Distributional dynamics of *Daphnia* species in a rock-pool environment

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The changes in distribution of *Daphnia longispina, D. magna* and *D. pulex* on a group of islands containing 507 rock-pools were followed over a three-year period with at least two samples per year. Of the pools 48 % were inhabited at least during some period and two-species coexistence was observed in 12 % of the pools. The distribution of invasions (155 cases) corresponded closely to the expected frequencies calculated as the product of frequencies of occupied and unoccupied patches. Empty pools and those occupied by other species were invaded with equal probability. Median distances to the closest source area were the same (5—9 m) in all species, but distances of up to 500 m were recorded. Of the populations existing at the start of the study 25—30 % became extinct, whereas 80 % of the populations established during the first study year and 33 % of those established during the second year disappeared. It is suggested that the distribution of daphnids is maintained by populations inhabiting favourable rock-pools. From these source areas hazardous marginal areas are continuously invaded, but with little success.

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1. Introduction

The rock-pools of the outer archipelago of the Baltic represent a fragmented and heterogeneous aquatic environment. The conditions among habitat patches vary widely. Salinity, the degree of eutrophy, and the content of humic matter can differ considerably even between neighbouring rock-pools. The temporal heterogeneity is also considerable. During the dry periods the more shallow pools tend to dry up and then even a single shower can refill them. During the winter most rock-pools freeze completely. Organisms living in such an environment either need efficient means of dispersal or must be able to survive in a dormant condition over unfavourable periods. On the other hand, the pronounced patchiness can stabilize otherwise destructive population processes, such as interspecific competition or predator—prey interactions. The process can lead to local extinction of one of the populations involved, but dispersal and the continuous disappearence and reappearence of the patches can still maintain the species. Starting with Levins (1969) and Levins & Culver (1971), modelling such processes has been the favourite pastime of several workers, and there is no doubt that the mechanism can act in reality. Pajunen (1971) suggested that

the heterogeneity of the rock-pool environment was important in stabilizing the populations of two corixid species and later (Pajunen 1979, 1982) gave a more detailed analysis of factors stabilizing the interspecific competition of rock-pool corixids. The great between-patch heterogeneity of the rock pool environment makes it exceptionally suited to the study of dispersal—extinction processes (Ranta 1982).

The three cladoceran species, *Daphnia longispina* O. F. Müller, *D. magna* Straus and *D. pulex* De Geer are obvious candidates for performers of the dispersal—extinction game. Their distribution in rock-pools is peculiar. In the outer archipelago only a fraction of the apparently suitable rock-pools are inhabited at a given time, and only relatively seldom do two species occur simultaneously. Levander (1900) noted that *D. longispina* and *D. pulex* seldom coexisted but tended to occupy certain rock-pools in different years. Lagerspetz (1955) convincingly showed the scarcity of mixed daphnid populations, and on the basis of laboratory experiments suggested that differences in habitat preference were the main factor responsible. Ranta (1979) maintained that interspecific competition was the main factor limiting coexistence, and presented data collected during a single season, comparable to

that of Lagerspetz (1955), as supporting evidence. Hanski & Ranta (1983) developed a detailed model, and used it to analyse the earlier material. Their model was a typical immigration—extinction model, with a competition driven booster. The main weakness of their analysis was the assumption that the disappearence of a population in a patch results in local extinction. The possibility of repopulation from locally produced ephippia was disregarded, and this naturally maximizes the frequency of extinctions. As is usual in competition studies, there are two at least partly conflicting explanations for the observed distribution: reactions to environmental differences and interspecific competition. Of the alternatives, the latter is attractive in allowing the workers to develop elegant theoretical models. However, it seems possible that the question can be decided by following the actual field process more closely. This paper represents the results of an attempt to follow the dynamics of daphnids in rock-pools over a three-year period.

2. Material and methods

Daphnid populations in the study area were followed by sampling with a small hand net. When sampling, an attempt was made to cover all parts of the pool. The sample was emptied into a white container and if the density of daphnids was high enough, a random subsample of some 100 individuals was taken. This was then augmented by a smaller sample of odd-looking individuals. If the density was low, only a selected sample consisting of at most one half of the captured individuals was taken. I believe that the sampling method was capable of detecting a species well below a frequency of 1%. The animals were preserved in ethanol and the species of each individual determined in the laboratory.

