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Diet specialization in a fluctuating population of *Saduria entomon*: a consequence of resource or forager densities?

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Intraspecific competition has been shown to favor diet specialization among individuals. However, the question whether the competition takes the form of interference or exploitative in driving diet specialization has never been investigated. We investigated individual diet specialization in the isopod *Saduria entomon*, in relation to forager and resource biomasses in a system that exhibits predator–prey fluctuations in density. We found that individual diet specialization was only affected by the biomass of their preferred prey (*Monoporeia affinis*) and not by *Saduria* biomass; diet specialization was higher when *Monoporeia* biomass was low compared to when there were high *Monoporeia* biomass. Population diet breadth increased at low *Monoporeia* biomass whereas individual diet breadths were marginally affected by *Monoporeia* biomass. Overall, this led to the increase in diet specialization at low *Monoporeia* biomass. This study shows that predator–prey dynamics might influence diet specialization in the predator and that resource biomass, not forager biomass might be important for individual diet specialization.

Numerous theoretical and empirical studies show that intraspecific competition is a diversifying force in nature (Dieckmann and Doebeli 1999, Bolnick 2004, Svanbäck and Persson 2004, Svanbäck and Bolnick 2005). For example, intraspecific competition may affect habitat choice in populations, such that only the preferred habitat is used at low degrees of competition, and more than one habitat is used at high levels of competition (Rosenzweig 1991, Svanbäck et al. 2008). Strong intraspecific competition may also favor diet specialization among individuals (Svanbäck and Persson 2004, Svanbäck and Bolnick 2007, Tinker et al. 2008). "Individual diet specialization", occurs when a population is composed of ecologically heterogeneous individuals, each of which uses only a subset of the population's overall resource base (Bolnick et al. 2003). As variation among individuals is necessary for natural selection and hence adaptation, it is important to understand the mechanisms underlying diet specialization. In this paper we investigate the relative importance of exploitation and interference competition for individual diet specialization, an issue that has not been addressed before.

In exploitative competition, individual resource use is affected by the amount of resources that remains after it has been exploited by others. The optimal diet model was originally developed to predict how the diet of a forager is influenced by the density and quality of available resources (Stephens and Krebs 1986). It has also been used to predict how individual diet specialization changes with increasing competition for resources (Svanbäck and Bolnick 2005). Svanbäck and Bolnick's model assumes that individual consumers differ in their handling time or attack rates on various prey. As a result, decreased density of preferred prey causes some but not all individuals to add less preferred prey, or different individuals to add different less preferred prey. Either outcome results in greater individual diet specialization. Thus, diet use and specialization is driven by resource densities (exploitative competition), and especially the density of the most preferred resource (Stephens and Krebs 1986, Svanbäck and Bolnick 2005).

Besides being exploitative, competition can also take the form of interference. In interference competition individuals interact with each other directly, such that one individual prevents another from exploiting the resources within a portion of the habitat or at certain times. This is normally seen in animals that defend territories but the extreme case of interference is cannibalism. Interference competition has in some cases been presumed to lead to diet variation among individuals when individuals defend territories with different resource bases (reviewed by Bolnick et al. 2003). In mobile cannibalistic individuals, diet specialization may arise through interference if resources are patchily distributed and individuals searching for food tend to avoid aggressive contacts with conspecifics. In this case it is expected that consumer density, rather than prey density, influences the degree of diet specialization. Pure exploitative and pure interference competition may be rare, especially in systems of mobile and cannibalistic consumers, suggesting that both consumer and prey densities affects the degree of diet specialization.

In this study we will investigate the relative importance of exploitative and interference competition for individual diet specialization in the isopod *Saduria entomon*. We study this in a benthic food web in the northern Baltic Sea where the food web and the density dynamics have been extensively studied and sampled yearly since 1983 (Leonardsson 1991a, Sparrevik and Leonardsson 1998, Albertsson and Leonardsson 2001, Bergström et al. 2006, Englund et al. 2008). *Saduria* is mobile and cannibalistic, which suggests that both interference and exploitation competition are potentially important for individual diet specialization. We expect the degree of diet specialization in *Saduria* to be most strongly related to preferred prey density if competition is primarily exploitative, whereas it should be most strongly related with consumer (*Saduria*) density if interference dominates.

