

Predation by the rock-pool insects *Arctocoris carinata*, *Callicorixa producta* (Het. Corixidae) and *Potamonectes griseostriatus* (Col. Dytiscidae)

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Two corixid species (*Arctocoris carinata*, *Callicorixa producta*) and one dytiscid species (*Potamonectes griseostriatus*) are common and abundant insect predators in rock-pools on islands in the Baltic Sea. Characteristic zooplankton in rock-pools are large *Daphnia* species, whilst chironomid larvae are common benthic animals. Laboratory experiments were made to disclose the impact potential of these predatory insects on their *Daphnia* and chironomid prey.

When offered 1.7, 2.7 and 3.8 mm *D. magna* in equal abundance both the number of prey eaten and diet width increased with predator size. All species and instars examined showed higher feeding rates on small-sized *Daphnia*.

When adults of the three insect species were fed in shallow (8 cm) aquaria in separate tests either with 2.2 mm *D. magna* or with 15 mm chironomid larvae, both prey types were eaten by the corixids with about comparable feeding rates. *P. griseostriatus* exhibited higher feeding rates on chironomids. The feeding rates of over-wintered corixids were considerably lower than those of non-over-wintered adults.

When the two prey types were offered together in shallow (8 cm) aquaria all species ate significantly more chironomids than *Daphnia*. The experiment was repeated with corixids in 25 cm deep aquaria. The feeding rates on *Daphnia* were now higher in both corixid species, but the differences between *Daphnia* and chironomid feeding rates were small.

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1. Introduction

Predator-prey interactions in fresh-water habitats have received considerable attention in recent years. For the most part the research has revolved around predation by vertebrate planktivores residing in large water bodies (for a review, see Zaret 1980). On the other hand, the great majority of aquatic habitats are small fresh-water ponds and pools (Wiggins et al. 1980). With decreasing size of the water body both the significance of aquatic insects as the top-predators and the temporal instability of the habitat increase. Not very much is known about the foraging behaviour of insect predators in temporary habitats (Peckarsky 1984).

Rock-pools are small, and shallow water basins on islands of the Baltic Sea (Levander 1900, Lindberg 1944, Ranta 1982). Owing to the small size and temporal instability corixids and diving beetles constitute

major predators in rock-pools (Lindberg 1944). According to Pajunen (1977 1983), the most common and abundant of these are the corixids *Arctocoris carinata* (Sahlb.) and *Callicorixa producta* (Reut.) and a diving beetle *Potamonectes griseostriatus* (Degeer).

In the present paper we consider the role of the three species (*A. carinata*, *C. producta*, *P. griseostriatus*) in the rock-pool microcosm. Our primary interest is to uncover what kind of effects these predators have on the zooplankton size spectrum. We are also interested in prey type choice by the three species, viz., they were given an opportunity to select between zooplankton (*Daphnia*) and benthic prey (chironomid larvae). In view of the small size of the predators it is likely that water depth might have considerable effects on foraging behaviour. For this reason we have studied the effect of increasing water depth on planktonic vs. benthic prey selection by these species.

2. Material and methods

2.1. Experimental animals

The study was made at the Tvärminne Zoological Station, University of Helsinki, located on the SW coast of Finland. Islands in the nearby archipelago harbour an abundance of rock-pools. To study the animal biota in rock-pools we selected 20 rock-pools from the islands Brännskär and Långskär. These rock-pools were within the size range of 2 to 10 m² and 25 to 50 cm in depth, generally without prominent macroscopic vegetation and with a thin and loose layer of sediment. This conforms to the typical rock-pool occupied by *A. carinata*, *C. producta* and *P. griseostriatus* (Lindberg 1944, Pajunen 1977, 1979). Samples of zooplankton were taken by towing a 50 µm mesh plankton net from the bottom to the water surface. Rock-pool insects were collected by towing the net sideways for a distance of about 1 m after thoroughly mixing the water and the sediment. The samples (taken in late July, 1984) were preserved in 70% ethanol. The aim of this sampling was to obtain a snapshot picture of the animal biota cohabiting with *A. carinata*, *C. producta* and *P. griseostriatus*.