During sampling care was taken to minimize the risk of transferring daphnids from one rock-pool to another. After taking a sample the net and other equipment was repeatedly washed in brackish sea water.

Obviously, all habitats suitable for daphnids should be included in the sampling scheme but the truly unhabitable patches excluded. Initially I was inclined to follow the example by Ranta (1979) and exclude the rock-pools lying close to the sea, but sampling late in 1982 indicated that under suitable conditions almost all rock pools could be occupied and most pools were included. I only excluded rock-pools of less than 10 cm in depth when their largest dimension was less than 50 cm and those losing water rapidly through fractures in the bedrock. Another difficulty was the estimation of the actual numbers of pools. The more shallow pools especially, when drying, tended to change into groups of close-lying smaller basins. Such groups were regarded as forming a single original pool.

The field work started in late June 1982 when all islands were sampled. Several islands having high numbers
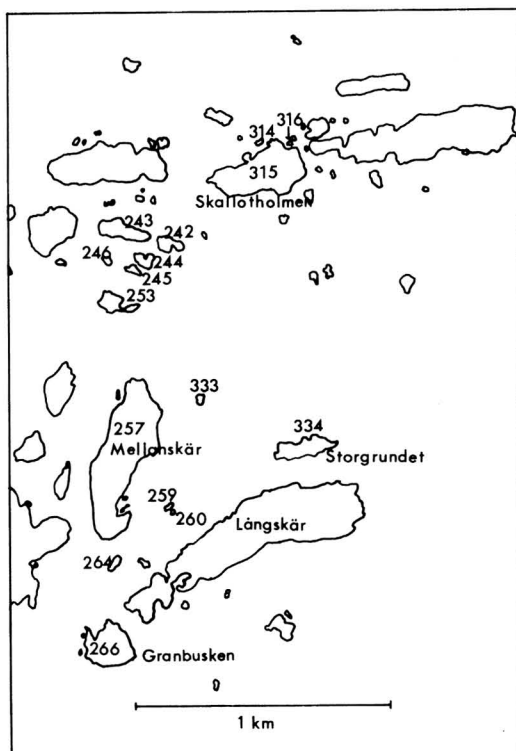

Fig. 1. The study area.

of occupied rock-pools were also visited later, in August—September. In 1983—1984 all islands were sampled in June and again in late July—August, so that for all rock-pools both the early season and the late-season species composition are known. In 1985 the sampling was carried out in early June, in the middle of July, and in late August. In all years additional samples were taken on several islands at shorter intervals.

An attempt was made to estimate the daphnid density in some rock pools using a glass cylinder with a diameter of 6 cm. The cylinder was pushed vertically through the water until the bottom rim reached the sediment, then the upper end was closed without disturbing the sediment and a piece of glass sheet was applied so as to cover the bottom. The contents of the cylinder were passed through a succession of sieves and the individuals were counted and released into the pool.

3. The study area

The study area was selected to include both typical forest-covered islands of the outer archipelago belt and outer-lying treeless islands. Islands that were in use for other research activities or teaching were excluded as it was assumed that such activities could easily increase the risk of the accidental transfer of daphnids from one rock-pool to another. The area is shown in Fig. 1, and the characteristics of the islands are described in Table 1, including the names and the numbers currently used in the

Table 1. The islands studied. The numbers refer to the Island Register used at Tvärminne Zoological Station.

Number	Name	Area, ha	Pools
242	Prackan	0.42	18
243	Fyrgrundet	1.03	11
244		0.34	27
245		0.19	21
246		0.09	1
253	Lasarettet	0.69	32
257	Mellanskär	8.68	91
259		0.09	8
260		0.04	2
264		0.13	10
266	Granbusken	2.31	126
314		0.05	3
315	Skallotholmen	4.97	46
316		0.03	7
333		0.10	21
334	Storgrundet	1.11	83

Table 2. The distribution of daphnids in the study area. The expected numbers are calculated from the products of overall occurrence probabilities.

