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Intra- and interspecific predation in rock-pool corixids (Hemiptera, Corixidae)

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The efficiency of intra- and interspecific predation by adults and the later larval stages of *Arctocorisa carinata* and *Callicorixa producta* was studied in the laboratory using 1st- and 2nd-stage larvae as prey. Animals which had been killed had characteristic punctures on their dorsal sides.

The efficiency of individual predators varied greatly. The average attack rates were low, but *A. carinata* was significantly more efficient than *C. producta.* No differences were found between the two last larval stages and adults of the species studied. The predator functional response appeared to be linear over the prey density range recorded in the field. Predator density had no effect on the attack rate.

Larvae of *C. producta* were the more vulnerable to attack, but no differences could be detected between 1st and 2nd larval stages of any one species. It is assumed that the difference between the two species is due to differences in evasive prey behaviour.

In field conditions the mortality of small larvae is correlated with the density of larger individuals. The attack rates observed in the laboratory are sufficient to explain the observed patterns of mortality. Cannibalism is potentially an important mechanism of population limitation in the rock-pool environment.

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1. Introduction

In rock-pool populations of the corixids *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.) the numbers of larvae show a regular fluctuation. As the minimum numbers of small larvae occur when the numbers of 4th- and 5th-stage larvae are greatest, it was assumed (Pajunen 1977) that the larger larvae interfered with the growth of small larvae or were cannibals. Although many aspects of corixid ecology in rock-pools can be studied by direct observation, the small size of the first larval stages makes observation of predation difficult. Therefore, a laboratory study was necessary.

Cannibalism is an extreme form of social dominance, in which the predator, usually larger in size than the prey, totally inhibits the use of resources by another conspecific individual by killing it. In addition to obtaining food, the predator secures additional resources for its future use. The widespread occurrence of cannibalism (Fox 1975a, Polis 1981) is thus understandable. Social dominance and other types of unequal resource allocation also contribute to the stability of populations (Łomnicki 1978, 1980).

When two related species share a habitat, interspecific and intraspecific predation may occur simultaneously. Their effects are often difficult to separate, and they can, at least temporarily, place the populations under a common limiting mechanism. The two rock-pool corixids show a complete habitat overlap. *A. carinata* is the more dominant competitor, but the heterogeneous and fragmented environment allows *C. producta* to persist as the fugitive species (Pajunen 1979a, 1979b, 1982). Differences in cannibalistic behaviour might explain the observed differences in competitive ability.

2. Material and methods

Mature adults were collected from rock-pools and batches of oviposited eggs were allowed to develop in the laboratory. Hatched larvae were removed daily and reared in aquaria containing pool water and sieved pool detritus. The larvae were fed on frozen chironomid larvae. The cultures were handled as described by Pajunen & Sundbäck (1973). The 1st- and 2nd-stage larvae used as prey had spent 1–3 days in their respective stages.

Adults and large larvae which were used as predators were collected from rock-pools and kept in the laboratory for not more than four days prior to the tests. They were fed daily. An attempt was made to use individuals from pools in which conditions, such as high population density, favoured cannibalism. Individuals about to moult were not used. Each predator was tested once.

Clear rectangular plastic containers with bottom areas of 17 × 24 cm^2 were used in the experiments. They were filled with 2 l of pool water and sieved pool detritus was added to form a 1 mm layer at the bottom. Three small stones were provided for resting support, and in tests with several predators, three 3 cm × 3 cm pieces of plastic netting was added. After the small larvae and the predators had been introduced the containers were covered with lids. They were kept in a laboratory close to the window and artificial illumination was used on cloudy days. After 24 h the predators were removed and the contents were sieved to recover the small larvae. Dead larvae were inspected with the aid of a stereomicroscope to establish the cause of death. Only 0.3 % of the small larvae used were not recovered. Replicates in which 15 % or more of the larvae were dead but had not been killed by predators, moulted or were missing, were excluded. In order to obtain sufficient number of replicates, the experiments were extended over several weeks. An attempt was made to disperse all combinations tested evenly over a study period. Periodic shortages of some prey types occurred resulting in some of the experiments being cancelled. The tests were started when the densities of large larvae in the field were close to the yearly maxima and prey depletion was likely to occur.

