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Ratio-dependent functional responses—tests with the zooplanktivore *Mysis mixta*

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ABSTRACT: The response of a consumer to varying densities of its food resources is essential to consumer-resource interactions, yet the proper way to describe this interaction (the functional response) has been intensively debated. Traditionally, consumption has been assumed to be solely a function of resource abundance (prey dependent). However, it has lately been suggested that consumption depends on the ratio between resource and consumer abundances (ratio-dependent functional responses). In this paper, we experimentally tested if the consumer density influences food consumption rates. As the consumer, we used a dominant Baltic Sea zooplanktivore, the mysid shrimp *Mysis mixta*. The prey used were of 3 types; the large but slow *Daphnia magna*, the small and slow *Artemia* sp., and a natural assemblage of Baltic Sea copepods that exhibit strong escape responses. Our results show that intraspecific interactions occurred among the consumers, supporting the hypothesis that a functional response can be dependent on the consumer density.

KEY WORDS: Ratio-dependent functional responses · Predation · *Mysis mixta* · Zooplankton · Baltic Sea

INTRODUCTION

The relationship between a consumer and its food resources is one of the most basic interactions in nature. It is described by a functional response (Holling 1959), i.e. the relationship between food density and the rate at which an individual consumes its food. The quantitative characteristics of this relationship are still being intensively debated. Traditionally, food consumption is assumed to increase with increasing food abundance, up to some level at which the consumer is satiated. Arditi and co-authors (Arditi & Ginzburg 1989, Arditi & Akçakaya 1990, Arditi et al. 1991a) suggest, however, that instead of using prey abundance as the independent variable, the ratio between prey and predator abundance should be employed (ratio-dependent functional responses).

The way that the functional responses are determined is not only of interest in itself, but has consequences for food web interactions and population dynamics. Population models based on prey-dependent functional responses predict that enrichment, favoring the production of prey, will increase the biomass of the predator but not that of the prey (Rosenzweig 1977, Oksanen et al. 1981; however, see Abrams 1997 for exceptions). Such enrichment is also predicted to decrease food web stability (Rosenzweig 1971). When using ratio-dependent functional responses in these population models, the predictions become very different. Enrichment is predicted to increase biomasses of both prey and predators, while food web stability is unchanged (Arditi & Ginzburg 1989).

Although functional responses describe the direct interaction between a consumer and its food, most contributions in favor of the ratio-dependent approach (Arditi & Ginzburg 1989, Arditi & Akçakaya 1990, Arditi & Berryman 1991, Arditi et al. 1991a, 1992, Hanski 1991, Akçakaya 1992, Arditi & Saïah 1992, Berryman 1992, Ginzburg & Akçakaya 1992, Akçakaya et al. 1995, Berryman et al. 1995, McCarthy et al. 1995, Stow et al. 1995), as well as the strong oppo-

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sition against it (Oksanen et al. 1992, Ruxton & Gurney 1992, Abrams 1993, 1994, 1997, Diehl et al. 1993, Gleeson 1994, Murdoch 1994, Holmgren et al. 1996, Bohannan & Lenski 1997), have been based on observations and models of population dynamics, not on actual analyses of functional responses. Some of the opponents of the ratio-dependent approach also stress that there are very few direct observations supporting such a relationship (Abrams 1994, 1997, Lundberg & Fryxell 1995, Abrams & Walters 1996).

In the current paper, we present results from experiments with the zooplanktivorous opossum shrimp *Mysis mixta* Lilljeborg. This species is one of the dominant zooplanktivores in the Baltic Sea (e.g. Hansson et al. 1990, Rudstam et al. 1992), and therefore it is important to understand the factors influencing its predation rate. The shrimps were fed 3 types of prey: the large but slow *Daphnia magna* Straus, the small and slow *Artemia* sp., and a natural assemblage of Baltic Sea copepods that have a strong escape response and are the natural prey of *M. mixta*. (cf. Rudstam et al. 1989). The results show that the food consumption of *M. mixta* is influenced by intraspecific, density-dependent interactions. Its efficiency as a predator decreases with its abundance.