The predators for the experiments were mainly collected from rock-pools on the island of Brännskär, about 1 km east of the Zoological Station. Freshly collected insects, with food *ad libitum*, were brought to the laboratory, and sorted into groups of 5 individuals of the same species and instar. These animals were then immediately used in the experiments, which were between 25 May and 4 August 1984.

The water flea *D. magna* Strauss, collected from rock-pools on the nearby islands, was used as the plankton prey. The sizes of the experimental *Daphnia* were standardized by sieving them through a mesh series (mesh sizes 3.0, 2.5, 2.0, 1.5, 1.0, 0.5 mm; Nuutinen & Ranta 1986). In the size-selection experiments the *Daphnia* remaining on the 0.5, 1.5 and 2.5 mm mesh (*D. magna* body lengths were 1.7, 2.7 and 3.8 mm). The corresponding energy contents for the three size classes are 21, 95 and 189 µg organic carbon, and their respective swimming speeds are 17, 27 and 33 cm/min (Nuutinen & Ranta 1986). These *Daphnia* sizes were selected as they are easy to score and count by naked eye. In other experiments with *Daphnia* the specimens remaining on the 1.0 mm mesh were used (2.2 mm, 26 µg organic carbon, swimming speed 23 cm/min). Red chironomid larvae (*Camptochironomus* spp., organic carbon content 2800 µg) of length 15 mm and collected from rock-pools were used as benthic prey.

The experiments were run between 1100 and 1600 hours in a laboratory (ambient temperature 20–25°C) at a light intensity of about 200 lux. After each experimental run the animals used were released back into rock-pools. Altogether we used 590 individuals of *A. carinata* (larval stage III [body length 3.1 mm], IV [4.5 mm] and V [6.3 mm], and adults [8.7 mm]), 615 individuals of *C. producta* (larval stage III [2.8 mm], IV [3.8 mm] and V [5.2 mm], and adults [7.2 mm]), and 410 individuals of *P. griseostriatus* (larval stage II [4.0 mm] and III [6.4 mm], and adults [4.9 mm]) in our laboratory experiments [body length measurements for corixids after Pajunen (1977) and for *P. griseostriatus* after Sisula (1971)]. Depending on the date on which the experiments were made, we were obliged to use either over-wintered or non-over-wintered adults of the three species. Moreover, the daily availability of prey sizes and types somewhat affected the design of the experiments.

2.2. Experiments

Size-selective planktivory

In the size-selection experiments *D. magna* of 1.7, 2.7 and 3.8 mm body length were provided at a density of 5:5:5 per aquarium. Plastic jars (about 9×12×10 cm) were used as experimental aquaria. These were filled to a depth of 8 cm (750 ml) with rock-pool water. In the experiments five predator individuals, each of the same instar and species, were placed in the jar and *Daphnia* were poured in. The jar was covered by a plastic lid. Alongside the experimental aquaria we always maintained one control aquarium having a similar prey composition but no predators. Sixty minutes from the start of the experiment the *Daphnia* remaining in the different size classes were counted. The difference in *Daphnia* numbers between the experimental and control jars constitutes the feeding rate by the predators. In a few experiments *Daphnia* mortality occurred in the control jars at the end of runs lasting longer than 60 minutes. For this reason we restricted the duration of the experiments to 60 minutes. The consequence of this, however, was that in the smallest instars examined the number of prey eaten was too low to permit adequate statistical tests. The predators used in these experiments were the 1984 summer generation (Table 3).

