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The population dynamics of rock-pool corixids living on supplementary food (Hemiptera, Corixidae)

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Naturally established corixid populations living in four rock-pools were given frozen *Chironomus* larvae to supplement their diet. Initially the amount was 50–100 larvae/m^2, and this was gradually increased to 300–400 larvae/m^2. Supplementary feeding rapidly increased the egg production and, initially, the survival of corixid larvae. Population densities and the numbers of individuals completing development increased markedly. A net immigration of adults was detected during the first four weeks of the experiment. Later a strong emigration of adults occurred, and larval mortality increased, leading to the characteristic mid-season drop in total biomass. During late summer a comparable new cycle with corresponding high densities occurred. These results suggest that rock pool corixid populations are food-limited. The main regulating mechanisms are density-dependent changes in survival of small larvae and dispersal of mature adults. The balance between immigration and emigration will change with changing food availability and leads to concentration of adults in high resource patches.

1. Introduction

The rock-pools of the outer archipelago of the Baltic form a simple and fragmented aquatic system. A single rock-pool is often structurally homogeneous, resembling a man-made aquarium. The number of animal species permanently present is small, and the food web is simple (Ganning 1971). Although the relationship between ecosystem complexity and stability is far from clear, very simple systems seem more likely to show signs of instability. Such systems can be expected to be short-lived, but in a patchy environment, processes leading to local non-equilibrium can be balanced by sufficient between-patch dispersal (Hutchinson 1951, Huffaker 1958, Taylor 1988).

The populations of two corixid species, *Arctocorisa carinata* (Sahlberg) and *Callicorixa producta* (Reuter), show several of the expected characteristics. The species are in non-equilibrium competition, but the process is balanced by temporal habitat heterogeneity and differences in dispersal (Pajunen 1982). During the reproductive season these populations fluctuate widely, typically in a cyclic manner. Scramble competition in a simple environment can cause such an outcome. Pajunen (1977) suggested that the rapidly growing corixid populations could locally decimate their prey. The increasing competition for food would then increase the mortality of smaller larvae. Cannibalism by older individuals was assumed to be significant in competition. The individuals completing development would then emigrate, and the prey populations could again grow, allowing another breeding cycle to begin. A more detailed analysis (Pajunen 1986) confirmed the existence of cyclic variation in the mortality of small larvae, but it also showed that variation in the rate of recruitment in the first larval stage contributed to the population fluctuations. The strong effect of corixids on the bottom fauna has been demonstrated experimentally (Salmi 1987).

The size of corixid larvae depends on the availability of food. As food level also has an influence on the rate of development, small size can be taken as indicating slow development (Pajunen 1986). Under natural conditions high density rapidly leads to considerable reduction in size of developing larvae.

When the main features of an ecological process become established, further collection and analysis of field data is bound to yield less and less additional information. An experimental approach in which some of the input to the system is modified and the responses recorded is often more economical. The rock-pools are well suited for such experimental studies. Their small size facilitates environmental manipulation, and replicates are easily arranged. Although the rock-pools are structurally simple, they nevertheless are natural systems, coupled with other rock-pools. Experiments can thus be expected to give results more general than those obtained in the laboratory. As the food level appeared to be important in density limitation, feeding experiments were chosen.

The field work was carried out at the area of Tvärminne Zoological station in 1975. The habitat has been described in earlier studies (Pajunen & Jansson 1969, Pajunen 1977).

2. Methods

2.1. Estimation of numbers and biomass

The four study pools were selected from the 19 rock-pools studied earlier (Pajunen 1977). Desirable characteristics included rapid colonization by adults in the spring and consistent population cycles with minimal year-to-year variation. All four rock-pools lie near the main winter habitat (a permanent pond) of adult corixids. M1 and Gb3 were medium-sized rock-pools (maximal surface area 4–5 m^2). In both, the mortality of small corixid larvae was continuously high, and the cycles relatively irregular. M2 and M3 represented typical small-sized rock-pools (1–2.5 m^2) with low initial mortality of small larvae and regular cycles.

The removal method used for estimation of active developmental stages of corixids has been described in Pajunen (1972) and Brummer (1988). The main improvement then introduced in the basic removal estimation (Zippin 1956) was the pooling of data from several separate sampling occasions prior to the estimation of the probability of capture. Sampling consisted of using a small hand net to capture a part of a population. We chose a standardized procedure and repeated the capture six or nine times, depending on the size of the pool. The field procedure was identical with that used by Pajunen (1972). The current data could thus be pooled with the earlier data (1966–68) in Pajunen (1977), thus effectively doubling the material available. The accuracy of daily estimates consequently increased: 95% confidence limits differing by 20–30% of the estimated stage-specific numbers. As earlier, the water level was kept above a specified minimum level by addition of tap water during rainless periods. The pools were visited at alternating 4- and 5-day intervals, less frequently in late August–September.

Daily biomass was calculated using either stage-and-species-specific wet weights given by Pajunen (1977) or stage-and-species-specific organic carbon content (Salmi 1987).

2.2. Measurement of size

In larvae of the last three stages, total length from the front edge of the frons to the tip of the abdomen was measured with a stereomicroscope and an eyepiece micrometer. The sample consisted of 50–70% of the numbers present. The size distributions were used to determine the species proportions. The average size of the daily sample was also used to estimate rate of development.

