

Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions

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ABSTRACT: We investigated prey selection by the 2 most important planktivores in the northern Baltic, the Baltic herring *Clupea harengus membras* L. and the mysid shrimp *Mysis mixta* Lilljeborg. We hypothesised that the intensity of prey selection by herring is positively related to prey size and that deviations from this relationship can be explained by prey escape capabilities. For the non-visually hunting mysids we assumed that prey size is less important than in herring and that escape capabilities of the prey explain a larger fraction of selectivities. To evaluate these hypotheses, we obtained selectivity indices for *C. harengus membras* and *M. mixta* from previous studies made either in the field (herring) or in the laboratory (mysids). We then quantified the escape performances of the 5 most abundant crustacean zooplankton species in the Baltic Sea by videofilming the plankters escaping from an artificially created water flow (siphon). As hypothesized, herring behaved as size-selective predators: prey selectivity rank was *Temora longicornis* > *Eurytemora affinis* > *Pseudocalanus elongatus* > *Acartia* sp. > *Bosmina longispina maritima*. In *M. mixta*, the selectivity rank was surprisingly similar, only the cladoceran *B. longispina maritima* was relatively more positively selected than in herring. Comparing the observed predator selectivities with the results of the siphon experiments allowed us to identify cases where the predators appeared to show 'true' positive selection for a certain prey (*E. affinis*) and where the selection was 'truly' negative (*P. elongatus*). On the basis of these results we suggest that large-sized copepods are important food for both herring and mysids and that a hydrography-induced shift towards a cladoceran-dominated zooplankton community may decrease the food gain by Baltic herring.

KEY WORDS: Prey selection · Escape reactions · *Clupea harengus* · *Mysis mixta* · Mesozooplankton · Baltic Sea

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INTRODUCTION

In the aquatic environment, it is not prey abundance but rather the encounter rate between predator and prey that determines prey availability for a predator. The encounter rate depends on 3 factors, namely prey concentration, prey detection distance and the velocity difference between predator and prey (Gerritsen &

Strickler 1977). For visually hunting planktivorous predators, prey detection distance is directly related to prey visibility, which is a function of prey size (Brooks & Dodson 1965, Gardner 1981, Wetterer 1989, Luo et al. 1996), pigmentation (Zaret 1972, Zaret & Kerfoot 1975, Buskey 1994, Tsuda et al. 1998) and behaviour (O'Brien et al. 1976, Williamson 1980, Zaret 1980, Yen & Strickler 1996). The non-visually hunting invertebrate predators, in turn, need to use hydrodynamic or olfactory cues to detect the prey (e.g. Strickler 1975). In contrast to the visual cues, the hydrodynamic distur-

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bance produced by zooplankters may not be directly related to their body size. The non-visually hunting predators may therefore detect fast swimming or abruptly jumping small prey from a longer distance than they detect slowly swimming larger prey (see Tiselius et al. 1997).

The active and passive predation-avoidance mechanisms of prey also greatly affect the outcome of the predatory interaction. The escape abilities of various zooplankton species have been demonstrated with many predator types, ranging from carnivorous copepods, cladocerans, jellyfish and mysids (Yen & Fields 1992, Browman et al. 1989, Suchman & Sullivan 1998, Viitasalo et al. 1998, respectively) to various fish species (e.g. Drenner et al. 1978, Drost et al. 1988, Heath 1993). Most zooplankton species can detect an approaching predator from the hydrodynamical disturbance it creates (Singarajah 1969, Strickler 1975) and attempt to escape before or during the attack, either by displaying a strong leap (e.g. Browman et al. 1989) or a 'dead-man response' (Kerfoot 1978). Also, after capture morphological defences such as spines may still make the predator reject the prey (e.g. Dodson 1974, Barnhisel 1991).

Thus, prey 'selection' is the end product of all components of the predation cycle, i.e., search, encounter, approach, attack and handling (Holling 1959, Gerritsen & Strickler 1977, Kerfoot 1978). Selectivity indices that show prey ingestion rates in relation to prey availability (e.g. Chesson 1978, Pearre 1982) present the end result of the whole interaction, and can thus be used to evaluate the 'vulnerability' (Pastorok 1981) of different prey types. However, to know *why* a certain prey species is more vulnerable to predation than another, we need to obtain accurate estimates of escape performances of each prey species, and to relate these to the observed selectivities. However, few studies have attempted to explain predator selectivities with independently quantified prey escape capabilities. A better understanding of the different components of the predation cycle will help us to estimate in which cases prey ingestion rates can be predicted from encounter rates, and in which cases the interaction is complicated by the predation-avoidance mechanisms of the prey.

