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Long-term variation of link strength in a simple benthic food web

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Summary

1. The predatory isopod *Saduria entomon* (L.) and its amphipod prey *Monoporeia affinis* (Lindström) are key components of the food web in the northern Baltic Sea, together representing 80–90% of the macrobenthic biomass. We use 20 years of stomach content data for *Saduria* to investigate how diet dynamics affect the stability of the interaction between *Saduria* and *Monoporeia*.

2. Consumption of the main prey, *Monoporeia*, fitted a type III functional response. Consumption rates of the most important alternative prey, mysids, were found to be unrelated to mysid densities but negatively related to the density of *Monoporeia*. The fit of consumption data to a model that assumes passive prey selection was poor. Thus we conclude that some form of active choice is involved.

3. The effect of consumption of mysids, the alternative prey, on the stability of this system was investigated using a 'one predator–two prey' model with stochastic environmental variation. Analysis of the model suggests that feeding on mysids leads to a decreased extinction risk for the predator, *Saduria*, and reduced density oscillations for both *Saduria* and its main prey, *Monoporeia*.

Key-words: complexity, flexible feeding, optimal diet choice, stability, switching

Introduction

Empirical observations indicate that the structural properties of food webs, such as connectance, species richness and the strength of links, vary over time (Winemiller 1990; Schoenly & Cohen 1991; Scheuerell *et al*. 2005). This variation can be caused by adaptive behaviours of both predators and prey. Predators may alter their diet in response to changes in prey densities, and prey may change antipredator strategies in response to changes in the densities of predators (Stephens & Krebs 1986; Sih, Englund & Wooster 1998). Behavioural responses can be rapid (Stephens & Krebs 1986), but their expression may require a longer time if learning (Hughes & Croy 1993), plastic morphological changes (Olsson, Svanbäck & Eklöv 2007) or evolutionary changes are involved (Joshi & Thompson 1997). The term 'adaptive links' has been used to describe interactions that vary in strength due to this kind of adaptive behaviour (Kondoh 2003).

A well known optimal foraging model predicts that predators should specialize on the most rewarding prey until the density of this prey falls below a threshold level (Charnov 1976; Stephens *et al*. 1986). Below this threshold density, predators should include alternative prey in the diet, assuming that different prey can be searched simultaneously. This behaviour is often referred to as adaptive, or optimal, diet choice. If a trade-off prevents predators from feeding efficiently on more than one prey type, for example by spatial separation of prey types, the optimal strategy for a forager is to switch to the most profitable prey. This behaviour may lead to an ideal free distribution of foraging efforts (Milinski & Parker 1991; Krivan 1997).

Studies of short-term behavioural responses often report the expected patterns, although responses are frequently not as well defined as predicted (Stephens *et al*. 1986), and pronounced deviations from adaptive diet choice are observed for evasive prey (Sih & Christensen 2001). Mathematical analyses of density dynamics in systems with a single predator species and two prey species show that optimal diet choice and switching behaviours often increase the probability of a stable equilibrium or reduce the amplitude of oscillations, when compared with a system containing an indiscriminate generalist predator (Krivan 1996, 1997; Abrams 1999; van Baalen *et al*. 2001). Such studies have also identified factors that influence the stabilizing effect of adaptive foraging, for example whether behavioural adjustments are instantaneous or delayed (Abrams 1999; Kondoh 2003), whether density responses are sharp or gradual (van Baalen *et al*. 2001), and whether or not trade-offs prevent simultaneous searching for two prey species (van Baalen *et al*. 2001).

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Analyses of more complex food web configurations confirm this general pattern (Pelletier 2000; Kondoh 2003, 2006). Such analyses also demonstrate that switching can lead to a positive relationship between stability and food web complexity. This result offers a potential solution to the apparent contradiction between the complexity of natural food webs and mathematical models predicting that food web stability will decrease with increasing complexity (May 1973; Yodzis 1981; McCann, Hastings & Huxel 1998; but see DeAngelis 1975). Critical assumptions required to produce a positive stability–complexity relationship include rapid diet adjustments and a large proportion of the trophic links being adaptive (Kondoh 2003, 2006).

Food web links can also be dynamic as a result of adaptive adjustment of prey defences (Sih *et al.* 1998; Eklöv & Jonsson 2007). Theoretical analyses suggest that induced defences that are specific to particular predator species stabilize interactions in a wide variety of food web configurations, but positive stability–complexity relationships are predicted only for food webs of low complexity (Matsuda, Hori & Abrams 1994, 1996; Kondoh 2007).

Although empirical research on switching and optimal diet choice is extensive, it seems that field data are scarce or lacking for aspects that have been identified as critical for food web dynamics. These aspects include the rate of behavioural adjustments (Abrams 1999; Kondoh 2003), the proportion of food web links that are adaptive (Kondoh 2003, 2006), and the extent to which diet dynamics are caused by predator or prey behaviour (Matsuda *et al.* 1994, 1996; Abrams 1999; Kondoh 2003, 2007).

