Scaling up the functional response for spatially heterogeneous systems

Abstract

Scale transition theory is a framework for predicting regional population dynamics from local process functions and estimates of spatial heterogeneity. Using this framework, we estimated regional scale functional responses for a benthic predator–prey system in the Baltic Sea. Functional responses were based on laboratory experiments or field observations of stomach contents, and prey densities measured at a local scale (0.1 m²) or a regional scale (300 km²). Laboratory data overestimated consumption at high prey densities, whereas predictions based on local scale data tallied closely with consumption observed at the regional scale. The predicted regional functional response was different for increasing and decreasing prey densities, reflecting that predator and prey densities, as well as the covariance between them, exhibit oscillatory dynamics. We conclude that it is important to validate laboratory data with small-scale field observations and that scale transition is a powerful tool for scaling-up process functions in heterogeneous systems.

Keywords

Moment approximation, scale transition, spatial dynamics, heterogeneity, predator–prey dynamics, process resolution.

Introduction

The functional response, which describes consumption by predators as a function of prey density, is a key component of dynamic population models of trophic interactions. The shape of this function is crucial in determining the dynamics and persistence of interacting populations. Often, functional responses are estimated in small-scale laboratory systems and incorporated into mean-field models, where the dynamics of interacting species are described as functions of their mean densities. These models are then used to predict the dynamics of much larger natural systems (Gurney et al. 1990; De Roos & Persson 2001; Hjelm & Persson 2001; Bergström et al. 2006). This approach rests on the assumption that functional response parameters estimated in laboratory experiments are accurate. Studies showing that this assumption is violated as a result of reduced spatio-temporal scales and simplified community structure in experimental systems, suggest that we need to validate laboratory experiments with direct observations of functional responses in natural systems (LaFontaine de & Leggett 1987; Wilhelm et al. 2000; Englund & Cooper 2003).

A particularly important source of scale effects is the reduced spatial heterogeneity in small systems (He et al. 1994). Since predation is a nonlinear process, the ‘true’ functional response, which describes consumption in a heterogeneous system as a function of mean densities, should generally be different from the response estimated in a more homogeneous system. From this it follows that mean-field approaches can lead to biased model predictions if the effects of heterogeneity are not included. The problem has long been recognized by ecologists and has been referred to as aggregation error (O’Neill & Rust 1979; Rastetter et al. 1992), transmutation (O’Neill 1979), and scale transition (Chesson 1996). Other authors have used ‘the fallacy of the average’ (Welsh et al. 1988) and Jensen’s inequality for related problems (Ruel & Ayres 1999).

One approach to account for the effects of heterogeneity in mean-field models is to combine small-scale observations from homogeneous systems with field measurements of heterogeneity. This approach was first developed in studies of host–parasitoid interactions (e.g. Bailey et al. 1962; Hassell 1980), and more recent studies have used it to derive models of host–parasite and predator–prey interactions (Dobson & Hudson 1992; Barlow 2000; Nachman 2006a,b). A general framework, which is applicable to a wider range of interactions, was proposed by Chesson (1996, 1998) and Melbourne & Chesson (2006) under the
name ‘scale transition theory’. Recent studies that have used this framework to predict the effects of spatial heterogeneity on algae–grazer interactions, predator–prey dynamics and patterns of coexistence between competing plants (Melbourne et al. 2005; Bergström et al. 2006). An attractive feature of this approach is that the resulting large-scale models have an additive structure that allows for straightforward quantification of the contribution of different types of heterogeneity, measured at different scales, and acting via different nonlinear processes.

In a previous paper (Bergström et al. 2006), we used the scale transition framework to predict regional scale consumption and population dynamics based on a laboratory-estimated functional response and field estimates of heterogeneity. The organisms studied were the benthic isopod Saduria entomon and its amphipod prey Monoporia affinis; these two form a tightly linked predator–prey system in deep parts of the species-poor northern Baltic Sea.