Natural or anthropogenic changes in trophic status and hydrographical conditions of the sea may significantly influence the zooplankton community structure. For instance, in the North Sea (e.g. Aebischer et al. 1990, Fransz et al. 1991) and the Baltic Sea (Segerstråle 1969, Vuorinen & Ranta 1987, Lumberg & Ojaveer 1991, Viitasalo et al. 1995b) many zooplankton taxa have been shown to display strong long-term variations in connection with hydrography and climate. Flinkman et al. (1998) have also suggested that these

hydrography-driven variations in zooplankton availability may have contributed to variations in herring growth in the northern Baltic Sea. One of our main objectives was therefore to verify which zooplankton species are the most easily caught, and which are the most difficult species to catch by Baltic planktivores. On the basis of this information we wanted to estimate the effects of changes in zooplankton communities on 'food availability' for these predators.

With these objectives in mind we investigated prey selection by the 2 most important planktivores in the northern Baltic, the Baltic herring *Clupea harengus membras* L. (hereafter referred to as 'herring') and the mysid shrimp *Mysis mixta* Lilljeborg. We hypothesised that the intensity of prey selection by herring is positively related to prey size (Blaxter & Hunter 1982, Flinkman et al. 1992) and that deviations from this relationship can be explained by prey escape capabilities. For mysids, that mainly hunt for zooplankton in the night by using mechanoreception (Mauchline 1980, Rudstam et al. 1989), we assumed that prey visibility is less important than for herring, and that prey escape capabilities may therefore explain a larger fraction of the observed selectivities. To evaluate these hypotheses we obtained selectivity indices for Baltic herring and *M. mixta* from previous studies made either in the field (herring) or in the laboratory (mysids). We then quantified the escape performances of the 5 most abundant crustacean zooplankton species in the Baltic Sea against an artificially created water flow. This allowed us to evaluate the selectivity patterns of herring and mysids in light of prey escape responses.

MATERIALS AND METHODS

Selectivity in *Clupea harengus membras*. The herring selectivity data are from Flinkman et al. (1998). The material, consisting of herring stomach samples and simultaneously taken zooplankton samples, was collected in the northern Baltic Proper and western Gulf of Finland in August 1985 and 1991. The fish were caught with a research trawl hauled between 10 and 30 m depths, on 4 to 6 consecutive nights at 4 different stations. Each station consisted of 2 or 4 trawl sites located 10 n miles apart; 170 fish were analysed in 1985 and 200 in 1991. The total length of the fish selected for stomach-content analysis varied from 15 to 17 cm and their age from 2 to 6 yr.

Plankton samples were taken using 2 different methods. In 1985, all plankton samples were taken with a 100 µm mesh WP-2 net: 3 vertical hauls (from 25 m to the surface) were taken before and 3 after each trawl haul. In 1991, both vertical and horizontal samplings

were employed. Horizontal samples were taken by attaching 3 'nackthai' plankton samplers (100 μm mesh) to the trawls. A Student's *t*-test indicated no significant difference between the zooplankton sampling methods. For more details on sampling see Flinkman et al. (1998).

One hundred plankters were identified from each herring stomach and plankton sample, and a chi-square-test-based selectivity index, *V* (Pearre 1982), was calculated using the average abundance percentages for each size category in stomachs and in respective plankton samples. The *V*-index is a useful measure of prey selection because, in contrast to many other indices, it is zero-valued for no selection, is fairly robust as regards the effect of rare species in the community, and is statistically testable (cf. Boyd 1976, Lechowicz 1982, Pearre 1982). The *V*-indices were then compared with the body size of the prey species. From the predator's perspective, prey 'size' is mainly a function of the profile area of the prey (e.g. O'Brien et al. 1976). However, as we had no data on the profile area of each prey, we chose to use wet weight (from Hernroth 1985 and Viitasalo 1992) as an index of prey size. We assume that the wet weight is a better approximation of prey size than, e.g., prey length, which varies greatly according to the length of appendages (such as furca in copepods). Also, as we were interested in the hydrodynamic disturbance created by different-sized prey, we wanted to use a measure more directly related to the body volume of the plankters than body length. For more details on analyses see Flinkman et al. (1998).

Selectivity in *Mysis mixta*. The mysid selectivity data are from an experimental study by Viherluoto & Viitasalo (2001a). The material was collected in June to October 1998 from an open-sea area in the western Gulf of Finland (depth 65 to 80 m). Mysids were collected with a 500 μm mesh net (diameter 0.8 m) and zooplankton with a 100 μm mesh net (diameter 0.6 m) by vertical hauls from near bottom to the surface. After sampling the mysids and zooplankton were put in separate insulated containers filled with seawater and transported ashore into a temperature-controlled room (13°C, light:dark cycle of 16:8 h). Mysids were identified, transferred into a 10 l aerated container with 0.2 μm filtered seawater, and acclimated to the laboratory conditions without food for ~24 h. The zooplankton were kept in the transport container in natural seawater with aeration.