Methods

Study system and field sampling

The isopod *Saduria entomon* is found throughout the Baltic Sea where it occupies soft bottom sediments (Haahtela 1990, Leonardsson 1991a). In the northern Baltic Sea, *Saduria* preys mainly on the amphipod *Monoporeia affinis* but the diet can also include other benthic invertebrates as well as fish and conspecifics (Sparrevik and Leonardsson 1998, Bergström and Englund 2002). At depths greater than 40–50 m in the northern part of the Baltic Sea, the Gulf of Botnia, the benthic community is dominated by *Saduria* and *Monoporeia*. It is believed that *Saduria* and *Monoporeia* make up a tightly coupled predator–prey system (Aljetlawi et al. 2004, Bergström et al. 2006) as other predators of these species are scarce at these depths (Leonardsson 1991b). It has furthermore been shown that *Saduria* and *Monoporeia* exhibit oscillatory density dynamics, cycling over a period of 6–8 years. The most important alternative prey for large and intermediate sized *Saduria* are Mysid shrimps (Englund et al. 2008) which are pelagic predators that sometimes feed near the bottom (Zouhiri et al. 1998), and eventually end up there when they die due to non-predatory causes.

The density dynamics of this food web in the Gulf of Botnia (63°20’N, 20°20’E) have been studied in an environmental monitoring program. Samples were taken in late May or early June each year during the period 1983–2002 at depths between 46–129 m. A van Veen grab (0.1 m^2) was used to collect three replicate samples at each station and the program was designed to produce quantitative density estimates for macrobenthic organisms as *Saduria* and *Monoporeia*. It was not aimed for smaller organisms such as copepods and ostracods due to the use of a sieve with a 1.0 mm mesh.

Analyses of stomach contents

To obtain estimates of diet specialization for *Saduria* in the field, we used stomach content of individuals collected at 10 of the stations in the monitoring programme (N15–N24 in Leonardsson 1991b), and analyzed for another study (Englund and Leonardsson 2008, Englund et al. 2008). Englund et al. (2008) analyzed 263 individuals collected during the period 1983–2002. They were in the size range 25–35 mm, which includes the modal size in most years. The individuals were collected at the same 10 sites each year, separated spatially by on the average 10.7 km. For the analyses of stomach contents, identifiable remains of prey exoskeletons were recovered and measured. The number of diet items (average 3.6, range: 1–37 items per stomach) in the stomach of an individual was determined based on the size and number of different body parts. One limitation of this method is that soft bodied prey such as dead fish and newly molted conspecifics are less likely to be detected than those with a hard exoskeleton.

Quantifying niche breadth and individual diet specialization

We used the proportion by number of each prey type in an individual’s stomach to estimate the individual diet breadth using Levins’ D (Levins 1968) where $D = 1/\Sigma p_j^2$ and p_j is the proportion of the diet that is represented by diet category j. The average proportion of each prey type in the whole population was then used to measure the population’s diet breadth, also using Levins’ D.

We quantified diet specialization by first calculating the mean overlap between each individual’s diet and the population diet $\overline{PS_i}$. PS_i was calculated as $PS_i = \sum_j \min(p_{ij}, q_j)$, where p_{ij} is the frequency of diet category j in individual i’s diet, and q_j is the frequency if diet category j in the population as a whole (Bolnick et al. 2002). The degree of diet specialization (V) was then calculated as $V = 1 - \overline{PS_i}$. This means that the degree of diet specialization ranges from 0 when all individuals use the full range of resources used by the population, towards higher decimal values when individuals are more heterogeneous and use smaller subsets of the resources used by the population. $\overline{PS_i}$ were calculated using Indspec 1.0 (Bolnick et al. 2002). In these analyses we define populations based on the grouping of individuals into either 1) density combinations, or 2) year of capture.

Data analyses

We analyzed the data in three different ways. First we investigated if individual diet specialization in *Saduria* was due to exploitative or interference competition. Second, as the *Saduria–Monoporeia* system is experiencing density fluctuations over time, we analyzed the effect of yearly density on individual diet specialization in *Saduria*. In this analysis we used the *Monoporeia* density as determinant for diet specialization in *Saduria* as *Monoporeia* was found to be the main determinant for diet specialization in the first analysis. Third, we verified that the increase in individual diet specialization came from increased population diet breadth.

