

## Zooplankton predation by rock-pool fish (*Tinca tinca* L. and *Pungitius pungitius* L.): an experimental study

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We studied plankton predation by two fish that inhabit rock-pools, the tench (9.4–14.7 cm body length) and the ten-spined stickleback (small (2.3 cm) and large (3.9 cm) fish were treated separately). Fish were allowed to choose between small (1.5 mm *Daphnia longispina*, 0.3 J) and large (2.3 mm *D. magna*, 2.8 J) prey in different densities and ratios. In both fish species the net energy gain by feeding on *D. magna* is higher than by feeding on *D. longispina*.

In experiments with both prey the tench preferred *D. magna* to *D. longispina*. Furthermore, the large sticklebacks proved to prefer *D. magna*, while the small sticklebacks had a preference for the less rewarding *D. longispina*. The proportion of *D. magna* decreased in the diet of the small sticklebacks with an increase in its abundance in the 1:1 two-prey experiments. No change in the diet composition was observed in the tench or in large sticklebacks in these experiments. In all two-prey experiments both fish species always ingested either a few or many of the less preferred prey.

In experiments where fish were allowed to forage on plankton varying in size from 0.2 mm to 4 mm, the tench first eliminated large (1.5–4 mm) plankters, while the sticklebacks concentrated on foraging small (0.2–2 mm) plankters.

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### 1. Introduction

The rock-pools on the Baltic islands are small and numerous water basins formed in shallow depressions in the rock bed (Levander 1900). Many of the pools close to the sea receive their water from waves and surf, while the freshwater pools are maintained by rains, and therefore the smallest of them may dry out during droughts. In other words, salinity and durational stability are the two most important variables in rock-pools (Ranta 1982). The fauna of rock-pools is diverse, characterized by microcrustaceans (Järnefelt 1940), water insects (Lindberg 1944), flagellates (Droop 1953) and rofifers (Björklund 1972). Owing to the small size and temporal instability of the pools, vertebrate planktivores only rarely inhabit them.

In the Tvärminne archipelago, SW Finland, the smooth newt (*Triturus vulgaris* L., Ranta & Nuutinen 1985), and at least two species of fish (the tench, *Tinca tinca* L., and the ten-

spined stickleback, *Pungitius pungitius* L.) are known to occupy a number of permanent rock-pools (K. Purasjoki, pers. comm., and own observations). Typical rock-pool zooplankters are cladocerans, such as *Daphnia magna*, *D. longispina*, *D. pulex*, *Scapholeberis mucronata* and *Polyphemus* sp. (Järnefelt 1940, Lagerspetz 1955, Ranta 1979).

Vertebrate planktivores, relying on visual cues while hunting for their prey, preferentially forage upon larger plankters. It follows that small plankters predominate in waters with visually hunting predators (Zaret 1980). On the other hand, invertebrate predation, i.e., preference for smaller prey, results in a dominance of large plankters (Brooks & Dodson 1965, Macan 1977, Durbin 1979, Zaret 1980, Greene 1983, and many others). As the rock-pool system in the Tvärminne archipelago harbours both ends of the planktivore gradient we studied experimentally the effects of both vertebrate and invertebrate predation upon the zooplankton community. This paper

discusses the consequences of fish predation on species composition and body-size distribution in rock-pool zooplankton.

## 2. Material and methods

### 2.1. Rock-pool fish

This study was made at the Tvärminne Zoological Station of the University of Helsinki. Almost all islands and islets of the Tvärminne archipelago have several rock-pools. While most of the rock-pools are small and thus temporary, some of the largest islands have rock-pools up to the size of ponds. These are permanent water bodies. In this area ten-spined sticklebacks belong to the native fauna of a small number of rock-pools (Långskär, Isskär, Lillhamnen, Spikarna) whereas tench has been introduced (in the 1930s) to a large pond on the island of Långskär (L. Koli, pers. comm.). In this pond the tench population thrives well, though only a few specimens attain a body length greater than 20 cm (own observations).

The tench used in our experiments were captured from the Långskär pond with a 10 mm net weir. In the laboratory, fish were kept in 20 l plastic aquaria (two per aquarium) filled with the Långskär pond water. While in captivity, fish were fed either with the commercial aquarium fish food Tetramin or with living *Daphnia* and copepods collected from rock pools on the nearby islands. The fish were allowed to adjust to laboratory conditions for about a month before the experiments were started (June 8–25, 1983). In the experiments we used the four individuals (standard body lengths 9.4, 9.6, 12.0 and 14.7 cm) which became least disturbed by our presence while observing their feeding behaviour in the experiments.

