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Prey selection by larvae of Potamonectes griseostriatus (Degeer) (Coleoptera, Dytiscidae)

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Predation by *Potamonectes* larvae was investigated in temporary rock pools. Of 350 prey individuals collected, 84 % were chironomid larvae and 8 % Potamonectes larvae. The main factor influencing prey selection was the ability of other prey types to escape approaching predators. Successive developmental stages of the predator preferred different size classes of prey, small individuals being reluctant to attack large prey. Chironomid larvae in bottom sediment were not attacked. Prey refuges and cannibalism contribute to the stability of predator-prey interaction.

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1. Introduction

The temporary rock pools of the outer archipelago of the Baltic represent structurally simple ecosystems. Although one can detect differences between neighbouring rock pools and successional series of pool types have been described (Levander 1900, Lindberg 1944, Forsman 1951), a single rock pool is hardly more complex than a laboratory aquarium. This simple environment offers good opportunities to study the relationship between stability and complexity of ecological systems. The heterogeneity of a rock pool environment increases stepwise as one compares the processes occurring in a single pool with those occurring on a wider scale. The component processes of interaction are thus easy to analyse. Two species can be in non-equilibrium interaction at one level and the stabilizing mechanism can act at another. Competition between rock pool corixids (Pajunen 1979a, b, 1982) is an example of this type.

Potamonectes griseostriatus (Degeer) is an important predator, inhabiting a variety of rock pool types. The adults have considerable powers of dispersal and they can use resources available in several pools. The larvae, on the other hand, must rely on local resources for completion of development. This paper describes the predation and prey selection by *Potamonectes* larvae, with special emphasis on the stabilizing processes occurring at the level of single rock pools.

2. Material and methods

The field work was carried out at Tvärminne Zoological Station on the southern coast of Finland in 1979-81. The main part of the material was collected in late June and early July, when larvae of all size classes were found simultaneously. The study area and the rock pool environment have been described by Pajunen and Jansson (1969).

The larvae were observed visually and magnifying glasses were used to examine the small larvae. A larva consuming its prey had a charcteristic posture and could be distinguished even when the prey was not immediately visible. With some practice, the larva could be compelled to swim upwards from the bottom and it could then be captured without disturbing the loose bottom sediment. The material was preserved in ethanol.

An attempt was made to investigate rock pools of different types in a random manner, but deep pools and those with cloudy water were difficult to study effectively. The material collected thus represents a rought average of prey consumption in shallow, clear-water rock pools,the principal habitat of the species.

The size of *Potamonectes* larvae was assessed by measuring the breadth of the head immediately behind the ocelli. The clear trimodal frequency distribution allowed precise identification of the three larval stages. The geometric mean of maximum length and breadth of the head capsule was used as the index of size for the main prey type, chironomid larvae.

3. Results

3.1. Predation behaviour

Potamonectes larvae search for the prey by walking along the bottom sediment and the rocky sides of the pools. Periods of stationary waiting often intersperse bouts of activity. During development the proportion of active search increases markedly. Small first-stage larvae seem to remain stationary most of the time, whereas the last-stage larvae are almost constantly active and spend a considerable amount of time in investigating crevices in the rock and solid objects on the bottom sediment. The larvae can change location by swimming. Their course is then straight and they do not seem to react to other swimming animals. Nevertheless, some instances of successful prey capture by swimming larvae have been observed.

Some larvae remain burrowed into the bottom sediment. Their behaviour was difficult to observe. There was no indication of their moving longer distances in the sediment and it is assumed that they were resting or consuming prey captured on the surface of the sediment.

A larva reacts to moving animals in its immediate vicinity; even chironomid larvae moving inside their tubes can trigger an attack. Prey coming inside the immediate striking distance triggers a biting reaction. No conspicuous attack movement is made and escaping prey is not pursued. At least under laboratory conditions, a larva may bite an approaching animal larger than intself but immediately releases its grip and retires. Simultaneous attack followed by immediate escape reactions usually occur when two *Potamonectes* larvae of about equal size meet. Small larvae tend to avoid the apporach of larger larvae.

The captured prey is held by the mandibles and the larva assumes the characteristic posture: the head is bent slightly upwards and the tip of the abdomen raised. The larvae with prey appear to remain stationary, but they evidently retreat to shelter when disturbed by other larvae. The handling of prey is a prolonged process, taking at least 10–20 minutes under laboratory conditions. In spite of this, larvae with prey were found infrequently, an hour's search yelding some 10–15 individuals, mostly with freshly caught prey. Cases of two larvae contesting a prey animal were rare.

