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Animal communities in rock pools

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Studies on the structure of animal communities in rock pools in the Baltic area are reviewed. Rock pools are patchy habitats characterized by low durational stability. This, together with pool size and water quality mainly determines the distribution of rock-pool organisms, as judged by data on flagellates, rotifers, corixids, daphnids and water beetles. Immigration to and extinction from pools create an ever-changing kaleidoscope of species occurrence in rock pools. Thus, examination of distribution patterns of species in rock pools is not sufficient to assess the significance of interspecific competition in affecting community structure.

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1. Introduction

The rock pools on the islands of the Baltic Sea are mosaically distributed habitats characterized by unpredictable changes in their water content. Rock pools usually form in shallow depressions in the rock. Many of the pools close by the shore receive their water from waves and surf, while the freshwater pools are maintained exclusively by rain. Rainless periods occur in most years, mainly during the first half of the summer, and desiccation can be expected during periods of drought. Usually the second half of the summer is rainy, though severe drought may intervene. Even a brief rain shower may, depending on the topography, fill a rock pool to overflowing. The probability of drying up varies from pool to pool, depending on the volume, the amount of vegetation and on fractures in the rock bed. When conditions deteriorate, the rock pool organisms either have to escape from the habitat or spend the unfavourable period in some kind of dormant form.

Although the pools vary in their physicochemical characteristics, it is easy to find similar pool types on every island and on almost every islet. These pools provide an excellent object for study of the factors governing the structure of ecological communities. As the pools are very small and structurally simple, their equivalents are easy to establish in the laboratory. The high number of pools facilitates experimentation in the field. However, the dominating method in rock pool studies has been sampling and description of the species living in the pools, and comparison of their numbers and the characters of rock pools (Levander 1900, Järnefelt 1940, Lindberg 1944, Droop 1953, Björklund 1972 are good examples).

In the following I will briefly review the studies on animal species living in rock pools. My emphasis is on community oriented studies, i.e. no attention will be paid to papers merely discussing population dynamics of single species. Even though rock pools also exist in areas other than the coast of the Baltic Sea (Levander 1901, Ghilarov 1967, Edwards 1968, Miller 1969, Jones 1974, Wiggins et al. 1980, Cantrell & McLachlan 1982), most of my examples are from the studies on animal life in rock pools on islands off the southern coast of Finland. Finally, with a reanalysis of data on the occurrence of water beetles in different rock pools, I shall study the most relavant subjects of modern community ecology (viz., factors affecting species richness and coexistence).

2. Typification of rock pools

Early planktological studies in Finland soon led the interests of hydrobiologists to the study of rock pools. At the turn of the century Levander (1900) published the results of his long-term studies (1889-1899) on the biota of rock pools on 11 islands close to the 'summer laboratory' on the island Esbo-Löfö (near Helsinki). The paper became the paradigmatic standard for subsequent studies on rock pool biota; the most recent study following Levander's example was by Björklund (1972). The obvious reason for Levander's paper becoming a landmark paper was that he suggested a descriptive ('natural') classification of rock pools into 9 different types (Table 1). His classification covers the full range of rock pools (Tümpeln, stehende Kleingewässern) from brackish water pools sporadically connected with the sea up to fresh water pools covered with vegetation. Levander's emphasis was on the gradual succession of each pool, due to land uplift, from type 1 pools up to type 9 pools. Levander's (1900) classification has

Table 1. The classification of rock pools by Levander (1900) and by Järnefelt (1940). The correspondence between the two classifications is only approximate.

	Levander (1900)	Järnefelt (1940)
	Pools with brackish water	
I	Intertidal sea water pools at sea level but normally isolated from the sea and only in continuity during rough weather and times of abnormally high water.	Thalassohaline pools
II	Permanent rock pools in the normal splash zone; never in continuity with the sea.	
III	Stagnant brackish pools, above the normal splash zone receiving sea splash very rarely. Subject to drying out.	Tykohaline pools
IV	Seaweed pools. Rock pools or marsh pools at sea level in which seaweed, carried by storms, lies rotting.	
	Pools with fresh water	
V	Ephemeral rain pools, above the splash zone; fresh water with no vegetation, and subject to drying out.	Ephemeral β-limnohaline pools
VI	Permanent rain pools: (a) with clear water and no vegetation (b) with peaty water and some vegetation.	Permanent β-limnohaline pools
VII	Moss pools. Permanent or ephemeral pools with *Drepanocladus* spp. lining the sides and bottom, but the water surface is free.	α -limnohaline pools
VIII	Rock sphagneta. *Sphagnum* spp. filled hollows with no free surface water.	
IX	Marsh, large or medium-sized pools with a muddy bottom and vegetation.	

been acknowledged by almost all later investigators, though most of them have introduced some modifications to the original 9 types (Häyrén 1914, Lindberg 1944, Droop 1953, Ganning 1971, Björklund 1972).