The ten-spined sticklebacks used in our experiments were captured using a pond net from the sea littoral (as we did not want to disturb rock-pool populations of this species). Sticklebacks were divided into two size classes, large (mean length 3.9 cm,  $SD = 0.19$ ,  $n = 22$ ) and small (2.3 cm,  $SD = 0.18$ ,  $n = 22$ ). The fish were kept in 10 l plastic aquaria, 5–10 individuals per aquarium, and fed with Tetramin and living *Daphnia* and copepods. Before our experiments sticklebacks were acclimatized for a week to the pond water. Stickleback experiments were made between August 4 and September 6, 1983.

The fish used in the experiments were deprived of food for about 12 hours.

### 2.2. Experimental design

The prey were size-standardized *D. magna* and *D. longispina*. Standard length was accomplished by accepting only the smallest specimens of *D. magna* which remained on a 2 mm mesh sieve (body length without tail spine  $2.3 \pm 0.3$  mm,  $n = 20$ ), and the largest specimens of *D. longispina* which remained on a 1.3 mm mesh sieve ( $1.5 \pm 0.1$  mm,  $n = 20$ ). Their energy contents were 2.8 and 0.3 J, respectively (Ranta & Nuutinen 1985). In the 'community' experiments (see below) plankters ranging from 0.2 to 4 mm in body length were used. All the prey animals were from rock pools on the nearby islands. Three types of experiment were performed:

A. Feeding efficiency of both small and large sticklebacks was studied in experiments where fish were allowed to feed in separate runs on the 2.3 mm *D. magna*, and on the 1.5 mm *D. longispina*. The aquarium size was 65×40 cm, filled with 40 l of the pond water (up to 15 cm water depth). The feeding efficiencies of single stickleback individuals were measured for 5 min in prey densities of 5, 25 and 100 *Daphnia* per aquarium. Four replicates were made for each *Daphnia* size.

Sticklebacks were placed into experimental aquaria about one hour before the experiment, and the experimental ration of *Daphnia* was placed into small glass jars. At the beginning of the experiment *Daphnia* were poured into the aquarium. A stopwatch was started when the fish fed on the first *Daphnia*. *Daphnia* eaten were recorded with a counter and eaten prey were replaced (in the experiment with 5 *Daphnia* per aquarium prey were replaced immediately; in that with 25 *Daphnia* prey were replaced three at a time; and in that with 100 *Daphnia* prey were replaced five at a time). Thus the feeding rates refer to constant prey densities. The experiment was terminated after 5 min.

*Daphnia* handling times by sticklebacks were recorded with a stopwatch in 5 l aquaria with a prey density of 10 *Daphnia* per aquarium. In these measurements, prey were not replaced, and only a few initial feeding occasions (3–6) were measured for each fish. The handling time was defined as the time elapsed from a successful strike until a search for a new prey was initiated. With the tench, prey handling times were so quick that they were impossible to determine with our manual methods. No differences in handling times dependent on prey size could thus be observed in the experiments with tench feeding on *Daphnia*.

B. Experiments with alternative prey. In these experiments fish were allowed to forage on 2.3 mm *D. magna* and 1.5 mm *D. longispina*. The experiments with two prey, each replicate lasting 5 min with each fish species, were made in 65×40 cm aquaria filled with 40 l water. In the first set of experiments, fish were allowed to feed on the two prey in 1:1 combinations in four densities (10:10, 30:30, 50:50 and 100:100). Secondly, we examined prey choice by the fish in a series of experiments where the relative proportion of the preferred prey type was gradually diminished in the following ratios (preferred to non-preferred prey) 5:25, 5:50, 5:100 and 5:200. Lastly, two experiments were made where the ratio of the two prey types was either 10:50 or 50:10.

In the two-prey experiments we recorded the type of prey eaten in sequence. Prey densities were held constant by replacing the prey eaten as follows:

Density	Replacement
5	immediately
10–30	three at a time
50	five at a time
100–200	ten at a time

The number of replicates per prey ratio was five in the tench experiments and ten in the stickleback experiments. Sticklebacks for the experiments were randomly selected from the laboratory stock, while in tench a randomly selected individual (out of the four) was used for two runs per prey ratio. Experiments (A) and (B) were run in the laboratory under a 200 lux light. When examining results of prey choice it should be remembered that in laboratory experiments the fishes were occasionally disturbed.