2.3. Estimation of rate of development

Pool temperature was continuously measured with Wallac 1000-Ohm Ni-resistors and Joens six-channel recorders. Precision was to 0.5°C. Temperature was assessed at 2 h intervals, and time - temperature distribution was calculated for each day by linear interpolation at 1°C temperature intervals. The expected daily developmental progress was then calculated as the sum of temperature-specific times weighted by temperature-specific developmental rates given by Pajunen & Sundbäck (1973). The intervals between sampling occasions were expressed as sums of daily values. The effect of density on development was then estimated for the first two larval stages with the aid of regression of average developmental progress (v_a) on size in 3rd stage (s). The regressions were obtained by analysing the earlier 1966–68 data (Pajunen 1986) as follows:

A. carinata $v_a = 4.292 - 1.106s$
C. producta $v_a = 4.175 - 1.234s.$

The regressions explained 40 and 39% of total variation. The dependence between duration of 1st (v_1) and 2nd (v_2) stages was calculated as

$$v_2 = 0.934v_1 + 0.173.$$

The method for calculating transformed time scales is described in Pajunen (1986). The time scales are stage-and-species specific, representing different nonlinear transformations, but for practical purposes, approximate linear transformations between two time scales are sufficiently accurate, at least for short time-intervals.

2.4. Supplementary food

Frozen red *Chironomus* larvae, available commercially for fishing bait, were used for supplementary food. Chironomid larvae have been used routinely as food for laboratory cultures of rock-pool corixids for several years, and all developmental stages seem to be able to consume them. The size of *Chironomus* larvae varied from 10 to 15 mm, and were thus larger than most chironomid larvae normally occurring in rock-pools. The daily consumption level at the inital stages of the experiment was 50–100 ind./m^2, but was gradually increased to 300–400 ind./m^2. If noticeable amounts of unused food were detected at the bottom surface after 24 h, the daily ration was kept constant for some days.

The density of natural prey was not monitored. Later studies have shown that in rock-pools with low corixid density, chironomid larvae of size class 5–10 mm occur at densities of 3000–5000 ind./m^2. Densities of smaller larvae are considerably higher, but these contribute little to the total biomass. Daily supplement of food was thus considerable. In comparison to the numbers of corixids present, furnishing supplementary food meant that during the population maxima there was about one experimentally added chironomid larva available daily per adult corixid or large corixid larva. It is probable that the food not used immediately by different predators were eaten by scavengers or even by otherwise herbivorous chironomid larvae. At least some surplus food could thus be stored in the bottom-dwelling animals.

3. Results

3.1. Population density and stage-frequency curves

The overwintered generation in 1975 was strong, and the rock-pools were already repopulated in early May. Spring dispersal usually starts when daily maximum air temperatures exceed 10°C (Pajunen & Jansson 1969). There then occurred a spell of cold weather during the first days of June, retarding development and probably synchronizing the moulting of 1st-stage larvae. When the rock-pools were visited between 10–13 June, the first larvae were already in the 4th stage or older. Supplementary feeding was begun, and the feeding rate gradually increased. Maximal feeding level was reached towards the middle of July. Then the feeding level was kept constant, until terminated in mid-August.

Corixids seemed to prefer thawed *Chironomus* larvae to natural food. Usually, within a minute after the thawed larvae were introduced, corixids resting nearby became active and started feeding, and in a few minutes a dense shoal of predators formed around the introduced larvae. Adults and large larvae often dragged the *Chironomus* larvae for considerable distances, distributing them widely. One may assume that the body contents seeping through the cuticle of thawed larvae act as a strong attractant facilitating the use of supplementary food.

Changes in stage-specific daily numbers are presented in Fig. 1. The time scale used is physiological, the time unit being the mean 1st-stage duration. The subsequent analysis rests heavily on the use of physiological time. The first sampling from 10–12 June showed that densities of small larvae were very high in M1 and Gb3, 586 ind./m^2 and 340 ind./m^2, respectively. The densities fell rapidly, however. In M2 and M3 the maxima were somewhat lower. Although data for early June are lacking, the start of the cycles can be reconstructed on the basis of the data for later stages. The results suggest that the values recorded from 10–12 June represent 1st-stage peak values, and that the first larvae appeared between 20–25 May, somewhat later in M2. The decrease in daily numbers of small larvae after the peak in Gb3 and M1 presumably represented a phase of normal cyclic fluctuation.

In all study pools, the period of decreasing daily numbers in 1st-stage larvae was short, and only in M1 were typical low values observed. Already from 23–24 June the numbers of 1st-stage larvae started increasing in Gb3 and M1. In M2 and M3 the increase started somewhat later. In Gb3 and M1 the daily numbers continued increasing up to the end of July, then an abrupt decrease followed. In M2 and M3 the trend was more variable. In both pools there was a sudden drop in daily numbers in late July. Analysis of survival rates showed that mortality was rapidly increasing at this time and recruitment was not sufficient to compensate for its effects.

The changes in numbers of later larval stages resemble closely those of the 1st stage. The peaks of the early season maxima were in all pools relatively high. In M2 and M3 the period of low survival in July resulted in the characteristic widening of the region of low density. In the late season there was clearly some compensatory mortality and the peak height remained roughly at the level earlier in the season. The peaks were remarkably wide, however, and the numbers of individuals completing a stage were thus high.

Delimitation of early and late summer peaks (Pajunen 1977) was easy in Gb3 and M1, the pronounced late-June minima providing reference points. In M2 and M3 densities were lower, and it is possible that the densities would have increased later, even without supplementary food. Nevertheless, the early season cohort was separated using the dates 25–26 June as limits for 1st-stage larvae. Corresponding limits for 5th-stage larvae were estimated with the aid of the 1st-stage physiological time scale. The early season peaks thus contain individuals having completed the early development without supplementary food, whereas all individuals during the late season could use this type of food for most of their development.