First, as the individuals analyzed for diets came from a variety of *Saduria* and *Monoporeia* biomass combinations we divided the individuals into four groups of low and high biomass of *Saduria* and *Monoporeia*, respectively, excluding individuals from intermediate biomass combinations (Supplementary material Fig. S1). This would ensure that the individuals within a group experience fairly similar environments when it comes to competitor and resource biomasses. Though, the division into these groups were arbitrary defined, changing the limits would give similar results and

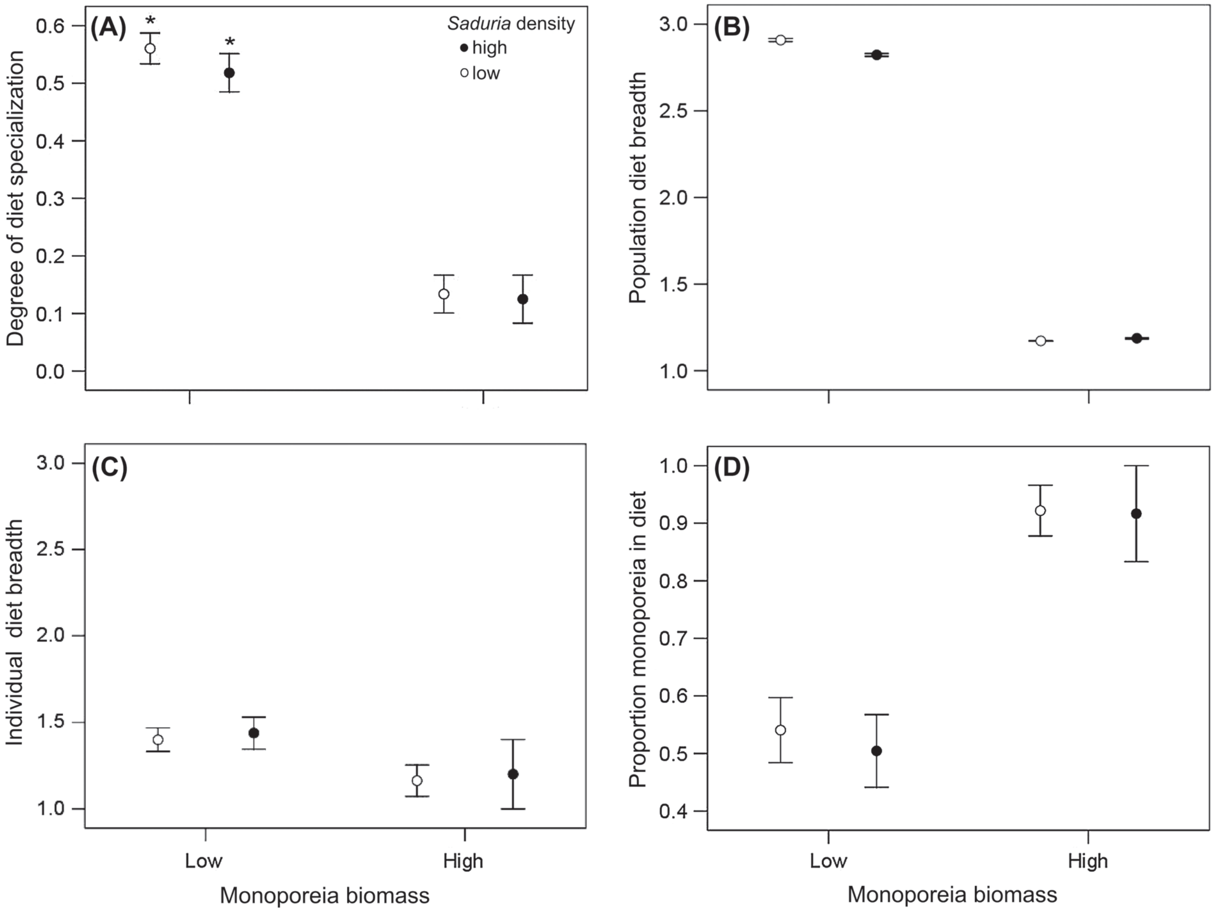

Figure 1. Relationships between the biomasses of consumers and resources (*Saduria* and *Monoporeia*) and (A) the degree of diet specialization (V), (B) population diet breadth, (C) individual diet breadth, and (D) the proportion of *Monoporeia* in the diet of *Saduria*. Mean ± SE are given. An asterix in (A) denotes a degree of diet specialization different ($p < 0.05$) from random, see text for explanation.