We also wished to assess whether the corixids were able to distinguish between *Daphnia* with and without eggs. Trials for this experiment were run using the 2.2 mm *Daphnia*. The aquaria held 10 individuals of both *Daphnia* types (making a total of 20 *Daphnia*) and the predators tested were non-over-wintered *A. carinata* and *C. producta* adults. In the trials we used 5 individuals of predators per aquarium. The quantities of the two *Daphnia* types remaining were checked 5 hours after the start of the run. Jars without corixids were used as controls (no mortality was observed in the control jars).

Prey choice

We first examined the predation rate by adults of the three species fed with 2.2 mm *D. magna* at a prey density of 10 individuals per 750 ml water in the 8 cm deep plastic jars. Secondly, adults of the three species were fed with 10 individuals of 15 mm chironomid larvae in the same jars. Thirdly, the two prey types were provided together in the ratio of 10:10 in the 8 cm deep jars. Finally, 10 2.2 mm *D. magna* and 10 chironomid larvae were placed in 25 cm deep plastic jars (diameter 12 cm, filled with 3 l of rock-pool water). The sides of these jars were covered with black plastic. Only about 10 cm of the upper part was left uncovered. This provided gradually darkening light conditions towards the bottom of the aquarium, and caused the *Daphnia* to swim for most of the time in the uppermost water layers of the jar. A 2 cm wide strip of plastic insect netting ran from the surface to the bottom in both types of aquaria. This provided a perch and resting site for the diving insects.

The experiments were run with 5 predators per jar and the number of prey types remaining were scored after 60 minutes. Alongside the experimental runs we always maintained one control aquarium having a similar number of prey but no predators. In the 'shallow' aquarium experiments both over-wintered and non-over-wintered adults of the two corixid species were tested, while only non-over-wintered adults of *P. griseostriatus*

Table 1. Number of replicates made and insect types used in the alternative prey experiments (W = over-wintered adult generation, S = non-over-wintered adult generation, – = no experiments made).

Experiments	Predators				
	<i>A. carinata</i>		<i>C. producta</i>		<i>P. griseostriatus</i>
	W	S	W	S	
Single prey					
<i>Daphnia</i>	10	5	11	11	19
Chironomids	5	10	7	10	11
Two prey					
Shallow water	10	10	10	10	15
Deep water	–	21	–	11	–

were examined. In the 'deep' aquarium experiments only non-over-wintered adults of the two corixid species were tested (Table 1). The explanation for this heterogeneity is the poor availability of these insect types during the period when the experiments were being run.

3. Results

3.1. Fauna of rock-pools

The two corixid species were found in almost all rock-pools inspected, while the most common diving beetle species of the Tvärminne area, *P. griseostriatus*, was found less often (Table 2). The data listed in Table 2 show that in these rock-pools the prey animals *Daphnia* and chironomid larvae were widely distributed and abundant. They also frequently coexist with the rock-pool insect predators examined in this study. Other taxa, with the exception of copepods, occurred more sparsely and less abundantly.

3.2. Size-selective predation

All the predator species and instars examined proved to have their highest feeding rates in the smallest *Daphnia* size class (Fig. 1). A comparison of the observed numbers eaten against the 1:1:1 ratio expectation permits rejection of the null hypothesis of

Table 2. Occurrence of the three predator species [*A. carinata*, *C. producta* and *P. griseostriatus*; larvae (L) and adults (A) are treated separately] in 20 rock-pools (size range 1.5–10 m²) together with other animal taxa inhabiting rock-pools. The abundance of the taxa are scaled as follows: – = not found, 1 = 1–5 individuals in the sample, 2 = 6–50 individuals and 3 > 50 individuals (*n* = number of rock-pools with occurrences).