In 1978–80 when most experiments with single predators were carried out, the temperature of the containers was 21–24°C. In 1984 the temperature was somewhat lower, 19–21°C.

Both species were found to be inefficient cannibals and the number of experiments in which all the prey survived was high. The distributions of numbers attacked were skewed and the sample variances heterogeneous. Detailed statistical analysis of such data is difficult. As larvae that had been eaten were not replaced and the predators' response appeared to be linear, theoretically the most attractive transformation is the attack rate (Thompson 1924, Royama 1971)

$$a = -(\ln (\text{proportion surviving})) / (\text{number of predators}).$$

The attack rate allows comparison between tests which used different prey or predator densities and considerably diminished the heterogeneity of variances. However, the skewed distributions were retained. Simple log (numbers killed + 1) transformation was more efficient in this respect. It is more conservative in giving less weight to replicates with a large number of killed larvae. Log $(x + 1)$ was used as the primary transformation in analyzing data with fixed prey density.

The dietary value of small larvae was assessed by measuring the organic carbon content of intact and cannibalized larvae using the combustion method of Salonen (1979).

3. Results

3. 1. Cause of death

Most dead larvae had several ragged holes on their dorsal side, and their body contents had been dissolved. In no cases were such holes seen on the ventral side. As dead small larvae tended to lie on their dorsal side at the bottom, the position of the punctures was consistent with the assumption that the larvae had been attacked before death. No holes were found in 30 dead larvae collected from the cultures of small larvae. This finding and the size of punctures indicate that they were made by large larvae.

The proportion of dead larvae without punctures was low. These non-predatory deaths occurred in contagious fashion in 1978–80, and amounted to 5.3 % of total number tested. This additional mortality did not hamper the analysis, and its effects were further diminished by the exclusion of replicates with several non-predatory deaths. In 1984 non-predatory mortality was 1.2 % and no replicates needed to be rejected on the basis of non-predatory mortality.

In 1979 310 1st-stage larvae and 60 2nd-stage larvae were tested at densities varying from 5 to 40 individuals per container without predators. The average daily mortality was 4.3 %, close to the values of the test material.

Table 1. The organic carbon content in mg (mean and its standard error) in intact and consumed small larvae.

	C. producta	*A. carinata*
1st stage, intact	0.0165 ± 0.0004	0.0238 ± 0.0002
carcass	0.0096 ± 0.0003	0.0133 ± 0.0010
proportion consumed	0.42	0.44
2nd stage, intact	0.0452 ± 0.0019	0.0899 ± 0.0024
carcass	0.0144 ± 0.0008	0.0224 ± 0.0013
proportion consumed	0.68	0.75

3.2. Food value of small larvae

When small larvae were introduced into small jars containing hungry 5th-stage larvae of *A. carinata*, they were rapidly cannibalized. The organic carbon content of intact small larvae and those of carcasses are given in Table 1. As the size of the prey increased, the proportion of extracted food appears to increase too. This may be because the relative thickness of the cuticle is smaller in the 2nd stage. Although all the consumed carcasses appeared to be empty, it is also possible that the predators find it easier to utilize the tissues of larger prey in greater extent than those of 1st-stage larvae. The details of energy requirement of corixids are not known, however the data for *Notonecta undulata* Say (Toth & Chew 1972) has been used as reference values. A 5th-stage larva of *A. carinata* and a 4th-stage larva of *N. undulata* have the same dry weight, and the latter needs a minimum of 0.46 mg/d (dry weight) of food for successful development. The carbon content of dry insect tissue is close to 0.5 (Salonen et al. 1976). A 5th-stage larva of A. carinata can consume 2–3 medium-sized chironomid larvae per day, corresponding to a total of 0.5 mg of organic carbon. The values suggest that small larvae may not be a particularly attractive type of prey, unless they are easily captured. The direct energetic gain of corixid cannibalism is thus small unless the victims are larger larvae.