In this paper we present empirical data on these aspects for a simple benthic food web in the northern Baltic Sea. This food web is dominated by the isopod *Saduria entomon* (L.) feeding on crustacean prey. Temporal variation is investigated using 20 years of diet data for this predator. Diet data are also used to parameterize a 'one predator–two prey' model that is used to examine the effect of diet dynamics on the stability of the system.

Methods

STUDY SYSTEM AND BACKGROUND DATA

The predatory isopod *Saduria entomon* is found in areas with soft bottom sediments throughout the Baltic Sea (Haahtela 1990; Leonardsson 1991a). Its main prey in the northern Baltic Sea is the amphipod *Monoporeia affinis* (Lindström), but its diet may also include other macro- and meiobenthos, dead fish and conspecifics (Sparrevik & Leonardsson 1998; Bergström & Englund 2002). *Monoporeia* is a deposit-feeder (Lopez & Elmgren 1989) and can be very abundant, with densities frequently reaching 10 000 individuals m^{-2} (Leonardsson 1991b). In the low-salinity, northern part of the Baltic Sea, the Gulf of Bothnia, the benthic community is dominated by *Saduria* and *Monoporeia* at depths >40–50 m. As other predators of these species, such as benthivorous fish, are scarce at these depths (Leonardsson 1991b), it is believed that *Saduria* and *Monoporeia* make up a tightly coupled predator–prey system (Aljetlawi, Sparrevik & Leonardsson 2004; Bergström, Englund & Leonardsson 2006), which exhibits oscillatory density dynamics, cycling over a period of 6–8 years (Andersin *et al.* 1978; Leonardsson, Laine & Andersin 2002). Mysid shrimps are the most important alternative prey for *Saduria* in the study area. Mysids are pelagic predators that sometimes feed near the bottom (Zouhiri *et al.* 1998). Mysids can reduce the densities of benthic copepods, but there seems to be little direct interaction with *Monoporeia* (Albertsson 2004).

In Fig. 1 we outline the web of interactions within which *Saduria* and its prey are embedded. The combined biomass of the dominant predator, *Saduria*, and its main prey, *Monoporeia*, is on average 83·1% of the total benthic biomass, emphasizing the importance of the links to theses species. A notable uncertainty concerns the importance of benthivorous fish, especially the four-horned sculpin (*Myoxocephalus quadricornis*), that may feed on *Saduria* (Leonardsson 1991b). During the late 1990s, the alien polychaet *Marenzelleria* sp. colonized the area but its densities were negligible during the time period of interest for the current analysis. Cod was present during the first 5 years of the time-series, as a consequence of offspring dispersal from a huge recruitment during late 1970s in the Baltic proper.

The density dynamics of this food web have been studied in an environmental monitoring programme in the Gulf of Bothnia, at 63°20′ N, 20°20′ E. Samples were taken at 11 stations within a 300-km^2

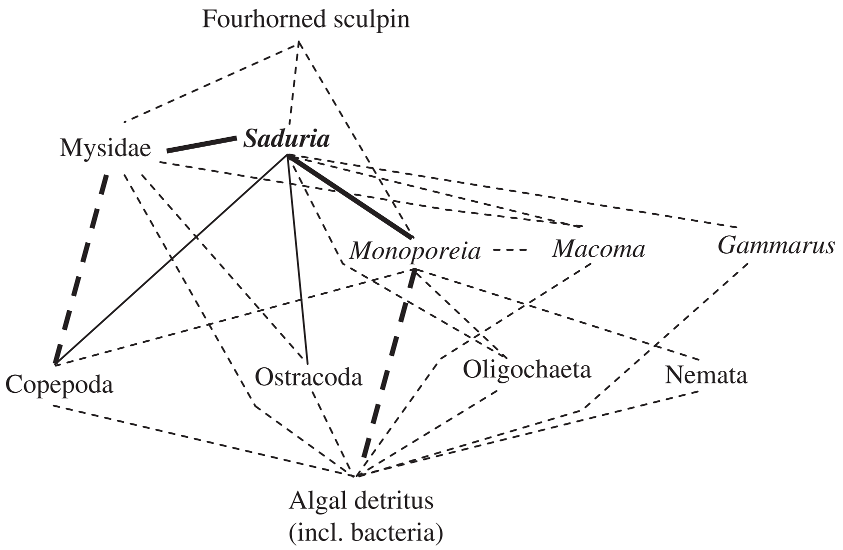

Fig. 1. The benthic food web in deep areas of the northern Baltic. Thin lines, links expected to be weak due to low densities; thick lines, strong links between abundant species; solid lines, links documented in this study; dashed lines, links observed in other studies (Albertsson & Leonardsson 1991; Leonardsson 1991a; Albertsson 2004).

area in late May or early June each year during the period 1983–2002. The depth at these stations is 46–129 m. A van Veen grab (0·1 m^2 area) was used to collect three replicate samples at each station. The distance between samples was 1–30 m, and the distance between nearby stations was 2–7 km. The programme produced density estimates for macrobenthic organisms such as *Saduria*, *Monoporeia* and mysids, but not for smaller organisms such as copepods and ostracods.