	Rock-pools 1–20																			<i>n</i>	
<i>A. carinata</i> L	1	2	2	1	1	1	1	1	–	–	1	–	1	–	–	2	–	1	1	1	14
<i>A. carinata</i> A	2	2	1	1	1	1	–	1	1	1	1	1	1	–	2	–	1	1	1	–	16
<i>C. producta</i> L	2	–	1	–	2	1	1	2	–	1	–	1	1	2	1	2	2	1	1	–	15
<i>C. producta</i> A	1	2	2	1	1	1	1	1	–	–	1	–	1	–	–	2	–	1	1	1	14
<i>P. griseostriatus</i> L	2	1	–	–	–	1	1	–	–	–	–	–	–	–	2	–	2	–	–	–	6
<i>P. griseostriatus</i> A	1	1	1	–	–	1	–	–	–	–	–	–	–	–	1	–	–	1	–	–	6
<i>Daphnia magna</i>	3	–	1	–	2	–	2	–	3	3	2	3	3	1	–	–	–	–	–	–	10
<i>D. longispina</i>	–	–	–	–	3	–	3	2	–	–	–	–	–	3	3	3	3	3	3	3	10
<i>D. pulex</i>	–	–	3	3	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Chironomidae L	3	2	1	2	1	1	2	2	2	–	1	2	3	2	1	2	2	1	1	–	18
Copepods	2	3	3	–	2	1	2	–	3	3	3	3	3	2	3	3	2	2	2	2	18
<i>Chydorus</i> spp.	1	3	2	–	–	2	3	–	–	–	–	–	2	–	1	1	2	–	2	–	10
Oligochaeta	–	1	–	–	–	–	–	–	1	1	1	2	3	–	–	–	1	1	1	–	9
<i>Sca. mucronata</i>	–	–	–	2	2	1	–	1	–	–	–	–	–	–	–	–	–	–	2	1	6
<i>Gammarus duebeni</i>	2	–	–	–	–	–	1	–	–	3	2	–	–	–	–	–	–	–	–	–	4
<i>Polyphemus</i> sp.	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3
Hydracarina	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3
Dytiscidae spp.	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	2
Culicidae L	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	2
Limnophilidae L	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2

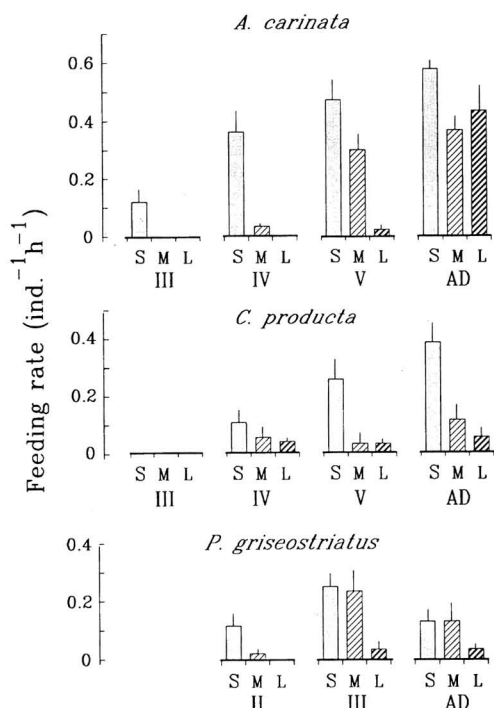


Fig. 1. Size selective zooplankton predation by *A. carinata*, *C. producta* and *P. griseostriatus*. Feeding rates (mean \pm SE) are given as *Daphnia* eaten per individual within a time span of 60 min. In the experiments three different *Daphnia* size classes (S = 1.7 mm, M = 2.7 mm and L = 3.8 mm) were used. Adults and three larval instars (III, IV, V) were tested in corixids, and adults and two larval instar (II, III) in *P. griseostriatus*.

random feeding, with the exception of *A. carinata* adults and IV-instar larvae of *C. producta* (Table 3).

It is known that the swimming activity of *Daphnia* increases with body size (Nuutinen & Ranta 1986). Consequently, a predator encounters *Daphnia* of different sizes with different frequency. The encounter rates should therefore be weighted with the corresponding *Daphnia* swimming activities. Independently of the method of deriving the null expectation, small-sized *Daphnia* are eaten more often than expected due to chance (Table 3).