Peak-height values for study pools, expressed as the mean of three largest daily values, are given in Table 1. The total number of individuals having passed mid-stage (the area under the transformed stage-frequency curve with correct physiological time scales, see section 3.3) are given in Table 2 for the 1st and 5th stages. At the first sampling date, a considerable number of individuals had already completed the 1st stage. The number of these 1st-stage larvae was estimated from cumulative total numbers of the first sampling occasion, assuming complete survival and that the individuals still in the 1st stage were in mid-stage. The result obviously is an underestimate, but is at least in M2 and M3 close to reality. The species proportions for the 3rd and 5th stages are given in Table 3. *C. producta* is about the half of the size of *A. carinata* and this should be considered in density comparisons. The wet weight of a *C. producta* 5th-stage larva is 0.555 that of *A. carinata*, and these values were reflected in the calculations.

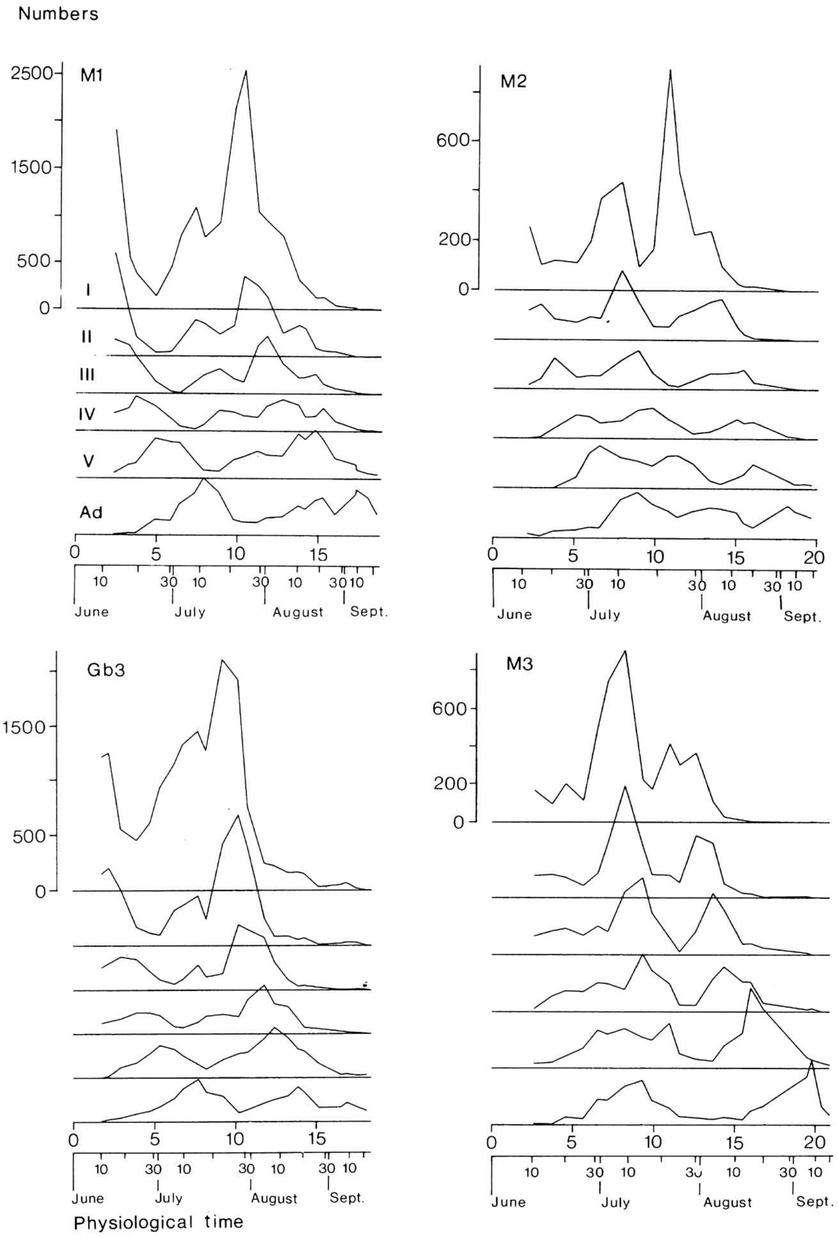

Fig. 1. Combined stage frequency curves in study pools in 1975. Graphs, from top: 1st-, 2nd-, 3rd-, 4th-, 5th-stage larvae and adults, common time scale in 1st-stage physiological time units (stage durations), starting point 1st June. Lower scale in days. The average surface areas of the rock-pools are as follows: Gb3: 3.7 m^2, M1: 3.2 m^2, M2: 0.87 m^2, M3: 1.7 m^2.

Table 1. Peak height values of 1st and 5th larval stages and maximal daily numbers of adults.

Pool		Peak height (ind.)			Relative peak height (ind./m²)	
		1st	5th	Adults	1st	5th
Early season	Gb3	1241	260	319	333	70
	M1	1216	395	274	379	123
	M2	189	146	159	216	167
	M3	164	198	192	97	117
Late season	Gb3	1833	395	274	492	106
	M1	1897	467	441	581	145
	M2	620	122	112	707	139
	M3	365	309	232	216	183

Table 2. Values of integral functions of 1st- and 5th-stage stage-frequency curves for early and late season peaks. For corrected 5th-stage relative values, relative species-specific weights are used (an individual of *C. producta* is 0.555 of the weight of *A. carinata*.