3.3. Predator functional response

It was beyond the resources available to study the functional response of all later developmental stages of the two species using different prey types, and the 5th stage preying on conspecific 1st-stage larvae was selected as a representative study. The prey densities varied from 5 to 80 individuals per container. The highest values correspond to a density of 2000 individuals/m^2 and are thus above the values encountered in the field (Pajunen 1977). As predator behaviour is quite stereotyped, it was assumed that the results could also be generalized for other developmental stages. For A. carinata a single individual was used. As the attack rate of C. producta was known to be low, a predator density of five individuals were used for this species. The experiments were carried out in 1979 and 1984, respectively.

The numbers killed as a function of initial prey density are shown in Fig. 1. A linear relation is evident in both cases. The mean attack rates at different prey densities did not differ significantly. Thus the risk of being attacked is constant in the range of prey densities likely to be encountered in field conditions.

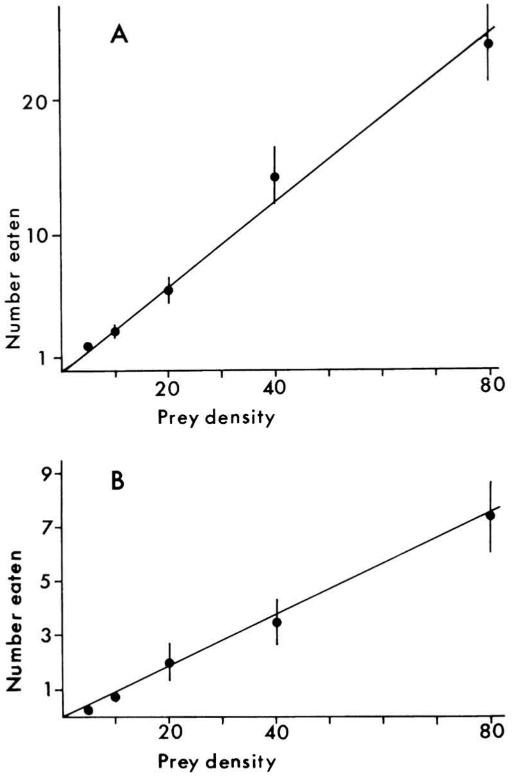

Fig. 1. The dependence of mean number killed on the inital prey density (numbers per container). The lines give ± standard errors. — A: Five 5th-stage larvae of *C. producta* preying on conspecific 1st-stage larvae, 19 or 20 replicates per treatment. — B: Single 5th-stage larvae of *A. carinata* preying on conspecific 1st-stage larvae, 16–20 replicates per treatment.

Table 2. The mean attack rate (*a*), its standard deviation (s_a) and the number of replicates (*n*) in tests with different numbers of 5th-stage larvae of *A. carinata* attacking conspecific 1st-stage larvae. Prey density was 20 individuals per container.

Predator number	*a*	s_a	*n*
1	0.130	0.127	19
2	0.161	0.108	18
5	0.220	0.148	18

3.4. The effect of predator density

Predator density in field conditions varies widely, even when only a single developmental stage is considered. Several predators can either facilitate the capture of the prey, for example forcing the prey to move about, or they can interfere with each other. The effect of predator density was tested using 1, 2 or 5 5th-stage larvae of *A. carinata* and conspecific 1st-stage larvae as prey. A prey density of 20 individuals per container was selected as a compromise, being low enough for easy handling and still high enough to allow even inefficient predators to catch some prey.