Despite repeated attempts with the 3rd instar larvae of *C. producta* these had very low feeding rates on *Daphnia*. It required 90 individuals in 18 tests (lasting 5 h each) for a total of 3 *Daphnia* eaten to be observed (Table 3). The reason for this low feeding rate is either that *D. magna* of the size used in our experiments are too large for such small (body length

2.8 mm) predators (most likely), or that the 3rd instar *C. producta* are not plankton predators at all (less likely).

There is a positive correlation between the body size of the predator and the proportion of the two largest *Daphnia* size classes in the diet (Spearman rank correlation $r_s = 0.6$, $P < 0.05$ [the 3rd instar of *C. carinata* not included]). Also, larger predators have higher feeding rates on *Daphnia* (Fig. 1).

In the 5 h experiments with *Daphnia* as prey with and without eggs, and with the non-over-wintered corixid adults as predators we obtained the following results:

	'without'	'with'	n	G	P
<i>A. carinata</i>	54 (56%)	43 (44%)	11	1.25	0.264
<i>C. producta</i>	43 (61%)	28 (39%)	16	3.19	0.074

In other words, both predators clearly do not prefer egg carrying *Daphnia*.

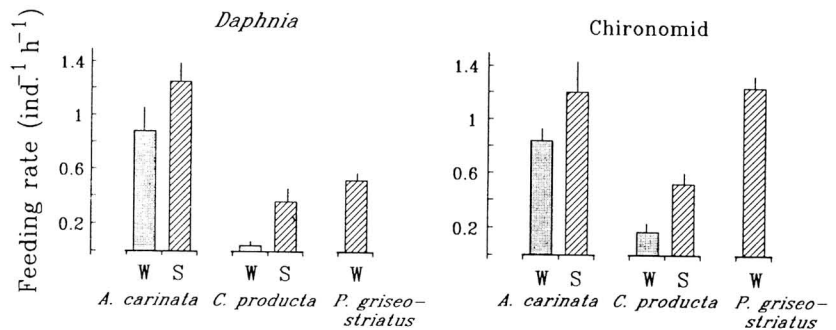
We analyzed the organic carbon contents (Salonen 1978) of 2.2 mm and 3.8 mm *Daphnia* after adult corixids had imbibed the extractable body fluids from them. *A. carinata* is able to extract 46% ($n = 43$) of the carbon in 2.2 mm *Daphnia* and 59% ($n = 40$) in 3.8 mm *Daphnia*. The corresponding values for *C. producta* are 69% ($n = 40$) and 60% ($n = 31$). The differences between species are statistically non-significant.

Assuming that these insects are able to extract about 60% of organic carbon from the *Daphnia* body independent of *Daphnia* size makes it possible to calculate the amount of biomass (in terms of organic carbon) eaten per hour. The 60% extraction efficiency parallels that observed with other aquatic insects: 60% efficiency in *Ranatra dispar* (Bailey 1986), 55–77% in *Notonecta* (Fox & Murdoch 1978), 86% in *Dytiscus fasciventris* (Kruse 1983). It follows that in the two corixid species biomass eaten per hour increases with body size, while in *P. griseostriatus* the adults obtained about 36% less biomass compared to the 3rd instar larvae (Table 3).

