·076	0·083	0·059	0·093
η_N	−0·101	0·058	−0·217	0·014
η_P	−0·232	0·049	−0·330	−0·135

Fig. 4. Expected survival of *Monoporeia affinis* specimens belonging to the age classes 0+, 1+ and 2+, respectively, at different values of the correction factor when the fecundity was 30 eggs per female.
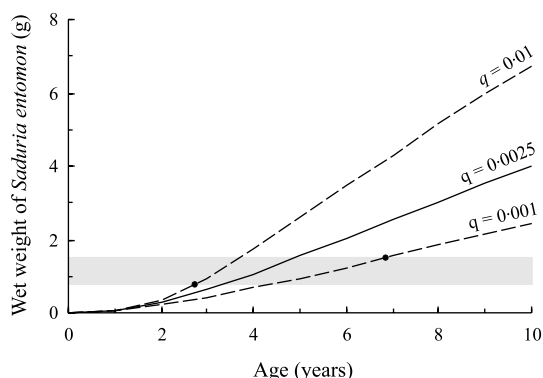

Fig. 5. The growth pattern of *Saduria entomon* from birth to an age of 10 years, for three different values of the correction factor, q, in the attack rate. $q = 0.0025$ best described the prey mortality in the field. These results correspond to that found when the size of 1-year individuals was set to 15 mm length. The growth parameters are given in Table 2. The upper and lower limits of the shaded area correspond to the 20%- and the 80%-quantile, respectively, of female maturation sizes in the study area. The dots denote the lower and upper limits to the life-cycle length.

density of small prey than on large when increasing q. The sensitivity analyses of the metabolic parameters did not change these results as long as they stayed within biologically reasonable values. However, the conversion coefficient had a more direct influence of the growth rate, almost a one-to-one relationship. Lack of data to compare with these model predictions makes the results qualitative, but the predicted growth rates seem reasonable according to our current knowledge and the correction factor overlap with that in the survival analysis.

THE COMPLETE FUNCTIONAL RESPONSE

The functional response surface was hump-shaped in relation to the prey size when evaluating it in the prey size and density dimensions (Fig. 6a,b). This evaluation considered one prey size available to the predator at a time. There was a sharp drop in predation rate towards very small prey sizes, and a slower decline towards large prey sizes. The marked hump became less pronounced when accounting for the entire predator population size-structure (Fig. 6c). The size-refuge for the smallest prey almost disappeared, and the size-refuge for large prey became more pronounced.

Discussion

The size-dependent attack rate estimated from our functional response experiments was a bent hump-shaped function of predator and prey size. In contrast, Thompson (1975) found no hump-shaped attack rate when incorporating both predator and prey size. A probable explanation of the contrasting results is the small ranges of predator and prey size used in the experiment by Thompson (1975). More complex attack rate surfaces should be expected when a wide range of predator and prey sizes is involved (McArdle & Lawton 1979). The handling time of the smallest predators increased with prey size in our experiment. In contrast, the handling time of the largest predators showed no clear change as the prey size increased. Other studies have shown that independent of predator size, handling time increased with prey size (Thompson 1975; Gibson, Yin & Robb 1995). One possible explanation to the contrasting results is that handling time in our study is underestimated in large predators and large prey due to partial prey consumption. This conclusion is supported by observations of remnants of large (2+) *M. affinis* in other functional response experiments with large *S. entomon* as predators (A. Aljetlawi, personal observations).