The experiments were conducted in 1.18 l glass bottles with 1 mysid in each. To determine prey selectivity at different prey concentrations, the mysids were provided 4 or 5 different dilutions (with 3 to 6 replicates) of the zooplankton mixture (0.5 \times to 15 \times). A nominal '1 \times ' concentration was set to ~20 copepods l^{-1} , which is a

normal concentration in the study area in summer (Viitasalo et al. 1995b). The bottles containing the mysids and the prey were placed on a plankton wheel rotating at 0.5 rpm for 12 h, of which 8 h was in darkness. The experiment was ended by pouring the mysids and zooplankton onto a 50 μm sieve and preserving with acid Lugol's solution. The numbers of prey remaining in the bottles was counted microscopically, and the selectivity index *V* was calculated for each mysid as for the herrings, by comparing the ingestion rates of different prey with their percentage availability in the prey community (Pearre 1982).

The selectivity indices on a certain prey taxon varied substantially between the experiments done in different seasons and with different-sized mysids (Viherluoto & Viitasalo 2001a). The data reported here represent average selectivity indices on crustacean zooplankton (copepods and cladocerans) for all mysids tested during the 5 experiments made in June to October 1998 (102 mysids, body lengths varying from 3 to 19 mm). The selectivity indices should therefore be taken as rough estimates of overall preference of the whole *Mysis mixta* population.

Experiments with artificial flow. To investigate the escape capabilities of the most abundant prey taxa, we videofilmed adults or large juveniles of 4 copepod species (*Acartia* sp., *Eurytemora affinis*, *Pseudocalanus elongatus*, *Temora longicornis*) and 1 cladoceran species (*Bosmina longispina maritima*) escaping from suction created by a siphon. The data are those of Viitasalo & Rautio (1998) and Viitasalo et al. (1998) supplemented with new data on *P. elongatus*. A Pasteur pipette was fixed vertically into a 1 l Plexiglas aquarium and connected to a silicon tube hanging outside the aquarium; this created a suction of water to which the zooplankters reacted. To enable measurements of distances in 3 dimensions, 2 video cameras were fixed at right angles to the aquarium, the 2 images were combined onto 1 monitor with a digital image mixer, and the images were recorded with a videocassette recorder (resolution 50 frames s^{-1}). Four parameters—escape position, escape speed, total escape distance, and escape success—were determined for each escape with an image-analysing program (Viitasalo et al. 1998). To quantify the flow field created by the siphon, we added almost neutrally buoyant phytoplankton particles to the water and measured their speeds when approaching the pipette. By noting the reaction distances of the zooplankton species within this flow field, we determined the threshold fluid velocity gradient (s^{-1}), which induced an escape reaction in each escaping plankter. Because the fluid flow may be disturbed close to the pipette body, only escapes that took place below the level of the opening of the pipette were taken into account. Further, in

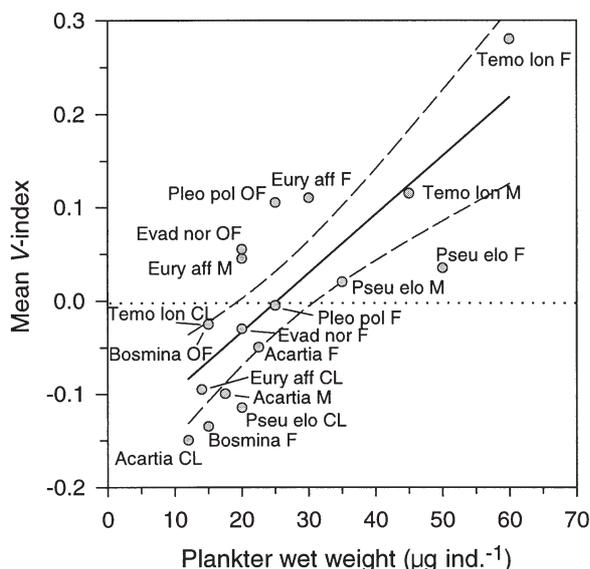


Fig. 1. *Clupea harengus membras*. Selectivity indices, V , for 18 most abundant prey species/stages found in herring stomachs plotted against prey wet weight. Values above horizontal dotted line indicate positive selection, those below line negative selection. Continuous line indicates significant linear regression ($y = -0.1593 + 0.006296x$) between the data sets, dashed lines indicate 95% confidence limits. Data collected in the Archipelago Sea, northern Baltic Sea, in 1985 and 1991 (Flinkman et al. 1998). Acartia: *Acartia* sp.; Bosmina: *Bosmina longispina maritima*; Eury aff: *Eurytemora affinis*; Evad nor: *Evadne nordmanni*; Pleo pol: *Pleopsis polyphemoides*; Pseu elo: *Pseudocalanus elongatus*; Temo lon: *Temora longicornis*. CL: large copepodite; F: female; M: male; OF: egg-carrying female

cases where a plankter performed several sequential jumps (between which the flow repeatedly drew the plankter towards the pipette), only the first escape was taken into account. The escape success of the plankters was, in turn, determined as a percentage of 'interactions' that ended in a successful escape. An interaction was defined as beginning when a plankter was for the first time entrained in the flow, and ending when the plankter was captured by the siphon or was able to escape farther away from the pipette mouth and continued to swim freely around.