Two types of mean prey density were calculated: regional mean density and local mean density. The regional mean density is simply the average prey density across all samples. The local mean density is the mean of the densities experienced by the predators, assuming that a sample (0·1 m^2) provides a reasonable measure of the density experienced by a predator. Specifically, the local mean is a predator-weighted average of prey density:

$$\bar{N}_{\text{local}} = \frac{1}{k}\sum_{i=1}^{k} N_i P_i / \sum_{i=1}^{k} P_i$$

where N_i and P_i denote the density of prey and predators, respectively, in each of k samples.

ANALYSES OF STOMACH CONTENTS

To obtain estimates of consumption rates for *Saduria* in the field, we analysed the stomach contents of individuals collected during the monitoring programme. A total of 263 individuals in the size range 25–35 mm were used, and the individuals were taken from samples that covered a wide range of *Monoporeia* densities (0–15 000 m^{-2}), during the period 1983–2002. Identifiable remains of prey exoskeletons were recovered and measured. The overwhelming majority of the remains were from *Monoporeia*. Other taxa found in the stomachs were Copepoda, Ostracoda and mysids. One limitation of our method is that soft-bodied prey are less likely to be detected than those with a hard exoskeleton. Thus it is possible that feeding on dead fish, *Marenzelleria sp.*, and cannibalism on newly moulted individuals remained undetected.

The van Veen samples taken at a station were stored temporarily in tubs placed on deck until they could be processed and preserved. The *Saduria* in the last of the three samples processed had more stomach contents than in the first two samples at some stations. This may indicate that *Saduria* started to feed in the tubs after a lag phase, therefore only data from the first two samples were used.

Numbers were converted to biomass using measurements of body length or other body parts and length–mass regressions. The remains of mysids were often fragmented to such an extent that the biomass could not be determined from length–mass regressions. Thus the mean size of mysids in the benthos was used when converting numbers into biomass. Translating stomach contents into ingestion rates requires an estimate of the half-life of detection: the time during which an ingested prey could be recovered from the stomach contents. *Saduria* ($N = 36$) were kept individually for 20 days in 1-l containers at 4 °C, with clean sand as the bottom substrate. They were fed 4 mg *Monoporeia* or mysids every fourth day to allow them to adjust to the feeding regime experienced in most years when *Saduria* were feeding on mysids. The temperature was chosen to match the May–June temperature at the sampling stations. At the end of the feeding period, each *Saduria* was fed a mysid weighting 4 ± 0·5 or 9 ± 0·5 mg. After 5, 10·5, 15, 20, 25 and 30 h, the predators were killed and the gut contents examined. Logistic regression showed that there was a significant relationship between detection rate and time ($t = -2{\cdot}70$, $P < 0{\cdot}01$), but not prey size ($t = 1{\cdot}28$, NS). Thus we used a model with time as the single predictor and calculated the half-life of detection (H) as the time at which there is 50% probability of detecting a prey. The estimated value ($H = 21{\cdot}3$ h, SE = 2·0) was then used to translate the biomass of mysids found in stomachs (S) to the amount consumed (E) in 24 h using $E = 24 \times S/H$. In a previous experiment, where *Monoporeia* was used as prey, it was found that the half-life of detection varied with the long-term average food intake according to $H = 22{\cdot}87 - 0{\cdot}761E$ (Englund & Leonardsson 2008). This relationship was used to adjust the estimated consumption of mysids for each year, using the average feeding rate for that year as a measure of E.

MODELLING THE CONSUMPTION OF MONOPOREIA AND MYSIDS

Diet variation can be a direct result of changes in the relative densities of prey, or it can reflect behavioural decisions. As a null model for the consumption of *Monoporeia* and mysids by *Saduria*, we used a two-species functional response model that did not involve active behavioural choice:

$$E_{\text{mo}} = \frac{a_{\text{mo}} N_{\text{mo}}^{\beta}}{1 + h(a_{\text{mo}} N_{\text{mo}}^{\beta} + a_{\text{my}} N_{\text{my}}^{\alpha})} \qquad \text{eqn 1}$$

$$E_{\text{my}} = \frac{a_{\text{my}} N_{\text{my}}^{\alpha}}{1 + h(a_{\text{mo}} N_{\text{mo}}^{\beta} + a_{\text{my}} N_{\text{my}}^{\alpha})} \qquad \text{eqn 2}$$

where E_{mo} and E_{my} are the consumption of *Monoporeia* and mysids expressed as biomass, a_{mo} and a_{my} are attack rates, h is handling time, and β and α are parameters that control the shape of the response. The exponent of N_{mo} was set to $\beta = 2$ in agreement with Aljetlawi *et al.* (2004), who found that *Saduria* have a type III functional response when feeding on *Monoporeia* in aquarium experiments. The corresponding exponent for mysid density (α) was fitted to the data as no prior information was available. Note also that we assume the mass specific handling time (h) is equal for the two prey species. We fitted this model to data on consumption and local densities of the two species by minimizing sums of square, and weighting the residuals with the number of stomachs studied each year. Because the two models share parameters, we fitted them simultaneously by minimizing the total sums of square, scaling the residuals to give the two prey species approximately equal weight, and using the restriction all parameters >0.