the same conclusions (Supplementary material Fig. S2). We then analyzed the degree of diet specialization, individual diet breadth and the proportion of *Monoporeia* in the diet using separate two-way ANOVAs with individuals from the groups as replicates. As the diet of a population can appear heterogeneous if there is limited diet information for each individual in the population, for example, if stomach size is small or resource competition constrains the number of prey consumed per individual; gut contents may underestimate niche widths. Therefore, to test whether the observed degree of diet specialization, V, differs from random expectations, we used a nonparametric Monte Carlo procedure implemented in IndSpec 1.0 to generate replicate null diet matrices drawn from the population distribution (Bolnick et al. 2002), from which the significance of the observed value can be computed. We used 10 000 replicates in Monte Carlo bootstrap simulations to obtain p-values for V. Furthermore, to obtain a null distribution of the population diet breadth to test for significance among the density combinations we also used 10 000 replicates in Monte Carlo bootstrap simulations.

Second, we used linear regressions to investigate the relationship between the main determinant of diet specialization (*Monoporeia* biomass, determined from the previous analysis) and the diet breadth measures (Levines' D) as well as the degree of diet specialization, V. In these analyses we used the yearly averages and individual stomachs within a year as replicate. The spatial covariance between predator and prey densities varied substantially between stations and years. This means that the overall mean density of prey is an inaccurate descriptor of the prey density experienced by the predators. Thus we used a predator weighted biomass for *Monoporeia*. The predator weighted biomass is the mean of the biomasses experienced by the predators used in the analysis, assuming that a sample ($0.1\ m^2$) provides a reasonable measure of the density experienced by a predator (see Englund and Leonardsson 2008 and Englund et al. 2008 for more details). Due to too few stomachs analyzed in 1989, 2001 and 2002 ($n = 2$, 2 and 1, respectively) we omitted these years from these analyses.

Third, to test if the population had a more heterogeneous diet (high degree of diet specialization) during years with high population diet breadth we regressed the degree of diet specialization on Levines' D. Here we also used a resampling procedure following Bolnick et al. (2007) to create a null expectation for the relationship between population diet breadth and the degree of diet specialization. Then to evaluate whether our observed trend can be explained by this null model alone we used a general linear model to test for a difference between the slopes of the observed and the simulated degree of diet specialization against population diet breadth.

Results

Diet specialization in *Saduria*

The degree of diet specialization in *Saduria* was only dependent on the *Monoporeia* biomass (Fig. 1A; ANOVA, *Monoporeia* biomass: $F_{1,113} = 49.73$, $p < 0.001$) and not on *Saduria* biomass or the interaction between *Monoporeia* and *Saduria* biomasses (*Saduria* biomass: $F_{1,113} = 0.19$, $p = 0.662$, *Monoporeia* × *Saduria*: $F_{1,113} = 0.083$, $p = 0.774$). From MonteCarlo simulations it was evident that only when there were low biomasses of *Monoporeia* the index of diet specialization, V, was found to differ from a null expectation ($p < 0.05$). The reason for the higher degree of diet specialization in low *Monoporeia* environments was an increase in the population diet breadth compared to the high *Monoporeia* environments (Fig. 1B; Median test: DF = 3, $\chi^2 = 4000$, $p < 0.001$) whereas there were no differences in individual diet breadths among the density combinations (Fig. 1C; ANOVA, *Monoporeia* biomass: $F_{1,113} = 2.29$, $p = 0.133$, *Saduria* biomass: $F_{1,113} = 0.059$, $p = 0.809$, *Monoporeia* × *Saduria*: $F_{1,113} < 0.001$, $p = 0.998$). At high density of *Monoporeia*, all *Saduria* fed primarily on *Monoporeia*, leading to a higher proportion of Monoporeia in the populations diet compared to at low biomass of *Monoporeia* (Fig. 1D, ANOVA, *Monoporeia* biomass: $F_{1,113} = 11.91$, $p = 0.001$, *Saduria* biomass: $F_{1,113} = 0.032$, $p = 0.857$, *Monoporeia* × *Saduria*: $F_{1,113} = 0.018$, $p = 0.893$).