3.3. *Daphnia* and chironomids as alternative prey

The experiments in which adults of the three species were fed with a single prey type in separate tests lead to the following conclusions. Firstly, both prey types were eaten with comparable feeding rates (Fig. 2). The only exception is *P. griseostriatus*, which feeds on chironomids to about three times the extent

Fig. 2. Feeding rates (see Fig. 1) on *Daphnia* and chironomids (mean \pm SE) by adults (W = over-wintered, S = non-over-wintered) of *A. carinata*, *C. producta* and *P. griseostriatus* in shallow water (8 cm) tests when the two prey types were given in separate experiments.



to which it consumes *Daphnia* (t -test, $t = 6.035$, $df = 28$, $P < 0.001$). Secondly, in terms of the numbers of prey eaten per hour *A. carinata* ranks first, while *C. producta* is the least effective (Fig. 2). Thirdly, the numbers of prey eaten by non-over-wintered corixid adults exceed the feeding rates by over-wintered adults on both prey types (Fig. 2). However, the difference with *Daphnia* as prey is not significant in *A. carinata* (t -test, $t = 1.27$, $df = 13$, $P > 0.1$).

When the two corixid species and the beetle species were offered a choice between *Daphnia* and chironomid larvae they always ate more chironomids in the shallow aquaria (Fig. 3, t -tests, always at least $P < 0.05$). This test was repeated with non-over-wintered corixid adults in 25 cm deep aquaria. The increased water depth greatly reduced feeding rates on chironomids (*A. carinata*, $t = 13.021$, $df = 29$, $P < 0.001$; *C. producta*, $t = 7.683$, $df = 19$, $P < 0.001$). No

Table 3. Number of different-sized *D. magna* eaten by rock-pool insects during the 1st hour of the experiments (n = number of replicates). Numbers in brackets for *C. producta* 3rd instar refer to *Daphnia* eaten during 5 h. The observed numbers are compared with G -tests against two null hypotheses, Gr = size classes are eaten in a 1:1:1 ratio, Ga = corrects encounter expectations with moving activities of different-sized *D. magna* (Table 1), $df = 2$ in all comparisons (critical values are $P_{0.05} = 5.99$, $P_{0.01} = 9.21$, $P_{0.001} = 13.82$). In the cases where the expected values do not fulfil the requirements of the G -test (Sokal & Rohlf 1981) no test is made (indicated by -). The estimate of organic carbon obtained ($\mu\text{g C/h}$) is based on the assumption that the predators can extract 60% of the energy from a *Daphnia* of a given size (see text).

Predator & instar	Prey: <i>D. magna</i>	<i>n</i>	body length (mm)			<i>Gr</i>	<i>Ga</i>	Carbon μg C/h
			1.7	2.7	3.8			
<i>A. carinata</i>								
adult		11	32	20	23	3.01	15.90	76
V		10	24	15	1	26.13	43.98	75
IV		12	22	2	0	37.92	55.59	7
III		14	8	0	0			
<i>C. producta</i>								
adult		12	23	7	3	19.41	36.08	17
V		12	15	2	2	16.08	27.00	9
IV		11	6	3	2	–	–	0.2
III		18	(2)	(1)	(0)			
<i>P. griseostriatus</i>								
adult		17	12	12	3	7.04	14.24	14
III		10	13	12	2	10.20	18.71	22
II		10	6	1	0	–	–	3

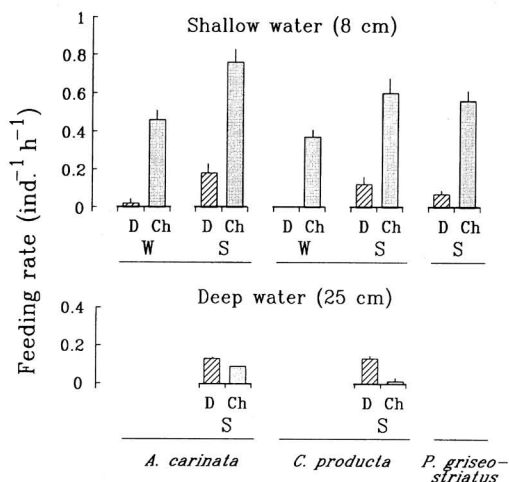


Fig. 3. Feeding rates (see Fig. 1) on *Daphnia* (D) and chironomids (Ch) (mean \pm SE) by adults (W = over-wintered, S = non-over-wintered) of *A. carinata*, *C. producta* and *P. griseostriatus* when the two prey types were offered simultaneously. The experiments were run both in shallow and deep water with non-over-wintered corixid adults.

such differences were observed in the feeding rates on *Daphnia* (Fig. 3). The drop in feeding rates on chironomids results from an apparent switch to feeding on *Daphnia* in deeper water.