	D. longispina	D. magna	D. pulex
D. longispina	73		
D. magna	17	39	
D. pulex	6	2	11
Total[a]	96	58	19
Probability of occurrence	0.189	0.114	0.037
Expected numbers			
D. longispina	81		
D. magna	11	45	
D. pulex	4	2	13

[a] 148 occupied, 359 empty.

Island Register established at Tvärminne Zoological Station. The smaller islets were as a rule treeless, containing only small patches of meadows. There is considerable variation between the islands as regards the density of rock-pools, and on larger islands Mellanskär (No. 257) and Skallotholmen (No. 315) most of the pools are concentrated in certain areas. The rock-pools of the study area represented most major pool types, only those with dense vegetation and large brackish water pools with vertebrate predators being lacking. For a general description of the rock-pools, as well as for the classification of different pool types, the papers of Levander (1900), Järnefelt (1940), Lindberg (1944) and Droop (1953) should be consulted.

The weather during the study period favoured the existence of rock-pools. In 1983 during the early summer dry period the more shallow rock-pools tended to dry out, but in later years the dry period was shorter than average. In July—August sufficient rains occurred to keep even the more shallow pools permanently filled. Examples of the yearly variation of rainy periods are given in Pajunen (1971).

4. Results

4.1. The initial distribution

The changes in population densities from one sampling occasion to another were great enough to be detected by simple netting. In rock-pools occupied by two species the populations often tended to vary independently, and one of the species could be temporarily absent. Obviously a single sampling occasion was not sufficient to show the real distribution of the species even in deeper semi-permanent rock-pools. For this reason it was decided to use the combined data of 1982 and those of June 1983 as a basis for the initial distribution. Any changes from this set of data were then regarded as being the results of immigrations or extinctions.

The initial distribution of the species is given in Table 2.

The results correspond closely to earlier results. *D. longispina* and *D. magna* occupy a considerable proportion of rock-pools in the Tvärminne archipelago, while *D. pulex* occurs only sporadically. *D. magna* inhabits rock-pools on small treeless islets, i. e. places where the salinity of the rock-pool water is liable to be high, whereas the other species mostly inhabit rock-pools situated in more sheltered places. These two species also commonly occur in dystrophic rock-pools characterized by a high content of humic matter. The drainage area for such pools is characterized by thick patches of vegetation, often including conifers or miniature bogs. The differences in habitat selection are not clear-cut, however, and the habitat requirements of the species overlap widely. The data are in close agreement with the results of Ranta (1979).

It is tempting to analyse the occurrence data using the null hypothesis that each species has a fixed probability of inhabiting a randomly selected rock-pool. Then the expected frequency of coexistence can be calculated as a product of species-specific occurrence frequencies, and if it is found to differ from the observed frequency, the result can be used as evidence of non-random distribution and a suitable theory can be invented. Thus, Hanski & Ranta (1983) used the results of Ranta (1979) in an attempt to show that co-occurrence was less frequent than expected. However, it should be realized that the frequency of empty rock-pools is crucial to the analysis. Delimita-

tion of the set of rock-pools inhabitable is by no means simple. Obviously, totally unsuitable habitats should be excluded, but on which characteristics should the selection be based? Ranta (1979) excluded very small pools and those "within reach of salt water", including only 315 of some 600 rock-pools available. In the course of the present field work pools very close to the sea were found to contain even the less tolerant D. longispina under suitable conditions. It is reasonable to point out that the calculated occurrence frequencies depend strongly on the number of unoccupied rock-pools included. With sufficient pruning of data the species-specific occurrence frequencies can be increased until the real co-occurrence frequencies fall sufficiently below the expected values. In the present material only the smallest shallow rock-pools were excluded. The co-occurrence tended then to be more common than expected by the total occurrence frequencies. There is thus no need to suggest the existence of any factor limiting coexistence.