When comparing among years, the degree of diet specialization was negatively related to the biomass of *Monoporeia* (Fig. 2A; $R^2 = 0.491$, $F_{1,15} = 14.5$, $p = 0.002$), confirming the previous results. Both population diet breadth and individual diet breadth decreased with *Monoporeia* biomass (Fig. 2B; population diet breadth: $R^2 = 0.391$, $F_{1,15} = 9.62$, $p = 0.007$, individual diet breadth: $R^2 = 0.260$, $F_{1,15} = 5.28$, $p = 0.036$). Even though both population diet breadth and individual diet breadth increased with the level of competition, population diet breadth increased faster than the individual diet breadth (Fig. 2B; *Monoporeia* biomass: $F_{2,31} = 6.03$, $p = 0.006$). When testing for diet specialization and diet breadths for the lower ranked prey (mysidae) we did not find any significant relationships ($p > 0.14$ for all comparisons).

Is *Saduria* more specialized in years of high total niche width?

The degree of diet specialization increased with population diet breadth (Fig. 3) both for the observed values ($F_{1,15} = 38.08$, $p < 0.001$) and for the null model simulated values ($F_{1,15} = 49.59$, $p < 0.001$). However, the degree of diet specialization increased more steeply for the observed values than for the null model values ($F_{2,31} = 46.13$, $p < 0.001$) indicating that *Saduria* is more specialized in years of high total niche width. The same relationship was found when diet specialization was calculated on the four groups based on biomass (Fig. 1A–B, Supplementary material Fig. S1), i.e. the degree of diet specialization increased with the groups diet breadth (Supplementary material Fig. S3) both for the observed values ($F_{1,3} = 907.58$, $p = 0.001$) and for the null model simulated values ($F_{1,3} = 364.96$, $p = 0.003$), and the degree of diet specialization increased steeper for the observed values than for the null model values ($F_{2,5} = 492.77$, $p < 0.001$).

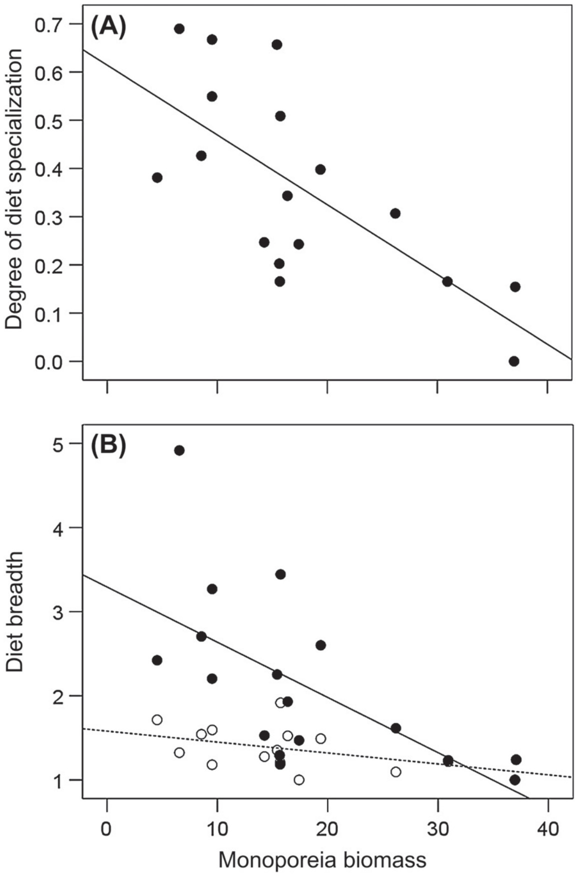

Figure 2. Correlation between *Monoporeia* biomass (g m^{-2}) and (A) degree of diet specialization, V, in *Saduria* and (B) population diet breadth (filled symbols and full drawn line) and individual diet breadth (open symbols and dotted line).