We also used an exponential model, $be^{-cN_{\text{mo}}}$, to describe the consumption of mysids. b and c are fitted parameters. This model was chosen to match the observed field patterns (see Results). To describe the combined consumption of the two prey, the following models were fitted to data using the procedure described above.

$$E_{\text{mo}} = \frac{aN_{\text{mo}}^{\beta}}{1 + h(aN_{\text{mo}}^{\beta} + f)} \qquad \text{eqn 3}$$

$$E_{\text{my}} = be^{-cN_{\text{mo}}} \qquad \text{eqn 4}$$

The parameter f denotes the encounter rate of *Saduria* with mysids. It was found by solving the equation:

$$be^{-cN_{\text{mo}}} = f/(1 + h(aN_{\text{mo}} + f)).$$

Estimated parameters are presented with bootstrapped standard errors (Manly 1997).

A MODEL OF THE *SADURIA–MONOPOREIA* SYSTEM

A dynamic model developed by Bergström *et al.* (2006) was used to investigate how feeding on alternative prey affects the stability of the interaction between *Saduria* and *Monoporeia*. We used this model because it has been shown to reproduce important aspects of the dynamics of the system, such as the 6–8-year cycles observed in the field. The model describes the dynamics of regional mean densities, but uses moment approximation to account for the effects of spatial variances and covariances of predator and prey densities. Only a brief description of the model is given here, as a detailed derivation and tests of many of its assumptions are provided in a previous paper (Bergström *et al.* 2006). The basic model for a well mixed system has the form:

$$\frac{dN_{\mathrm{mo}}}{dt} = g(N_{\mathrm{mo}}) - f(N_{\mathrm{mo}}, N_{\mathrm{my}})P \qquad \text{eqn 5}$$

$$\frac{dP}{dt} = qP[f(N_{\mathrm{mo}}, N_{\mathrm{my}}) + v(N_{\mathrm{mo}}, N_{\mathrm{my}})] - dP \qquad \text{eqn 6}$$

where N and P are the densities of the prey, *Monoporeia*, and the predator, *Saduria*, measured as biomass per unit area, $g(N_{\mathrm{mo}})$ is the growth function for *Monoporeia*, $f(N_{\mathrm{mo}}, N_{\mathrm{my}})$ and $v(N_{\mathrm{mo}}, N_{\mathrm{my}})$ are the functional responses of *Saduria* feeding on *Monoporeia* and mysids, respectively, and d and q are the death rate and conversion efficiency of *Saduria*. 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 responses for *Monoporeia* and mysids are given either by equations 2 and 3 or by equations 3 and 4. Below we show that consumption rates are independent of mysid densities. N_{my} can therefore be treated as a constant.

A model for a system that is not well mixed is obtained through moment expansion of the basic model (for details of moment methods see Bergström *et al.* 2006; Melbourne & Chesson 2006). A second-order approximation yields:

$$\frac{d\bar{N}}{dt} = g(\bar{N}) - f(\bar{N})\bar{P} + g''(\bar{N})\sigma_N^2/2 - f''(\bar{N})\bar{P}\sigma_N^2/2 - f'(\bar{N})\sigma_{N,P} \qquad \text{eqn 7}$$

$$\frac{d\bar{P}}{dt} = q[f(\bar{N})\bar{P} + f''(\bar{N})\bar{P}\sigma_N^2/2 + f'(\bar{N})\sigma_{N,P}] + q[v(\bar{N}) + v''(\bar{N})\bar{P}\sigma_N^2/2 + v'(\bar{N})\sigma_{N,P}] - d\bar{P} \qquad \text{eqn 8}$$

This model describes the dynamics of regional mean densities based on functions estimated in well mixed systems and moment terms that incorporate the effects of variances and covariances of predator and prey densities on nonlinear submodels.

The variance in prey density σ_N^2 and the covariance between predator and prey densities $\sigma_{N,P}$ were estimated from field data presented by Englund & Leonardsson (2008). The variance in prey density was well described by a power model $\sigma_N^2 = zN_t^{\lambda}$ where $z = 1{\cdot}10$ (SE = 0·62) and $\lambda = 1{\cdot}57$ (SE = 0·05) ($r^2 = 0{\cdot}96$). The covariance was modelled as a function of predator biomass at time t, and prey biomass at time t and $t - 1$, $\sigma_{n,P} = uN_t + vN_{t-1} + xP_t$, where $u = -3{\cdot}41$ (SE = 1·11), $v = 3{\cdot}45$ (SE = 1·35), and $x = -3{\cdot}11$ (SE = 1·24) ($r^2 = 0{\cdot}76$). The parameters r, K, f, d and h were taken from Bergström *et al.* (2006); Englund & Leonardsson (2008): $r = 0{\cdot}003$ day^{-1}, $K = 59{\cdot}7$ g m^{-2}, $f = 0{\cdot}7$, $d = 0{\cdot}0035$ day^{-1}, $h = 60$ days, and the feeding parameters a, b, α and c were estimated in this study as described above.