In this paper we extend this work, using field observations of stomach contents and prey densities, to produce field estimates of the functional response of Saduria on a local scale (0.1 m²) and a regional scale (300 km²). This allows us to examine the validity of previous findings for the study system and, more generally, to test components of the scale transition framework. Specifically, we investigate: (a) whether the laboratory-estimated functional response agrees with the local-scale functional response observed in the field; (b) whether the observed regional scale functional response can be predicted from the local-scale functional response and heterogeneity measured in the field; and (c) how the choice of observation scale for measuring spatial heterogeneity influences the accuracy of the predicted regional functional response. We find that the regional scale functional response is phase dependent, i.e. different for increasing and decreasing prey densities, a pattern that was predicted by the scale transition framework.

SCALE TRANSITION THEORY

The scale transition framework for scaling up population dynamics is described in detail elsewhere (Chesson et al. 2005; Bergström et al. 2006; Melbourne & Chesson 2006), so here we only provide a brief summary. An important component of the framework is the mathematical method of moment approximation (also called moment expansion) (Rastetter et al. 1992; Chesson et al. 2005). This method can be used to extrapolate nonlinear mathematical functions: data collected in small-scale homogeneous systems can, therefore, be used to predict the output of more heterogeneous natural systems. The effect of spatial variation on process output is quantified by statistical moments, such as spatial variance, covariance, skew, etc. along with terms that measure the nonlinearity of the function. A second order approximation of a functional response model that is linear in \( P \) (predator density), i.e. where there is no interference or facilitation between predators, and nonlinear in \( N \) (prey density) due to satiation, is given by:

\[
G(N)P \approx f(N)P + \frac{f''(N)P\sigma_N^2}{2} + f'(N)\sigma_{N,P} \tag{1}
\]

(see Bergström et al. 2006 or Chesson et al. 2005 for model derivation). The function \( G(N) \) can be interpreted as the functional response that can be used in a mean-field model of a large heterogeneous natural system and \( f(N) \) as the functional response estimated in a smaller more homogeneous system. The function \( f(N) \) can be estimated from laboratory experiments, or from small-scale field observations of consumption and prey densities. Two additive terms, henceforth called ‘variance effect’ and ‘covariance effect’, describe the effects of the two different types of heterogeneity. These terms contain derivatives describing the nonlinearity of the small-scale function, and the variance in prey density \( \sigma_N^2 \) and the covariance between predator and prey densities in the large-scale system, \( \sigma_{N,P} \).

Equation 1 suggests that the form of the function for the more homogeneous environment is insufficient when extrapolating from a relatively homogeneous to a more heterogeneous system. For such extrapolation, we also need measures of the spatial variance of prey density and the spatial covariance between predator and prey densities. Thus, in order to parameterize the right side of the equation for the Saduria–Monoporia system, we used field estimates of variances and covariances and either a functional response estimated from local consumption and local densities in the field, or a response estimated from laboratory experiments. Testing the accuracy of eqn 1 also requires that \( G(N)P \) is measured in the field. This was achieved by recording consumption as a function of the regional mean density of prey.

STUDY SYSTEM

The benthic fauna in deep areas of the northern Baltic Sea is dominated by the predatory isopod Saduria entomon (L.) and the amphipod Monoporia affinis (Lindström) (Haattela 1990; Leonardsson 1991a). Saduria feed mainly on Monoporia, except in years with very low Monoporia densities, when mysid shrimps can be an important food source. Occasionally the diet also includes dead fish, conspecifics, and other macro- and meio-benthic taxa (Sparrevik & Leonardsson 1998). Monoporia is a deposit feeder (Lopez & Elmgren 1989), that can reach densities as high as 10 000 ind. m⁻² (Leonardsson 1991b). Given the numerical dominance of Saduria and Monoporia, it is believed that they form a tightly coupled predator–prey system (Aljetlawi et al. 2004;
Bergström et al. 2006), that exhibits oscillatory density dynamics with a cycle length of 6–8 years (Andersin et al. 1978; Leonardsson et al. 2002). Aljetlawi et al. (2004) studied the functional response of Saduria preying on Monoporia in aquarium experiments and found that the response was well described by a sigmoid function.

**METHODS**

To parameterize eqn 1 we estimated mean densities and spatial variances and covariances for Saduria and Monoporia in the field. Stomach contents of Saduria and experimentally determined gut evacuations rates were used to estimate consumption rates at different Monoporia densities.