Discussion

In this study we found that the degree of diet specialization in *Saduria* was correlated with resource densities and not to forager densities, suggesting exploitative competition to be the factor determining diet specialization. The degree of diet specialization was greater at lower biomass of *Monoporeia*. Both population diet breadth and individual diet breadth increased with decreasing *Monoporeia* biomass when comparing among years. Exploitative competition led to increased diet specialization because population diet breadth increased at a faster rate than individual diet breadth, due to increased between-individual diet variation. Increasing diet specialization with increasing levels of intraspecific competition has been shown before for fish (Svanbäck and Bolnick 2007, Svanbäck and Persson 2004) but this is the first study showing that diet specialization is due to resource density and not forager density a result suggested by optimal diet models (Stephens and Krebs 1986, Svanbäck and Bolnick 2005). Our results are also the first to show that the strength of intraspecific competition also might explain diet specializations in natural populations' of invertebrates (but see Agashe

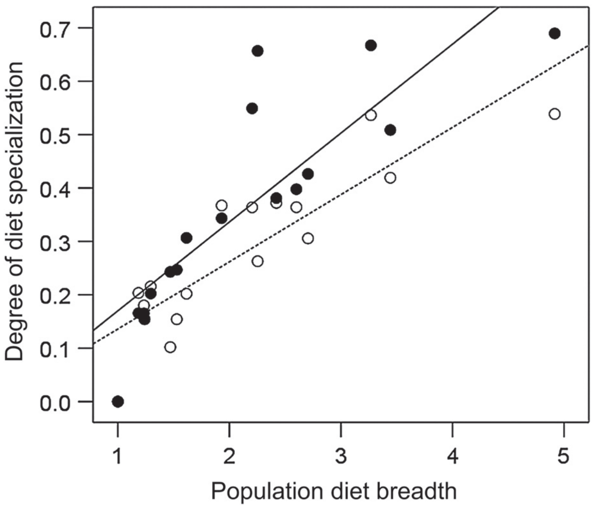

Figure 3. Correlation between degree of diet specialization (V) and the total niche width (population diet breadth) of the population. The empirical results are shown with filled symbols and solid line. Open symbols and dotted regression line indicate the expected trend under a null model in which diet arises solely by individuals randomly sampling from a limited set of prey from a shared prey distribution.

and Bolnick 2010 for a lab population). As many invertebrate species have been shown to exhibit individual diet specialization within populations (Bolnick et al. 2003) our results thus suggests that a positive relationship between diet specialization and the intensity of exploitative competition might be more common than previously thought.

Why is exploitative competition and not interference competition causing diet specialization in *Saduria?* One possible explanation is that the interactions from exploitation are stronger than the interactions from interference (cannibalism) in this system. Other studies have showed that interference in the form of territorial defense may lead to diet variation among individuals (reviewed by Bolnick et al. 2003). In these studies, diet variation is due to that territories differ in their resource base. Thus, interference may affect individual diet specialization but, whether interference in the form of cannibalism may lead to diet specialization needs further investigations, e.g. will interference influence diet specialization among individuals more if the effect of cannibalism is stronger?

Diet specialization among individuals has been shown to be driven by intraspecific competition (Svanbäck and Persson 2004, Svanbäck and Bolnick 2005, 2007) or predation (Eklöv and Svanbäck 2006) but other food web interactions such as interspecific competition and intraguild predation may also influence diet specialization (Bolnick et al. 2010). The underlying mechanisms are believed to be functional tradeoffs that prevent any given individual from using the whole set of available resources (Bolnick et al. 2003). These tradeoffs can be morphological, cognitive or physiological (Persson 1985, Lewis 1986, Schluter 1995, Estes et al. 2003, Svanbäck and Eklöv 2003, Olsson et al. 2007). We don't know which of these tradeoffs is affecting *Saduria* diet choice but basically it can be any or all of them at the same time. For example, for other crustaceans, the morphology of mouth parts have been hypothesized to be related to handling time of different prey types (Harlioglu 2000). Physiological tradeoffs such as digestive enzymes have also been a suggested mechanism for diet specialization in crustaceans (Christensen 1977). Cognitive constraints where individuals need to learn search images, search behaviors or prey handling behaviors can, however, also be important in restricting individual diet specialization (Persson 1985, Lewis 1986). Search behaviors have been thought to be related to prey use in *Saduria*. For example, when foraging, *Saduria* have been shown to use either a sit and wait strategy or hunt actively, walking on the sediments (Bergström and Englund 2002). These two strategies can be hypothesized to be adaptations to catching the more mobile mysids (sit-and-wait) or the less mobile *Monoporeia* (actively hunting) (Leonardsson and Johansson 1997, Englund and Harms 1999). However, it still remains to be determined if the foraging modes of *Saduria* generates tradeoffs leading to individual diet specialization as suggested by this study.