RESULTS

Selectivity in *Clupea harengus membras*

The herring behaved as size-selective predators. There was a statistically significant positive correlation between plankter wet weight and the average selectivity index V (Pearson correlation coefficient $r = 0.79$, $p = 0.0001$, $n = 18$). The large-sized *Eurytemora affinis*

females, *Temora longicornis* adults and egg-carrying *Pleopsis polyphemoides* were the most positively-selected taxa, whereas the copepodite stages of *Acartia* sp., *E. affinis* and *Pseudocalanus elongatus*, as well as *Acartia* sp. males and *Bosmina longispina maritima* females were negatively selected (Fig. 1).

We analysed the predatory interactions between herring and their prey by determining which prey species deviated most from the selection-wet weight regression line in Fig. 1. Table 1 shows the magnitude of these residuals for each prey taxa. The species and stages with the most positive residuals (i.e. egg-carrying *Pleopsis polyphemoides* and *Evadne nordmanni*, and *Eurytemora affinis* adults) were either poor escapers or were 'truly selected' by herring, regardless of their size and escape capabilities. The species with the most negative residuals (*Pseudocalanus elongatus*, *Acartia* sp. and the non-ovigerous *Bosmina longispina maritima*) were either good escapers, or were actively avoided by herring. It must be noted that these results are sensitive to departures from the linear hypothesis, and need to be interpreted with caution. However, we concluded that the small cladocerans were actively selected when they carried conspicuous eggs, and that 2 copepod taxa, *Acartia* sp. and *P. elongatus*, were more negatively selected by herring than predicted by their size.

Table 1. *Clupea harengus membras*. Deviations from the linear regression between prey wet weight and herring prey selectivity index, V (Fig. 1). Positive value indicates that the taxon was more positively selected by herring than predicted by its size, negative value indicates the opposite. OF: egg-carrying female; F: female; M: male; CL: large copepodite; *values outside 95% confidence limits (see Fig. 1). Data presented in order of decreasing selectivity

Species, stage	Deviation from linear regression
<i>Pleopsis polyphemoides</i> , OF	0.107*
<i>Evadne nordmanni</i> , OF	0.088*
<i>Eurytemora affinis</i> , F	0.080*
<i>Eurytemora affinis</i> , M	0.078*
<i>Temora longicornis</i> , F	0.062
<i>Bosmina longispina maritima</i> , OF	0.040
<i>Temora longicornis</i> , CL	0.040
<i>Evadne nordmanni</i> , F	0.003
<i>Pleopsis polyphemoides</i> , F	-0.003
<i>Temora longicornis</i> , M	-0.009
<i>Eurytemora affinis</i> , CL	-0.024
<i>Acartia</i> sp., F	-0.032
<i>Pseudocalanus elongatus</i> , M	-0.041
<i>Acartia</i> sp., M	-0.051*
<i>Acartia</i> sp., CL	-0.066*
<i>Bosmina longispina maritima</i> , F	-0.070*
<i>Pseudocalanus elongatus</i> , CL	-0.082*
<i>Pseudocalanus elongatus</i> , F	-0.120*

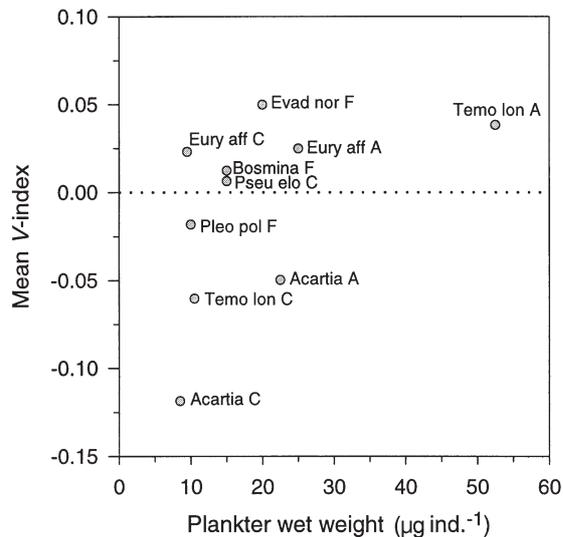


Fig. 2. *Mysis mixta*. Selectivity indices, V , for 10 most abundant prey species/stages, plotted against prey wet weight. Data from experimental study in 1998 with mysids collected at Hanko Peninsula, SW coast of Finland (Viherluoto & Viitasalo 2001a). Values above horizontal dotted line indicate positive selection, those below line negative selection. Abbreviations as in Fig. 1

Selectivity in *Mysis mixta*

Mysis mixta were not clearly size-selective in their feeding (Fig. 2), i.e., there was no significant correlation between plankter wet weight and the mean V -index (Pearson $r = 0.47$, $p = 0.172$, $n = 10$). However, while there was a large scatter on the lower end of prey wet weights, the largest prey items (*Evadne nordmanni*, *Eurytemora affinis* and *Temora longicornis* adults) had the highest selectivity indices. Only *Acartia* sp. adults were clearly more negatively selected than could be expected from their size (Fig. 2).