MATERIALS AND METHODS

As a general description of the searching efficiency (a) of a predator, Arditi & Akçakaya (1990) suggested the equation:

$$a = \alpha \times p^{-m} \quad (1)$$

where α is a constant, p is the predator density, and m is a constant describing the predator density dependence. In classical prey-dependent functional responses, the value of m is 0 (consumption is proportional to prey abundance and is not influenced by the abundance of the predator). If $m > 0$ the functional response is influenced by predator abundance, and if $m = 1$ the functional response is strictly ratio-dependent.

As a measure of the searching efficiency (a) of *Mysis mixta*, we have used the prey capture rate (A), estimated as (derived from Arditi & Akçakaya 1990):

$$A = \frac{1}{P \times T} \ln\left(\frac{N_0}{N_T}\right) \quad (2)$$

where P is the number of mysids in an experimental container, T is the duration of the experiment (in minutes), and N_0 and N_T are prey density at the beginning and at the end of the experiment. This equation accounts for the prey depletion that occurred during the experiments. However, the equation is valid only if the predator has a Type I (linear) functional response, or if prey depletion is small (i.e. prey density is relatively constant).

To maintain relatively stable prey availability, the experiments were performed with high prey densities, where depletion effects should be moderate. Since the prey depletion was expected to be stronger in containers with more mysids, these containers were generally started with slightly higher prey abundances. The intention was to keep average prey availability the same regardless of the number of mysids in the container. The average prey abundance was estimated for each experimental container, using the equation:

$$N_{\text{mean}} = N_0 \times \left(\frac{e^{\ln\left(\frac{N_T}{N_0}\right)} - 1}{\ln\left(\frac{N_T}{N_0}\right)} \right) \quad (3)$$

One group of replicates in the experiment with *Daphnia magna* had comparably higher mysid densities (15 container^{-1}). To avoid large differences in starting abundances of *D. magna*, relative to the other treatments in this experiment, and to avoid substantial prey depletion, the experimental design was slightly different and the average prey abundance was estimated differently (see below).

Mysis mixta were collected at night during August in a coastal area of the northern Baltic proper (58° 49′ N, 17° 35′ E, bottom depth of 25 to 35 m). We used a 1 m^2 plankton net (0.5 mm mesh size) which was towed horizontally for approximately 100 m at depths between 17 and 32 m. Except for the experiment with *Daphnia magna* as prey, the studies were done within 3 d after *M. mixta* were collected. During the 5 mo between capture and running the experiment with *D. magna*, the mysids were kept at a constant temperature (9°C) in a storage aquarium and fed with newly hatched brine shrimp nauplii (*Artemia* sp.). Prior to all experiments, the mysids were starved for at most 20 h (Table 1). All experiments were performed in darkness using sand-filtered Baltic Sea water (salinity 6.5 ± 1 on the practical salinity scale).

***Mysis mixta* fed *Daphnia magna*.** To test if predator density influences food consumption, 2, 5, 10 or 15 mysids (5 replicates each) were incubated at 9°C for 4 h with *D. magna* as prey (8 l circular containers, 27 cm diameter). The *D. magna* used were young animals from a laboratory culture (average size 680 to 720 µm, see Table 1 for more details). Because we expected differences in prey depletion between containers with different numbers of predators, measures were taken to keep the average prey abundance (Eq. 3) the same in all containers, independent of the numbers of mysids. This was achieved by varying the starting densities of *D. magna* (Table 2). To avoid large differences between starting and ending abun-

Table 1. Summary of experimental conditions used in studies of the feeding of *Mysis mixta* (all experiments incubated in darkness)

	Prey type		
	Daphnia magna	*Artemia* sp.	Baltic zooplankton[a]
Container size (l)	8	1	26.6
Experiment duration (h)	4	1	24
Temperature (°C)	9	9	13
No. of mysids (l^{-1})	0.25–1.9	1 or 3	0.38 or 0.75
Size of mysids (mm, $\bar{X}$ ± SD)[b]	16.6±0.5	12.6±0.7	16.0
Size of mysids (mg dry weight)	8.9±1.3	4.8±0.9	7.4
Mysid starvation before experiment (h)	18–20	18	12–16
Size of prey (µm)	680–720	~180	90–1200
Average weight of prey (µg dry weight)	31	2	1.6

[a]Zooplankton composition (%) in Expt 3a/3b. Copepods: *Acartia* 29/40, *Eurytemora* 44/31, *Pseudocalanus* 26/24. Other zooplankton (mainly cladocerans and some nauplii): 1/4
[b]Length from tip of rostrum to the end of telson

dances in incubations with 15 mysids, those tests were initiated with 160 *D. magna* in each container. After 2 h an additional 20 *D. magna* were introduced into each container.