Results

TEMPORAL VARIATION IN FEEDING RATES

The diet of *Saduria* was dominated by *Monoporeia* in most years (Fig. 2). Mysids were mainly eaten in years with a low density of *Monoporeia*. Copepods and ostracods comprised a negligible fraction of the diet, but it should be noted that copepods were eaten mainly in years with low densities of *Monoporeia* (Fig. 2).

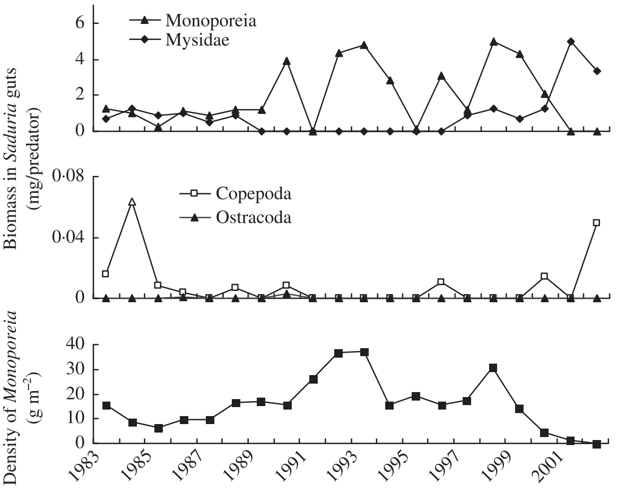

Fig. 2. Local mean densities of *Monoporeia* and diet of the predatory isopod *Saduria* in the period 1983–2002, as determined by analyses of stomach contents.

The temporal variation in consumption of mysids did not reflect changes in the densities experienced by the predator (the local mean density of mysids). Rather than the expected positive relationship (e.g. a type II or III functional response), a non-significant negative correlation was found (Fig. 3a, Spearman's rank correlation, $r_s = -0{\cdot}32$, $N = 20$, NS). To test the alternative hypothesis, that consumption of mysids was driven by the density of the preferred prey, we plotted consumption of mysids against the local mean density of *Monoporeia* (Fig. 3b). A significant negative relationship was found ($r_s = -0{\cdot}61$, $N = 20$, $P < 0{\cdot}005$), supporting this alternative hypothesis.

The passive choice model (equations 1 and 2) was fitted to data on the consumption rates for the two prey species (Table 1). The estimated exponent for mysid density was $\alpha = 0$, which suggests that the consumption of mysids was not related to mysid density. The model provided a reasonable description of consumption of mysids at high densities of *Monoporeia* (Fig. 4), but did not account for the high consumption at low densities of *Monoporeia*. The alternative phenomenological model (equations 3 and 4) was more strongly supported by the data, based on Akaike's information criterion (AIC) (Fig. 4; Table 1).

The abundance of copepods in *Saduria* stomachs was significantly correlated with the benthic density of *Monoporeia*, whereas the corresponding relationship for the abundance of copepods was not significant ($r_s = -0{\cdot}57$, $N = 20$, $P < 0{\cdot}005$, $r_s = -0{\cdot}08$, $N = 20$, NS, respectively, Fig. 3c,d). The functional responses of these species could not be investigated as data on their densities in the field were not available.

Changes in link strength could also be caused by prey adjusting their antipredator behaviour in response to high