**Background data**

Benthic densities of Monoporia and Saduria are recorded as part of an environmental monitoring program in the Gulf of Bothnia, at 63°20’N, 20°20’E. Samples are taken at 11 stations within a 300 km² area in May–June each year. The depths at these stations vary between 46 and 129 m. A van Veen grab (0.1 m² area) is used to collect three replicate samples at each station. The samples are taken within a radius of approximately 30 m from the station, and the distances between stations are 2–7 km.

We used data for the period 1983–2005 to calculate mean prey densities at both the regional and local scales. The regional scale mean is the average density across all samples. Here each sample is a single observation. The local scale density refers to the local density experienced by a predator. In this case there is a single observation per predator: we assume that a sample (0.1 m²) provides a reasonable measure of the density experienced by a predator. Density data are also used to estimate the spatial variation at two scales: ‘between samples at individual stations’ and ‘between stations within regions’, henceforth referred to as the sample scale and the station scale.

**Estimating scale-dependent heterogeneity**

Because variances and covariances are scale dependent, it is critical that they are measured at an appropriate scale. The extent of the sampling program should match the extent of the population(s) of interest (Bergström et al. 2006). Finding the appropriate sampling resolution is more complicated and requires consideration of the resolution of the nonlinear process of interest. The resolution of a process is defined as the smallest scale of spatial variation of a driving variable that affects the outcome of the process (Englund & Cooper 2003; Bergström et al. 2006). Variation at scales smaller than the resolution scale is thus not ‘detected’ by the process. The inclusion of such small-scale variation will therefore distort predictions of the large-scale outcome of the process. For example, the variance effect on a satiating type II functional response is caused by a higher degree of predator satiation in patches with high prey density. Variance in prey density at scales that are small compared to the mobility of the predator will not matter, because similar prey densities will be experienced by hungry and satiated predators (see Bergström et al. 2006 for a detailed discussion of process resolution).

Given our experience of Saduria mobility and the distance between samples (< 30 m), it seems possible that the sample scale may be smaller than the resolution scale of this process and should, therefore, be excluded from our estimates of prey variance. To examine whether the resolution of our variance and covariance observations needs to be adjusted, we measure the effect of including or excluding the sample scale variance or covariance on the fit between observed consumption and the predicted regional scale functional response. To estimate the variance and covariance components associated with the sample scale and the station scale, we ran One-way ANOVAS and ANCOVAS for each year (Sokal & Rohlf 1995; Underwood 1997).

**Variance and covariance models**

Measured variances and covariances can be incorporated directly into eqn 1 to adjust the consumption observed in each year (e.g. Bergström et al. 2006). However, this approach is of limited value if the aim is to find a functional response that can be incorporated into a model of regional predator–prey dynamics. The reason is that variances and covariances are dynamic entities that are expected to vary with prey and predator densities (Taylor et al. 1980; Keeling et al. 2002). One solution is to express variances and covariances as functions of predator and prey densities. The spatial variance of a population can usually be modeled as a power function of its mean density (Taylor et al. 1980). Finding a model for the covariance is more challenging, since empirical studies of its density-dependence do not seem to be available. However, analyses of metapopulation models of enemy–victim systems (Keeling et al. 2002), and our previous analysis of the Saduria–Monoporia system (Bergström et al. 2006) suggest that covariances may be modeled as a function of both past and present densities.

**Analyses of stomach contents**

To obtain estimates of consumption rates in the field, we analyzed the stomach contents of Saduria collected as part of the monitoring program. A total of 263 individuals were selected from samples taken each year between 1983 and 2002, covering a wide range of Monoporia densities (0–15 000 ind. m⁻²). Individuals in the range 25–35 mm
were chosen to reflect the average size of Saduria in the area. All identifiable remains of prey found in the stomachs were measured. The overwhelming majority belonged to Monoporeia. For this species, eight different measures of legs, antenna and cerci were taken. The measurements were then translated to biomasses using length–mass regressions, based on 25 individuals ranging from 0.5 to 8 mg wet mass. The number of individuals in a single stomach was determined based on the size and number of the different body parts. Other taxa found in the stomachs were Copepoda, Ostracoda, and Mysidae spp. The biomasses of these taxa were negligible, with the exception of Mysidae in years when Monoporia densities were very low.