**C. Community experiments.** In these experiments fish were allowed to forage upon an array of plankters (small cladocerans, cyclopoid copepods and *Daphnia*) which varied in body length (0.2–4 mm). An artificially constructed zooplankton sample was divided into four sub-samples by a plankton sample splitter (Edmondson & Winberg 1971). Two to three hours before each experiment fish were introduced into three 40 l aquaria, the fourth aquarium (without fish) served as a control. In the experiments with tench there was a single fish per aquarium, and with sticklebacks there were five small or three large fish per aquarium. Two 'community' experiments were run with the tench (July 22 and 25, 1983) and two with the sticklebacks. In the first experiment with sticklebacks there were two aquaria with small fish and one with large fish (July 26–27), in the second experiment (July 27–28) two of the experimental aquaria had large fish and one small fish. Experiments with the tench lasted 30 min (prevailing light was  $\geq 500$  lux), and experiments with sticklebacks 24 hours (natural light and dark rhythm). The experimental aquaria were kept outdoors and covered on all four sides with a black plastic sheet to make the light conditions uniform.

When the experiment was terminated fish were taken out of the aquaria and the remaining zooplankters were sieved on a  $50 \mu\text{m}$  mesh sieve. Plankters were preserved in 70% ethanol, and measured with an ocular micrometer under a  $\times 12$  dissecting microscope to the nearest 0.08 mm. All differences between control and experimental aquaria are interpreted as being due to fish feeding.

### 3. Results

#### 3.1. Feeding efficiency

Handling times of *D. magna* and *D. longispina* by small sticklebacks were 21.3 s ( $SD = 14.9$ , range 8–100) and 4.3 s ( $SD = 2.0$ , 1.5–11.6) and by large sticklebacks 7.0 s ( $SD = 4.8$ , 2–29) and 1.5 s ( $SD = 0.9$ , 0.4–3.3;  $n = 50$  in each case). Differences between small and large prey handling times were statistically significant in both stickleback size classes (Mann-Whitney  $U$ -test, small  $z = 8.56$ , large  $z = 8.22$ ,  $P \ll 0.001$  for both comparisons). Furthermore, comparisons between small and large sticklebacks showed that for both prey types the handling times by large sticklebacks were significantly shorter than by small ones ( $z = 7.30$  for *D. magna*,  $z = 7.29$  for *D. longispina*,  $P \ll 0.001$  in both cases). The most likely explanation for the observed difference is that the mouth diameter in small sticklebacks is 1.7 mm ( $SD = 0.1$  mm,  $n = 22$ ), while in large sticklebacks the corresponding figure is 2.5 mm ( $SD = 0.1$  mm,  $n = 22$ ). The wide range of *D. magna* handling times in small sticklebacks shows that they also manage to eat *D. magna* fairly quickly. To be able to do this, the longest dimension of a *Daphnia* should be