In our derived theoretical attack rate function the size scaling of predator and prey mass was important for the shape of the function. The size scaling may depend partly on predator foraging mode. The size scaling of the search area and capture efficiency is expected to vary between predators with different foraging mode, e.g. visual hunters, tactile hunters and
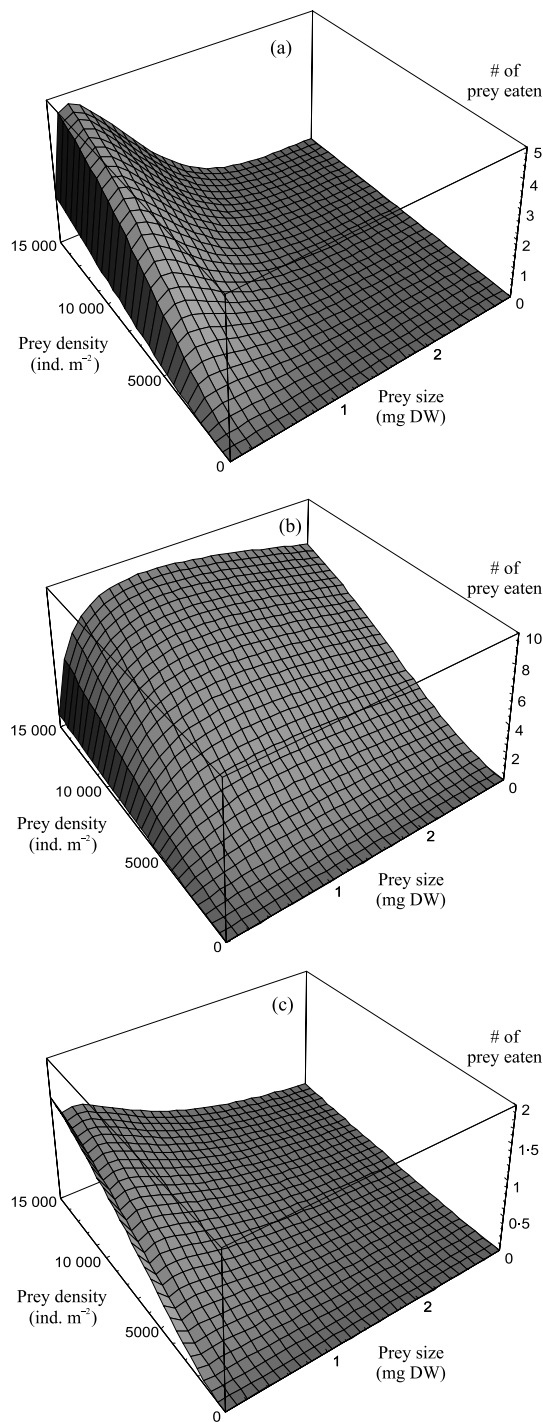
experimentally derived functional response parameters (Fig. 4). Multiplication of the attack rate by the correction factor, q, in the order 0.001–0.003 was needed to predict successfully the survival of the 0+, 1+ and 2+ age-classes. The predicted survival of *M. affinis* size-classes 1+ and 2+ was more or less unaffected by the change in the fecundity (20 vs. 30 eggs per female), indicating that the young-of-the-year should not contribute greatly to the predators total handling time. The q-value that best described the survival of 0+ and 2+ *M. affinis* implies that the attack rate estimates from the experiments were overestimated by a factor of 400.

The predicted predator growth curves that generates a realistic life-cycle length of 3–7 years required q-values in the range; $0.001 < q < 0.01$ (Fig. 5). When increasing q, the growth of the predators decreased for sizes below 0.4 g wet weight. Above that size the growth increased with q. The decrease in the smaller predators' growth was due to a stronger negative feedback on

Fig. 6. The size-dependent functional response of *Saduria entomon* when foraging on one size class of *Monoporeia affinis* at a time. In (a) the predator size is 0·2 g wet weight, in (b) the predator size is 2·0 g, in (c) all size classes of *Saduria entomon* were represented with the frequency of each size corresponding to that found in the field.