In the shallow aquarium experiments the feeding activity of non-over-wintered corixid adults was higher (this holds true for both prey types, *t*-tests, always at least $P < 0.05$) than the feeding activities of over-wintered adults (Fig. 3A).

The corixids are able to extract 64% ($n = 32$) of the organic carbon from a chironomid larva. This makes about 1800 $\mu\text{g C/h}$ for feeding on one chironomid, while their energy gains were 12–18 $\mu\text{g C/h}$ when feeding on a 2.2 mm *D. magna*. In terms of energy extracted, corixids feeding on a chironomid larva acquire about twice as much energy than they do when they prey on a water flea. Multiplying the observed numbers of *Daphnia* and chironomid larvae eaten by their corresponding energy rewards indicates that *Daphnia* are of very much minor importance as a food for the corixid species (Table 4). The difference in the chironomid feeding rates of corixid adults in shallow and deep water results in a considerable drop in their energy intake (Table 4) in deep water.

Table 4. The amount of organic carbon extracted ($\mu\text{g C/ind./h}$) by the predators in the alternative prey experiments. The estimates are based on the assumption that the predators are able to extract 60% of organic carbon from *Daphnia* and 1800 $\mu\text{g C/h}$ when feeding on a chironomid larva (see text). Over-wintered adults are referred to as W, non-over-wintered as S.

Adult type	<i>Daphnia</i>	Chironomid
One prey type available		
<i>A. carinata</i> W	13	1410
<i>A. carinata</i> S	19	2020
<i>C. producta</i> W	1	286
<i>C. producta</i> S	6	874
<i>P. griseostriatus</i> W	8	2080
Both prey types available simultaneously		
Shallow water		
<i>A. carinata</i> W	1	773
<i>A. carinata</i> S	3	1277
<i>C. producta</i> W	0	622
<i>C. producta</i> S	2	1008
<i>P. griseostriatus</i> W	1	740
Deep water		
<i>A. carinata</i> S	2	151
<i>C. producta</i> S	2	17

4. Discussion

It is an established fact that *A. carinata*, *C. producta* and *P. griseostriatus* are voracious predators which feed on a wide variety of prey types available in the rock-pools, including even smaller conspecifics (Lindberg 1944, Pajunen 1983, Pajunen & Ukkonen 1987). The present data clearly demonstrate that the rock-pool predator insects are size-selective. In all species and instars examined feeding rates were highest on the smallest *Daphnia* size classes. In Zaret's (1980) terminology they conform to size-dependent predators. In the present case it is obvious that *Daphnia* of the largest size class (3.8 mm) effectively manage to escape many of the capture attempts by approaching predators. The smallest predator able to feed on them is the 4th instar *C. producta* larva (3.8 mm). The finding that the prey size spectrum used increases with increasing body size parallels observations on *Notonecta* (Sih 1981, Scott & Murdoch 1983).

Rock-pools on the Baltic Sea islands harbour three species of *Daphnia* (Ranta 1979, Pajunen 1986, Bengtsson 1988). According to Bengtsson (1986) minimum juvenile and adult sizes of the species are

D. longispina 0.6 and 1.4 mm, *D. pulex* 0.6 and 1.5 mm and *D. magna* 0.8 and 2.4 mm. A comparison of these sizes to those used in the size selectivity experiments and to the results obtained suggests that juvenile stages of all three *Daphnia* species are vulnerable to corixid and *Potamonectes* predation. With the reproductive *Daphnia* it is obvious that *D. magna* is the species least affected by these predators.