To estimate the prey capture rate in containers with 15 mysids, we first had to estimate the prey density in the middle of the experiment ($N_{0.5T}$), before the addition of *Daphnia magna*. Assuming that the prey capture rate was the same before and after the addition of *D. magna*, we have the following equations (derived from Eq. 2):

$$A = \frac{1}{P \times 0.5T} \ln\left(\frac{N_0}{N_{0.5T}}\right) \quad (4)$$

$$A = \frac{1}{P \times 0.5T} \ln\left(\frac{N_{0.5T} + 20}{N_T}\right) \quad (5)$$

These equations allowed us to calculate $N_{0.5T}$:

$$(N_{0.5T})^2 + 20N_{0.5T} = N_0 \times N_T \quad (6)$$

Prey capture efficiencies were then calculated using Eq. (4) or Eq. (5), and the average prey abundances in these containers were calculated (based on Eq. 3) as:

$$N_{\text{mean}} = 0.5 \times \left\{ N_0 \times \left[\frac{e^{\ln\left(\frac{N_{0.5T}}{N_0}\right)} - 1}{\ln\left(\frac{N_{0.5T}}{N_0}\right)} \right] + (N_{0.5T} + 20) \times \left[\frac{e^{\ln\left(\frac{N_T}{N_{0.5T}+20}\right)} - 1}{\ln\left(\frac{N_T}{N_{0.5T}+20}\right)} \right] \right\} \quad (7)$$

***Mysis mixta* fed *Artemia nauplii*.** To test for ratio dependence with another type of prey, we used newly hatched brine shrimp (*Artemia* sp., ~180 µm). Here, 1 or 3 mysids were incubated together with 500 *Artemia* for 1 h at a temperature of 9°C (1 l circular containers, 10 cm diameter, 5 replicates).

***Mysis mixta* fed Baltic zooplankton.** To examine if the prey capture rate of *M. mixta* was influenced by intraspecific interactions when fed their natural prey,

Table 2. Experimental setup to test if the density of *Mysis mixta* influences their feeding on *Daphnia magna*. We used 5 replicates for each 'treatment' (i.e. number of mysids). The 'average no. of *D. magna* container^{-1}' is the average of N_{mean} (from Eq. 3 for containers with 2 to 10 mysids and Eq. 7 for containers with 15 mysids). Average numbers of *D. magna* are not statistically significantly different (ANOVA: $F_{3,4}$ = 2.57, p > 0.09)

No. of *M. mixta* container^{-1}	No. of *D. magna* container^{-1} at start	Average no. of *D. magna* container^{-1}
2	150	138
5	160	143
10	168	139
15	160 + 20[a]	135

[a]Twenty *D. magna* added in the middle of the experiment (after 2 h)

they were offered wild-caught Baltic Sea zooplankton. These plankton were collected on the same nights as the mysids, at approximately the same depth, and in the same manner. The zooplankton net was smaller (0.2 m^2 opening, 90 µm mesh size) and shorter tows were employed. Catches were dominated by a few species of copepods, i.e. *Acartia* sp., *Eurytemora affinis* (Poppe) and *Pseudocalanus minutus elongatus* (Boeck), constituting together >96% of the zooplankton by number. By collecting zooplankton at the same depth as mysids, we obtained a natural prey composition (the zooplankton diet of *M. mixta* in the Baltic is dominated by copepods; Rudstam et al. 1989, 1992, Hansson et al. 1990). The quantity of phytoplankton in the samples was very small compared to that of zooplankton, as the net tows were made below the euphotic zone. Furthermore, we used a relatively large meshed net (90 µm) as compared to the <20 µm phytoplankton that domi-

nated the phytoplankton community during this period (S. Hajdu, Dept. Systems Ecology, Stockholm Univ., pers. comm.).