In fact, the outer archipelago is relatively unsuitable for studying the problem of coexistence. The frequency of unoccupied rock-pools is always high, and the collected material thus inefficient for detecting the limitation of coexistence. Obviously, such data should be collected from the rock-pools near the inner limit of their occurrence, on larger more sheltered islands. Here the probability of extinction should be smaller and the proportion of occupied rock-pools greater. The main drawback is the scarcity of D. magna in this area.

The simple statistical analysis forces one to assume that the rock-pools are identical respecting features affecting extinction and immigration. This is obviously not true. If populations in some pools live in a less hazardous environment, these are included in the group of pools inhabited at the start of the study, whereas the pools invaded only in the course of the study should contain examples of a more hazardous environment. For this reason the set of initially occupied rock-pools is a valuable reference material.

4.2. Invasions

When a species is found in a rock-pool where it was not previously found, this can be the result of successful immigration or of

Table 3. The number of invasions grouped according to the characteristics of the target pool.

Target	Invading species		
	D. longispina	D. magna	D. pulex
Empty	60	51	3
D. longispina	–	13	8
D. magna	12	–	3
D. pulex	4	1	–
Total	76	65	14

moulting from ephippia produced locally prior to the start of the investigation. Information on the duration of the dormancy of ephippia is scanty and no detailed data applicable to field conditions seem to exist yet. In the absence of contrary information it was assumed that a significant proportion of ephippia deposited in a summer produce new individuals during the next summer. This means that a quarantine period of one summer is sufficient to discriminate between immigration and an intermittent local population. As the initial distribution is the combination of 1982 late summer data and 1983 early summer data, it was taken as a basic distribution, and all new records were interpreted as immigrations.

Immigrations, including recolonization of previously occupied rock-pools are given in Table 3. The frequencies of the immigrations roughly correspond to the initial occurrence frequencies of the three species. The frequencies of the species outside the study area are not known with certainty, but the situation on Långskär, the most significant source area, is known to be comparable. The results of earlier studies (Lagerspetz 1955, Ranta 1979) suggest that D. pulex is always a rare species and that the other two occur with nearly equal frequency. The use of initial frequencies is thus possible. The frequencies of observed immigrations depend also on the number of rock-pools not occupied by the species in question, and should thus be proportional to the product of the frequencies of occupied and unoccupied pools. Such a relation between D. longispina, D. magna and D. pulex is 4.25 : 2.81 : 1. The numbers of invasions do not differ significantly from this theoretical distribution. Immigrations by D. longispina were particularly common in 1985, and in the light of such great year-to-year variation no great weight can be applied to the differences between the species. The data thus suggest that

Table 4. The distribution of the distances from invaded rock-pools to the closest source pool.

Distance in m class limit	D. longispina	D. magna	D. pulex
5	22	18	7
10	20	18	3
15	14	7	0
20	7	2	0
30	8	3	1
50	2	7	2
100	4	1	2
200	4	4	0
300	0	2	0
400	0	1	0
500	0	2	0
Median	9	7	5
Maximum	180	437	70
Observations	81	65	15

the species are quite similar in immigration efficiency.

The simple statistical analysis treats cases in which a species was obviously carried by overflow from one rock-pool to another, a distance of perhaps less than one metre, as equivalent to the invasion of a new island, several hundred metres from the nearest populations. In fact all three species showed successful long-distance invasions.

The distribution of minimum distances covered by immigrations is given in Table 4. In the determination of minimum distances, known sources outside the study area were also considered. In all cases where a group of rock-pools was invaded, it was assumed that one of the pools acted as a stepping stone from which the other pools were subsequently invaded. As expected, the distributions are pronouncedly skew. The medians do not differ significantly but this seems mainly to show the great frequency of short distance immigrations. *D. magna* appeared to be somewhat more prone to long distance immigrations.

D. pulex inhabited either solitary rock-pools from which the possibility of dispersal was limited (Storgrundet, southern part of Mellanskär) or groups of shallow temporary rock-pools (Skallotholmen, northern part of Mellanskär). In the latter habitats the species often appeared simultaneously in several pools, as if moving on a 20−50 metres wide front. Typically, the probable source pools situated west of the invaded rock-pools suggested an efficient windborne dispersal of

ephippia, perhaps during the early summer dry period.