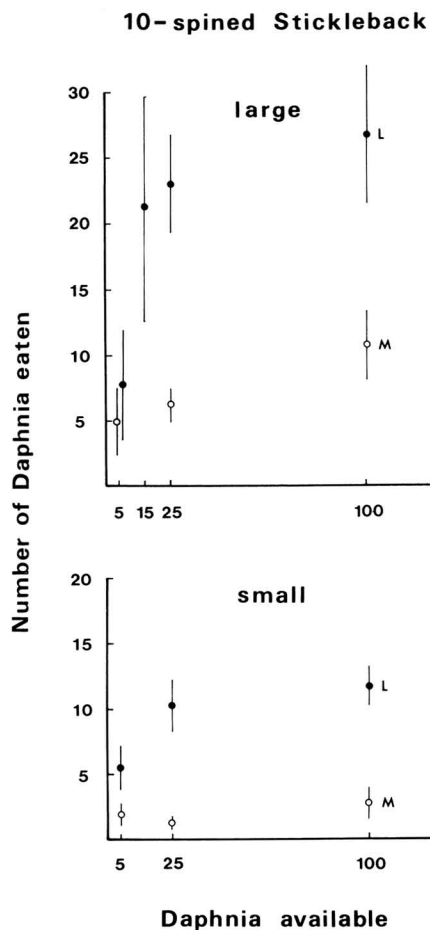


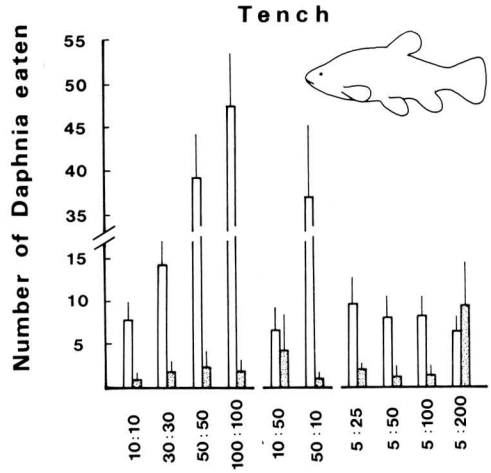
Fig. 1. Number of 2.3 mm *D. magna* (M, open circles) and 1.5 mm *D. longispina* (L, black dots) eaten (mean with two standard deviations) by large (3.9 cm) and small (2.3 cm) ten-spined sticklebacks as a function of prey density (results of 4 replicates of 5 min runs are shown).

parallel with the strike direction of the stickleback. However, *Daphnia* usually swim in an upright position and sticklebacks have to make a number of strikes to catch the prey. Energy gains from feeding on single *D. magna* and *D. longispina*, as scaled by handling times, are 0.13 J/s and 0.07 J/s, respectively, for small sticklebacks and 0.40 J/s and 0.20 J/s for large sticklebacks. Thus, all else being equal, feeding on *D. magna* is more profitable than feeding on *D. longispina*.

Our recording method does not allow accurate estimates of *Daphnia* handling times for the tench. The fish swallowed both prey sizes

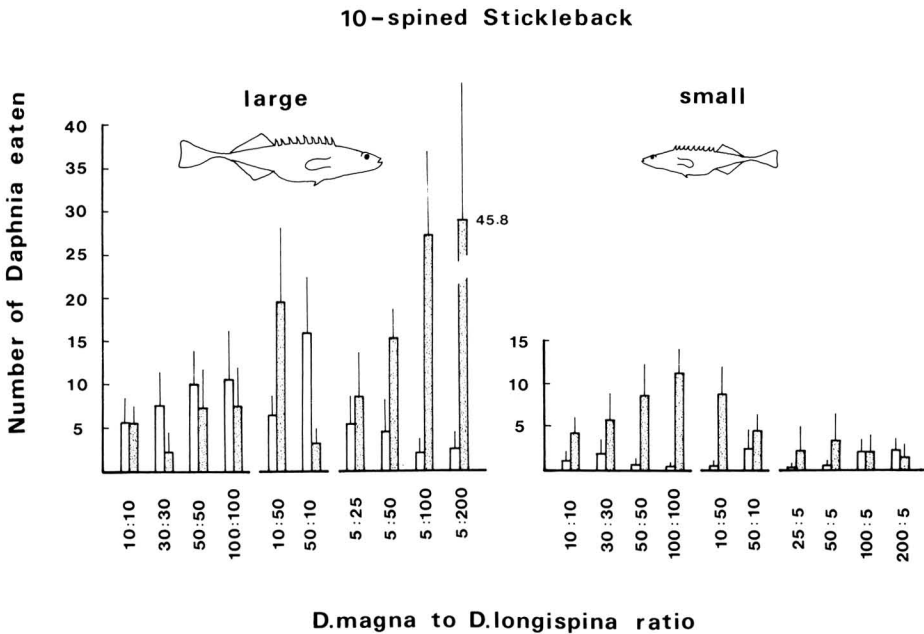
with ease and no detectable differences were observed between large and small prey. Thus, we assume that for the tench, the profitabilities of feeding on the two prey types are close to their energy contents (2.8 J for *D. magna* and 0.3 J for *D. longispina*), and therefore feeding on a *D. magna* gives c. 10 times more energy than feeding on a *D. longispina*.

In the foraging rate experiments sticklebacks fed more upon *D. longispina* than on *D. magna*. Large sticklebacks showed higher foraging rates (in numbers of *Daphnia* eaten) than small sticklebacks (Fig. 1). The observation is in accordance with the observations of *Daphnia* handling times. *D. longispina* feeding efficiency seems to reach an asymptote in prey densities between 25 and 100 prey per aquarium. With *D. magna*, no such clear functional response can be seen in large sticklebacks. In small sticklebacks difficulties in handling *D. magna* meant that they could not improve their efficiency even though prey density increased from 5 to 100 per aquarium.