Järnefelt (1940), in his extensive studies on the limnology of Finnish waters, also analysed the hydrochemical properties of rock pool water in 14 pools. The study attempts to relate planktic assemblages of algae (and to a lesser extent also zooplankters) to the limnological characters of the water. Although Järnefelt analysed 20 physico-chemical variables, his discussion stresses salinity. Consequently, Järnefelt (1940) suggested a new classification of rock pools based on water salinity (Table 1). The two different rock pool classifications have their merits and demerits. Levander's (1900) 'natural' typification is easy to use in the field, while Järnefelt's (1940) limnological classification gives more detailed information of the pool water.

3. Niche-theoretic approaches

The early studies of rock pool organisms focused on salinity as a factor governing the distribution of the species (Levander 1900, 1901, Järnefelt 1940, Lindberg 1944, Droop 1953, Lagerspetz 1955). Good examples are given by Droop (1953), who studied the distribution of flagellates in relation to salinity, and Lagerspetz (1955), who analysed the brackish water tolerance of three *Daphnia* species living in rock pools. A closer look at Droop's (1953) table 10 supports the significant role of salinity in determining which species are able to live in particular pools (Fig. 1A).

It is interesting to note that no apparent relationships emerge if one attempts to correlate species richness of flagellates and salinity (Fig. 1A). Moreover, the species number of planktic algae (data from Järnefelt 1940) does not correlate with the salinity of rock pool water (Fig. 1C). Similarly, if one looks at the number of rotifer species in the six different types of rock pools studied by Björklund (1972), the number of species found in pools of each of the six types are more or less the same (Fig. 1B). However, if the composition of the rock pool communities is compared, it becomes evident that rotifers inhabiting brackish water pools do differ from those living in the fresh water end of the continuum (Fig. 1B). These data suggest that species are "packed" (e.g., MacArthur 1972) along the salinity gradient.

Ghilarov (1967) was the first to refer explicitly to the Gause-Hutchinson framework in a study of rock pool animal communities. His data support the principle of competitive exclusion among ecologically closely related species. "The closely related species inhabit, as a rule, different water bodies. When such species live in the same water body they are of unequal dimensions" (p. 82). This applies especially well to four species of *Daphnia* (*D. longispina*, *D. pulex*, *D. magna*, *D. arctica*). He found only one of the species of this genus per pool at any given time. Similar observations are given by Lagerspetz (1955) and Ranta (1979) on three *Daphnia* species (*D. magna*, *D. pulex*, *D. longispina*) in the rock pools of the Tvärminne archipelago, southern Finland, although two species may coexist in Tvärminne pools.

A case in point is the study by Ranta (1979) on the distribution of the three *Daphnia* species in Tvärminne. The niches of the species were characterized by observing the distribution of the species in rock pools in which four environmental parameters (pH, organic carbon content and salinity of the water, and size of pool) were analysed. Even though the species differed somewhat in their tolerances, their niches overlapped considerably (table 7 in Ranta 1979). However, no pool was inhabited by all three species, and the proportion of two-species pools was about 10 % of all inhabited pools.