Pool		Ind.		Ind./m²		
		1st	5th	1st	5th	5th, corrected
Early season	Gb3	3277	631	879	169	162
	M1	4459	960	1389	299	282
	M2	653	310	745	354	258
	M3	787	535	465	316	186
Late season	Gb3	10195	1186	2736	318	314
	M1	9474	1361	2951	424	419
	M2	2959	460	3368	525	435
	M3	3507	955	2072	564	470

Table 3. Proportion of *C. producta* in 3rd- and 5th-stage larvae in study pools.

	Early season		Late season	
	3rd	5th	3rd	5th
Gb3	0.145	0.100	0.040	0.045
M1	0.243	0.124	0.059	0.025
M2	0.443	0.375	0.399	0.361
M3	0.955	0.925	0.339	0.359

In all pools the number of adults was high, and their stage-frequency curves corresponded closely to the form of 5th-stage curves. This suggests high survival rates during late larval development. In unfed rock-pools the numbers of adults were usually much lower than maximal numbers of 5th-stage larvae (Pajunen 1977). However, the daily numbers of adults depend strongly on migration. The data are analysed in section 3.5.

3.2. Biomass

The changes in total biomass expressed as mg organic carbon per unit of average pool surface area (mean of surface areas on days of sampling) appear in Fig. 2. Biomass per unit of current pool area is also included. In all rock-pools the biomass rose rapidly, and the early season maximal values were 350–700 mg/m². After the maxima the biomass decreased but rose later, and in August reached values of 400–500 mg/m². The biomass is of course strongly correlated with stage-specific numbers.

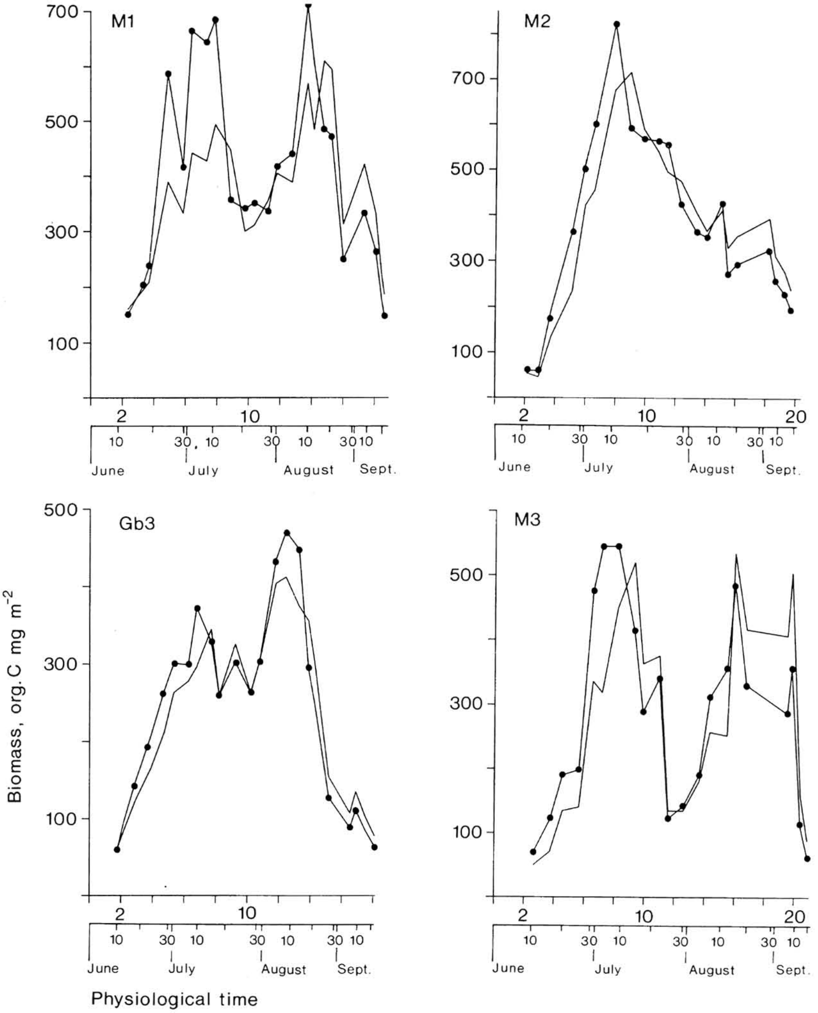

Fig. 2. Changes in total corixid biomass (organic carbon per m^2), calculations based both on actual pool surface area at sampling time (line with dots) and mean surface area (line). Time scale in 1st-stage physiological time units, lower scale in days.

3.3. Larval size and developmental rates

The size of corixid larvae depends on the availability of food. As food level also has an influence on the rate of development, small size can be taken as indicating slow development (Pajunen 1986).

Changes in larval-size appear in Fig. 3. The size of the first individuals in the 3rd stage is unknown, but again some inference can be based on later larval stages. *A. carinata* dominates in three of the pools; in M3, *C. producta* is dominant early in the season. The first individuals in the 3rd stage were relatively large, althrough in Gb3, significantly smaller than in others. In all pools the growth rates of small larvae then decreased, more slowly in M1, in which the total density drop was greatest. For the rest of the season the larvae were small. The periods of minimum densities of 5th-stage larvae and adults cause in all cases a significant increase in sizes attained by smaller larvae. The 5th-stage larvae