The selectivity indices of mysids were generally much lower (varying from -0.12 to 0.05) than those of herring. This was probably due to averaging the indices over several seasons, during which both prey size (Viitasalo et al. 1995a) and mysid size (Viherluoto et al. 2000) varied substantially.

Herring selectivity versus mysid selectivity

To determine any similarities between herring and mysid selection, we plotted the selectivity indices of *Mysis mixta* against those of herring (Fig. 3). This showed that, e.g., adult *Eurytemora affinis* and *Temora longicornis* were positively selected, and *Acartia* sp. copepodites and adults and *T. longicornis* copepodites negatively selected by both predators. However, the

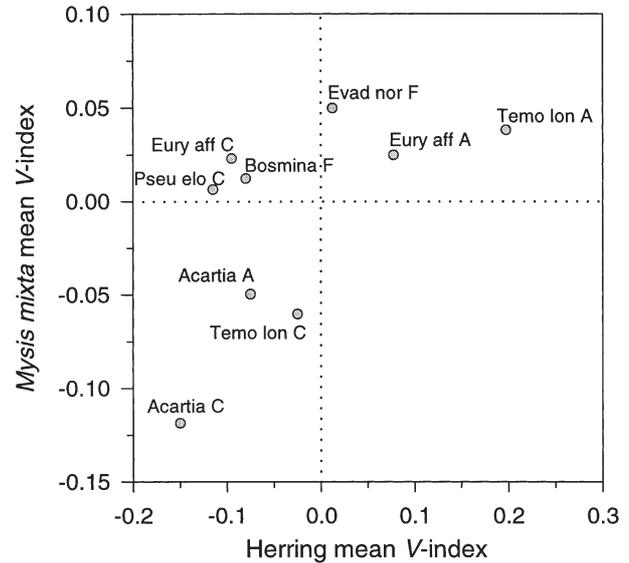


Fig. 3. *Clupea harengus membras* and *Mysis mixta*. Selectivity indices of mysids plotted against those of herring (data from Figs. 1 & 2). For herring, means for female and male copepods were used. Data points in lower left and upper right corners indicate similar selectivity by herring and mysids

correlation between the selection indices was not significant (Pearson $r = 0.56$, $p = 0.119$, $n = 9$), mainly because the selectivities for *E. affinis* copepodites, *Pseudocalanus elongatus* and *Bosmina longispina maritima* were different.

Zooplankton escape responses with artificial flow

The escape capabilities of *Acartia* sp. adults, *Eurytemora affinis* females, *Pseudocalanus elongatus* copepodites/adults, *Temora longicornis* adults and *Bosmina longispina maritima* females were tested against water flow created with a siphon. Fig. 4 shows all escape locations of the copepod species relative to the pipette. When only the escapes below the opening of the pipette were taken into account, the mean reaction distances of copepods were 0.52 and 0.53 cm for *Acartia* sp. and *E. affinis*, and 0.35 cm for both *P. elongatus* and *T. longicornis*. However, because the fluid velocities varied slightly between experiments, the corresponding average fluid-velocity gradients inducing an escape were 3.9 , 5.4 , 10.4 and 14.2 s^{-1} for *Acartia* sp., *E. affinis*, *P. elongatus* and *T. longicornis*, respectively (Table 2). There was large variation in the data, but, based on the mean fluid-velocity gradients eliciting escapes (Fig. 5: dotted lines), we ranked the 4 copepod species from the most 'alert' to the least 'alert' as follows: *Acartia* sp. \approx *E. affinis* $>$ *P. elongatus* $>$ *T. longi-*