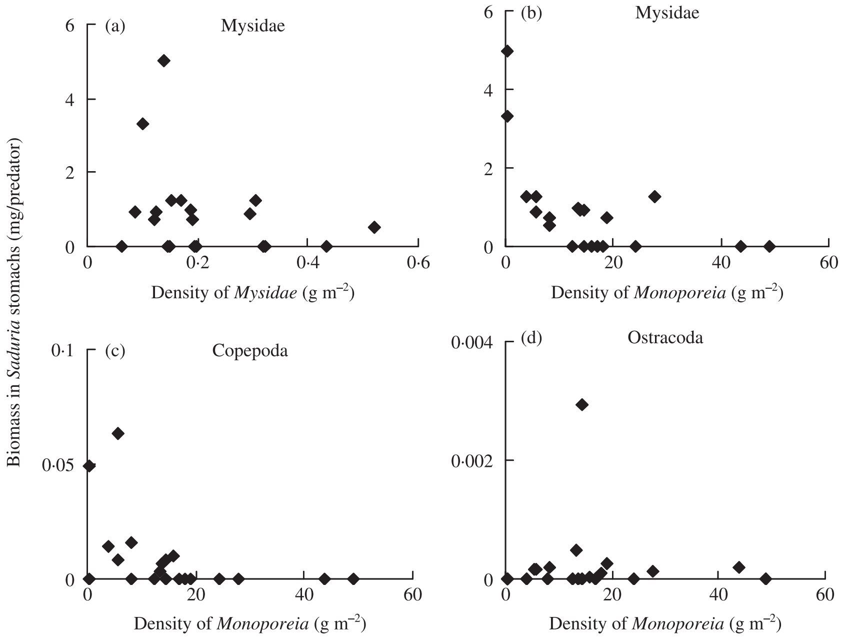

Fig. 3. Relationships between the biomass of mysids in *Saduria* stomachs and (a) local mean density of mysids in the field; (b) local mean density of the main prey *Monoporeia*. (c,d) Relationships between consumption of copepods and ostracods, respectively, and density of *Monoporeia*.

Table 1. Parameter estimates and values of Akaike's information criterion (AIC$_c$) for models used to describe the consumption of Mysids and *Monoporeia* by the predator *Saduria*

Parameter	Passive choice model	Exponential model
a_{mo}	$4{\cdot}76 \times 10^{-5}$ ($1{\cdot}38 \times 10^{-5}$)	$4{\cdot}00 \times 10^{-5}$ ($1{\cdot}1 \times 10^{-5}$)
b		0·0091 (0·0039)
c		0·21 (0·091)
α	0·0 (0·2)	
a_{my}	0·0028 (0·00064)	
AIC$_c$	–340·0	–346·9
Model likelihood	0·03†	1

†Model likelihood = 0·11 if α is treated as a fixed parameter set to zero.

Standard errors are given in parentheses. The passive choice model is specified by equations 1 and 2 in the text, and the exponential model by equations 3 and 4.

predation risk (a defence switch). Assuming that predator density could be used as a proxy for predation risk, we would expect a negative relationship between predator density and consumption per predator. However, no significant relationship was found for the prey taxa that have adaptive links to *Saduria* (*Monoporeia* $r_s = -0{\cdot}08$, $N = 20$, NS; mysids $r_s = -0{\cdot}33$, NS; copepods $r_s = 0{\cdot}24$, NS).

To investigate the temporal scale of adaptation, we calculated cross-correlations between lagged densities of *Monoporeia* (N_t, N_{t-1}, etc.) and prey biomasses in *Saduria* stomachs. Significant negative relationships were found between biomass in the diet and N_{t-1} for mysids but not for copepods (Fig. 5). Longer lag times produced non-significant or significant positive correlations. For a more detailed analysis, we fitted the model

$$E_{mys} = ae^{bN_t + cN_{t-1}}$$

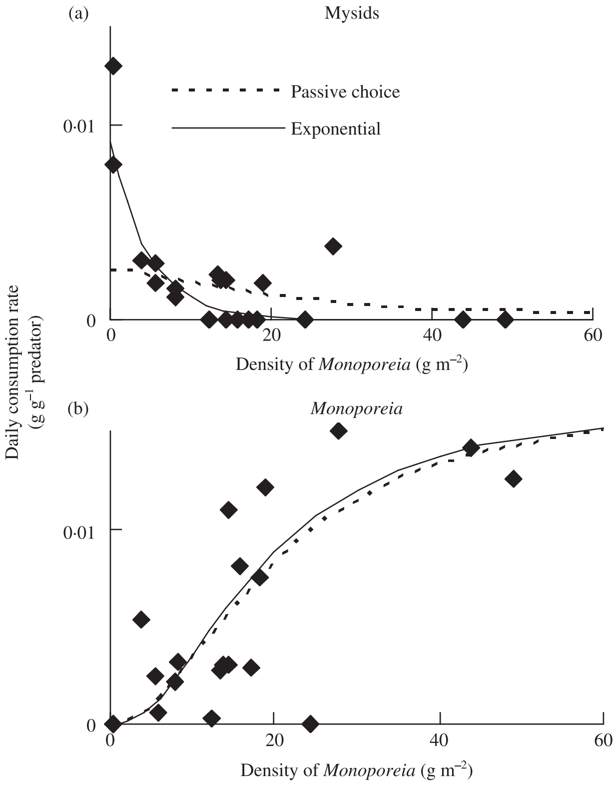

Fig. 4. Daily consumption rate by *Saduria* of (a) mysids; (b) *Monoporeia* in the field. Dotted line, best fit for a passive choice model specified by equations 1 and 2 in the text. The exponential model (solid line) is a phenomenological model given by equations 3 and 4 in the text.

where E_{mys} is the biomass of mysids in *Saduria* stomachs and a, b, c are fitted constants. This analysis identified a significant relationship with N_t but not with N_{t-1} (approximate t values 2·5 and 0·07), which indicates that the correlation