There exists at least one record of apparently sumultaneous multiple immigrations by *D. magna*. The species was absent from the rock-pools of northern Mellanskär in 1982 to early 1983. The area had been used for field studies for several previous summers, and although the species had earlier occurred in many rock-pools it was not found for several years. In late June to early July it was then found in two separate rock-pools, the distance between them being some 50 metres. The species then rapidly invaded several surrounding rock-pools, some of them being connected to the places of initial immigration by flowing water during rainy periods, but some being separate. Individuals of *Scapholeberis mucronata* O. F. Müller and the ostracod, *Heterocypris incongruens* (Ramdohr) were also found simultaneously in one of the groups of rock-pools, which suggests a simultaneous multispecies invasion.

The immigrations allow of an independent test of the possible effect of interspecific competition. If competition is strong the presence of another species in the place of immigration can either prevent successful establishment or at least lower its success.

Providing invasions occur at random, empty rock-pools and those inhabited by other species should be invaded in proportion to their frequency. As the situation is continuously changing, it was impossible to assess the frequencies for any given period, and thus the initial distribution was used, the rationale being that extinctions and invasions tend to remain at an approximate equilibrium. The analysis showed that both for *D. longispina* and *D. magna* the frequencies of immigrations in empty and occupied rock-pools closely corresponded to the frequencies of different target types. Chi-square tests carried out separately for each species did not indicate any significant differences. The material for *D. pulex* was too small for testing but the species in many cases invaded already inhabited rock-pools. Thus, the distribution of immigrations does not suggest that the presence of another daphnid species in any way interferes with successful immigration.

No cases of invasions in rock-pools occupied by two species were observed. Five of the invaded pools had initially had two species but had lost one of them prior to immigration.

Table 5. The distribution of daphnids in the study area, including invasions.

	D. longispina	D. magna	D. pulex
D. longispina	102		
D. magna	39	69	
D. pulex	18	5	8
alternating with			
D. magna	5		
D. pulex	1	1	

Table 6. The number and percentage of populations in initially occupied rock-pools becoming extinct during the study period.

	Extinct species		
	D. longispina	D. magna	D. pulex
Populations extinct			
D. longispina	14	3	2
D. magna	8	9	0
D. pulex	2	1	4
Total	24	13	6
Percent extinct			
D. longispina	19	18	33
D. magna	47	23	0
D. pulex	33	50	36
Total	25	22	32

D. longispina made eight reinvasions in pools it had previously occupied. For *D. magna* four comparable cases were observed.

Invasions naturally increase the number of inhabited rock-pools, and with lengthening of the study period more patches are inhabited at least temporarily. Table 5 gives the distribution of the inhabited rock-pools for the whole study period.

4.3. Extinctions

In order to guard against unrecognized re-population from locally produced ephippia, extinctions could only be studied in 1983—1984. The extinctions observed in rock-pools inhabited at the beginning of the study are given in Table 6. For all species the frequency of extinctions was similar, being about 25 %. No pool characteristics (size, depth, the degree of eutrophy, etc.) could be correlated with extinctions, and several permanent populations survived repeated drying up of their pools. Comparison between single-species pools and those inhabited by two species showed that *D. longispina* had relatively frequent extinctions when occurring together with *D. magna* (the frequencies are different at the 5 % significance level). The data for other species varied erratically and the cases were too few for reliable analysis. The data can be taken to support the case for competitive exclusion (Hanski & Ranta 1983; they give *D. magna* as the weakest competitor), but as the same trend could not be observed in the material consisting of rock-pools invaded during the study period (*D. magna* invading pools occupied by *D. longispina* frequently went extinct), no strong weight could be placed on the result. Exclusion, when real, should give consistent results.