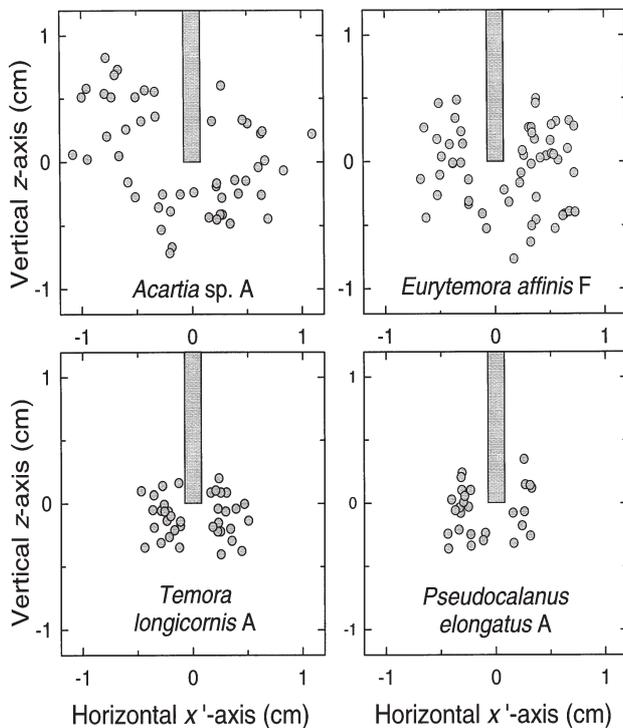


Fig. 4. Zooplankton escape experiment with artificial flow, showing escape locations of *Acartia* sp., *Eurytemora affinis*, *Temora longicornis* and *Pseudocalanus elongatus* relative to pipette siphoning water out of the experimental aquarium. Pipette is denoted by the shaded bar; opening of the pipette is at the origin of the coordinates. Third dimension (second horizontal axis, y) has been removed by projecting all escape points onto the x - z -plane (see Viitasalo et al. 1998)

cornis. The cladoceran *B. longispina maritima* did not show an escape response and was always captured by the siphon if entrained in the flow. This may however reflect its weak swimming abilities rather than its low hydrodynamical sensitivity.

Table 2. Zooplankton escape experiment with artificial flow. Mean (\pm SD) copepod reaction distances and corresponding thresholds for fluid-velocity gradient, escape speeds during the first 0.06 s of escape, and total escape distances. Data include only escapes below level of opening of the pipette (see Fig. 4)

Species (stage)	Threshold fluid velocity gradient (s^{-1})	Escape speed ($cm\ s^{-1}$)	Total escape distance (cm)	n
<i>Acartia</i> sp. (adults)	3.94 ± 5.05	4.05 ± 2.10	0.26 ± 0.16	25
<i>Eurytemora affinis</i> (females)	5.42 ± 6.74	5.51 ± 2.51	0.34 ± 0.17	28
<i>Pseudocalanus elongatus</i> (adults)	10.40 ± 12.29	4.31 ± 1.65	0.33 ± 0.21	16
<i>Temora longicornis</i> (adults)	14.19 ± 12.93	4.69 ± 1.75	0.51 ± 0.29	29

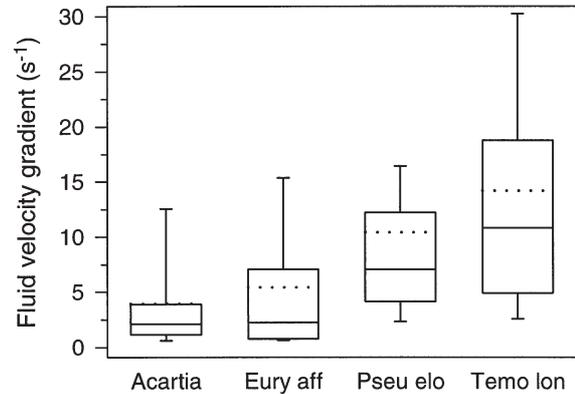


Fig. 5. Zooplankton escape experiment with artificial flow, showing fluid-velocity gradients (s^{-1}) that elicited an escape reaction in *Acartia* sp., *Eurytemora affinis*, *Pseudocalanus elongatus*, and *Temora longicornis*. Data correspond to escape locations below opening of the pipette (see Fig. 4). Small threshold value indicates escape further away from the pipette than a large threshold value. Ends of boxes: 25th and 75th percentiles; ends of whiskers: 10th and 90th percentiles of the data; middle horizontal lines: medians; dotted lines: averages

A more detailed inspection of the video films showed that *Eurytemora affinis* often first performed several small escape jumps and then finally released themselves from the flow with a very strong jump. Also, *Temora longicornis* could escape to a relatively long total distance (mean 0.51 cm; Table 2) compared to the other copepods (0.26 to 0.34 cm). In contrast, the 'alert' *Acartia* sp. performed the weakest escape jump (initial speed $4.05\ cm\ s^{-1}$, total distance 0.26 cm), and was often repeatedly entrained in the flow. Consequently, the final siphon capture success was clearly higher (33%) for *Acartia* sp. than for *E. affinis* (9%; Table 3). *Pseudocalanus elongatus* also exhibited a weak escape response and was often captured immediately or after 1 to 3 escapes (siphon capture success 86%). *Bosmina longispina maritima* was never seen to escape (siphon capture success 100%). In summary, the siphon capture success ranking was *B. longispina maritima* > *P. elongatus* > *T. longicornis* > *Acartia* sp. > *E. affinis* (Table 3).