The results of this experiment are given in Table 2. No significant differences were detected. It can be

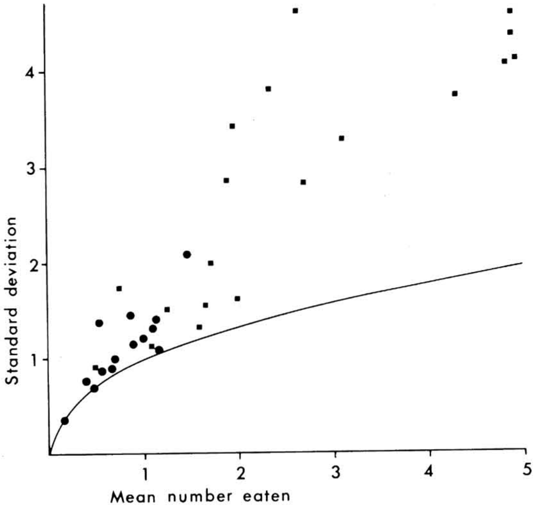

Fig. 2. The relationship between the mean number killed and the standard deviation of the distribution in experiments with 20 prey individuals and a single predator per container in 1978–80. The theoretical relationship of the binomial process is indicated by the line. The symbols indicate the predator's species as follows: Squares: *A. carinata*; dots: *C. producta.*

Table 3. The regression of ln(number killed + 1) on the five classifying variables (F = 29.5; df = 5, 630; $P > 0.001$): the regression coefficients (c), their standard deviations (s_c), the results of t-test for the significance of regression and the increase in squared multiple correlation coefficient by the inclusion of the predictor in question (*imcs*).

	c	s_c	t	*imcs*
Predator species	0.612	0.057	10.84	0.151
Prey species	–0.338	0.057	–5.97	0.045
Year of study	0.261	0.047	5.51	0.039
Prey devel. stage	–0.085	0.064	–1.34	0.002
Predator devel. stage	0.006	0.045	0.14	0.00002

concluded that the predator's efficiency is not affected by density, and attack parameters calculated using any predator density have a more general applicability.

3.5. Species- and stage-specific differences

Different predator and prey combinations were studied using a prey density of 20 individuals per container and a single predator. Fifth-stage larvae formed the main predator type and 1st- and 2nd-stage larvae were used as prey. Several combinations using overwintered adults and some with 4th-stage larvae were also tested, but the scarcity of small larvae precluded experiments with all the possible combinations. The experiments were carried out between 1978 and 1980. The data collected seemed to indicate that the study years differed considerably. Consequently, the attempt to obtain a balanced material failed. Relatively small numbers of tests were carried out in 1978, and all the values were close to those of 1979. Of the 17 predator and prey combinations used, 13 were tested both in 1979 and in 1980. In 11 cases the average attack rates were greater in 1980. Wilcoxon's signed rank tests indicated that this difference was significant at 2 % level. The difference is probably connected with the similar difference in population density in the rock-pools. In 1980 high densities of large larvae caused widespread and early food shortage which can be assumed to encourage cannibalism. The predators to be tested were given adequate amounts of food on days preceding the experiment. The previous field conditions probably influenced their subsequent behaviour.

The variation between replicates was considerable. Even when the attack rate was high, in some replicates the predator failed to kill any prey. As the individuals killed were not replaced, a binomial distribution can be assumed to be the limiting approximation of the sample distribution, when a constant attack rate between individual predators of a given species is assumed. In experiments with low average attack rate the variance of the number killed was in agreement with the binomial approximation, but all the tests with higher attack rates had significantly larger dispersions than expected (Fig. 2). This indicates a marked heterogeneity between individual predators.

The between-year differences complicated the analysis and a stepwise regression analysis was carried out as the first step in analysis. Log (numbers killed + 1) was regressed on the following variables: the species of the predator, the species of the prey, the developmental stage of the predator, the developmental stage of the prey and the study year. The analysis (Table 3.) showed that the species of predator, the species of the prey and the study year were significant predictors, but the developmental stages of the predator and the prey did not have significant additional information. The regression explained 19 % of the variation of attack rate which is an indication of the magnitude of the between-replicate variation. When attack rate was used as the dependent variable, the same predictors were included in the same order but only 17 % of the variance was explained. Further

Table 4. Mean daily attack rate (a), its standard deviation (s_a), mean numbers cannibalized (x), standard deviation (s_x), and number of replicates for different predator and prey combinations. Experiments using different developmental stages of predator and prey are pooled. The initial prey density was 20 individuals per container.