filter feeders (Werner 1988). The allometric scaling for these aspects was defined by γ in our function, and we expected γ to be positive for an active forager as *Saduria*. In contrast, our estimate using the experimental data was slightly negative. The interpretation of such results would be that the predators acted like filter feeders. This is not consistent with the non-significant

prey movement term in our results. However, if *S. entomon* isopods forage mainly in the uppermost sediment surface, the size fractioning of *M. affinis* with smaller individuals at the sediment surface (Hill 1984) may then explain our results. In other experimental studies of attack rate there are large differences of predator or prey size effects on the shape of attack rate function, changing from hump-shaped to monotonically decreasing or increasing patterns (Hewett 1980; Spitze 1985; Persson 1987; Parker 1993; Tripet & Perrin 1994). Differences in predator foraging mode may partly explain these diverging results in the literature. When the foraging mode changes from passive filter feeding to active search, the scaling exponent γ is expected to increase. If everything else is constant, the hump in the attack rate function will move from small to larger prey sizes as γ increases. For filter feeders there should be a smaller range of prey sizes within the increasing slope of the attack rate than for active foragers. Thus, the hump is more likely to be found in actively foraging species.

We used five predators of the same size class in the same aquaria, which may have caused some interference between the predators. Such interference affects feeding activity through the dilution of the attack rate (see Crowley & Martin 1989). However, despite the potential interference the attack rate in the aquaria was much higher than that estimated for field conditions. Interference among the predators may have acted via the prey to produce predator facilitation (Sih, Englund & Wooster 1998). In our experiments, foraging predators may have increased the swimming activity of the prey and the surrounding predators benefited thereby from the increased availability of prey. We do not know whether such positive effects could outweigh the negative effects of direct interference between predators.

It seems that the predator and prey size dimensions in the functional response allow for size-refuges of the prey. In the benthic ecosystem in the northern Baltic there are few invertebrate species in the same size order as *M. affinis* and *S. entomon*. This means that large *M. affinis* have large *S. entomon* as their main predator. The size refuge for larger *M. affinis* will therefore be relatively safe and promote coexistence with the predator. On the other hand, the smallest *S. entomon* may have access to meiofauna species that are abundant in the sediments. This type of relaxation of predation is likely to weaken the interactions between the predators and their prey species and stabilize the dynamics in the system (McCann, Hastings & Huxel 1998; Berlow 1999). The huge size variation among and within species is probably the key to the manifold of weak interactions. One study that shows this potential is that by Woodward & Hildrew (2002). However, the benthic ecosystem in the Baltic has few species, but the number of species increases from north to south. For many species the size range also increases from north to south. Thus, there is more room for complex interactions in the southern part of the Baltic and the dynamics in the benthic system is less fluctuating than in the northern part.

The impact of size-dependent functional responses on population dynamics is largely unexplored, but should have a considerable potential to affect the dynamics of size-structured populations and food webs (De Roos, Persson & McCauley 2003). The size-dependence in the attack rate seems to be important in that respect as it may result in various types of dynamics, stable, cyclic or chaotic (Persson *et al.* 1998). No study has investigated so far the influence on population dynamics from size scaling of both predator and prey mass in the attack rate. Because the majority of the animal taxa are size-structured (Ebenman & Persson 1988), such investigations are of major interest in understanding the mechanisms driving the population dynamics. Handling time is also considered to affect the stability of population dynamics in size-unstructured models, but to a lesser extent than the attack rate (Hassell & May 1973). Thus, there is a need for modelling of population dynamics with the inclusion of size-structure both in predator and prey. The predictions from such models should be compared with empirical data of predator–prey dynamics from size-structured populations.

Our approach in this study provides a method to obtain the parameters of the functional response in relation to prey and predator size that provides details for understanding the interactions in predator–prey systems. By using the obtained parameter estimates in a consumption model based on real data it allowed us to investigate the potential bias in the experimentally derived parameter estimates. If we are to predict the dynamics in real systems we need parameter values that do apply to natural conditions. Our approach is one way to solve the scaling problem from small-scale experiments up to the real world. The underlying idea is simple; it requires only basic knowledge about the life history of the organisms and high quality field data for the consumption and the growth model.