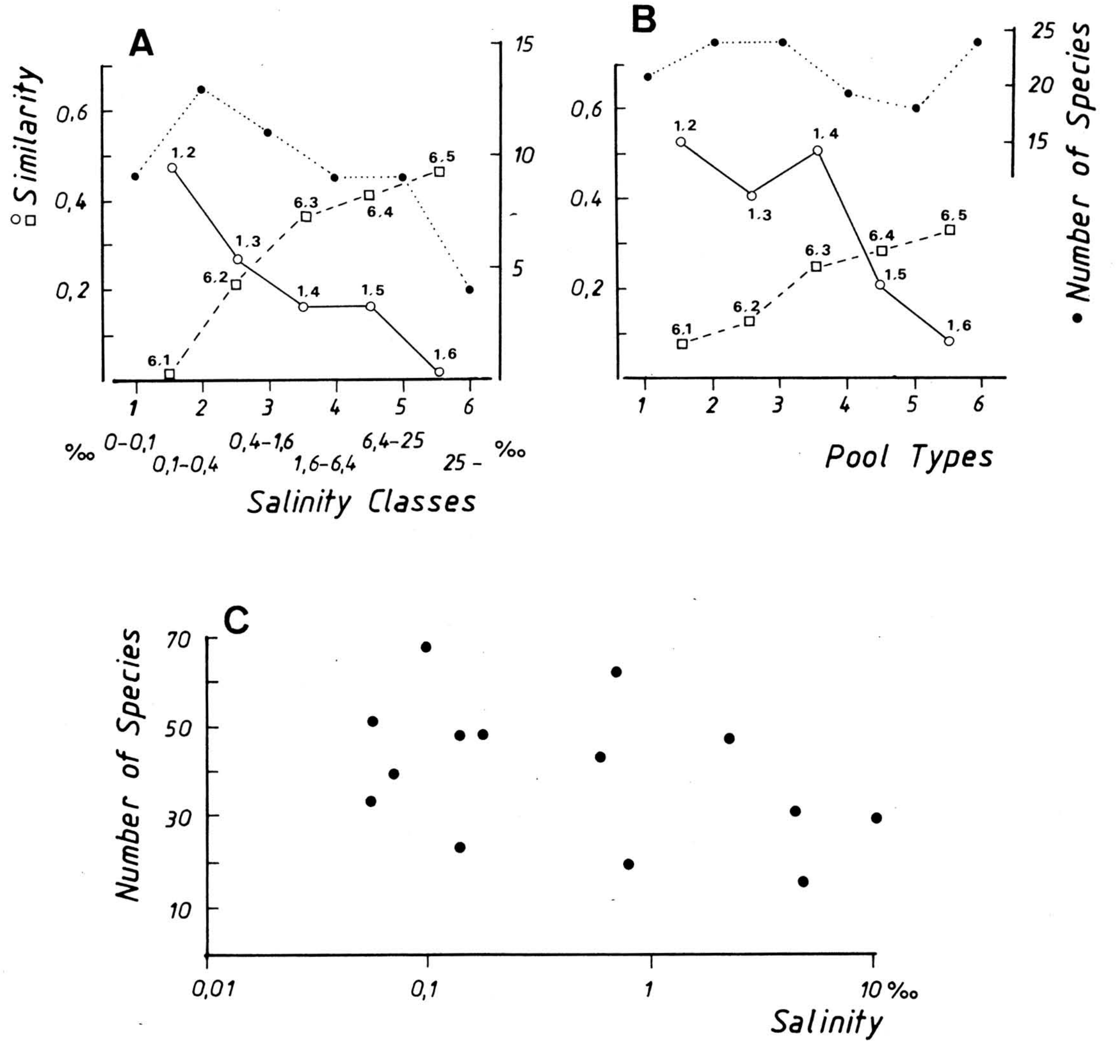

Fig. 1.–A. Flagellate species richness and community similarities in different water salinity classes (1–6). Similarities are given for comparisons between classes 1 and 2 (=1,2); 1,3; 1,4; 1,5; 1,6 and 6,1; 6,2; 6,3; 6,4; 6,5. Data from Droop (1953).

B. Rotifer species richness and community similarities in different rock pool types (1–6, highest salinity =1, lowest salinity =6). Data and pool typification are taken from Björklund (1972). Similarity comparisons are indicated as in Fig. 1A.

C. Species richness and water salinity in planktic algae in 14 rock pools. Data from Järnefelt (1940).

4. Rock pools — kaleidoscopic habitat patches

For aquatic organisms, rock pools are habitat patches that clearly differ from surrounding environments. Besides their mosaic-like distribution, rock pools are characterized by durational instability (disappearance and reappearance of pools), which rock-pool organisms have to cope with in order to survive and reproduce. Clearly, animal species from different taxa have differing strategies for overcoming the problem of survival over drought periods (Wiggins et al. 1980).

Principally, there are two possibilities, either to spend the whole life cycle in rock pools or to disperse elsewhere. The first case, year-round residents incapable of active dispersal, avoid desiccation either as dormant stages or by burrowing into the bottom sediment. This strategy has been adopted by the zooplankton and by most other groups of rock-pool species. Active dispersal is largely restricted to insect imagos. They enter rock pools in spring for oviposition. When conditions deteriorate they may leave the pool (provided that the wing musculature is not histolysed) and move to large and deeper pools. Recolonization of small pools after rain opens up new resources for exploitation by this group of species. Of course, some of the species with active dispersal have larvae which are able to hibernate for some time in the dry mud of rock pools (e.g., water beetles of the family Hydrophilidae). Thus, short dry periods merely interrupt their growth and maturation. However, even for these species, long dry periods are certainly fatal.

The crucial character of rock pool habitats for the animal species living in them is the length of the generation time (τ) in relation to the length of the period during which the pool remains suitable for breeding (H), τ/H (see Southwood 1977). Rock pools with $\tau/H>1$ are unsuitable for reproduction. Following this reasoning, and considering the fact that pools dry up and refill in a more or less unpredictable manner (between-pool variance in the length of the favourable period is large), one realizes that, at any given time, there are pools both occupied and unoccupied by a given species. The processes of colonization into and extinction from pools become dominant factors in the lives of animal populations in the archipelago of rock pools. The theoretical approaches to species coexistence and competition in patchy environments (Skellam 1951, Levins & Culver 1971, Horn & MacArthur 1972, Levin 1974, Slatkin 1974, Hanski 1981, 1982a) are highly significant for studies on animal populations in rock pools, as exemplified by Hanski & Ranta (1983).

A direct conclusion drawn from the references cited above is that habitat patchiness and varying colonization rates, with competition affecting the rate of extinction, enhance the possibilities of regional coexistence (here coexistence in an archipelago of rock pools) of similar species even though local coexistence (here coexistence within a rock pool) would be unlikely.