The van Veen samples were taken in triplicate and kept in tubs on board the boat until processed and preserved. We found that, at some stations, the Saduria in the last of the three samples had fuller stomachs than those in the two samples processed first. Since this may indicate that Saduria began to feed in the tubs after a lag phase, we only used data from the first two samples taken at each station.

**Gut evacuation experiments**

Translating stomach contents to ingested biomass requires a measure of gut evacuation rate, or a measure of the period during which a single prey individual can be recovered from the gut (e.g. the half-life of detection). Preliminary observations suggested that the digestive rate of Saduria varied with the long term average consumption rate. To quantify this effect, we kept Saduria (length 25–35 mm) for 23 days on four different feeding regimes: no food, 4 mg Monoporia every fourth day, 4 mg every day, and 8 mg every day. The Saduria were kept individually in 1 l containers at 4 °C, with clean sand as the bottom substrate. They were “hand fed” using a pair of tweezers. The temperature was chosen to match the May–June temperature at the sampling stations. The time between the last feeding event and the evacuation experiment was 24 h for the treatment given 8 mg/day, 48 h for 4 mg/day, and 96 h for 1 mg/day. For the evacuation experiment each Saduria (n = 80) was fed a single 3.5 mg Monoporia. After 3, 8, 10, 15 and 24 h, Saduria were killed and their gut contents examined. The time during which the prey could be recognized (half-life of detection) was estimated using logistic regression. Estimated half-life values (H) were then used to translate the biomass of Monoporia found in stomachs (S) to the amount consumed (C) in 24 h using

\[
C = 24 \times \frac{S}{H}. \tag{2}
\]

The half-life of detection (H) varied between 22.1 h for predators kept without food to 16.8 h for those acclimated to 8 mg of food per day (logistic regression, \(\chi^2 = 27.9, df = 2, P < 0.001\)). As the logistic model predicts a linear relationship between food level (C) and half-life of detection we could summarize the results using the equation

\[
H = 22.87 - 0.761 \times C. \tag{3}
\]

This equation was substituted into eqn 2 and used to calculate the yearly mean consumption per predator.

**RESULTS**

The functional response observed at a local scale in the field

The local functional response \(f(N)\) was estimated directly from the observed consumption in the field, i.e. consumption was expressed as a function of the local density estimated at the sample scale \((0.1 \text{ m}^2)\) (Fig. 1, error estimates in Appendix S1). A function of the form

\[
f(N) = aN^b/(1 + abN^b) \tag{3}
\]

was fitted to these data. Depending on the value of the exponent \(b\), this model can describe a satiating type II response \((b = 1)\) or sigmoid responses of different shapes \((b > 1)\). Since the values for mean consumption per year were based on varying numbers of guts \((n = 2–32)\), we weighted each yearly mean using \(N\). Our first model provided an estimate of handling time: \(h = 65.1 \pm 28.8\) (estimates of \(a\) and \(b\) not shown). This estimate could be validated using observations from the feeding experiment. Saduria receiving 8 mg food/day occasionally stopped feeding for a couple of days, suggesting that 8 mg/day is close to the maximum feeding rate than can be sustained for

![Figure 1](https://example.com/image.png)

Figure 1 Observed and modeled local consumption by Saduria preying on Monoporia. Observations are yearly mean values for the period 1983–2002. The x-axis is the mean density experienced by predators measured at the scale of a sample \((0.1 \text{ m}^2)\). The solid line is a functional response model of the form \(f(N) = aN^b/(1 + abN^b)\) fitted to the data. The dotted line is the model estimated by Aljetlawi et al. (2004) from laboratory experiments.
The sample scale.