Predator		Prey									
		A. carinata					*C. producta*				
		a	s_a	x	s_x	n	a	s_a	x	s_x	n
A. carinata	1978–79	0.075	0.143	1.28	2.21	100	0.145	0.189	2.25	2.64	113
	1980	0.211	0.290	3.21	3.92	76	0.337	0.366	4.92	4.32	63
C. producta	1978-79	0.043	0.066	0.81	1.15	37	0.041	0.063	0.76	1.15	106
	1980	0.028	0.045	0.53	0.85	66	0.059	0.081	1.09	1.43	75

analysis of the data was undertaken by pooling the data for different developmental stages. The small material collected in 1978 was included in 1979 data. The mean attack rates for the pooled material are given in Table 4.

The unequal number of replicates in the pooled material limited the type of analysis that could be done, and only a three-way analysis of variance was carried out. The analysis disclosed significant predator – prey (at 0.1 % level) and predator – year (at 1 % level) interaction components. All factors (the species of predator, the species of prey and the study year) with interactions were significant at 0.1 % level. The interactions and main effects could not be separated. The lack of prey – year interaction suggests that the influence of the species of the prey remained constant throughout the study period, and the significant interaction component was due to the more rapid increase in the predation of *A. carinata* in 1980.

The main factor contributing to differences between groups was the species of the predator. *A. carinata* was consistently more efficient. Another, weaker factor was the species of the prey. *C. producta* was more vulnerable in most tests. No consistent differences between 1st and 2nd stages of any species could be found in analysis using logarithmic transformation. On the other hand, the average attack rates of *A. carinata* preying on 1st-stage larvae were high for both species. This indicates that tests with large numbers of prey killed were more frequent when the prey were 1st-stage larvae.

3.6. Field data

There is a marked cyclic variation in the recruitment of small larvae and all the developmental stages have pronounced peak occurrence periods, usually two per summer. The stage-specific peak densities in 1966–68 material (Pajunen 1977), calculated per unit of pool surface area were usually 100–300 individuals/m^2 for small (1st and 2nd stages) larvae and 50–100 individuals/m^2 for larger larvae. The high values usually occurred in early summer, late summer densities being considerably lower. Adult densities were always lower than those of 5th-stage larvae. The field densities, even when several stages are combined, lie in the density range used in the experiments, and we believe that the laboratory results can be generalized. The structure of small rock-pools is very simple and the feeding behaviour of corixids occurs on the smooth surface of bottom material. The difference between experimental and field conditions is much smaller than is usually the case.

Although the rate of cannibalism appears to be small, it can, in fact, be an important mortality factor. The total developmental time of the first two stages is about 10–15 days. Assuming that the attack rate obtained for *A. carinata* is effective in the field, large larvae at densities of 25 individuals/m^2 can eliminate one half of the small larvae present in 5 days, and cannibalism at the maximal densities observed would result in the total decimation of larvae in the first two stages. Even though the possibility of escaping predation is probably better in the field than in the laboratory, cannibalism may be a significant mortality factor.

Pajunen (1983a, 1986) developed a method for determining the time-varying mortality of small larvae. The method uses physiological time to transform the integrals of original stage-frequency functions to represent the numbers of individuals passing through successive mid-stages. Survival between mid-points of successive stages is then measured as a ratio of the increase in numbers at suitable time intervals. The ef-