The framework outlined above has been applied directly to the system of two species of rock pool corixids (*Arctocorisa carinata* and *Callicorixa producta*) by Vepsäläinen (1978a) and Pajunen (1979a, b, 1982) and to the three *Daphnia* species inhabiting rock pools by Ranta (1979) and Hanski & Ranta (1983). As the corixids disperse by active flight of imagos and the daphnids by means of passive transport the results obtained by these authors are worth a brief review.

4.1. Rock pool corixids

Vepsäläinen (1978a) discussed the coexistence of the corixids *A. carinata* and *C. producta* on the basis of predictions derived from the theory of *r* and *K* selection (MacArthur & Wilson 1967, Pianka 1970, Stearns 1976). After examining 17 life history and population ecology characters, the larger species (*A. carinata*) proved to be more *K*-selected than the smaller species (*C. producta*). Vepsäläinen's (1978a) conclusion was that the coexistence of the two corixid species in temporary rock pools appeared to be facilitated by division of the environment on the time axis.

Pajunen (1979a, p. 140) opened his series of studies on the competition between the rock pool corixids (Pajunen 1979a, b, 1982; see also Pajunen 1977) by listing the facts suggesting that *strong* competitive interactions function between the two species: (1) The habitat utilization by the two species is similar. Quantitative differences in the use of different-sized pools occur only for a part of the reproductive season. (2) The species are similar in terms of their reproductive phenology. (3) The structure of the habitat is simple, the pools are small with respect to the swimming power of even the smallest larvae. This contributes to diminished possibilities for habitat segregation. (4) Densities of mixed populations are frequently high enough to result in considerable mortality.

Pajunen (1979a) compiled evidence indicating that in stable situations *C. producta* would be excluded by *A. carinata*, whereas in an unpredictable and patchy environment *C. producta* can maintain its populations regionally because it has a clearly better dispersal ability than its congener. Besides, in the late season *C. producta* is able to utilize smaller water bodies effectively.

In two subsequent papers, Pajunen (1979b, 1982) goes on to quantify interspecific competition. With a ratio diagram analysis and data accumulated earlier (Pajunen 1977) he was able to demonstrate convincingly that the competition coefficients per unit of biomass are 1.45—1.50 for *A. carinata* and 0.66—0.68 for *C. producta* (Pajunen 1979b). In an experimental field analysis, Pajunen (1982) was able to show that the competition between the two species was nothing but for food. The species have completely overlapping resources which are utilized with almost equal efficiency. This contradicts the competition coefficients given above. However, the problem is overcome as Pajunen introduces the idea of size-related interference. The larger larval stages of both species are cannibalistic on smaller larvae, and as

C. producta is about half the size of *A. carinata*, interspecific interference (predation) clearly favours the larger species.

Pajunen's results are of great interest to the present debate on the significance of competition in affecting the structure of animal communities (MacArthur 1972, Diamond 1975, Connell 1975, 1980, Simberloff 1978, 1980, Connor & Simberloff 1978, Grant & Abbott 1980, Levins & Lewontin 1980, Alatalo 1982; this issue). If nothing else, they are at least a caution against drawing too direct conclusions about competition in action (/nonaction) simply on the basis of presence/absence data of the distribution of supposed congeners over a set of habitat patches (cf. Simberloff 1978, Connor & Simberloff 1978).

4.2. Three species of Daphnia in rock pools

Although the three *Daphnia* species, *D. magna*, *D. pulex*, *D. longispina*, have greatly overlapping habitat niches they rarely coexist in the same rock pools (Ranta 1979). As an explanation of the scarcity of coexisting populations, I proposed a resource-competition hypothesis. The species are filter feeders and the size of ingested particles is relative to the body length of the species (Burns 1968). The body sizes of the species range as follows: *D. magna* 0.86—5.0 mm, *D. pulex* 0.67—3.5 mm and *D. longispina* 0.59—2.5 mm [combined data from Green (1956) and Ranta (1979)]. Thus, the overlap is prominent. The laboratory experiments by Frank (1952, 1957) and Neill (1975) demonstrate convincingly that smaller species invariably overcome the larger species, thus lending support to the hypothesis by Ranta (1979). Ranta (1979) suggested that frequent local extinctions and random colonizations of empty pools maintain the observed pattern of regional (within-island) coexistence despite the fact that local (within-pool) coexistence is unlikely owing to resource competition. This was subjected to a theoretical analysis by Hanski & Ranta (1983). Our hypothesis, supported with data from the literature, was that the largest species (*D. magna*) is the best colonizer and the worst competitor, the smallest species (*D. longispina*) is the best competitor and the worst colonizer, while *D. pulex* is intermediate in both respects.

A model was constructed to analyse the number of pools occupied by *Daphnia* on islands with varying numbers of rock pools. The model predicts that regional coexistence is facilitated by an increase in the number of pools on islands. This agrees with the field data, only the largest islands with most pools having all three species. A 'priority effect' is possible but unlikely in the model, and it was not observed in the field: all the

Table 2. Distribution of 22 water beetle species in 20 rock pools in the Tvärminne archipelago (data from Lindberg 1944). The rock pools are arranged in the order of decreasing salinity. The abundance of the species is indicated as 1 = sparse, 2 = less sparse, 3 = abundant, 4 = very abundant. Upper tolerated salinities for the species are given according to Lindberg (1937, 1948). P = number of occupied rock pools.