If there are sharp differences between the rock-pools as regards the probability of daph-nid extinction, those initially occupied should include pools with a low extinction probability as a subgroup. The fate of the immigrations observed can be seen in Table 7. Comparison with initially occupied pools demonstrates clearly that extinctions in newly established populations are more frequent. In all three species nearly 80 % of the immigrations of 1983 were extinct by the end of 1985; the difference from initially occupied pools is highly significant. Even the invasions occurring in 1984 suffered relatively high losses (30 %) in a single year. The probability of extinction varies considerably from one rock-pool to another, and this leads to relatively permanent populations in some pools and to temporary populations in others. Of the initially occupied rock-pools, 18 were invaded by a new species, 15 of the cases in 1983. Of these, 10 populations (67 %) went extinct, but eight of these belonged to a massive invasion by *D. magna* on Mellanskär, and are thus actually replicates of the same process. It is thus possible that the great stability of some rock-pools only applies to a particular species.

Extinctions can obviously have several causes. A rock-pool can be so shallow that it dries up before the population can produce ephippia. Brackish water entering rock-pools is harmful to all species. *D. longispina* and *D. pulex* do not tolerate the salinity of sea water (Lagerspets 1955), and although *D. magna* tolerates considerable salinity in laboratory conditions, all field evidence shows that active stages of this species rapidly disappear after sea water enters a rock-pool occupied by it. It is also possible that sudden changes in the

Table 7. The extinction frequency of populations established by invasion.

	1983	1984	1985	Reinvasions in 1985
D. longispina				
Invasions	17	19	40	6
Extinctions	14	8		
Per cent extinct	82	42		
D. magna				
Invasions	18	29	18	0
Extinctions	14	8		
Per cent extinct	78	28		
D. pulex				
Invasions	4	3	3	1
Extinctions	3	1		
Per cent extinct	75	33		

Table 8. Population densities for large and small (passing through the 1.5 mm sieve) individuals of D. magna in two rock-pools representing favourable and unfavourable environments in 1984. The densities (means of six samples ± SE) represent numbers per 27 cm². In the last sampling on Mellanskär all large individuals had disappeared, and the majority of small individuals were D. longispina.

Skallotholmen No 11			Mellanskär No 15		
Date	Large	Small	Date	Large	Small
12.6.	10.2±2.8	46±13	12.6.	3.5±1.4	48±14
19.6.	19.5±2.3	85±11	19.6.	3.8±1.7	13.8±4.1
27.6.	87±7	357±37	28.6.	0.8±0.5	41±9
10.7.	64±15	168±26	6.7.	2.0±0.9	56±8
4.8.	31±7	202±55	13.8.	0	—

ionic composition of pool water, such as those connected with heavy rains after a prolonged dry period, can be harmful. However, such catastrophic events must occur soon after invasion, otherwise the production of ephippia can be expected to allow the population to survive over the unsuitable period.

Nevertheless, several extinctions seemed to be the result of gradual diminution of the population inhabiting an apparently suitable rock-pool. Populations of D. magna on Mellanskär, established by multiple invasions in June 1983, were studied in more detail. In late 1983 the population densities in most pools were remarkably high, and great numbers of ephippia covered the bottom. During the winter a particularly violent storm occurred, and most of the rock-pools were affected by high water level and waves. All bottom material, including several ten-kilogram stones, were carried away from the pools. Nevertheless, sparse populations of D. longispina and D. magna were observed in most of the pools in early June 1984. Samples taken at two-week intervals suggested that the population densities constantly remained much lower than in 1983 and no clear midsummer peak could be observed. From one of the rock-pools inhabited by D. magna quantitative samples were taken. The results, including a thriving population on Skallotholmen for comparison, are given in Table 8.

The population densities give the number of individuals per 27 cm² of bottom area. The rock-pool on Skallotholmen is about twice the depth of that on Mellanskär. Nevertheless, the density difference is considerable, and in the

Mellanskär data there is no clear buildup of the population. This is particularly evident in the consistently low numbers of small individuals (individuals passing through a 1.5 mm sieve) and their failure to enter the group of large individuals. The low population density then apparently prevented the production of ephippia. In the middle of July a period of heavy rains followed, and most of the remaining individuals disappeared. In August only D. longispina was present in small numbers. In other rock-pools on Mellanskär the process was comparable.