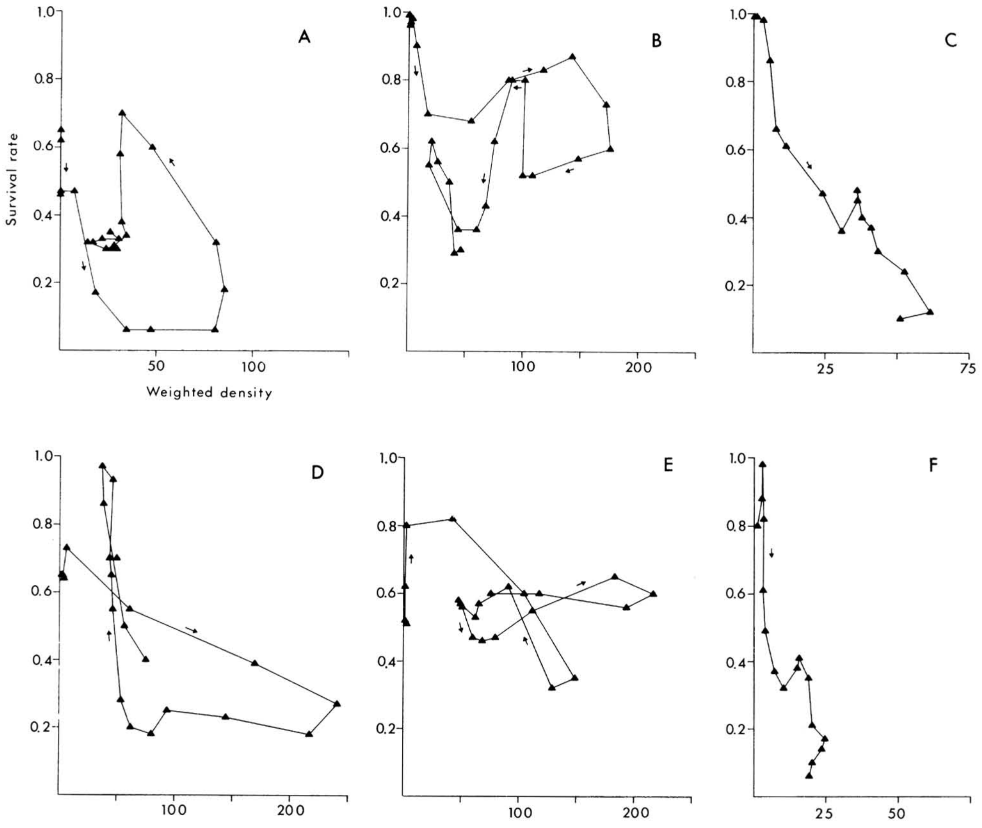

Fig. 3. Examples of the relationship between mean stage-specific survival rate of small larvae and the combined weighted density of later developmental stages in the field material. The weights used are the relative species-specific cannibalistic efficiencies. The difference between succesive data points is usually 3–4 d (the normal sampling interval), the arrows show the temporal direction. In graphs depicting data for a three-month summer season (A, B, D and E), the increase of mortality in mid-summer and the decrease of mortality when the adults of the first cohort emigrate can be seen. The sets (B, D and E) represent the changes in a single rock-pool (M 2 in Pajunen 1977) during three successive summers. (C and F) represent pools refilled in early July.

fect of population density on development was included in the time scales with the aid of the regression of the larval size and the length of developmental period. In most cases the mortality of small larvae increased as the numbers of 4th- and 5th-stage larvae increased, and decreased only after the numbers of large larvae again fell and the moulted adults emigrated. As the numbers of large larvae increased the rate of development of small larvae decreased, with the resultant increase in the time that all the mortality factors had to act. Examples of the mortality changes are given in Pajunen (1986). In most cases survival between 2nd and 3rd stages was consistently somewhat higher than between 1st and 2nd stages. This suggests that in the field prey size has some influence.

Now as the relative efficiencies of later developmental stages of the two species are known, the relationship between the mortality of small larvae and the density of large larvae can be investigated in greater detail. The efficiency of *C. producta* as a cannibal is about 26 % of the efficiency of *A. carinata*. Weights 0.26 and 1.0 were accordingly used to calculate the effective densities of cannibals. The densities of larvae were estimated at alternating 3- and 4-day intervals. The mortality of small larvae was estimated at intervals of one stage duration (5–10 d), the point estimates averaged by fitting a smooth curve by eye, and the survival rates for the sampling days estimated from the curve.