	Rock pools (numbering after Lindberg 1944)																					
	1	2	4	3	6	17	7	5	14	13	8	16	12	19	10	15	9	18	20	11	P	Tolerated salinity (‰
Dytiscidae																						
Coleambus impressopunctatus	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	8.1
Potamonectes griseostriatus	2	4	3	3	4	–	3	3	3	3	3	–	–	–	1	–	–	–	–	–	11	9.8
Hydroporus erythrocephalus	–	–	–	–	–	2	–	–	–	–	–	–	1	1	2	–	–	1	–	–	5	8.7
H. tristis	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	1	1	–	–	4	6.1
H. melanocephalus	–	–	–	3	–	–	1	–	–	3	–	3	2	4	2	–	3	4	4	3	11	2.8
H. obscurus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	0.2
H. melanarius	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	2.5
Platambus maculatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	5.7
Agabus bipustulatus	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	1	–	3	1	–	5	7.0
A. congener	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	1	–	–	3	2.3
A. subtilis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4.6
Ilybius subaeneus	–	–	–	3	–	–	3	–	3	3	3	2	1	2	3	2	1	–	–	1	12	2.5
I. aenescens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	–	–	–	2	7.1
Rhantus frontalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	6.6
Acilius sulcatus	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	1	4.0
Gyrinidae																						
Gyrinus opacus	–	–	–	3	–	–	1	–	–	–	3	–	4	3	4	2	1	2	–	1	10	2.8
Hydrophilidae																						
Helophorus flavipes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	7.3
Hydrobius fuscipes	–	–	1	–	–	–	–	–	1	–	–	–	–	2	–	–	1	1	2	–	6	2.8
Anacaena limbata	–	–	–	–	–	2	–	–	3	–	1	2	–	2	–	2	3	2	3	1	12	6.1
Enochrus sahlbergi	–	–	–	–	1	3	–	–	1	4	1	3	2	–	1	–	–	1	2	–	10	8.8
E. fuscipennis	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	1	5.2
E. affinis	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	2	6.7
Species totals	1	1	2	4	2	6	4	1	4	6	5	4	6	10	9	7	9	9	5	4		
Salinity (‰)	8.0	6.6	1.5	1.0	0.9	0.7	0.4	0.3	0.3	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1		

single-species islands were occupied by *D. magna*, and all the two-species islands by *D. magna* and *D. pulex*. Interspecific differences in colonization and competitive abilities appear to determine a predictable change in abundance relations along a gradient of increasing rock pool density. The rock pool *Daphnia* is an example of similar species coexisting in a heterogeneous environment but diverging on a productivity gradient (rock pool density) because of exploitative competition (Hanski & Ranta 1983).

5. Water beetles in rock pools — a case study

Håkan Lindberg (1937, 1944, 1948) made extensive studies on the distribution of water beetles (Haliplidae, Noteridae, Dytiscidae, Gyrinidae and Hydrophilidae) in different kinds of water. His 1944 paper gives a detailed list of the occurrence of 22 species of water beetles in 20 rock pools in the Tvärminne archipelago (Lindberg 1944: table 5). This set of data (Table 2), supplemented with other observations by Lindberg (1937, 1944, 1948), serves here as a data base for my analysis of factors affecting the structure of water beetle communities in rock pools.

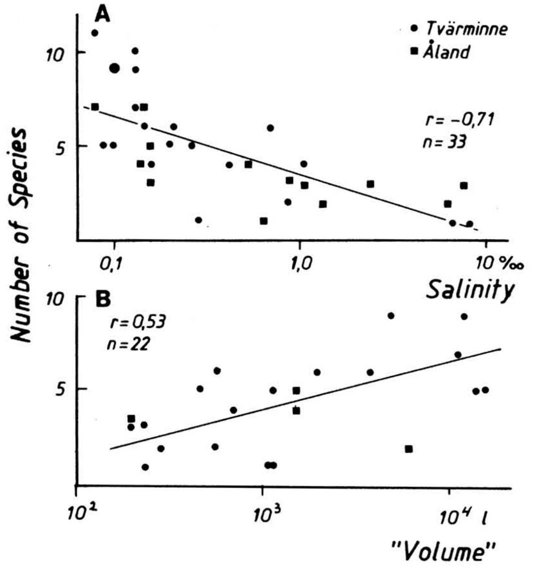

Fig. 2. Relationship (A) between water salinity and species number, and (B) between rock pool volume and species number in water beetles living in rock pools. The data are taken from Lindberg (1944), the observations from the archipelago of Tvärminne and Åland are indicated with different symbols (large dot = two overlapping observations).