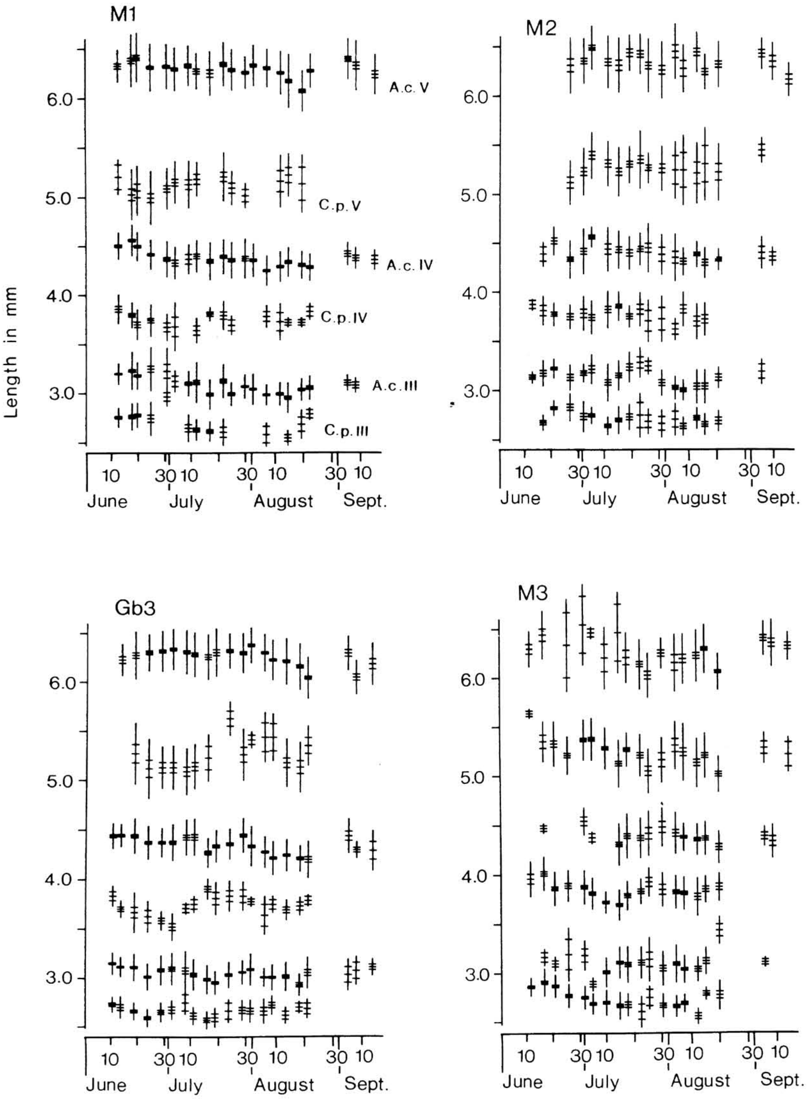

Fig. 3. Changes in total length of three last larval stages. For each sampling date, mean ± *SE* (ticks) and ± *SD* (total line) are shown. The two species form regularly alternating size classes, the smallest size class is the 3rd stage of *C. producta*, the largest the 5th stage of *A. carinata*. Time scale is in days.

were consistently large. The termination of supplementary feeding in August caused a rapid decrease in the size attained.

The clear early- and mid-season minima facilitate recognition of corresponding segments of successive stage-frequency curves. The estimation of duration of larval stages is thus easy. As with the earlier data (Pajunen 1986), physiological time-scales constructed directly from field temperature-records and developmental-rate func-

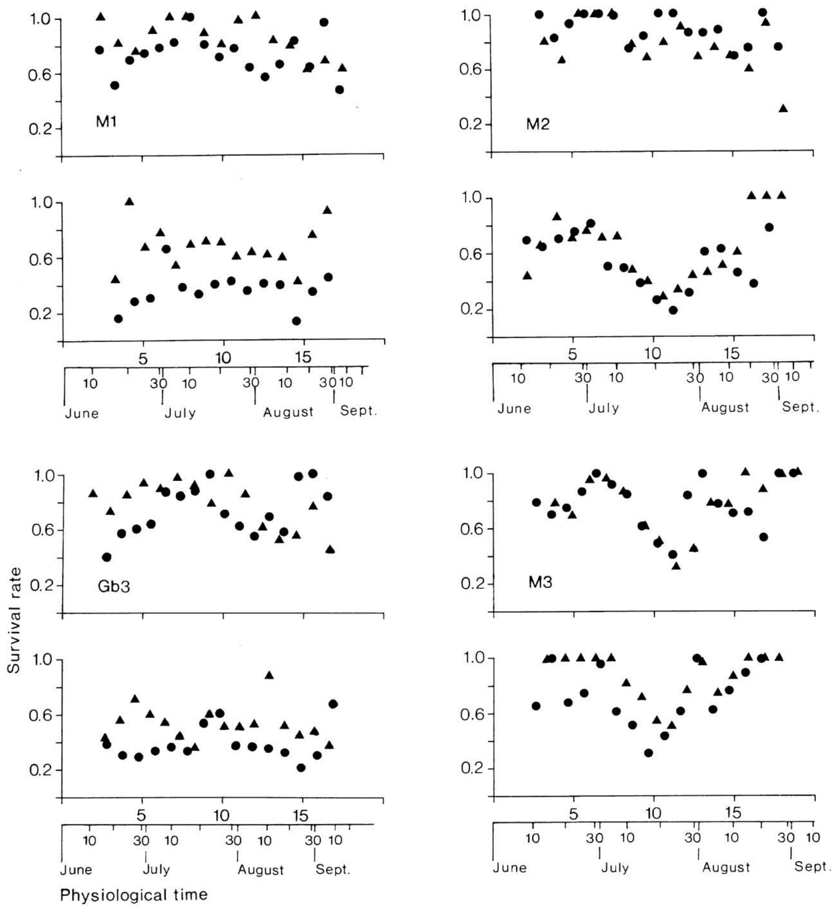

Fig. 4. Seasonal variation in survival rates (from one mid-stage to the next) in 1975. Upper graph: circles: 3rd–4th stage, triangles: 4th–5th stage. Lower graph: circles: 1st–2nd stage, triangles: 2nd–3rd stage. Common time scale in 1st-stage physiological time units, lower scale in days.

tions obtained in the laboratory at constant temperature (Pajunen & Sundbäck 1973) somewhat underestimated the true rate of development. When the time-scales were corrected using the new information based on larval growth (Pajunen 1986), the new scales predicted real field development with considerable precision. This suggests that the correlation between size and developmental time remains unchanged even in experimental feeding, and that high population density always causes some energy drain which cannot be compensated by providing easily acquired food.