According to a survey by Ranta and Pajuniemi (unpubl.) *Daphnia* species are by far the most common and abundant meso-zooplankton taxa in rock-pools. The population densities of *D. magna* and *D. longispina* score an average index value of 40, whilst the smaller cladocerans (*Eubosmina*, *Alona*, *Alo-nella*) score density index values of from 0.01 to 7. It is tempting to suggest that the documented preference by the rock-pool predator insects make *Daphnia* the most common and abundant meso zooplankton taxon in these pools.

When given a choice between plankton prey and bottom dwelling prey all the predator types fed markedly more on chironomid larvae than on *Daphnia*. This conforms to earlier knowledge (Lindberg 1944, Pajunen 1983). In terms of energy, feeding on chironomids is 2 to 3 orders of magnitude more profitable than feeding on *Daphnia*. Despite this large difference in energy returns the predators also ate some *Daphnia*.

The feeding rate of over-wintered corixids is markedly lower than that of the non-over-wintered individuals. A tentative explanation for this difference could be higher energy needs on the part of the newly hatched adults in conjunction with the development of flight muscles and sexual maturation. It is also possible that these corixids already build up their energy reserves (e.g., brown fat) in the autumn ready for over-wintering and egg laying the next spring.

Corixid adults are less efficient predators on bottom-living chironomid larvae when the water depth is increased from 8 to 25 cm. This small difference led to about a 90% reduction of feeding rates on chironomids. According to Pajunen (1979: 139) 62% of rock-pools ($n = 538$) on four islands in the Tvärminne archipelago have a maximum depth of 9 cm or less, and only 8% of them have a maximum depth of ≥ 25 cm. The water depths used in our experiments are thus fairly realistic. Whether the observed difference in chironomid feeding rates is due to capture difficulties in the deep water, to decreased encounter rates, or to surface water dominated time usage by the corixids, remains to be checked by further studies. However, this observation suggests that corixids

should concentrate their foraging on chironomid larvae in shallow water. It would be more advantageous for chironomid larvae to reside in the deeper parts of corixid inhabited rock-pools.

A switch in foraging behaviour due to changes in prey availability is by no means uncommon in aquatic insect predators. Formanowicz (1982) observed that larvae of a diving beetle, *Dytiscus verticalis*, changed from active seekers to 'sit and wait predators' when prey densities increased. Similar observations are documented for odonate larvae (see Peckarsky 1984 for a review). An observation paralleling our findings is reported by Cockrell (1984), who was able to show that *Notonecta glauca* had higher feeding rates on benthic prey compared to plankton prey in shallow (8 cm) aquaria. Increasing the water depth to 28 cm forced them to concentrate more on planktonic prey. In Cockrell's experiments *Notonecta* spent a higher proportion of their time close to the bottom in shallow aquaria than they did in deep water.

It is a widely supported fact that invertebrate predators are capable of affecting their prey populations (reviews in Zaret 1980, Peckarsky 1984). For example, *Hygrobat* water mites may reduce chironomid population densities in lake sediments to 80% compared to mite-free control areas (Winkel 1985). The size spectrum of zooplankton is observed to switch towards a larger size in acidified lakes in Sweden, where corixids and *Chaoborus* are the new top predators (Henrikson & Oscarson 1981, 1985, Nyman et al. 1985). It was shown by Dodson (1974) that *Chaoborus* are able to decimate their *Daphnia* prey populations in small ponds. Scott & Murdoch (1983) demonstrated the same pattern in small tanks with *Notonecta* as predator.

In view of the small population size of corixids and *Potamonectes* relative to population sizes of the rock-pool *Daphnia* it is less likely that they could decimate the *Daphnia* populations. Experimental field manipulations in the Tvärminne rock-pools by Pajunen and Salmi (pers. comm.) demonstrate that at the beginning of the second half of the summer, when corixid larval populations (especially the late stages) are at their highest, corixids are able to decimate their chironomid larval prey populations.

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