3.2. Types of prey

The material collected consisted of 350 prey individuals. Most of them were freshly caught and contained undigested tissues. The frequencies of different types are given in Table 1. Nearly all animals in the rock pools seem to be attacked, provided they are of suitable size. In addition to animals living on the bottom sediment, the prey included animals living in the bottom sediment as well as planktonic forms. Thus, the actual availability of prey types cannot be directly compared to their abundances. Direct observation suggested that the relative availability of prey types on the bottom sediment varies much less than their frequencies among prey, and that the main factor influencing prey frequencies was the ability to escape predation. Chironomid larvae were vulnerable only when moving on the surface of the sediment or swimming near the bottom, but they did not react to approaching predators and could not escape by swimming. On the other hand, small corixid larvae reacted to all approaching larger animals and changed their resting sites before the potential predator came within striking distance. Plankton seldom descended near the bottom and many species reacted to the approach of larger animals with sudden escape movements.

Table 1. The percentage of prey types in the sample of 350 prey individuals.

Chironomid larvae	83.7
Potamonectes larvae	8.3
Daphnia longispina and *D. magna*	3.1
Chironomid pupae	2.0
Corixid larvae	0.6
Others	2.3

Only one larva of *Limnephilus vittatus* (Fabr.) was included in the material. Contacts between *Limnephilus* and *Potamonectes* larvae were frequent, but the trichopteran larval case effectively prevented successful attacks.

Chironomid larvae form the main group of bottom fauna in the rock pools. Samples of 10 × 10 cm of bottom layer contained up to 80 individuals in the most intensely investigated pools and densities can be locally much higher. Lindeberg (1958) reported daily emergence of up to 1000 adults per m^2. The majority of larvae live in the bottom sediment, many species in larval tubes, and are vulnerable only when changing site by swimming. Although their high frequency among prey can be connected to lack of escape behaviour, their capture and handling by *Potamonectes* larvae is quite stereotyped and suggests some specialization to this prey type. The first bite seems to be directed near the head of the prey and the tissues in the head region are consumed first. Of 293 chironomid larvae obtained, 192 showed localized signs of feeding. In 63 % only the head part was consumed, in 25 % both the head and tail regions contained dissolved tissue, and in 12 % damage was restricted to the caudal part. In 101 larvae, feeding had either progressed too far for precise analysis or no signs of feeding could be detected.

Table 2. The developmental stages of predators and conspecific prey. Five of the killed last-stage larvae were newly moulted.

Predator	Prey			
	1st	2nd	3rd	Total
1st	1	–	–	1
2nd	11	2	–	13
3rd	4	3	8	15
Total	16	5	8	29

3.3. Cannibalism

The incidence of intraspecific predation was high, but this was not surprising with regard to the simultaneous attacks frequently observed when two larvae met. Now and then such an encounter is bound to end in success for one of the antagonists. Table 2 gives the developmental stages of predator and prey.

In all cases of cannibalism, the predator was larger or at same developmental stage as its prey. In six cases the prey was newly moulted and still soft, five of the cannibalized last-stage larvae being of this type. The material is scanty, but seems to indicate that the second-stage larvae were more efficient than the last-stage larvae in capturing the first-stage larvae. It is possible that the second-stage larvae, being smaller, do not trigger escape reactions as easily as larger individuals. Another factor may be the difficulty in handling small prey.

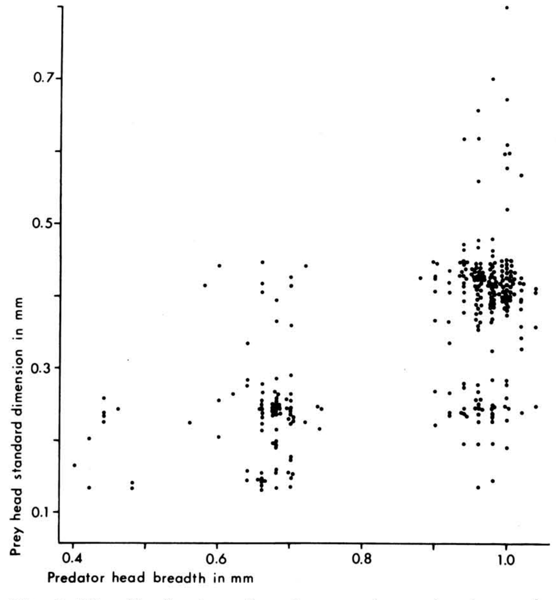

Fig. 1. The distribution of predator and prey head capsule sizes. The standard dimension is the geometric mean of maximum head capsule breadth and length.

3.4. Size-dependent prey selection

The number of chironomid species inhabiting rock pools is considerable (Lindeberg 1958). They have four larval stages and, consequently, a wide range of prey sizes is available. Laboratory experiments suggested that *Potamonectes* larvae were reluctant to attack the largest chironomid larvae encountered. This indicates that the predators recognize the size of the prey and make size-dependent selection.