3.4. Survival rates and transfer functions

When correct physiological time scales are known, both the numbers passing through successive stages and the stage-specific mortality can be estimated. Time-varying biased survival rates (Pajunen 1983) calculated between mid-points of successive larval stages using a time-interval one stage in length are given in Fig. 4. Again the rock-pools studied represent two types. Survival rates of small larvae (1st and 2nd stages) in Gb3 and M1 were at the beginning of summer considerably lower (0.2–0.4) than in M2 and M3

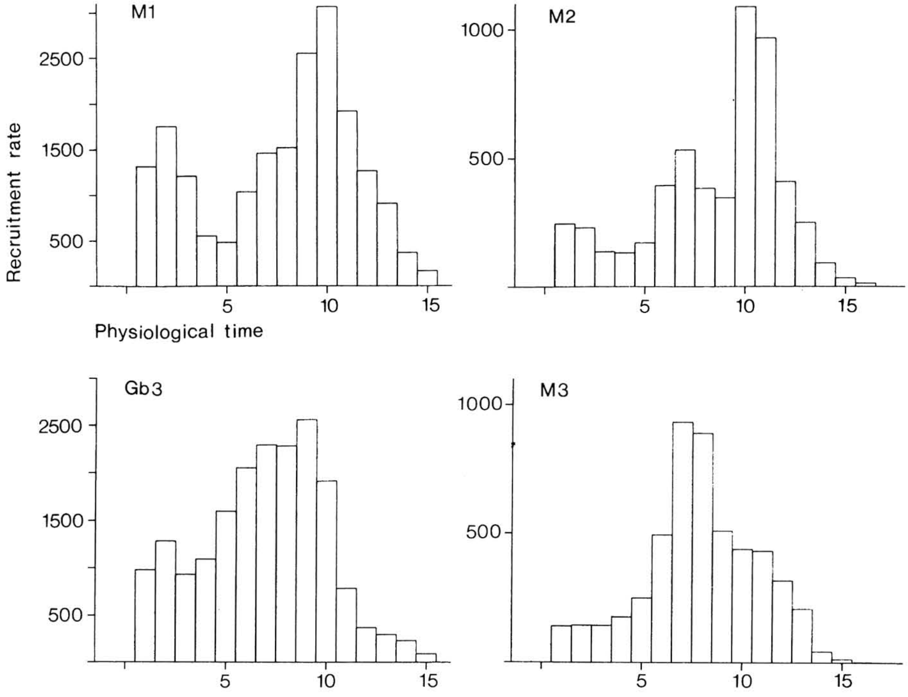

Fig. 5. Seasonal changes in approximate 1st-stage recruitment rate (individuals per one stage duration).

(0.8–0.9). Survival of larger larvae was 0.5–0.6, somewhat higher in M2. The supplementary feeding was effective in raising the survival rates of large larvae in all pools. The survival rates of small larvae rose moderately, at least between the 2nd and 3rd stages. In M3, the high initial survival precluded further change. Then survival rates began to fall. Due to the high inital level, the change in M2 and M3 was quite dramatic, and its effect was noticeable even in stage-frequency curves, in which clear, if short-lived minima occurred. In August the survival rates, especially those of small larvae, rose again. In Gb3 and M1 the decrease was smaller, although the lowest survival rates recorded were comparable. Both pools exhibited a short period of better survival in mid-July.

Changes in survival rates were in close correlation with the changes in population density, especially those of large individuals. The maxima of 5th-stage larvae occurred earlier in Gb3 and M1, and in mid-July there were conspicuous minima. In M2 and M3 the period of high numbers of large larvae terminated only towards the end of July. The total biomass, calculated per unit of current pool surface area (Fig. 2), shows comparable differences. In Gb3 and M1, values close to the maximal level occurred earlier, and the density fluctuations were weaker than in M2 and M3. This explains the consistently low survival in Gb3 and M1. The periods of high survival rates were in all cases characterized by low density, and even the magnitude of changes was similar.

After mid-July when the dispersal rate increased, survival rates of small larvae decreased as well, indicating decreased resource availability and possibly increased cannibalism.

When the survival rates of small larvae are known, approximate 1st-stage transfer functions can be calculated by partitioning the survival between the stages and by assuming that the estimated survival rates for the later half of the 1st stage also apply for the first half. The recruitment rates calculated at one stage interval are presented in Fig. 5. This recruitment is probably underestimated, and the extreme values are displaced by about one-half of stage-duration. However, the general form of the transfer function can be determined.

Comparison with the functions derived from earlier field data (Pajunen 1986) shows clear differences. In all pools the recruitment rate begins increasing soon after the start of supplementary feeding, and the maximal values, two to three times earlier peak rates, occur in mid-July. The midsummer mimimum frequently observed in 1966–68 material is absent, although some indication can be seen in M2. The emigration of the adults in mid-July effectively terminates further recruitment, but the great numbers produced are sufficient to form the strong late season cohort.