D. magna to D. longispina ratio

Fig. 2. Average numbers of 2.3 mm *D. magna* (open columns) and 1.5 mm *D. longispina* (stippled columns) eaten by tench in different *D. magna* to *D. longispina* ratios (vertical bars show one standard deviation). In all two-prey ratios *D. magna* was preferred statistically significantly (*G*-tests,  $P < 0.001$ ) over *D. longispina*.



D. magna to D. longispina ratio

Fig. 3. Average numbers of 2.3 mm *D. magna* (open columns) and 1.5 mm *D. longispina* (stippled columns) eaten by large (3.9 cm) and small (2.3 cm) ten-spined sticklebacks in different *D. magna* to *D. longispina* ratios (vertical bars show one standard deviation). With the following exceptions large sticklebacks preferred *D. magna* statistically significantly (*G*-tests;  $P < 0.05$  in ratios 50:50 and 100:100, in other  $P < 0.001$ ) over *D. longispina*: 10:10, 50:10 and 5:100. In small sticklebacks preference was for *D. longispina* (*G*-tests,  $P < 0.001$ ) in all two-prey ratios.

### 3.2. Alternative prey

In the two-prey experiments, the tench preferred *D. magna* to *D. longispina* in all prey ratios and densities significantly more than expected on the basis of a random encounter hypothesis (Fig. 2). The same conclusion also holds for large sticklebacks, with a few exceptions (Fig. 3). With the small sticklebacks the results were the opposite (Fig. 3). Although the net energy gain by small sticklebacks was twice as high from feeding on *D. magna* as from feeding on *D. longispina*, small sticklebacks in the two-prey experiments ate proportionally more *D. longispina* than expected on the basis of a random encounter hypothesis.

The theory of optimal foraging (Pyke et al. 1977) states that when the abundance of a better food type in the environment reaches a certain level, the predator, foraging optimally, should concentrate solely on the better prey type. On the other hand, the 'apparent size' hypothesis (O'Brien et al. 1976, Eggers 1977, 1982) predicts a 'smoothed' change in planktivore diet width with increasing abundance of the larger food type. It follows that, according to the 'apparent size' hypothesis, the proportion of the larger prey item (*D. magna*) should increase in the fish diet as its density increases. On the other hand, if the *D. magna* densities used in our experiments were above the critical level predicted by the theory of optimal diet (see, e.g., Townsend & Hughes 1981) the fish should abruptly specialize on the energetically more rewarding *D. magna*. That is, both hypotheses predict some kind of decrease in the fishes' diet width.

Table 1 lists mean percentages of *D. magna* in the diet of the tench and sticklebacks in experiments with increasing prey density. In tench experiments the proportion of *D. magna* in the diet increases with *D. magna* density (in the 1:1 two-prey experiments) as expected. In sticklebacks, however, no such trend was observed (Table 1). In large sticklebacks the highest *D. magna* proportion (84%) eaten was in the 30:30 prey density but it decreased towards the highest prey densities. In contrast, small sticklebacks ate fewer and fewer *D. magna* as its density increased (Table 1, Fig. 3). This trend does not comply with the expectation based on net energy gain.

We compared *D. magna* percentages eaten in pairs between the different 1:1 two-prey experiments with the Mann-Whitney *U*-test. Though an increasing trend in the *D. magna*

Table 1. Percentage of *D. magna* in diets of the tench and small and large sticklebacks in the 1:1 *D. magna* (M) to *D. longispina* (L) mixed-prey experiments (mean %M of the replicate runs is given together with the standard deviation, *SD*). The *D. magna* percentages are compared in pairs using Mann-Whitney *U*-tests; test values (*z*) and corresponding probabilities (*P*) are given.