Within 2 h of collection, the zooplankton were passed through coarse meshed screen to remove larger animals such as fish, mysids and polychaetes. The zooplankton were kept for 12 h in approximately 700 l of 12°C sand-filtered seawater. The water surface was skimmed with a 90 µm mesh sieve to remove cladocerans trapped by surface tension, while the bottom of the aquarium was siphoned to remove dead zooplankton. The remaining 'zooplankton concentrate' was gently stirred to ensure a homogenous distribution of zooplankton. Different volumes of this 'concentrate' were diluted with sand-filtered seawater to give zooplankton abundances of approximately 1×, 5× and 9× expected ambient zooplankton densities (based on *in situ* zooplankton abundances in our study area during that period of the year [August], as reported by Rudstam et al. 1989, Hansson et al. 1990 and Johansson et al. 1993). These ambient densities were derived from samples covering the entire water column; small-scaled patchiness is likely to allow mysids to feed in considerably higher prey densities (cf. Rudstam et al. 1989, Hansson et al. 1990, references in Mohammadian et al. 1997). The prey concentrations in the experiments were thus within the range that mysids can be expected to face in nature. As we expected prey depletion to be higher in replicates with 20 mysids, these were stocked with larger volumes of the 'zooplankton concentrate' than the containers with 10 mysids. Furthermore, these supplemented volumes varied over the concentration gradient, since the prey depletion was expected to be higher in containers with low prey concentrations. Through this procedure we attempted to keep the average zooplankton density (Eq. 3) the same in each kind of zooplankton treatment (1×, 5× and 9× ambient zooplankton densities), irrespective of the number of mysids incubated. The experimental setup and volumes of the zooplankton concentrate used are shown in Fig. 1.

At 12 to 16 h after the animals were collected, non-transparent black polyethylene bags were filled with 26.6 l of water containing the zooplankton. Following this, 10 or 20 mysids were added to each bag. Excess air was removed from the bags, which were then closed and incubated for 24 h at 13°C. During incubation the suspended bags had a diameter of 24 cm and a length of approximately 70 cm. To end the incubation, the bags were cut open, drained and rinsed. Zooplankton and mysids were collected by filtering the water through a 90 µm mesh net. The zooplankton were preserved in 5% disodium tetraborate buffered formaldehyde (Dybern et al. 1976) and counted under 12× to 50× magnification.

This experiment was repeated twice (Expt 1 and 2), each time with 4 replicates per 'treatment' (10 or 20 mysids and 1×, 5× or 9× ambient zooplankton concentrations). In the first of the experiments, 1 sample with 10 mysids and 1× zooplankton was destroyed. We also had 8 containers with 1× ambient zooplankton concentrations but without mysids. Of the latter replicates, 4 were incubated in the same way as the containers with mysids, while 4 were sampled immediately after the start of the experiment. The containers incubated without mysids served as controls for the background mortality of zooplankton (on average 8%). A pilot experiment, without mysids and with 4 zooplankton densities (⅓×, 1×, 3× and 9× ambient zooplankton density) and 5 replicates each, did not indicate density-dependent background mortality. Since we do not know whether mysids also fed on zooplankton that died from causes other than mysid attacks, we calculated the average of all 8 replicates without mysids. This value was then multiplied by a 'density treatment factor' to estimate the starting density (N_0 in Eq. 2). The 'density treatment factor' was calculated from the volume of zooplankton concentrate added to a container (see Fig. 1) divided by 0.49 l, which was the volume added to containers with the 1× ambient zooplankton density.

Statistical analyses were made with SPSS for Windows Ver. 8.0.2.