Fig 3. gives some examples of the results. The survival of small larvae (the average of the survival between mid-stages of 1st and 2nd stage and 2nd and 3rd stage) is expressed as a function of the weighted combined density of 4th- and 5th-stage larvae and adults. As can be seen, the mortality of the small larvae is intimately connected with the density of large larvae. In many rock-pools the mortality is at first low, but increases as the density of large larvae increases. The change is more pronounced in small shallow rock-pools (C and F) refilled in late June and repopulated by corixids before the prey populations had much time to develop. In more permanent pools the minimum survival rates vary considerably, and in pools with a high nutrient content, considerable densities of large larvae have been recorded before small larvae survival decreased appreciably. A clear time lag in the change of mortality is often observed. The differences in weighted density of large larvae between the rock-pools are much lower than the differences in numerical densities (Pajunen 1977, 1986). There are obviously other mortality factors acting at least in certain types of rock pools, but the timing of the changes in mortality of small larvae is consistent with the assumed rate of cannibalism. There are indications that large larvae, occurring at the densities observed, can decimate the local population of chironomid larvae. The rapid decrease of natural prey can then result in a sudden increase of cannibalism.

4. Discussion

The great inter-individual variation in predator effectiveness in spite of standardized experimental conditions was remarkable. Similar variation between individual predators has been reported in other studies. Hardman & Turnbull (1980) working on the wolf spider, *Pardosa vancouveri* (Emerton) suggested that differences in developmental history and differences in the contents of different gut compartments were responsible. Such variation considerably limits the applicability of results from laboratory studies to field conditions. Nevertheless, the present experimental results and field data were in agreement. The main difference was the lower than expected mortality in the rock-pools. This is understandable, as more complex bottom structure can be expected to provide better shelter from predators for the small larvae.

The cannibalistic behaviour of corixids appears to be very simple. The linearity of the predator response suggests that the handling time for the relatively small prey is quite short and that only a very small proportion of contacts between prey and predator lead to successful capture. Linear functional response in cannibalistic interactions between larvae of *Tetragoneuria cynosura* (Say) was reported by Crowley et al. (1987).

The independence of predation from predator density suggests that the prey can avoid predators efficiently and the attack distance must be short. Corixids are relatively inefficient cannibals. This suggests that the small larvae differ from ordinary prey in their behaviour.

A small corixid larva typically spends much time perched on the bottom and changes station suddenly with a rapid swimming action. Observations made in the rock-pools suggest that small larvae take evasive action when larger animals approach them and this makes them difficult to catch. The ventral orientation of the mouth parts of corixids makes direct observation of preying difficult and the composition of corixid diet in field conditions is not known. Comparable information exists for larvae of the dytiscid *Potamonectes griseostriatus* (Degeer). These polyphagous predators attack all animals of suitable size they encounter on the bottom surface. The proportion of small corixid larvae in their diet was less than 1 %, much smaller than would be expected on the basis of the probability of encounter (Pajunen 1983b). Small corixid larvae seem to possess efficient escape behaviour patterns.

In *Notonecta hoffmanni* Hungerford the rate of cannibalism depends on the level of predator starvation and on what additional prey is available (Fox 1975b). A comparable mechanism probably exists in rock-pool corixids. The changes of total corixid biomass in rock-pools are rapid, suggesting sudden resource depletion during the period of maximal numbers of large larvae. Comparable changes in the incidence of cannibalism can thus be expected. The differences observed in the 1979 and 1980 laboratory results suggest that the predators are able to some degree improve their cannibalism skills by practice.

The appearence of the species of the prey among significant experimental factors was unexpected. In predation studies, considerable interest has been shown in predator selection of prey types and the effect of prey behaviour has largely been overlooked. As the developmental stage of the prey did not emerge as a significant factor, and 2nd-stage larvae of *C. producta* are larger than 1st-stage larvae of *A. carinata*, the effect of prey species cannot be explained solely by size. The results indicate that small *A. carinata* larvae are better in evading larger larvae. The difference may be due to that fact that *A. carinata* is a more efficient predator.