	M:L	%M	SD		<i>z</i>	<i>P</i>
Tench						
a	10:10	89	10	ab	0.213	0.416
b	30:30	89	9	ac	0.853	0.197
c	50:50	95	4	ad	0.640	0.261
d	100:100	96	3	bc	1.386	0.083
				bd	1.492	0.068
				cd	0.853	0.197
Stickleback						
small						
a	10:10	21	20	ab	0.643	0.260
b	30:30	29	24	ac	1.058	0.145
c	50:50	10	12	ad	1.512	0.065
d	100:100	4	5	bc	1.890	0.029
				bd	2.646	0.004
				cd	0.756	0.225
large						
a	10:10	48	13	ab	3.780	0.001
b	30:30	84	15	ac	1.739	0.041
c	50:50	60	14	ad	0.907	0.182
d	100:100	56	22	bc	2.570	0.005
				bd	2.684	0.004
				cd	0.416	0.339

percentage was observed in the tench, none of the differences were statistically significant at the *P* = 0.05 level (Table 1). As the trend in large sticklebacks was inconsistent with the prediction it also follows that some of the statistically significant differences (e.g., 30:30 vs. 50:50 or 30:30 vs. 100:100) are contrary to the prediction (Table 1).

With the present data no specialization on *D. magna* was found in either small or large sticklebacks (Fig. 3). Furthermore, the decreasing number of *D. magna* eaten by small sticklebacks with increasing *D. magna* abundance (Fig. 3) contradicts the prediction.

A comparison of the total numbers of *Daphnia* eaten in the two-prey experiments against the number of *Daphnia* available reveals some interesting facts. Firstly, in 1:1 prey ratios, there was a clear increase in numbers of *Daphnia* eaten by the tench with an increase in *Daphnia* availability (Fig. 4). However, no clear improvement in the capture rate was observed in the two-prey experiments where the density of *D. magna* (preferred prey) was held at 5 and that of *D. longispina* was gradually increased (Fig. 4). In sticklebacks the

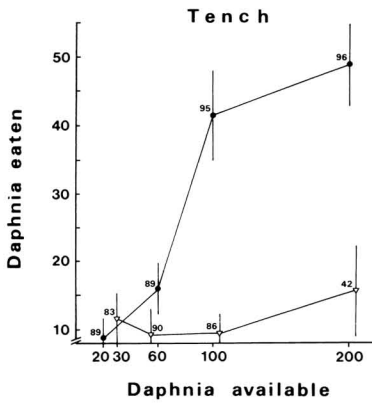


Fig. 4. Number of *Daphnia* eaten by tench (mean  $\pm$  SD of the replicate runs;  $n = 5$ ) as a function of *Daphnia* available in the two-prey experiments (black dots indicate 1:1 prey ratios, triangles are for the mixed-prey ratios where the density of the preferred prey (*D. magna*) was held constant and that of *D. longispina* was gradually increased (5:25, 5:50, 5:100, 5:200). Numbers indicate percentages of *D. magna* in the diet of the tench in the different two-prey ratios.

situation is more complex. Small sticklebacks show a foraging pattern similar to that of the tench (Fig. 5A). However, *Daphnia* foraging by large sticklebacks was more effective in the two-prey experiments (where the density of *D. magna* (preferred prey) was kept constant and that of *D. longispina* increased) than in the 1:1 two-prey experiments (Fig. 5B). Although large sticklebacks preferentially forage on *D. magna*, the percentage of *D. magna* included in the diet abruptly diminished from about 20% (5:50) to 7% (5:100) while no such sudden change in prey choice was found in either small sticklebacks or tench (Figs. 4 and 5).

This is interesting, as the stomachs of freshly caught tench from the Långskär pond were filled with 0.9 mm long *Acanthocyclops vernalis* (own observations). On the sampling day (May 26, 1983) cyclopoid density in the pond was c. 3/litre, which corresponds closely to the *D. longispina* densities (1.3–5/litre) used in the 5:50 – 5:200 *D. magna* : *D. longispina* experiments. In other words, at the same small-prey densities in the wild, tench intensively forage small prey items, while in the laboratory, when a low density of large *D. magna* was also available they continue to search for these rarities. Detailed evaluation of this result requires more specific experiments.

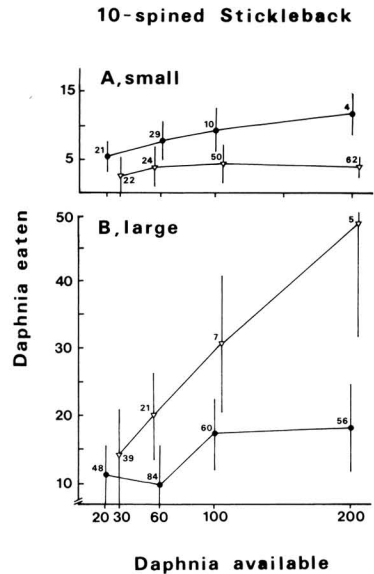


Fig. 5. Number of *Daphnia* eaten by small (A) and large (B) sticklebacks (mean  $\pm$  SD of the replicate runs;  $n = 10$ ) as a function of *Daphnia* available in the two-prey experiments (black dots indicate 1:1 prey ratios, triangles are for the two-prey ratios where the density of the preferred prey (*D. longispina* for small, and *D. magna* for large sticklebacks) was held constant (5:25, 5:50, 5:100, 5:200). Numbers indicate percentages of *D. magna* in the diet of stickleback in the different two-prey ratios.