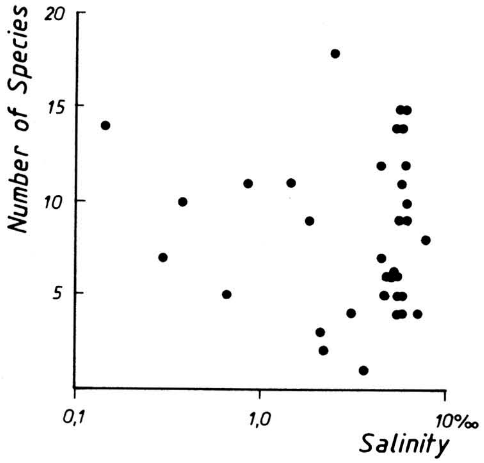

Fig. 3 Relationship between water salinity and species number in water beetles living in the sea littoral. Data from Lindberg (1937).

Lindberg (1944) was well aware that the physico-chemical properties of rock pools have a great impact on the faunal diversity. He was mainly interested in the effects of the salinity of rock pool water on water beetle distribution. A significant negative correlation emerges between log salinity and the number of water beetle species in rock pools (Fig. 2A). It has been established in studies of species richness in patchy habitats that species number increases with increasing patch size (MacArthur & Wilson 1967, and many others). Rock pools are no exception, for species number and log rock pool volume (maximum depth × maximum area) correlate positively (Fig. 2B). A positive correlation can also be found between species number and log area (r=0.43, df=31, P<0.05), and between species number and log depth (r=0.45, df=22, P<0.05).

Let us return to the question of species richness and water salinity. Lindberg (1937) studied the distribution of water beetles in the sea littoral in the Tammisaari-Tvärminne area. He sampled 31 littoral localities and four smaller water bodies which regularly received sea water. The total number of species encountered was 61, and the salinity in the sampling sites varied from 0.14 ‰ to 7.3 ‰. Interestingly enough, no correlation can be found between water salinity and the number of species (Fig. 3).

Comparing the two sets of data (Fig. 2A and Fig. 3) one finds that the salinity range covered is almost the same. However, the salinity has a clear effect on species richness only in rock pools, while in the sea littoral species diversity seems to be independent of water salinity. When comparing the two species lists, a few facts deserve particular attention: (1) the rock pool species do not include any species from the families Noteridae and Haliplidae; (2) with a few exceptions (*Potamonectes griseostriatus*, *Hydroporus melanocephalus*, *H. obscurus*, *Agabus subtilis* and *Gyrinus opacus*), all water beetles inhabiting rock pools can also be found living in the sea littoral; (3) only about one quarter (17) of the total of 61 species living in the sea littoral are found in rock pools; moreover, (4) on the mainland, close to Lindberg's (1937, 1944) study sites, one finds three species of *Gyrinus* (*G. natator*, *G. substriatus*, *G. minutus*; Jan Landin, unpubl.) in fresh water basins. It is interesting to note that *G. opacus* is not found in these habitats while the fauna of the sea littoral also includes *G. natator* and *G. minutus* (Lindberg 1937). Similarly, two of the largest dytiscids (*Dytiscus marginalis* and *D. circumcinctus*, both about 30—35 mm long) are found in small water bodies on the mainland but not in the rock pools.

5.1. Species assemblages, chaos or order?

The first answer to the posed question will be sought by analysing whether any of the aquatic families of Coleoptera is more suited to life in rock pools than the others. Table 3 lists the number of species in different water beetle families living in rock pools, as compared to those found in the sea littoral and in the Finnish fauna (species list from Silverberg et al. 1979). The answer is clearly no — no family of aquatic Coleoptera is more suited to living in rock pools — the only difference being in species totals (Table 3).

One of the persisting explanations given for observed differences in the distribution of animal species over a number of habitat patches (see Table 2) has been interspecific competition. The feeding experiments by Lindberg (1944: pp. 79-108) demonstrate that most of the water beetle species in rock pools feed on the same food items (larvae of Chironomidae and *Ephydra* flies, and *Daphnia* species), thus indicating competition for food. Another explanation, originating from the theory of the niche, would be that coexisting species differ in some (hidden?) dimension of their niches which facilitates coexistence, as each of them has its own main habitat elsewhere. In the following I will attempt to find out whether the data given in Table 2 support the idea that competition affects the distribution of the water beetle species in rock pools.

Table 3. Number of species in different water beetle families found in rock pools (Lindberg 1944) as compared to the species numbers found in the sea littoral (Lindberg 1937) and in the Finnish fauna (Silfverberg et al. 1979). Expected numbers are calculated on the basis of the Finnish fauna (χ^2 statistics are given with corresponding probabilities).

	Rock pools			Sea littoral			"Finland"	
Family	Obs	(%)	Exp	Obs	(%)	Exp	Obs	(%)
Haliplidae	0	(0.0)	1.8	6	(9.8)	5.1	17	(8.3)
Noteridae	0	(0.0)	0.2	2	(3.3)	0.6	2	(1.0)
Dytiscidae	15	(68.2)	14.2	29	(47.5)	39.3	132	(64.4)
Gyrinidae	1	(4.5)	0.9	5	(8.2)	2.7	9	(4.4)
Hydrophilidae	6	(27.3)	4.8	19	(31.1)	13.4	45*	(22.0)
Totals	22			61			205	
				χ^2		P		
Rock pools vs. "Finland"				2.33		0.674		
Sea littoral vs. "Finland"				6.94		0.139		
Rock pools vs. sea littoral				4.16		0.385		

*)Non-aquatic species are excluded.