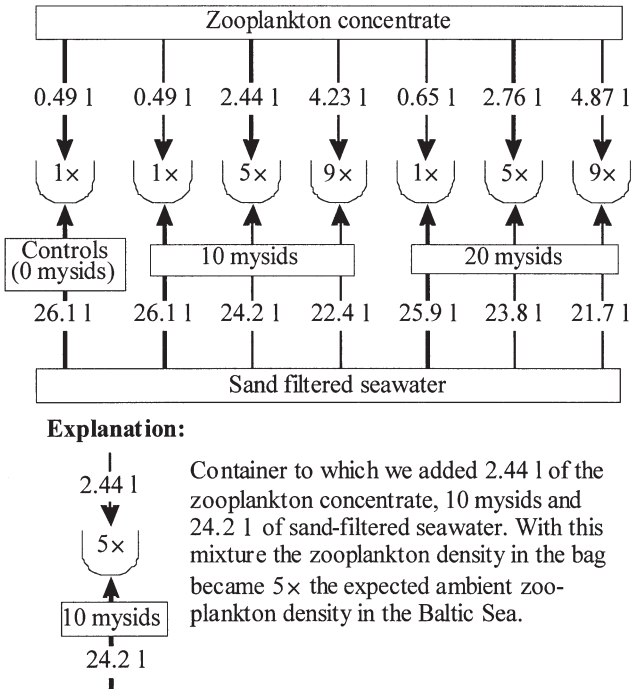

Fig. 1. Illustration of the experimental setup in the 2 tests with *Mysis mixta* and Baltic Sea zooplankton. For each treatment with mysids we had 4 replicates, while there were 8 controls, i.e. containers without mysids. All containers were incubated for 24 h, except for half of the controls, which were sampled after 0 to 2 h

RESULTS

In the experiment with *Daphnia magna*, the prey capture rate (*A* in Eq. 2) decreased significantly with increasing number of mysids (Spearman's rank correlation: $r_s = -0.78$, N = 20, $p < 0.01$; Fig. 2). A similar result was derived in the experiment with *Artemia* as prey (ANOVA with the number of mysids per container [1 or 3] as the factor and log-transformed *A* values as the dependent variable: $F_{1,8} = 47$, $p < 0.001$; Fig. 3).

The 2 experiments with Baltic Sea zooplankton as prey were analyzed together, since the regression line between *A* and N_{mean} did not differ significantly between the experiments (tested according to Dixon & Massey 1969: $t = 1.93$, df = 43, $p > 0.05$) or between the different mysid densities within the 2 experiments ($t = 1.12$, df = 19 and $t = 1.29$, df = 20, both $p > 0.05$). To test for effects of mysid density on the prey capture rate, we used a General Linear Modeling approach with a General Factorial design. The factors used were the number of mysids per container (10 or 20) and the experiment (1 and 2). Average zooplankton density (N_{mean}) was used as a covariate and the log-transformed *A* value was used as the dependent variable. The effect of mysid density on prey capture rate was highly significant ($p < 0.001$, Table 3, Fig. 4) and the same in both experiments (no significant interaction between the 2 factors, $p > 0.8$). There were, however, differences in prey capture rates between the 2 experiments ($p < 0.001$).

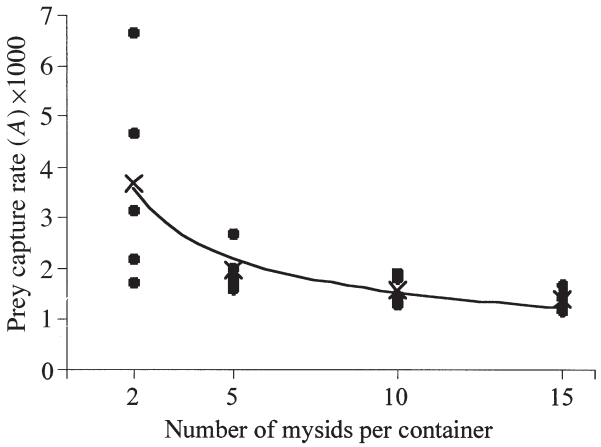

Fig. 2. Relationship between the number of *Mysis mixta* per container and their prey capture rate (*A* in Eq. 2) when feeding *Daphnia magna*. Values shown by dots and their mean with crosses. The variation among replicates decreased with increasing number of mysids per container. This is caused by consumption differences among individual mysids, which influenced the consumption per container more when there were few mysids in the containers. When there were many mysids in a container, individual consumption differences were balanced out and the variation in the average consumption per container became small. Line shows the estimated relationship between *A* and *P*, estimated from Eq. (1) after replacing *a* and *p* with *A* and *P* respectively ($m = 0.53$ and $\alpha = 5.2 \times 10^{-4}$)