Herring and mysid selectivities versus siphon selectivity

We also evaluated the selectivity patterns in herring and mysids by plotting selectivities of the 2 predator species against siphon selectivity. The plot of the herring selectivity rank against the

Table 3. Summary table of mean selectivity indices, V , and selectivity rank for herring (*Clupea harengus membras*) and mysids (*Mysis mixta*), and siphon capture success of 'prey' in experiments with artificial flow. For herring and *M. mixta*, a high rank (4 or 5) indicates positive selection, a low rank (1 or 2) rejection. Siphon capture success is shown as percentage, with number of interactions in parentheses (see 'Materials and methods' for explanation)

Species (stage)	Herring		<i>M. mixta</i>		Siphon capture success	
	V	Rank	V	Rank	%	Rank
<i>Acartia</i> sp. (adults)	-0.075	2	-0.050	1	33 (49)	2
<i>Eurytemora affinis</i> (adults/females ^a)	0.078	4	0.025	4	9 (56)	1
<i>Pseudocalanus elongatus</i> (adults/copepodites ^b)	0.028	3	0.006	2	86 (29)	4
<i>Temora longicornis</i> (adults)	0.198	5	0.038	5	74 (50)	3
<i>Bosmina longispina maritima</i> (females)	-0.080	1	0.012	3	100 (21)	5

^aPredator selectivity indices determined for adults, siphon selectivity determined for females
^bHerring selectivity and siphon results determined for adults, *M. mixta* selectivity index determined for copepodites

siphon selectivity rank showed no correlation (Fig. 6A). Notably, *Bosmina longispina maritima*, that showed no escape response, was clearly rejected by herring (Rank 1), whereas the evasive *Eurytemora affinis* was strongly positively selected (Rank 4). Similarly, *Mysis mixta* selectivity did not correspond with siphon selectivity: *E. affinis* again had a high rank 4 (Fig. 6B). Finally, plotting *M. mixta* selectivity rank against that of herring (Fig. 6C) showed that, for copepods, the ranking was exactly the same. In contrast, the cladoceran *B. longispina maritima* was the least selected by herring but ranked third for the mysids.

DISCUSSION

Prey selection

In planktivorous predatory interactions, prey vulnerability should peak at intermediate prey sizes because prey escape capabilities usually increase with increasing prey size (Pastorok 1981, Greene 1988). However, we did not detect any hump in the prey vulnerability data for *Clupea harengus membras* (Fig. 1). This implies that, within the prey size range studied, herring did not have a threshold prey size above which the prey would be too difficult to catch. We can therefore maintain the hypothesis of a positive relationship between prey body size and herring selectivity. A size-selective tendency of herring, also demonstrated by earlier findings (Sandström 1980, Checkley 1982), is plausible since the largest prey are detected from the longest distance, which rapidly enlarges the volume of water the fish can clear from large prey (cf. Gerritsen & Strickler 1977). For the mysids, the selectivity data in Fig. 2 conforms better with the non-linear hypothesis (Pastorok 1981). This may indicate that the largest prey were close to the upper threshold of prey sizes available for *Mysis mixta*. It must however be noted that the

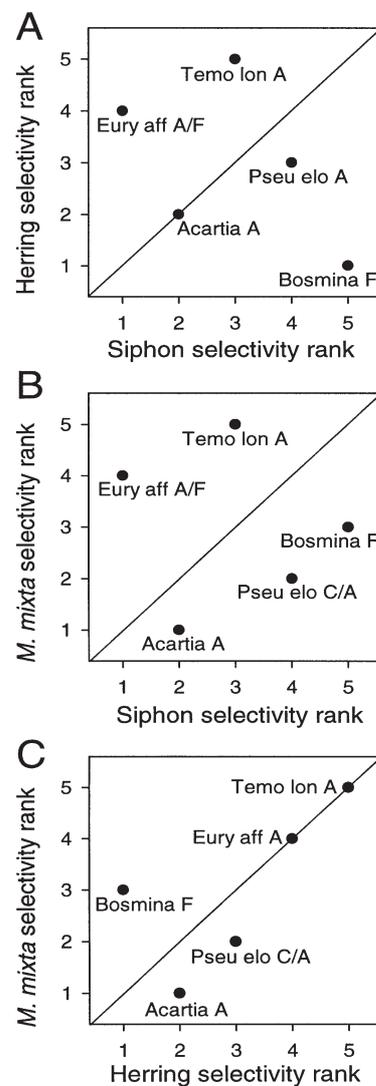


Fig. 6. Prey selectivity ranks of (A) *Clupea harengus membras* and (B) *Mysis mixta*, plotted against siphon selectivity ranks, and (C) plotted against each other. Rank data from Table 3; diagonal line represents the 1:1 line. A: adult; C: copepodite; F: female; species abbreviations as in Fig. 1

wet weight of copepods in the study area may vary seasonally by almost a factor of 2 (Viitasalo et al. 1995a). This may make the results for mysid selectivity more uncertain.