The small sample correction, AICc, proposed by Hurvich & Tsai (1989) was used.

\[ G(\text{field}) = aN_{\text{field}}^b/(1 + abN_{\text{field}}^b) \]

\[ G(\text{lab}) = aN_{\text{lab}}^b/(1 + abN_{\text{lab}}^b) \]

Region models

\[ G(\text{reg}) = aN_{\text{reg}}^b/(1 + abN_{\text{reg}}^b) \]

\[ G(\text{reg}) = aN_{\text{reg}}^b/(1 + abN_{\text{reg}}^b) \]

\[ G(\text{field}) = f_{\text{field}}(N_{\text{field}}) + MA \]

\[ G(\text{lab}) = f_{\text{lab}}(N_{\text{lab}}) + MA \]

The small sample correction, AICc, proposed by Hurvich & Tsai (1989) was used. M.A in models 6 and 7 denotes the variance and covariance effects calculated using moment approximation. \( N_{\text{reg}} \) is Monoporeia density estimated on the regional scale and \( N_{\text{loc}} \) is the density observed at the sample scale. \( f_{\text{field}} \) and \( f_{\text{lab}} \) denote functions estimated from field and laboratory data, respectively.

Comparison of the local scale functional response and the laboratory-estimated response

A comparison between the functional response model estimated by Aljetlawi et al. (2004) from laboratory experiments (dotted line in Fig. 1) and consumption rates observed in the field, demonstrates that the laboratory model performs poorly at high prey densities. This reflects the fact that the handling time estimated by Aljetlawi et al. was low. Based on AICc values, the support for this model (model 2 in Table 1) was substantially lower than for the local scale model (model 1 in Table 1).

Estimating variance and covariance models

Quantifying the two remaining terms on the right side of eqn 1 requires estimates of variances and covariances. Since these are dynamic entities, we searched for empirical models that can be used to express them as functions of the regional mean densities for the period 1983–2005. The total spatial variance in prey density, including variance at the sample and station scales, was estimated by a one-way ANOVA for each year and subsequently fitted to a power model (\( \sigma_N^2 = 1.10N_t^{1.57}; \ r^2 = 0.96, P < 0.001, \) Fig. 2a). Corresponding covariances were estimated with one-way ANCOVAs and modelled as a function of prey biomass at times \( t \) and \( t-1 \), and predator biomass at \( t \) (\( \sigma_{NP} = -3.41N_t + 3.45N_{t-1} - 3.11P_t; \ r^2 = 0.76, P < 0.01 \) for all parameters, Fig. 2b). Details of the model selection are presented in Appendix S2. The delayed density-dependence in the covariance model reflects the fact that the covariance is different depending on whether the prey densities are increasing or decreasing. As shown in Fig 2b, the covariance tends to be slightly positive for decreasing prey densities and strongly negative for increasing prey densities.

Comparing the predicted regional functional response with observed consumption

One consequence of the relationship between covariance and the change in prey density is that the predicted regional response, \( G(N) \), is different for increasing and decreasing prey densities. The oscillatory dynamics of this system suggest that we can classify the different years as being either in the increasing phase or the decreasing phase. To generate predictions for the two phases, we assumed that the change in prey density from one year to the next corresponded to the observed average prey population growth rate within each phase (\( \bar{r} = 0.3 \) and \(-0.8\), respectively) and that predator density was equal to the regional mean (\( P = 12.7 \text{ g m}^{-2} \)). The effect of relaxing these assumptions is investigated below. Figure 3a shows the resulting prediction for the regional functional response,
three predictor variables ($N_t$, $N_{t-1}$, $P_t$), between densities of predators and prey ($Saduria$ and $Monoporia$). The model best describing the covariance–density relationship included three predictor variables ($N_x$, $N_{x-1}$, $P$). To illustrate this somewhat complicated relationship, we used the model to standardize the covariances to a predator density of 10 g/m² and plotted the standardized covariance against the difference in prey density in consecutive years. The lines are derived from the fitted models.

To test whether the large-scale functional response is different for the increasing and decreasing phases, we compared a model that allowed the attack rate ($a$) and the exponent ($b$) to be different for the two phases (solid lines in Fig. 3b) with a model that assumed a single response, i.e. that the parameters were unaffected by changes in prey density. The phase dependent model exhibited a better fit and lower AICc values than the model with a single response (models 4 and 5 in Table 1). A $\Delta$AICc value exceeding 10 indicates that there is essentially no support for the model with a single response (Burnham & Anderson 2002). To confirm that it is the covariance dynamics that generate phase dependence, we also fitted the two types of models to the data at the local scale. As expected, we found that a single response model was more strongly supported by the data than a phase dependent model (models 1 and 3, Table 1).