The distribution of sizes of predators and captured chironomid larvae are given in Fig. 1. As only preserved material was available, chitinous structures were used as size indicators and a considerable amount of information was lost. An attempt was made to diminish the effect of species-specific differences in the prey head capsule by using the geometric mean of maximum length and breadth. The prey appears to fall into distinct size classes. This suggests that the first larval stages of large species of Chironomidae are the same size as later larval stages of the smaller species. There appears to be a clear size-dependent prey selection. Large prey is attacked only by last-stage *Potamonectes* larvae, and the small predators prey only on the two smallest prey size classes. The frequencies of prey size classes differ significantly. When prey larger than 0.5 mm are excluded, prey larger than 0.3 mm comprises 77 % of the diet of third-stage larvae but only 16 % of the diet of second-stage larvae.

The actual availability of prey of differing size is not known, but a rough comparison can be made with bottom samples collected from the six rock pools most intensely studied in early July. The pooled material contains 425 chironomid larvae; their size distribution is given in Table 3. The two median size classes dominate. The frequency of smallest larvae is certainly underestimated, however, as they tend to remain on the surface of the bottom sediment and are easily induced to swim.

4. Discussion

The results support the generally held opinion that dytiscid larvae are polyphagous predators. The high frequency of chironomid larvae in the diet of *Potamonectes* larvae is obviously the result of their being so vulnerable when migrating. Other

Table 3. Percentage distribution of head capsule size (mm) in 450 chironomid larvae collected from the six most intensely studied rock pools.

Class limit	0.10	0.15	0.20	0.25	0.30	0.35	0.40	0.45	0.80
Percent		6.6	4.5	33.0	8.0	2.6	11.1	34.0	0.2

potential prey types demonstrate efficient escape behaviour, rely on protective structures, or are so large that the predators do not attack. Chironomid larvae in their larval tubes or when moving in the bottom sediment are also relatively safe from predation by *Potamonectes* larvae. There are observations of large larvae trying to attack chironomid larvae in their tubes, but such attacks were only exceptionally successful.

Lindberg (1944) studied the predator-prey interactions of rock pool arthropods by offering different types of prey to solitary predators in small glass jars. The size of the jars probably precluded normal escape movements and *Potamonectes* larvae successfully attacked almost all small arthropods including *Daphnia* and small corixid larvae. Larger corixid larvae and *Gammarus duebeni* Lillj. individuals larger than the predator were not attacked. The laboratory studies thus seem to confirm the significance of prey size.

The behaviour of adult *Potamonectes griseostriatus* is flexible. They spend considerable periods moving along the bottom sediment and can bury into it, but they also swim readily. The great mobility of adults makes direct observation difficult and only large-sized prey such as chironomid larvae are easy to identify. The laboratory studies by Lindberg (1944) suggested that the diets of adults and larvae are qualitatively similar. However, the adults can capture prey while swimming and the diets can thus differ quantitatively. The adults can also leave the pools when prey becomes scarce. The larvae are thus more sensitive to local food shortages and differences in prey selection between adults and larvae are advantageous.

The present results suggest that even at the level of single rock pools there exist factors contributing to the stability of *Potamonectes griseostriatus* and its prey populations. The principal prey has at least temporary refuges and alternative prey types demonstrate behavioural or structural adaptations, making them invulnerable. A contributory factor is the rapid growth and recruitment of chironomid populations. The number of species is considerable and their successive generations overlap. New small larvae are thus recruited almost continuously. The interval between successive prey generations also seems to be shorter than that of predator generations.

Cannibalism also seems to contribute to the stability. During high population density, nearly 10 % of the prey consists of conspecific individuals, and so this may be an important limiting factor. When the principal prey becomes scarce, the incidence of cannibalism presumably increases, curtailing further increase in larval density. Cannibalism is relatively common in aquatic environments (Fox 1975, Polis 1981). It is suggested as the main limiting mechanism in rock pool corixids (Pajunen 1977, 1982). In the fragmented rock pool environment, rapid limitation of larval numbers is particularly advantageous, as developing individuals must rely on local resources during development. Furthermore, cannibalism favours the oldest larvae, i.e. those completing development more rapidly. On the other hand, cannibalistic population limitation has a built-in time lag, which often leads to cyclic fluctuation in numbers.

Potamonectes griseostriatus can be regarded as inefficient predator. Another species, which would also exploit chironomid larvae living in the bottom sediment could obviously attain considerably higher densities, but it would presumably deplete prey polulations, causing at least marked fluctuations in the system. *Potamonectes* larvae thus represent a kind of 'prudent' predator (Slobodkin 1961, 1974, Wilson 1978) in its simplest form.

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