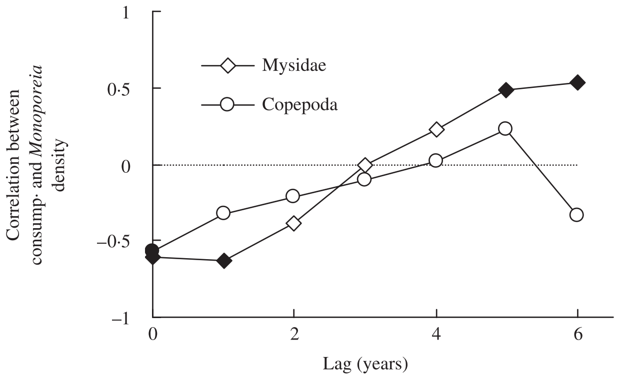

Fig. 5. Spearman's rank correlations between lagged densities of *Monoporeia* (N_t, N_{t-1}, etc.) and prey biomasses in *Saduria* stomachs as a function of the time lag. Filled symbols denote correlation coefficients significantly different from zero.

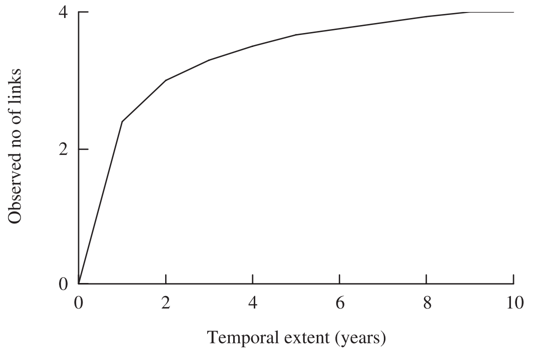

Fig. 6. Relationships between number of observed links and duration of the observations.

between E_{mys} and N_{t-1} may reflect collinearity between N_t and N_{t-1}.

Determining the number of links in food webs that contain dynamic links is complicated by the fact that the link structure varies over time (Kondoh 2003). Thus we examined the relationship between temporal observation scale and number of observed links. This was achieved by varying the duration of the observation period using every possible starting time. Observations from nine consecutive years were sufficient to guarantee that all links were detected (Fig. 6).

EFFECTS ON STABILITY OF DIET DYNAMICS

The model specified by equations 7 and 8 was used to investigate how diet dynamics affect the stability of the *Saduria–Monoporeia* system. We used the two-species functional response model (equations 1 and 2) to represent feeding on an alternative, donor-controlled prey that does not involve active prey choice, and the exponential model (equations 3 and 4) to represent a situation where there is active choice. The estimated parameter values for the two models are presented in Table 1.

Stability was quantified by the amplitude of density oscillations [ln(max/min)] and by observing the risk of extinction due to environmental variation. Such variation was introduced by adding normally distributed random between-year variation to prey-carrying capacity (mean $K = 59{\cdot}7$ g m^{-2}, SD = 20). Carrying capacity was therefore changed once every year. The effects on these measures of stability were studied by varying feeding rates from zero to the value recorded in the field. The system was modelled over 60 years, and a density of 0·01 g m^{-2} was used as the extinction threshold.

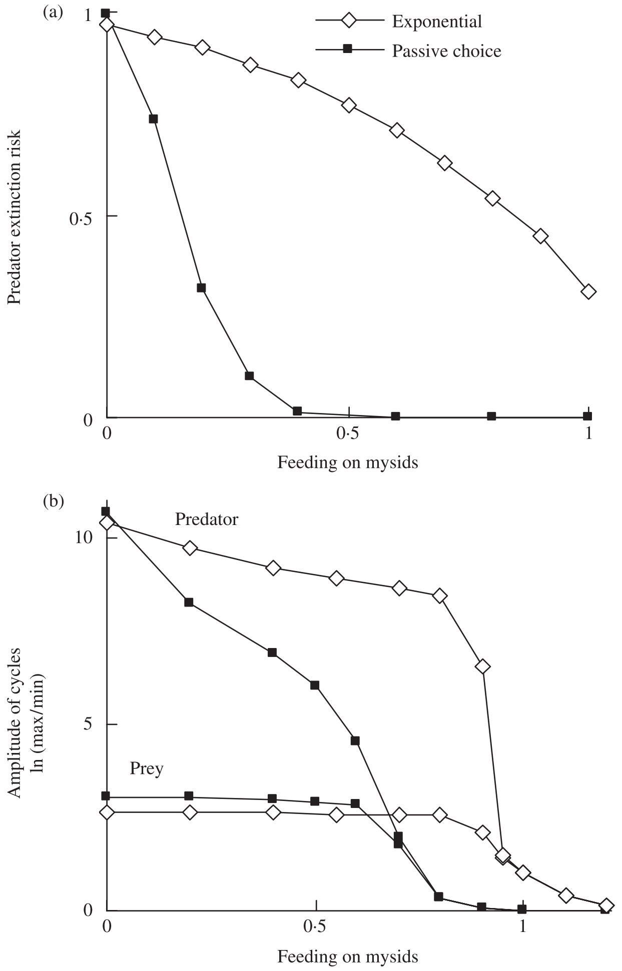

Fig. 7. Effects of consumption of alternative prey, mysids, on (a) the extinction risk for the predator, *Saduria*; (b) the amplitude of density oscillations for *Saduria* and its main prey *Monoporeia*. The *x*-axis represents the amount of feeding on mysids expressed as the fraction of the feeding rate observed in the field. Predictions were generated using equations 7 and 8 in the text. Environmental perturbations causing extinctions were introduced as random between-year variations in carrying capacity. Two different models were used to describe feeding by *Saduria* on mysids: a passive choice model given by equations 1 and 2 and an exponential model described by equations 3 and 4.