Figure 3a also shows that the quantitative fit of the prediction based on the local scale functional response and moment approximation was quite good. According to the AICc values, this model was more strongly supported by the data than the other models investigated (model 6, Table 1). A regional model, based on the laboratory-estimated response and the moment approximation, had substantially lower support (compare models 6 and 7 in Table 1).

To test the hypothesis that the resolution of our variance and covariance estimates did not match the resolution of the processes causing nonlinearity, we examined how exclusion of either the variance or the covariance at the sample scale affected the fit between observed regional consumption and predictions based on the local functional response model and moment approximation (i.e. model 6 in Table 1). If the variance and covariance at the sample scale are irrelevant, we expect that excluding this heterogeneity would enhance the fit between the model and the data. However, both manipulations caused small reductions in the fit (variance: $\Delta$AIC = 0.01, covariance: $\Delta$AIC = 0.03), suggesting that there was no mismatch between process and sampling resolution.

The regional functional response predicted by a predator–prey model

The assumption that predator densities and prey growth rates are constant within each phase is problematic because both are expected to vary within phases. To examine the effect of relaxing these assumptions, we incorporated the estimated local functional response into a dynamic predator–prey model. We used the model developed by Bergström et al. (2006) and refer to their paper for the derivation and a discussion of simplifying assumptions. The model for a small-scale system has the form:

$$\frac{dN}{dt} = g(N) - f(N)P$$

$$\frac{dP}{dt} = qf(N)P - dP$$

where $N$ and $P$ are the densities of the prey and the predator, respectively, measured as biomass/unit area, $g(N)$ is the prey growth function, $f(N)$ is the functional response of the predator, and $d$ and $q$ are, respectively, the death rate and conversion efficiency of the predator. Specifically, we assume that prey growth is logistic, $g(N) = rN(1-N/K)$, where $r$ and $K$ are relative growth rate and carrying capacity, and that the functional response for $Monoporia$ is given by eqn 3. A simplifying assumption made here, but not in Bergström et al., is that predators do not feed on alternative prey.

A model for a large-scale, heterogeneous system, is obtained through moment expansion of the basic model (see Bergström et al. (2006) and Melbourne & Chesson (2006) for details of moment methods). A second order approximation yields:
We used the functional response parameters estimated in this study; the other parameters were taken from Bergström et al. (2006) \( (r = 0.003 \text{ day}^{-1}, K = 59.7 \text{ g m}^{-2}, q = 0.7, d = 0.0027 \text{ day}^{-1}) \). The consumption pattern predicted by the model is shown in Fig. 3c. The difference between the increasing and decreasing phases is now larger than was predicted for fixed predator densities and prey growth rates in each phase (compare Fig. 3a and c).

**DISCUSSION**

Our empirical test of the scale transition framework showed that both qualitative and quantitative effects of heterogeneity could be successfully predicted. Using this framework we predicted that the regional functional response for *Saduria* should be phase dependent, i.e. different for increasing and decreasing prey densities. Field data on consumption rates agreed with this prediction and we found stronger quantitative support for the predicted functional response than for any of the other models investigated. Phase dependent functional responses have been observed in dynamic population models. The moment closure models of host–parasitoid dynamics analyzed by Keeling et al. (2002) and the individual-based predator–prey model analyzed by Donalson & Nisbet (1999) (e.g. their Fig. 12b) are two such examples. However, direct empirical observations of this phenomenon have, to our best knowledge, not been presented before.

The phase dependence of the functional response is a consequence of the covariance dynamics: increasing prey densities coincide with negative covariances and, thus, with a low consumption rate per predator. The converse pattern is observed for decreasing prey densities. Thus, it is important to consider what mechanisms generate this type of covariance dynamics. As a preliminary hypothesis, we suggest the following. Predators aggregate in patches with high prey densities during phases with high and decreasing prey densities; this leads to a positive covariance. These prey patches are then depleted as a result of local predator growth and local consumption of prey, leading to a negative covariance. The negative covariance persists long enough to allow prey density to increase to high levels in some patches. Evaluation of this hypothesis, and the formulation...
of more precise ones, requires analyses of spatially explicit models, in particular the relationship between covariance dynamics and the movement rules used by predators and prey. Previous behavioral studies suggest that Saduria can induce long range dispersal but reduce small-scale foraging activity of Monoporia (Sparrevik & Leonardsson 1995), which suggests that such movement rules can be quite complex.