The pattern of increase in diet specialization with an increase in generalization (higher population diet breadth) has been described for several other animal taxa (Bolnick et al. 2007). This pattern suggests that the *Saduria* population can be subject to frequency-dependent interactions that drive disruptive selection (Bolnick 2004, Pfennig et al. 2007, Bolnick and Lau 2008, Martin and Pfennig 2009, Svanbäck and Persson 2009) which in turn may lead to evolutionary divergence (Dieckmann and Doebeli 1999, Doebeli and Dieckmann 2000). However, evolutionary divergence may not be likely in the *Saduria–Monoporeia* system due to its cyclic nature. It has recently been shown that in cyclic populations, the fitness landscape will change with density and favor different phenotypes at different parts of the population cycles (Svanbäck and Persson 2009). Such density fluctuations will favor the evolution of phenotypic plasticity over evolutionary branching (Svanbäck et al. 2009).

The change in individual diet specialization with density dynamics might influence food web connections as the diet use of foragers will change with competition. For example, Fig. 4 illustrates the benthic food web in deep areas of the northern Baltic (described in other studies, e.g. Leonardsson 1991a, Albertsson and Leonardsson 2001, Englund et al. 2008). As shown in this study, however, at high abundance of *Monoporeia*, *Saduria* will mainly feed on *Monoporeia* whereas at low density of *Monoporeia*, the *Saduria* population as a whole will feed on several different prey types. Thus, the density dynamics in this system should alter connectance of the food web, and, thus, its dynamics. Using a model that only included the two dominant prey taxa, *Monoporeia* and mysids, Englund et al. (2008) found that the diet dynamics of *Saduria* reduced density oscillations in *Saduria* and *Monoporeia* and decreased the extinction risk of *Saduria*. Interestingly, Svanbäck and Persson (2004) found in a population of Eurasian perch *Perca fluviatilis* that fluctuates in density over time that population diet breadth increased with increasing perch population, suggesting that the food web dynamics seen in *Saduria* might be common. However, the effect of individual diet specialization and adaptive foraging on food web dynamics remains to be investigated.

In conclusion, we have shown that density fluctuations between predators and prey influence the degree of individual diet specialization in the predator. This diet specialization

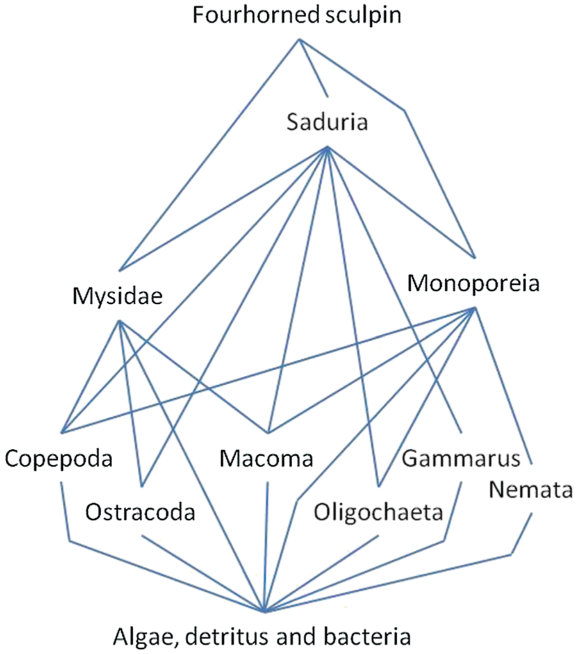

Figure 4. Illustration of the benthic food web in the deep areas of the northern Baltic (adapted from Leonardsson 1991a, Albertsson and Leonardsson 2001, Englund et al. 2008).

is dependent on resource levels and might in turn influence the length and the size (number of links) of a food web. Our results therefore suggest that including individual diet specialization into food web studies might increase our understanding of the complex structures of food webs.

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Supplementary material (available online as Appendix O18945 at <www.oikosoffice.lu.se/appendix>). Figure S1–S3.