The reasons for the gradual diminution of the population remain obscure. There can be no question of competitive exclusion. The population of D. longispina was at this time so small that ordinary netting often failed to record it. As the population density in the rock-pools on Mellanskär has since then been quite low, some long-term change in the populations of food organisms is possible.

4.4. Empty rock-pools

At the start of the study 359 of the rock-pools studied did not contain daphnids, and after the three-year immigration process daphnids failed to occuppy 260 of them. Three principal reasons seem to explain the existence of empty rock-pools. Perhaps the most important factor is the distance separating them from possible source areas. Solitary rock-pools or even groups of pools situated 100−200 metres from rock-pools occupied by daphnids were often empty. Such pools were found on larger islands; the southern tip of Mellanskär and southern shore of Skallotholmen both con-

tained solitary rock-pools, deep enough for continuous over-summer existence of daphnids. Small-sized and shallow pools formed another group. In these the populations are obviously relatively short-lived and ephippia allowing more prolonged local existence can be produced only under exceptionally rainy conditions. The third group consists of pools close to the sea. In these pools the high salinity of the water prevents successful immigration for extended periods, and the action of waves carries individuals and presumably also ephippia away. Only during periods characterized by calm weather, low sea level and extended rain are these pools available for active populations of daphnids. In 1984 and in particular in 1985 such conditions prevailed for most of July, and even *D. longispina* was able to establish populations in rock-pools close to the sea on exposed shores, such as the southern side of Granbusken. The factors can also act together. The rock pools on small islets (for example No. 333) are easily affected by storms and are located far from the source areas.

5. Discussion

Theories of competition in a patchy environment predict a rapidly changing irregular distribution, especially when the risk of local extinction from catastrophic events is high. In reality the picture of daphnid distribution obtained from the present material is essentially stable. Most of the rock-pools containing daphnids at the beginning of the study had the same species composition three years later. Admittedly, around these stable refuges typical extinction and immigration process occurred, indicating the existence of less stable marginal habitats. However, its contribution to the total stability of the system was small. Levander (1900) noted the great persistence of daphnid populations in some rock-pools, while rapid changes were characteristic of others.

Stability is also suggested by the similarity of the frequencies of rock-pools occupied by the three daphnid species in all studies carried out in the vicinity of Tvärminne Zoological Station. The minor differences can be explained by slightly differing study areas. Lagerspetz (1955) does not directly indicate his study area, but the information given suggests that most of the islands close to the Zoological Station were included. Ranta (1979) collected

his data more selectively and included a high number of treeless islands. This probably explains the great frequency of pools occupied by *D. magna* in his material.

The main reason for the relative stability is presumably the efficiency of ephippia in maintaining local populations. This was the function Hanski & Ranta (1983) deliberately ruled out in their model. They regarded ephippia as the agent of dispersal. However, without any means of active transfer available, it would be surprising if any of the numerous packages produced would not be neglected, especially as rock-pools do not seem to be favourite habitats of water birds, the main group of suspected tranporters. Ranta (1979) noted on the possibility of ephippia maintaining local populations. Hanski & Ranta (1983) attempted to evaluate the dispersive capacities of different species on the basis of species-specific hooks and spines on the ephippia, assuming a positive correlation between the average transfer distance and the complexity of the anchoring mechanism. As anchors can also be used to fasten objects on to the bottom of an aquatic environment, direct supporting evidence is needed. Regarding the rather limited range of the rock pool environment, long range dispersal is obviously maladaptive. Distances of several tens of kilometres would probably transfer the ephippia into habitats quite different from the original ones.

In addition to mechanical attachment, other features can also be important. Ephippia of *D. pulex* tend to rise to the surface of the water and are thus more easily transported by water overflowing into the rock-pools. They are also peculiar in fastening on to smooth surfaces, a factor certainly important in short range dispersal. The opinions of earlier workers about the relative merits of different aids for dispersal seem to be contradictory (Storch 1925, Berg 1931). Until further evidence becomes available, it is prudent to regard ephippia of the three species as equal in the game of dispersal.