3.5. Adult numbers

The changes in daily numbers of adults early in the season appear at first glance to depend mainly on local emergence of 5th-stage larvae. However, an important subsidiary factor can be dispersal. As adults were not marked, the only clue available is the possible discrepancy in species composition between the large larvae and the adults. If we assume that survival during the latter part of the 5th stage is the same as during the first half of that stage, the numbers present at the end of the stage can be calculated. The survival between midpoints of the 4th and 5th stages can be partitioned between the two stages. The average duration of the 5th stage in 1975 material is 1.61 the 4th stage duration, which means that a given rate (s) can be decomposed as rates $s^{0.383}$ and $s^{0.617}$, indicating survival during the half-stage durations of the 4th and 5th stages. The increase of stage-frequency integral between two sampling dates gives the approximate number of individuals passing the mid-stage. The estimated cumulative numbers of individuals completing development appear in Table 4. These estimates are obviously overestimates, as the individuals in final moult are large and easily dislocated when moulting, especially when local density is high.

Table 4. Total adult cumulative production as predicted on the basis of 5th-stage numbers and mid-stage to mid-stage mortality between 4th and 5th stages, and daily adult numbers estimated by removal netting in June–July. *C. p.* = *C. producta*, *A. c.* = *A. carinata*.

Rock-pool and date		Predicted		Estimated	
		C. p.	*A. c.*	*C. p.*	*A. c.*
Gb3	18. 6.	15	2	16	21
	23. 6.	5	43	33	41
	28. 6.	11	98	38	62
	2. 7.	17	165	42	98
	7. 7.	30	291	53	163
	10. 7.	40	360	119	183
	15. 7.	53	462	95	292
	18. 7.	54	491	29	239
	23. 7.	58	567	28	205
	28. 7.	63	631	2	79
M1	17. 6.	3	23	9	13
	19. 6.	6	48	10	10
	24. 6.	16	137	71	92
	30. 6.	38	292	59	93
	3. 7.	53	396	96	234
	8. 7.	82	578	157	287
	11. 7.	95	662	225	380
	16. 7.	108	760	76	376
	21. 7.	115	798	18	144
	24. 7.	121	843	19	118
	29. 7.	123	943	15	120
M2	20. 6.	4	4	19	8
	26. 6.	7	8	28	4
	1. 7.	11	15	31	12
	4. 7.	19	34	28	12
	10. 7.	54	105	80	75
	14. 7.	91	152	93	91
	18. 7.	122	173	37	100
	22. 7.	156	196	62	48
	25. 7.	173	214	40	44
M3	20. 6.	13	14	24	17
	25. 6.	47	16	24	8
	1. 7.	103	18	107	28
	4. 7.	151	20	112	19
	9. 7.	251	25	177	27
	14. 7.	349	29	193	43
	17. 7.	408	33	81	49
	22. 7.	441	72	72	17
	25. 7.	454	99	31	12

There were consistent differences between predicted and actual data. In all rock-pools the dominant species occurred in numbers that were about half those predicted. In all cases the minor species occurred in numbers that exceeded predicted values. This means that mortality during late development and during the early adult stage exceeds the predictions. As the source of immigrants is the same for all pools, it can be assumed that proportions of species among the immigrants remain constant. It is known that the initial differing preferences of the two species disappear during the late reproductive period of the overwintering generation. Assuming that a fixed proportion of numbers predicted to be alive at the end of the 5th stage survive to adults, and that they do not emigrate (flight ability is attained in 5–10 days, Young 1965), the number of immigrants and species-proportions can be estimated. In all pools consistent values should be obtained. When survival in the range 0.45–0.60 is assumed, calculations indicate that 0.7–0.8 of the immigrants were *C. producta*. Higher survival values were not compatible with the data for large rock-pools, and much lower values yielded diverging results. As *C. producta* is known to have a dispersal rate about twice that of *A. carinata*, these results seem to be realistic. There is thus considerable mortality during the final moult and early adult stage.

4. Discussion

The results of the experiments clearly showed that rock-pool corixids can efficiently use dead prey, but it is not known to what degree dead animals contribute to their natural diet. Their rapid response to *Chironomus* larvae suggest that they can react to wounded prospective prey in their vicinity and it is possible that partially-consumed prey and corixid individuals not successful in moulting are consumed.

Data on corixid densities and biomass in rock-pools of the study area are available for 1966–68 (Pajunen 1977, 1986). In early summer peak densities (the means of the three largest daily values) of 1st-stage larvae in high-density rock-pools varied from 100 to 370 ind./m^2, and values for the 5th stage were 50–150 ind./m^2. In the late season, the values were lower: 50–200 ind./m^2 and 30–90 ind./m^2, respectively. As regards the present study pools, the characteristic differences in survival rates between larger Gb3 and M1 and small M2 and M3 can be detected also in 1966–68 data. Average maximal densities and ranges (ind./m^2) were as follows in early and late summer:

	Early	Late
Gb3 and M1		
1st stage	123 (32–217)	120 (84–150)
5th stage	30 (15–33)	19 (5–38)
M2 and M3		
1st stage	185 (56–367)	137 (90–186)
5th stage	92 (54–143)	45 (27–74)

The lowest values of the range occurred in Gb3 and M2 in 1966, when the density of overwintered adults was very low, and the densities of 1st-stage larvae obviously were below the carrying capacity of the rock-pools. The difference between the larger and smaller rock-pools was also evident in the integrals of stage-frequency functions representing numbers per m^2 attaining respective mid-stages:

	Early	Late
Gb3 and M1		
1st stage	643 (230–821)	466 (297–689)
5th stage	65 (26–105)	46 (9–100)
M2 and M3		
1st stage	753(218–1542)	663 (267–927)
5th stage	192 (68–288)	130 (50–259)

Compared with these values, the densities and total numbers of small larvae in early summer of 1975 were essentially similar, but those of 5th-stage larvae were already somewhat elevated. During the late season all maximal densities in 1975 considerably exceeded values recorded earlier, the differences in numbers of individuals being more pronounced than peak-height values.