### 3.3. Effects upon zooplankton community

In the 'community' experiments where fish were allowed to feed upon an array of plankters varying widely in size (0.2–4 mm) the tench first eliminated the largest plankters (Fig. 6) and thus caused the frequency distributions of plankter body sizes to be dominated by small plankters. The observation is in accordance with the previous results, which showed that the tench has a preference for large plankters.

In these experiments, sticklebacks foraged more upon small plankters, thus normalizing the frequency distribution of plankter body sizes (Fig. 7). With both size classes this observation contradicts the observation that they gain more energy from the larger prey (*D. magna*) than from the smaller prey (*D. longispina*).

## 4. Discussion

Both the fish species studied were clearly



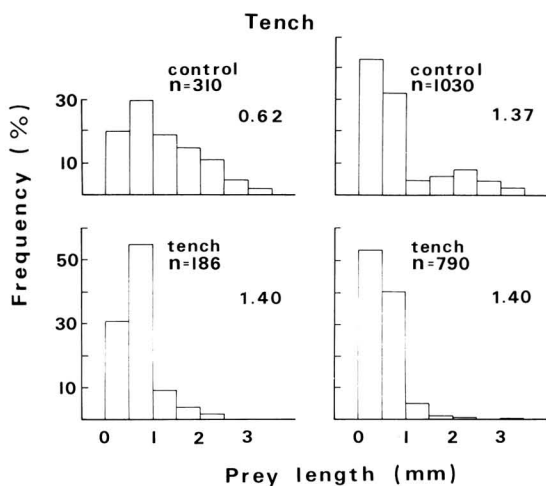


Fig. 6. Frequency distributions of zooplankter body lengths in aquaria without (control) and with tench (pooled histogram for three fish) in two 'community' experiments. The upper panels show the frequency distribution of zooplankter sizes given to the tench to feed on, and the lower panels show size distribution of plankters remaining in the aquaria after 30 min of tench feeding ( $n$  = sample size). Skewness values of the histograms are indicated.

size-selective predators. In all two-prey densities examined the tench preferred the larger *D. magna* to the smaller *D. longispina*. Similarly, large sticklebacks slightly preferred large prey. A clear contrast was observed between the diet choice of small sticklebacks in the two-prey experiments and their net energy gain while feeding on *D. magna* and on *D. longispina*. The small sticklebacks always took the less rewarding prey in a significantly higher proportion than expected on the basis of a simple random encounter hypothesis. Moreover, the proportion of *D. longispina* in their diet increased as the density of *D. magna* increased in the experimental aquarium. The observation contradicts the energy maximization expectation derived from the theory of optimal foraging (Werner & Hall 1974, Pyke et al. 1977, Townsend & Hughes 1981).

In the two-prey experiments no specialization on *D. magna* by the fishes was observed. It is likely that the prey densities used were so low that the encounter rates with the better quality prey (*D. magna*) remained below the critical limit as defined by the theory of optimal foraging. Gibson (1980) studied foraging by 4.7 cm three-spined sticklebacks (*Gasterosteus aculeatus*) on 1.4 and 2.4 mm *D.*