According to Hanski's (1982b) hypothesis animal species can be grouped into core and satellite species, on the basis of their local abundance and regional distribution. The core species are widely distributed, i.e. they occupy most of the sites suitable for them, they are locally abundant, and they are relatively well spaced out in niche space. The opposite characteristics belong to the satellite species. In the analysis below I have excluded two rock pools (1 and 2) as they have salinities (7.96 ‰ and 6.58 ‰) higher than what most of the species tolerate. *Hydroporus obscurus*, which has a narrow salinity range (0.19-0.11 ‰), is excluded. These deletions do not substantially change the emerging pattern (Table 2). Six of the species have the status of 'core species' (*Potamonectes griseostriatus*, *Hydroporus melanocephalus*, *Ilybius subaeneus*, *Gyrinus opacus*, *Anacaena limbata*, *Enochrus sahlbergi*). Now we can ask whether these six species are more widely distributed in the niche space than any six species randomly selected from the total of 21 species. (Body sizes are assumed to reflect adequately the particle sizes eaten, thus providing the best available estimates of food niches of the species.) The observed average of body length differences in the six species is 3.3 mm, and the expected average after 500 random draws is 4.1±1.4 mm. It is clear that in this set of data the 'core species' are not more widely distributed by body size than species in randomly selected sets of six species.

My next step was to investigate whether the species composition (in terms of body size differences) of any of the 20 rock pools was a 'non-random' draw from the species pool (Fig. 4). As the water quality varies from pool to pool, the 'species pool' was tailored in each case to include only the species which can live in the rock pools with that particular water salinity (salinity tolerance data from Lindberg 1937 and 1948). The results are as follows: in seven pools the distribution was wider than expected, but only in one case was the difference statistically indicative

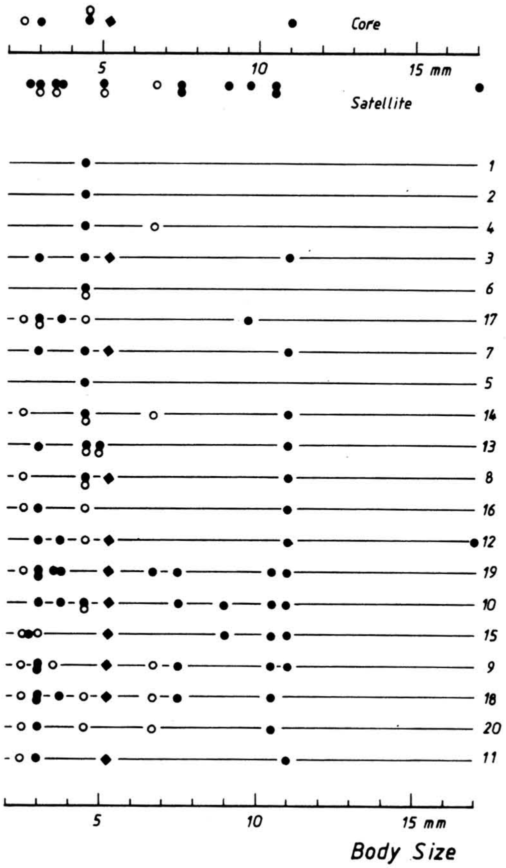

Fig. 4. Distribution of body sizes in water beetle species living in rock pools in the Tvärminne archipelago. Above, species are grouped according to their 'core' or 'satellite' species status (see text). Below, pool specific size distributions of water beetle species in 20 rock pools. Data and numbering of rock pools follows Lindberg (1944). The different water beetle families are indicated as: Dytiscidae = black dots, Gyrinidae = diamond, Hydrophilidae = open dots.

(pool 12, $P<0.1$). The observed distribution was less than expected in 10 cases, two of the differences being statistically significant (pools 6 and 14, $P<0.05$ in both cases). In three pools (1, 2 and 5) with only one species, no calculations could be made (Fig. 4). In conclusion, one finds little evidence here for the idea that species compete intensively.

Water beetles of the three families found in rock pools (Dytiscidae, Gyrinidae, Hydrophilidae) differ somewhat with regard to their ecologies. Dytiscidae and Gyrinidae are predators both as larvae and adults, while Hydrophilid larvae are predators and the imagos herbivores and/or detritivores. Hence it might be warranted to keep to the family level 'guilds'. Thus analysed, the observed size difference in Dytiscidae is 5.3 mm, the expected value being 4.7±2.5 mm (non-significant difference), in Hydrophilidae the corresponding figures are 2.0 mm, and 1.9±1.2 mm (non-significant). As there is only one Gyrinid species, no calculations could be made for it. Again, the observations failed to support the importance of competition. Note, however, that the trend in the size differences is indicative of a trend, observed values being higher in both cases.