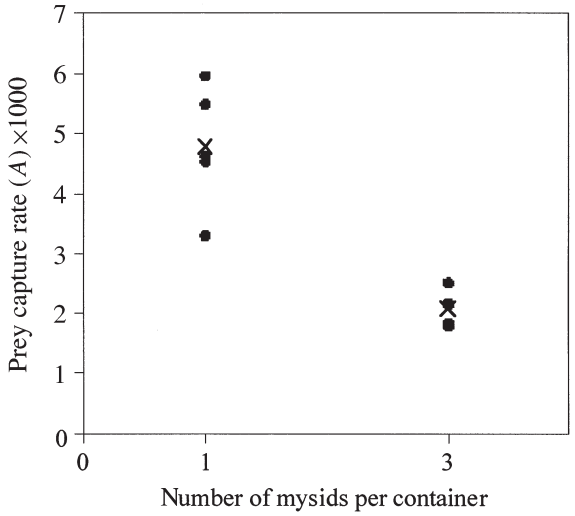

Fig. 3. Relationship between the number of *Mysis mixta* per container and their prey capture rate when feeding on *Artemia*. Values shown by dots and their mean with crosses

The estimates of prey capture rates used in these analyses account for prey depletion during the experiments (cf. Eq. 2), provided that mysids have a Type I functional response. If the functional response is of some other type and prey depletion is large enough, this may bias the results. The experiments with Baltic Sea zooplankton are best suited for examining this problem, since both prey and predator densities were manipulated. The statistical analyses of this experiment (Table 3) showed that prey capture rate de-

Table 3. Results of a General Linear Model analysis on data from the experiments with Baltic Sea zooplankton. The response variable is prey capture rate (*A*, log-transformed to homogenize variances); the factors are experiment (1 or 2) and number of mysids (10 or 20). Prey abundance (N_{mean}) is included as a covariate

Source of variation	df	SS	MS	*F*	p
Corrected model[a]	4	4.80	1.20	37.5	<0.001
Intercept	1	1427	1427	44622	<0.001
Prey abundance (l^{-1})	1	0.938	0.938	29.3	<0.001
Number of mysids	1	2.15	2.15	67.1	<0.001
Experiment	1	1.51	1.51	47.2	<0.001
Mysids × Experiment	1	0.001	0.001	0.040	>0.8
Error	42	1.34	0.032		
Total	47	5089			
Corrected total	46	6.14			

[a]$R^2 = 0.78$, adjusted $R^2 = 0.76$

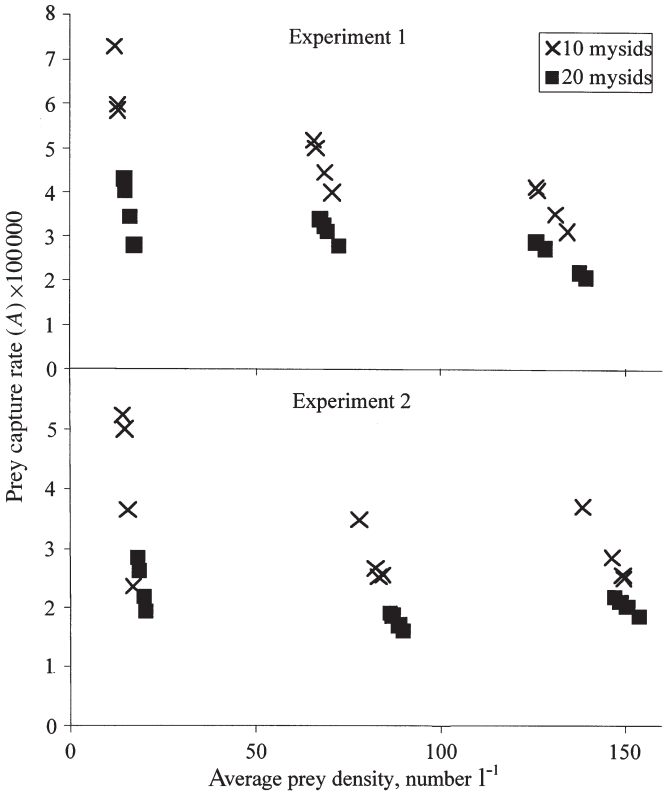

Fig. 4. Prey capture rates in 2 experiments with 10 or 20 *Mysis mixta* feeding on different densities of their natural prey, Baltic Sea zooplankton (mainly copepods). The 3 levels of zooplankton abundances represent approximately 1×, 5× and 9× ambient zooplankton densities in the Baltic in August