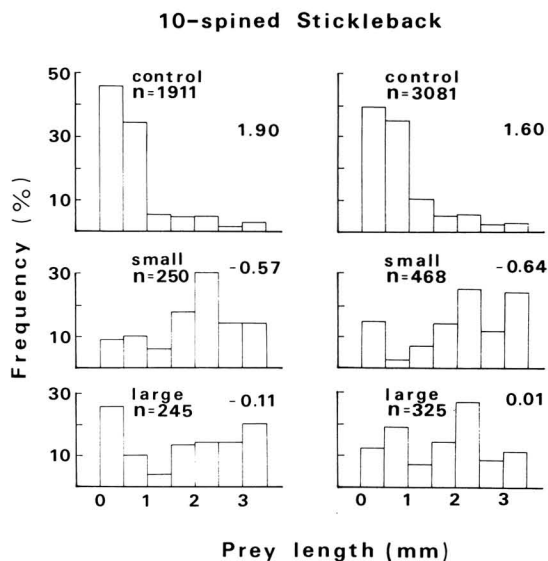


Fig. 7. Frequency distributions of zooplankter body lengths in aquaria without (control) and with small and large ten-spined sticklebacks in two 'community' experiments (in the first column two aquaria had 5 small fish each and one aquarium 3 large fish, in the second column two aquaria had 3 large fish each and one aquarium 5 small fish; histograms indicate pooled results for these aquaria). The upper panels show frequency distributions of zooplankter sizes given to sticklebacks to feed on, and the middle and lowest panels indicate size distributions of plankters remaining in the aquaria after 24 hours of stickleback feeding ( $n$  = sample size). Skewness values of the histograms are indicated.

*magna*. He calculated that the critical density of the larger prey should be much greater than in his experiments, where the maximum density of the 2.4 mm *D. magna* was 200/l. Furthermore, the studies by Werner & Hall (1974), O'Brien et al. (1976), Vinyard & O'Brien (1976), and Eggers (1977, 1982) have shown that calculating encounter rates is a tricky task because data are needed on reactive distances for both prey types, on the swimming speed of fishes, and on the shapes of visual fields.

The apparent size hypothesis (O'Brien et al. 1976; but see also Gardner 1981) says that the planktivore selects the prey item that appears to be the largest. In other words, sometimes small plankters close to the forager seem to be bigger than larger prey items further away. It follows, on the basis of the argumentation by, e.g., Eggers (1982), that with increasing density of the better prey type a gradual narrowing of the diet width is to be expected. The only statistically significant change obser-

ved was that small sticklebacks concentrated less and less on *D. magna* in the 1:1 two-prey experiments with increasing *D. magna* density. Recently Milinski (1982) demonstrated that three-spined sticklebacks (*Gasterosteus aculeatus*) preferentially foraged on familiar but less rewarding prey. Also, Furnass (1979) argues for habituation with familiar food types while explaining his 'non-optimal' results of plankton predation by perch fry.

Allowing tenches to forage for a longer time on an array of plankters varying widely in body length results in the elimination of the largest plankters. This observation is consistent with our two-prey experiments with the tench. It is also comparable to a number of other studies which have shown that vertebrate planktivores are able to change the body size distribution of plankters, viz., to cause frequency distributions of plankter sizes to be dominated by small plankters (for rock-pool newts, see Ranta & Nuutinen 1985; for other references, see the review by Zaret 1980). In contrast to these observations, our 24-hour 'community' experiments with sticklebacks resulted in a numerical dominance of plankters larger than 1.5 mm in body length. The difference between the two fish species studied most likely results from the differences in their mouth dimensions. The diameter of the large stickleback mouth averages 2.5 mm, while tenches have a mouth opening of about 10 mm. Thus sticklebacks were unable to feed on 3 mm or larger plankters.

In the long run, both the tench and sticklebacks foraging on plankton will evidently eliminate the largest plankters. With the tench

this will be accomplished fairly rapidly as they are able to ingest all plankter sizes encountered in temperate waters. This was proved in a field experiment where we introduced tench into rock-pools dominated by *D. magna* in the Tvärminne archipelago (Ranta et al., unpubl.). The experimental pools were divided into two halves, one half being the control; tench were introduced into the other half. Within about a month the tench had eliminated all plankters larger than 1 mm in body length. A longer time will be needed by sticklebacks, which would probably first eliminate 0.5–2 mm plankters. As there would be no more recruitment from these size classes, the largest size classes would age and eventually die out. This reasoning assumes that there are no refuges for the plankters, and in water bodies of the size and characteristics of rock-pools this is the case. However, in ponds and lakes, submerged littoral vegetation may serve as a sufficient refuge and fish and large plankters may coexist.

It was interesting to note that, in summer 1984, sticklebacks had managed to colonize the rock-pool from which we had collected *D. magna* for the laboratory experiments reported here. This rock-pool used to have a dense population of *D. magna* ranging from 1 to 5 mm in length (see fig. 7d in Ranta & Nuutinen 1985). As expected, the sticklebacks had managed to harvest *D. magna* to extinction.

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