Although my samples were not quantitative, notes were also made on females producing ephippia. In *D. pulex* such females tended to appear already in early June, at least in some rock-pools, when the population was not particularly dense. On the other hand, *D. magna* typically produced ephippia when the population density was high. The experience gained from the rock-pools on Mellanskär suggests that this species mainly reacts to a

high population density, whereas the other two species might be more subtle in their reactions.

Although no clear indication of the influence of interspecific competition could be demonstrated in the present material, it would be foolish to suggest that competition does not exist among daphnids in the rock-pool environment. The seasonal succession of algal species is rapid, meaning variation in the food level, and the daphnid populations tend to attain impressive densities. The coexisting populations are bound to have a competitive influence. The early laboratory experiments (Frank 1952, 1957) and later studies (Lynch 1978, Smith & Cooper 1982) all suggest that competitive interactions are a reality. Although there is a conspicuous size difference between adults of *D. magna* and the other two species (Hanski & Ranta 1983) the overlap of small individuals is sufficient to form a basis for strong competition. Why then are the species unable to influence each others' distribution? Little is known about the dietal differences in rock pool conditions. *D. magna* appears to attain considerably higher total biomass than the other two species, and this suggests that it is able to tap some exclusive resource. Large *D. magna* individuals often appear to descend to the bottom and possibly can use the uppermost surface of the bottom detritus. Large size would then be advantageous. Such differences would obviously lessen the influence of other species, but they are probably not sufficient and further explanations are needed.

There are obviously several explanations. Firstly, the changes in individual rock-pools are rapid. In the time needed for competitive exclusion the environmental conditions have changed several times, and it is always possible that the initially weaker competitor can gain a temporary advantage during some set of environmental conditions. The mechanism was proposed by Hutchinson (1953). Such changes in the rock-pool environment include partial drying and refilling of the pools with resulting changes in the concentrations of dissolved substances. During rains the water can carry considerable amounts of nutrients into pools, or dilute their concentrations drastically. All such changes can affect the exploitation efficiencies of coexisting species differently, and they can also affect the populations of food organisms.

The second explanation is the existence of dormant ephippia. There seems to be no detailed information available about the length of dormancy in natural conditions, but the considerable variation in the moulting of ephippial eggs seems to have been known for a long time (Storch 1925). According to Wesenberg-Lund (1939) a two year dormancy period is possible. Provided that ephippia are routinely produced even when conditions are favourable and that they have a sufficiently long dormancy period, they can maintain a population even over periods of competitive extinction of the species. If, in addition, the moulting is connected to the environmental conditions favouring the species, such a mechanism can maintain the species provided that the environment changes with sufficient frequency compared to the length of the dormancy period. Ephippia can also be carried outside the actual pool basin and be preserved for considerable periods in dry conditions.

The two mechanisms presented should be able to defeat the effects of non-equilibrium competition. They act at the level of individual rock-pools and no mechanism acting on a regional scale (such as the extinction — immigration process) is necessary. The difficulty/advantage for ecologists is that this process is now so complex that no amount of field data can show its true form, and the unbridled imagination of modellers cannot be checked.

Of the mechanisms the existence of a dormant stage is probably more important. This is evident when daphnids and typical rock-pool insects are compared. Insects rely on the simple extinction — immigration strategy, and having no automatic means to survive over unfavourable periods, they must use active dispersal. Starting from a low population density in early summer, they rapidly invade practically the whole available rock-pool environment, an in late August there hardly exists an unoccupied patch. Daphnids, on the other hand, seem to be able to use only a fraction of the available patches. Those less easily invaded are permanently vacant and even small-scale changes demand appreciable time. Factors acting in the preservation of earlier gains are favoured in this situation.

Rock-pools are caricatures of more complex aquatic systems. Daphnids form the main group of planktonic herbivores, and in empty rock-pools a considerable proportion of primary production probably remains unused. The insect predators concentrate mainly on

chironomid larvae, the major detritus-feeders and bottom herbivores, and there are indications that they are capable of reducing their density to very low levels. This means that in the rock-pool system much primary production simply accumulates as detritus and there exist vacancies for suitably constructed herbivores.

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