Examples of changes of daily biomass expressed as wet weight appear in Pajunen (1977). Typically the biomass increased rapidly and attained a short-lived peak coinciding with the maximal density of 5th-stage larvae. The maximal values, when calculated per average unit surface area, were somewhat lower in larger rock-pools. Expressed as organic carbon, the average early summer maxima were 114 mg/m^2 (range 72–162 mg/m^2) in Gb3 and M1, and 252 mg/m^2 (range 115–391 mg/m^2) in M2 and M3. In late summer the respective means were 86 mg/m^2 (range 32–168 mg/m^2) and 200 mg/m^2 (range 92–301 mg/m^2). Maximal biomass in 1975 was much higher, particularly in late season.

Jansson (1978) gives data about densities attained by *A. carinata* in laboratory cultures. Plastic containers with bottom area of 25×17 cm^2 were used, and frozen *Chironomus* larvae were given for food. New eggs were introduced daily until the oldest larvae moulted to the 3rd stage. When the 30–40 oldest larvae attained the 5th stage, younger larvae rapidly disappeared, and most old larvae emerged as adults during a time interval of about one week. The mean of 17 replicates was 34.2±2.1 adults (*SD* 8.8). This suggests that when food is not a limiting factor, strong behavioural limitation occurs when the density of large larvae reaches 800–1000 ind./m^2. The total number of individuals attaining the 5th stage during the late season in the present feeding experiments, 314–470 ind./m^2 (expressed as *A. carinata*), is relatively close to this limit.

The effects of supplementary feeding were as expected. The high food level rapidly increased the survival of large larvae; the resulting densities of 5th-stage larvae in early July were relativley high. The supplementary food reduced the typically heavy mortality in late development. In August the densites of large larvae remained at the level of early summer values or were even higher. The results thus support the assumption that the biomass in corixid populations tends to increase until food is exhausted.

The supplementary food also influenced adult dispersal. The moulted new adults evidently remained in their home pools, and the dispersal of the immigrants was low, leading high adult numbers. Then a relatively rapid emigration occurred simultaneously in all rock-pools. This period was characterized by low survival of small larvae and, especially in small rock-pools, by decrease in the size attained by 3rd- and 4th-stage larvae. The rate of supplementary feeding had stabilized to a steady level somewhat earlier. It is thus possible that the continuously growing corixid populations then started to use the normal bottom fauna more intensively, which led to prey scarcity. The adults responded by emigrating. Increasing mortality also contributed to the resulting drop in total biomass, which then evidently led to restoration of bottom fauna, and a new increase of biomass followed. As survival rates of large larvae in most cases remained at the original level (M3, in which the biomass change was largest was an exception) the change in food availability could not be considered serious. One must assume that mature adults, at least when occurring at high density, are very susceptible to the changes in food availability.

The rapid increase of numbers of 1st-stage larvae suggests that supplementary food rapidly encouraged further oviposition. In Gb3 the response was almost immediate; other rock-pools showed a clear rise in egg-production after a lag of some 5–10 days. The oviposition rate then continued to rise, in most cases to the middle of July, and the maximal rates were 2–3 times the maximal values observed earlier. Low values were observed only towards the end of July, as a result of strong emigration. The continuous recruitment resulted in wide late-season peaks and in high maximal densities of small larvae. These results indicate that in natural conditions the scarcity of food is the factor causing decreased oviposition and presumably emigration of the adults.

An increase of population density as the response to increased food levels is a standard result of most feeding experiments. In fact, the absence of such a reaction can be regarded as a strong indication of the existence of specific regulatory mechanisms such as territoriality. What is important in the present case is the rapidity of the reaction. The population density had increased considerably already in a period shorter than one generation, and the immigrants probably contributed substantially to the late- season peak densities. This suggests that in natural conditions only a proportion of the reproductive capacity of rock pool corixids can be realized, and peak population densities are set by the availability of food. Sufficiently intense dispersal of mature adults is thus advantageous, as otherwise much of the regionally available resources would remain unused. An ability to assess the availablity of food in a particular patch and undergo more extensive dispersal without ovipositing if resources are liable to be scanty would considerably increase the breeding success of females. Pajunen (1986) found some evidence for this kind of behaviour in the analysis of population data. The reaction of adults to increased food by continuing oviposition is consistent with this assumption.

Initially, supplementary food raised the survival rate of small larvae, but after the stage-specific densites rose to high values, changes typical of natural conditions were observed. In Gb3 and M1, survival of small larvae was constantly low, presumably reflecting the rapid increase in numbers of large larvae. In M2 and M3 the decrease in survival was more gradual, but all developmental stages were affected.

Under natural conditions, survival rates of small larvae decrease as densities of large larvae increase, and cannibalism is assumed to be the chief regulatory factor (Pajunen 1977, 1986, Pajunen & Ukkonen 1987). Availability of easily consumable food should decrease the incidence of cannibalism, but because densities in experimental populations were very high, direct comparison is difficult.

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