Finally, if one takes the six species with the status of 'core species' and calculates the number of rock pools in common and compares these figures with the expected number of shared pools (see Simberloff 1978), one finds that the observed number of shared pools is greater than expected in only two cases, and once they were equal. According to a sign test the probability of an equally rare or rarer event (2/14) is 0.006. This observation lends slight support to the conclusion that these species seem to coexist in fewer cases than expected from a simple model of random distribution.

To summarise, it is clear that little can be deduced about competition from the distibution of rock pool water beetles (Table 2) at local (within-pool) or regional (between-pool) levels. On the other hand, the evidence suggests (Lindberg 1944) that most of the water beetles in rock pools have the same food items. When coexisting they certainly diminish the amount of resources available in the rock pools. The question of whether or not this is any proof of competition remains open, and the answer awaits experimental tests.

5.2. Why are there so few species?

In describing the data it became evident that rock pools of a given salinity support fewer beetle species than found in the sea littoral with corresponding water salinity. Furthermore, only about one quarter (17/61) of the species living in the sea littoral seem to be able to invade rock pools, even though the range of tolerated water salinity (Lindberg 1937, 1948) is an excluding factor for only a few of the species. In the following I shall outline tentative hypotheses explaining the paucity of the rock pool fauna. It is certain that no single factor is responsible for the whole phenomenon for all species. It should be also mentioned that with the present data no quantitative significance can be given for any of the suggested factors.

The island effect (rock pool size) is responsible for about one quarter of the within-pool species richness (28 % of the variation in species number is explained by rock pool volume). Thus, from increasingly larger rock pools, one will certainly sample an increasing number of species. But note that most of the rock pools are small (Pajunen 1979a: table 1). However, because of the insularity of suitable habitats species also encounter the problem of finding the habitat. Only species with good dispersal abilities can find the patchy habitats. Not all species have equal dispersal abilities, and so a decrease in species richness can be expected. The small size of rock pools also implies few possibilities for microhabitat differentiation. Macrophytes are often necessary components in the habitats of water beetles but only a few of the rock pools have dense macrophyte vegetation. To my knowledge, this is the reason why the large *Dytiscus* species are not found in rock pools. Low spatial density of suitable habitats certainly excludes many of the potential rock pool colonizers.

The small rock pool size is also associated with the stability of the habitat patches. Most of the pools dry up and refill at least once per season. The durational instability of rock pools excludes species with poor dispersal and recolonization abilities. This is exemplified in *Gerris thoracicus*, a water-strider, which is the only *Gerris* species able to cope with the instability of rock pools. The presence of *G. thoracicus* in rock pools is made possible only by its extremely good dispersal potential and willingness to fly often from pool to pool (see Järvinen 1976, Vepsäläinen 1978b). The instability of rock pools also introduces instability into the water quality. For example, the salinity of a single pool may fluctuate widely, depending on the frequency of dry and rainy periods (Lindberg 1944 gives an extreme range from 0.1 ‰ to 4.6 ‰). It seems to be more difficult for an organism to become adapted (/adjusted) in the course of evolution (/development) to irregular fluctuations of some environmental factor than to one particular, even extremely high or low but constant, value of the factor (e.g. Dahl 1956, Ghilarov 1967).

The above discussion neglects the important fact that the habitat patchiness has an increasing effect on regional species richness. Only a few of the islands in the Tvärminne area have more than 10–20 rock pools. Consequently, inter-island distances might become a problem for migrants and thus reduce species richness.

6. Concluding remarks

Much of the present controversy about the role of competition between species in affecting their distribution (Connell 1975, 1980, Diamond 1975, Simberloff 1978, 1980, Connor & Simberloff 1978, Grant & Abbott 1980, Levins & Lewontin 1980, Bowers & Brown 1982, Pontin 1982, this issue) is due to difficulties arising from direct interpretation of observational data. Distribution lists or pairwise niche overlap values do not necessarily tell anything for or against competition. Take the rock pool corixids and daphnids as an example: *Arctocorisa carinata* and *Callicorixa producta* coexist frequently in the same pools. However, there is no doubt that these species do compete, while the three *Daphnia* species do not often coexist locally, owing to resource competition. Thus, observational data as such do not indicate whether or not the species distributions on local and regional scales are affected by competition. Similarly little, if anything, could be deduced for competition affecting the distribution of water beetles in rock pools. Clearly, more information is needed. The distribution of animal species is certainly a function of many different factors, competition being only one of the many. Thus, it is not suprising that one gets ambiguous results when attempting to rule out the significance of a single factor. We need controlled experiments, both in the field and in the laboratory (e.g., Connell 1980, Levin 1981). Rock pool systems are excellent objects for experimentation: they are simple in structure, small, and there are many of them. This makes them easy to manipulate and enables sufficient replicates for statistical tests.

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