It has been noted that knowledge of the shape of functional responses in natural systems is poor (Abrams & Ginzburg 2000) and we suspect that this paucity of data is because collection of such data is fraught with difficulties, some of which are apparent from our data. One approach, that can be used when estimating functional responses in the field, is to collect large-scale data and fit a small-scale model to this data (Rastetter et al. 1992). The resulting parameter values differ from the true values but may serve as reasonable approximations. A theoretical example where such an approximation works well is provided by Pascaul et al. (2002). However, in situations where the description of the large-scale functional response requires a different model structure, as is the case for the Saduria–Monoporia system, this approach is unlikely to be useful. In this situation it is crucial that an appropriate model structure can be identified. The scale transition framework was instrumental in identifying an appropriate large-scale model in this study, but if the empirical data are not too noisy, it may be possible to infer an appropriate model structure directly from field data. A second source of model misspecification is feeding on alternative resources. Our study also generated data on the functional response of Saduria feeding on mysids. This response was found to be a function of Monoporia density, rather than of mysid densities (G. Englund, unpublished data).

A second approach is to base predictions on laboratory-estimated functions. Our field data and the laboratory data presented by Aljetlawi et al. (2004) demonstrate that this approach can also be problematic. Aljetlawi et al. re-scaled observed attack rates using a parameterized population model and found that the laboratory-estimated rate was 20 times higher than could possibly be sustained in the field. High initial movement rates and aggregation along the walls of the experimental containers (Bergström & Englund 2002, 2004) are a plausible explanations for this bias. A comparison of the consumption rate predicted by the re-scaled model and our observations based on stomach data, shows that consumption was of the correct magnitude for low and intermediate prey densities, but much too high for high prey densities. This reflects the fact that the laboratory-estimated handling time, which was not re-scaled in Aljetlawi et al. (2004), was much higher than observed in the present study. One possible explanation for the short handling time observed by Aljetlawi et al. (2004) is that the experiments measured short term consumption (24 h) by starved predators; such measures are likely to reflect limitations caused by handling the prey rather than digestion (Jeschke et al. 2002). Surplus kills and partial prey consumption in the experiments, may also have contributed to this result.

In light of these results, it seems that estimating functional response data from local data is the best approach. Ideally, consumption should be quantified by direct observations (e.g. Norris & Johnstone 1998). However, inferring consumption from stomach analyses seems to be a viable alternative in systems where the gut evacuation process can be modeled accurately (Rindorf & Gislason 2005).

A functional response estimated from local data can be adjusted so that it describes consumption as a function of regional mean densities. This can be achieved using the approximate moment method applied here or, as demonstrated in Nachman (2006b), by deriving exact solutions. In the latter study, the covariance between predator and prey densities was modeled as a fixed aggregative response of predators to prey densities. This means that phase dependent covariance dynamics, which were observed in our study, could not be accounted for. We think that this is an important limitation because phase dependent covariance dynamics may be a common feature of oscillating systems. One example is so-called ‘hide and seek’ dynamics, where patches go through a cycle of local prey growth, followed by predator colonization, prey depletion, and predator extinction (Holyoak & Lawler 1996; Lei & Hanski 1997; Nachman 2001). Under such a cycle there should be alternating negative and positive covariances.

We conclude from this study that the scale transition framework is a powerful tool for scaling-up and for increasing our understanding of the widely recognized, but little understood, effects of spatial heterogeneity on predator-prey dynamics. More specifically, this study provides empirical evidence that large scale functional responses can be phase dependent in systems with oscillatory dynamics.

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REFERENCES


**SUPPLEMENTARY MATERIAL**

The following supplementary material is available for this article:

**Appendix S1** Summary statistics for functional response data.

**Appendix S2** Empirical variance and covariance models.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01159.x.

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