creased with increasing prey density (nonlinear functional response, consistent with, e.g., Types II and III responses). The lower prey capture rate in containers with 20 mysids thus cannot be explained by a stronger prey depletion than in containers with 10 mysids, since our results show increased capture rates with decreasing prey abundance. To further illustrate that the differences in prey capture rate between containers with 10 and 20 mysids cannot be explained by prey density differences, some additional analyses are presented from the first experiment with Baltic zooplankton as prey. At the highest prey concentration (9× ambient zooplankton density), the starting densities of zooplankton in containers with 10 and 20 mysids were 166 and 185 ind. l^{-1} respectively, while final concentrations were 98 and 92 ind. l^{-1}. These ~10% differences in start and final prey abundances, and the 2% difference in average abundance, cannot explain the 33% reduction in the prey capture rate in containers with 20 mysids compared to those with 10 mysids. This is not an extreme case, and similar values are derived if other comparisons are made on data from the 2 experiments with Baltic zooplankton as prey.

In the experiment with *Daphnia magna* as prey, there was no significant difference in the average abundance of *D. magna* among treatments (Table 2). Thus, by starting with different numbers of *D. magna* we kept the average prey abundance relatively constant and independent of predator density. However, despite this manipulation the prey capture rate decreased with increasing density of mysids. This decrease cannot be explained by prey depletion alone, as can be shown with an example similar to that above: in containers with 2 and 10 mysids, the starting numbers of prey were 150 and 168 ind. $container^{-1}$ respectively, and the average final numbers were 126 and 115 ind. $container^{-1}$. These ~10% differences, or the 1% difference in average number, cannot explain the 56% reduction in prey capture rate in containers with 10 mysids relative to those with 2 mysids.

The experiment with *Artemia* as prey also supports the conclusion that the prey capture rate is affected by predator density dependence, and is not an artifact caused by prey depletion. Containers with 1 and 3 mysids were all initiated with 500 *Artemia*, and average final numbers were 376 and 343 respectively. This gives a difference in the average density of 4 and 10% in final numbers. These differences cannot explain the 56% reduction in the prey capture rate in containers with 3 mysids relative to those with 1 mysid.

DISCUSSION

All of our experiments show that the prey capture rate of *Mysis mixta* is influenced by intraspecific interaction. Based on Eq. (1), and substituting *a* with *A* (Eq. 2), it is possible to estimate the predator density dependence constant *m*. With data like ours, this constant can be calculated correctly if the predator-prey relationship follows a Type I functional response (Arditi & Akçakaya 1990). If the functional response is of another type, it is unclear how this constant should be estimated (Abrams 1997). Given this uncertainty, we have calculated *m* values (by nonlinear regression) as if the functional response of the mysid was of Type I. The *m* values estimated from our 4 experiments were 0.53 for *Daphnia magna* as prey, 0.75 with *Artemia*, and 0.63 and 0.66 in the 2 experiments with Baltic zooplankton. These values are well within the range found by Arditi & Akçakaya (1990) in their analysis of 15 published datasets (range: 0.33 to 1.14) and close to their average (0.74).

Direct interference between the mysids (cf. Chivers et al. 1996), influence on the behavior of the prey (e.g. Folt & Goldman 1981, Abrams 1993), or some other interactions obviously decrease the feeding efficiency of mysids when their abundance increases. The hy-

pothesis of direct interference among the mysids is supported by the fact that we obtained similar results for different prey types (large and small prey that are slow [*Daphnia magna* and *Artemia*] and small prey with strong escape responses [Baltic Sea zooplankton, mainly copepods]).

It has been suggested that heterogeneity in the distribution of predators and prey, including spatial refuges for the prey, may result in predator-prey population dynamics as expected from functional responses dependent on predator density (Arditi et al. 1991b, Scheffer & De Boer 1995, Abrams & Walters 1996). In our experiments artificial spatial heterogeneity may have been introduced by the container walls, potentially influencing the behavior of the mysids and/or the prey. We tested some aspects of this unintentionally in a pilot study designed to determine appropriate equipment for the experiments with mysids and Baltic Sea zooplankton. Different containers were used, with the relationship between container volume and container wall area varying by a factor of 3. No significantly different consumption rates were obtained among different types of containers. In another study (Gorokhova & Hansson 1997), we have shown that container size has a rather limited effect on the food consumption of *Mysis mixta*.