Feeding on mysids reduced the extinction risk of the predator as well as the amplitude of density oscillations (Fig. 7). These effects were produced by both models, but were stronger for the passive choice model. For this model, predator and prey densities reached a stable equilibrium. The prey persisted in all simulations.

Discussion

In this study we present 20 years' diet data for the key predator *S. entomon* in the benthic food web in the northern Baltic Sea. This long time-series allows us to assess how food web structure varies over time. The data show that the link structure in the food web is variable, and that 9 years' observations should be sufficient to detect all the links observed in this study. Leonardsson (1991a), who performed stomach analyses of 246 individuals sampled in a nearby area in 1985, found the same prey taxa as we found in this study for the same year. The only difference was a single observation of *Gammarus* sp. by Leonardsson (1991a). These results show that 20 years' data is enough to detect all important links. A dynamic link structure has been observed in a wide range of food webs (Winemiller 1990; Schoenly & Cohen 1991; Scheuerell *et al.* 2005), suggesting that it is a general phenomenon.

We also find that the strength of observed links is dynamic. The relative importance of different taxa in the diet is variable, and for three of the four prey taxa there are indications that variable consumption rates are the result of active prey choice by the predator. This explanation is supported by the poor fit between data and a model of passive choice; the observation that consumption of the alternative prey, mysids, is unrelated to mysid densities; and the lack of evidence for diet adjustments driven by changes in prey behaviour. Although each of these observations must be considered to provide weak evidence, we argue that the most parsimonious explanation is active predator choice.

This pattern is in agreement with the assumption of adaptive foraging (*sensu* Kondoh 2003). However, it is not possible to use our data to distinguish between switching and optimal prey choice or non-optimal foraging strategies. Some useful information can, however, be obtained from behavioural observations. When foraging, *Saduria* either use a sit-and-wait strategy, remaining partially buried in the sediment, or hunt actively, walking on the sediment surface (Bergström & Englund 2002). As mysids are more mobile than *Monoporeia*, we expect that the sit-and-wait strategy is more effective for catching the former (Leonardsson & Johansson 1997; Englund & Harms 2001). This could potentially generate a trade-off that leads to switching, but it still remains to be determined whether the foraging mode of *Saduria* changes in response to variations in *Monoporeia* density.

Behavioural observations also suggest that prey responses to predation risk can influence the diet of *Saduria*. The immediate response of *Monoporeia* to high densities of *Saduria* is to decrease small-scale foraging activity, but to increase swimming, which may lead to large-scale dispersal (Sparrevik & Leonardsson 1995). Mysids also exhibit predator-avoidance behaviours (Lehtiniemi & Linden 2006), although behavioural interactions with *Saduria* have not been investigated. These observations illustrate that the behavioural interaction between predators and prey can be complex (Hammond, Luttbeg & Sih 2007), involving adjustments of both predator behaviours and defence strategies used by the prey.

The rate at which the diet is adjusted in response to variations in prey density is of interest because slow adaptations introduce a delayed density-dependence that may destabilize food webs and lead to a negative complexity–stability relationship (Kondoh 2003). The temporal correlation observed between *Monoporeia* densities and the consumption of mysids by *Saduria* suggests the possibility that adaptation occurs instantaneously and/or with a time lag of approximately 1 year. However, the multiple regression analysis did not provide evidence for a delayed response, probably due to collinearity arising from the temporal autocorrelation of *Monoporeia* densities. Thus we must conclude that the evidence for a delayed response is weak at best.

The analysis of the population model also shows that *Saduria*'s feeding on mysids increases its persistence and reduces the amplitude of density oscillations. For the passive choice model, densities even reached a stable equilibrium when we assumed the amount of feeding observed in the field data. This suggests that mysids have an important stabilizing effect on this system, even though their biomass is low. The average biomass of mysids (regional mean) is 0·8% of the total benthic biomass; the corresponding values for *Saduria* and *Monoporeia* are 43 and 39%, respectively. The finding that the passive choice model is more stabilizing than the exponential model appears to be in conflict with theoretical studies showing that optimal diet choice and switching behaviours lead to more stable dynamics than is produced in systems with an indiscriminate generalist predator (Krivan 1996, 1997; Abrams 1999; van Baalen *et al.* 2001). The explanation for this result appears to be that the stabilizing effect caused by the donor-controlled input of mysids across a wide range of *Monoporeia* densities, which is predicted by the passive choice model, is more important than the high input at low *Monoporeia* densities predicted by the exponential model.

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