Acknowledgements

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Appendix I

DERIVING AND VERIFYING THE ANALYTICAL SOLUTION OF THE FUNCTIONAL RESPONSE

The analytical solution to the number of prey eaten is found by solving the differential eqn 1·1 to yield $N(t)$, which is the number of prey remaining at time t. The number of prey eaten, N_E, is the difference between the initial prey density, N_0, and the final density, $N(t)$. The differential equation based on a sigmoid, type III, functional response denotes the continuous decline in prey numbers due to predation, given the attack rate, a, handling time, t_h, and number of predators, P.

$$\frac{dN}{dt} = -\frac{aPN^2}{1 + at_h N^2}$$

<div align="right">eqn 1·1</div>

Using separation of variables we obtain:

$$\int_{N_0}^{N(t)} -\frac{1 + at_h N^2}{aPN^2}\,dN = \int_{N_0}^{N(t)} \left(-\frac{1}{aPN^2} - \frac{t_h}{P}\right) dN = \frac{(N_0 - N(t))(1 + at_h N_0 N(t))}{aPN_0 N(t)} = \int_0^t 1\,ds = t.$$

<div align="right">eqn 1·2</div>

Solving for $N(t)$ yields two roots of which the positive, i.e. the biologically meaningful, is:

$$N(t) = \frac{aN_0(t_h N_0 - Pt) - 1 + \sqrt{4at_h N_0^2 + (1 - aN_0(t_h N_0 - Pt))^2}}{2at_h N_0}.$$

<div align="right">eqn 1·3</div>

To verify this solution we differentiate $N(t)$ with respect to time. To simplify the following analyses we define two constants, A and B, as: $A = aN_0(t_h N_0 - Pt)$, and $B = 4at_h N_0^2 + (1 - A)^2$, and replace the corresponding expressions with A and B in the equations:

$$\frac{d(N(t))}{dt} = -\frac{P}{2t_h}\left(1 + \frac{(1 - aN_0(t_h N_0 - Pt))}{\sqrt{4at_h N_0^2 + (1 - aN_0(t_h N_0 - Pt))^2}}\right) = -\frac{P}{2t_h}\left(1 + \frac{(A-1)}{\sqrt{B}}\right)$$

<div align="right">eqn 1·4</div>

If the solution is correct, replacing N in eqn 1·1 with the analytical solution of $N(t)$, eqn 1·3 will give the same answer as in eqn 1·4:

$$\frac{dN}{dt} = -\frac{aPN(t)^2}{1 + at_h N(t)^2} = \frac{P\left(A - 1 + \sqrt{B}\right)^2}{4at_h^2 N_0^2 \left[1 + \frac{\left(A - 1 + \sqrt{B}\right)^2}{4at_h N_0^2}\right]} = \frac{P\left(A - 1 + \sqrt{B}\right)^2}{t_h\left(B - (1-A)^2 + \left(A - 1 + \sqrt{B}\right)^2\right)}$$

<div align="right">eqn 1·5</div>

$$= -\frac{P}{2t_h}\left(\frac{\sqrt{B} + A - 1}{\sqrt{B}}\right) = -\frac{P}{2t_h}\left(1 + \frac{A - 1}{\sqrt{B}}\right)$$

This verifies the analytical solution. Finally, we rewrite the equation to obtain the number of prey eaten, $N_E(t)$, as a function of time.

$$N_E(t) = N_0 - N(t) = N_0 - \frac{aN_0(t_h N_0 - Pt) - 1 + \sqrt{4at_h N_0^2 + (1 - aN_0(t_h N_0 - Pt))^2}}{2at_h N_0}$$

$$= N_0 - \frac{\dfrac{aN_0(t_h N_0 - Pt) - 1}{aN_0} + \sqrt{\dfrac{4t_h}{a} + \left(\dfrac{1 - at_h N_0^2 + aN_0 Pt}{aN_0}\right)^2}}{2t_h}$$

<div align="right">eqn 1·6</div>

$$= N_0 - \frac{\sqrt{\dfrac{4t_h}{a} + \left(Pt - \dfrac{at_h N_0^2 - 1}{aN_0}\right)^2} - \left(Pt - \dfrac{at_h N_0^2 - 1}{aN_0}\right)}{2t_h}.$$