The size-selective tendency of *Mysis mixta* was evident in the case of 4 copepod prey (*Acartia* sp., *Eurytemora affinis*, *Pseudocalanus elongatus* and *Temora longicornis*; see Figs. 2 & 6). This could be due to mysid using vision in prey detection; at least Ramcharan & Sprules (1986) have shown that freshwater mysids are able to capture more prey in light than in darkness. However, our own recent experiments (Viherluoto & Viitasalo 2001b) have shown that Baltic *M. mixta* do not increase their feeding rates in the light. Thus we suggest that the selectivity of both herring and *M. mixta* is based on prey size, but that it is mediated by different mechanisms, i.e. visual cues in herring and hydromechanical cues in mysids.

There were clear differences in the escape capabilities of the zooplankton species, which partly explain the observed selectivities by herring and mysids. We thus interpret our results concerning the 5 most abundant prey species in the following way: Baltic herring preys preferentially on the largest and most conspicuous prey items, such as *Eurytemora affinis* females and *Temora longicornis*, and egg-carrying cladocerans (Fig. 1). The delayed escape response of *T. longicornis* (Fig. 5) also makes it an easy prey, and it was consequently the most positively selected species by both herring and mysids. *Acartia* sp., in turn, were negatively selected, probably because of their relatively small size and their alertness to hydrodynamic signals. The same conclusion was reached by Checkley (1982) for *Clupea harengus* larvae, which preferred *Pseudocalanus* sp. to the evasive *Acartia* sp. In contrast, the fact that the agile *E. affinis* adults were more positively selected than predicted by their size (Table 1) implies a 'true' selection by herring, whereas the negative selection by herring on the poorly escaping, relatively large-sized *Pseudocalanus elongatus* indicates 'true rejection'.

Predation-avoidance strategies

The 5 zooplankton species that we tested against the siphon flow showed different escape behaviours. Two species, *Acartia* sp. and *Eurytemora affinis*, were relatively alert, while *Temora longicornis* was less alert but attempted to escape by a strong leap. The early escape response of *Acartia* sp. can be explained by the conspicuous setae on its first antennae, which are used for hydrodynamic detection of ciliates and small rotifers (Stoecker & Egloff 1987, Jonsson & Tiselius 1990). This 'sensitivity strategy', whereby a plankter escapes from

a relatively long distance from a predator, allows a lower escape speed than in the less sensitive species. This however does not explain why the short-setae *E. affinis* was the best escaper, and other factors need to be evoked. Notably, *E. affinis* females carry large egg sacs containing up to 30 eggs. Thus, when encountering a predator, the female has more at stake than its own life, which may promote the evolution of strong escape responses. The other egg-carrying calanoid species in the Baltic Sea, *Pseudocalanus elongatus*, carries much smaller eggs sacs, which are also very easily detached from the female (M.V. pers. obs.). This conforms to its weaker escape capabilities compared to *E. affinis*. The egg-carrying cladocerans, in turn, show a very rapid parthenogenetic reproduction and can thus numerically outgrow their predators. They therefore need not possess as strong escape capabilities as copepods.

Field implications

One of our objectives was to estimate the effect of changes in zooplankton communities on food availability for Baltic planktivores. Several studies have shown that the populations of certain zooplankton species vary according to fluctuations in Baltic Sea hydrography. For instance, abundances of *Bosmina longispina maritima* and *Eurytemora affinis* have been shown to increase during periods of low salinity (Viitasalo et al. 1994, Viitasalo et al. 1995b), whereas high abundances of the neritic copepods (mainly *Pseudocalanus elongatus* and *Temora longicornis*) have been associated with elevated salinity (Vuorinen & Ranta 1987, Lumberg & Ojaveer 1991, Viitasalo et al. 1995b, Vuorinen et al. 1998). Based on the results of the present study, we can rank the 5 most abundant zooplankton taxa in the northern Baltic according to their 'profitability' for Baltic planktivores: *T. longicornis* > *E. affinis* > *P. elongatus* > *B. longispina maritima* > *Acartia* sp. We hypothesise that if Baltic salinity declines the food conditions of herring deteriorate. This supports the findings of Flinkman et al. (1998), who found that the weight-at-age of the northern Baltic herring declined by 50% during a low-salinity period dominated by *B. longispina maritima*. How an increase in the positively selected *E. affinis* would affect the food avoidability for herring, would depend on the age and size (i.e. predatory capabilities) of the herring, with large fish benefiting more than their smaller conspecifics. For the mysids, the consequences of changes in prey assemblages are harder to predict. A decrease in *T. longicornis* would be a disadvantage, whereas an increase in the easily predated cladocerans might be favourable. However, the semibenthic,

omnivorous habits of mysids may compensate for any negative changes in zooplankton availability.

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