Another possible explanation for our results would be that the mysids fed preferably on dying or dead prey. If this were the case, containers with fewer mysids would have proportionally more vulnerable prey available, and this would allow higher apparent prey capture rates in treatments with few mysids. This explanation is difficult to evaluate, as it is practically impossible to judge if individual prey are dying. In experiments with Baltic Sea zooplankton as prey, we had a mortality of about 8% in our control containers. Compared with the proportion consumed by the mysids (28 to 71%), this background mortality was small. The other 2 experiments (with *Daphnia magna* and *Artemia* as prey) were of short duration (4 and 1 h respectively), and, based on our experiences with these animals, the background mortality is likely to have been minimal.

Taken together, our results challenge the idea that the predator density dependence shown by *Mysis mixta* is an experimental artifact, caused by the surface area of the container or the occurrence of dead or dying prey. However, as long as we do not understand the mechanism behind the results seen in our experiments, we can neither rule out the possibility of experimental artifacts, nor can we evaluate the significance of predator density dependence in nature. The predator dependence is, however, of significance even if it is an experimental artifact. To understand predator-prey interactions in the wild, predation studies are often made under laboratory conditions. If resulting functional responses are influenced by interactions among the predators, that are irrelevant under natural conditions, laboratory results will be misleading (cf. Carpenter 1996).

In an earlier article in this journal, we reported studies on the functional response of *Mysis mixta* in the Baltic. Several experiments were made with 10 mysids feeding on natural Baltic Sea zooplankton in a 26.6 l container (i.e. the same procedure as in one of the experiments reported in this paper). Based on the results and a bioenergetics model for *M. mixta* (Rudstam 1989), we concluded that the average ambient Baltic Sea zooplankton density (integrated over the entire water column) is too low to support the observed growth of the species (Mohammadian et al. 1997). To explain observed growth rates, we speculated that mysids are able to detect patches of zooplankton where prey abundances are high enough to allow a consumption that is 2.5 to 6 times higher than what we predicted as possible under average ambient conditions. The results presented in the present paper, however, offer an alternative explanation, namely that the functional response we determined in that paper was influenced by interference among the mysids. Based on Eq. (1), and the average value of m (0.65) in the experiments with Baltic zooplankton as prey, the prey capture rate of 10 mysids in a container is 22% of that of a single mysid ($10^{-0.65}$ vs $1^{-0.65}$). A predator-density-dependent reduction of the prey capture rate could thus explain why our earlier experiments produced low food consumption rates and why we were unable to explain the *in situ* growth of *M. mixta* with the average prey densities observed in the field.

The calculations above raise the question on the relevance of the mysid densities used in the experiments. In the study area, we have found natural mysid densities of >300 m^{-2} at ~30 m deep stations (Rudstam & Hansson 1990), corresponding to >0.01 l^{-1}. The mysids are, however, not evenly distributed in the water column, but concentrated in layers that are a few meters deep(Rudstam et al. 1989), where concentrations probably may exceed 0.1 l^{-1}. During daylight hours, all mysids are very close to the bottom (Rudstam et al. 1989) and in patches the density exceed 10 l^{-1} (Hansson unpubl. obs. from a remote controlled camera). The mysid concentrations in the experiments (0.25 to 3 l^{-1}) were thus high but not unrealistic, and we cannot rule out the possibility that interactions among mysids can reduce their *in situ* food consumption.

A result similar to ours was reported by MacKenzie et al. (1990), who found that *in situ* food consumption by larval fish appears to be higher than predicted from functional responses derived in laboratory studies. The authors discuss 2 possible explanations for

their finding: that the *in situ* consumption rates are overestimated or that prey encounter rates in the wild are higher than expected from normal abundance estimates. An alternative explanation is that larval fish abundances under laboratory conditions were significantly higher than in nature, and that the experimental functional responses were influenced by density-dependent interactions among the fish larvae and hence underestimated the *in situ* food consumption.

Based on the predation experiments presented in this paper we conclude that functional responses dependent on predator density occur. Whether these are experimental artifacts or phenomena that influence animals in the wild is unknown, but in either case this may have considerable consequences for analyses and understanding of natural ecosystems.

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