Considerable attention has been given to the problem of the evolution of cannibalism. In groups of animals that exhibit a high level of parental care or when the investment to reproduction is otherwise high, the existence of cannibalism is problematic. On the other hand, in predators with relatively simple behaviour, cannibalism may be an extension of ordinary predation. The behavioural conventions inhibiting attacks on conspecific prey are perhaps too complex to be included in the repertoire of such animals. A simple mechanism preventing cannibalism is obviously specialized monophagy (Duelli 1981), but that is not always possible. The advantages of cannibalism for the individual cannibal are obvious. It obtains food when other prey types are scarce, and limits the number of potential competitors. Cannibalism in critical situations means a procedure of efficient resource allocation for the population, and the individuals most capable of surviving and reproducing are automatically preferred (Łomnicki 1978, 1980). The advantage gained by the population through this stabilization mechanism is clearly subsidiary to the gains of the individuals and there is no need to assume that it is directly selected for.

Much of the reproductive potential is wasted by cannibalism and for an efficient predator this type of population regulation is risky. As evolution proceeded, some mechanism limiting the effect of cannibalism, at least in periods of adequate resource availability, must thus have been acquired. As more efficient predatory behaviour and hence, increased cannibalism, is selected for at the level of the individual, the alternative is the evolution of efficient antipredatory behaviour. There are several possible ways of arranging this. Stage-specific differences in habitat preference introduce shelters for members of the population at risk. Conspecific prey can also acquire efficient escape behaviour that is not used by the normal prey. Rock-pool corixids are an example of this type. The species differences now recorded suggest that during evolution some equilibrium between cannibalism and its avoidance is established. When two species then occupy the same habitat, the more effective cannibal gains an advantage in interspecific competition (Pajunen 1979a, 1979b, 1982). Size-dependent habitat segregation is not possible in the monotonous rock-pool habitat, but in more structured environments it can be effective.The segregation of *N. hoffmanni* is an example of this phenomenon (Fox 1975a, Murdoch & Sih 1978, Sih 1982). Differences in stage-specific habitat selection of water-striders has been interpreted, at least in part, as an anti-cannibalistic system (Nummelin et al. 1984), but the importance of cannibalism as a mortality factor is not clear (Spence 1986).

As cannibalism in effect decreases the reproductive capacity of the females, one way to resolve the impasse is to maintain a balance between cannibalism and reproductive capacity. An example of this type is the correlation between the level of egg cannibalism and oviposition in different species and strains of *Tribolium* (Park et al. 1965, Sokoloff 1974). In patchy environments, resource-dependent cannibalism can be controlled by behavioural adaptations. In rock–pool corixids, after a given recruitment period, further oviposition in an occupied patch is wasteful. The correct strategy for mature females would then be to disperse from populated patches in an attempt to find unused places. An analysis of the fluctuation of numbers of small corixid larvae (Pajunen 1986) shows that the density of small larvae decreases even before mortality increases, and thus only a relatively low number of small larvae are actually cannibalised. Dispersal of ovipositing females from high density rock-pools when food availability is still relatively high is a probable explanation. The limitation of cannibalism by restriction of oviposition may be widespread in patchy environments (McNeil & Quiring 1983, Quiring & McNeil 1984a, 1984b).

The significance of competition in structuring animal communities is difficult to assess. Several of the early studies failed to provide conclusive evidence, and even now competition based on common resource use is difficult to demonstrate adequately. The effects of interference competition, of which interspecific predation is an obvious example, are more easy to demonstrate. The non-equilibrium nature of competition between the two rock-pool corixids was originally inferred from mortality differences during the last three larval stages, and later from the total overlap of resource use (Pajunen 1979a, 1979b, 1982). As the two first larval stages could not be distinguished in the field, no information on the possible difference in mortality at this point of the life cycle was available. The present laboratory results suggest that the competitive superiority of *A. carinata* can be extended even to the first larval stages.

Cannibalism as a means of interference competition can be assumed to be widespread. The relatively simple structure of aquatic habitats makes this type of interaction more probable in aquatic species (Istock 1965, Fox 1975b, Benke 1978, Benke et al. 1982, Johnson et al. 1985). Spatially restricted habitats, such as plant stems (Rathcke 1976), flower heads and galls (Zwölfer 1979) and host insects (Zwölfer 1971) are also structurally simple and the frequent occurrence of cannibalism in such environments is not surprising.

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